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The dangers of irreversibility in an age of increased uncertainty: revisiting plasticity in invertebrates

Ary A. Hoffmann and Jon Bridle

A. A. Hoffmann (https://orcid.org/0000-0001-9497-7645), School of BioSciences, Bio21 Inst., The Univ. of Melbourne, Vic, Australia. – J. Bridle (https://orcid.org/0000-0002-5999-0307) ✉ (j.bridle@ucl.ac.uk), Dept of Genetics, Evolution and Environment, Univ. College London, UK.

Plasticity in traits in response to environmental conditions can increase fitness, expanding the range of environments within which a genotype can generate viable and productive phenotypes, and therefore when and where populations can persist and diversify in ecological space. Adaptive forms of plasticity in invertebrates are diverse, ranging from polyphenism and diapause to behavioural thermoregulation and optimal foraging. Local patterns of environmental variation and developmental constraints will dictate which of these forms evolves. Here we review the core idea that the use of narrow developmental windows by invertebrates to attain specific types of phenotypic changes reduces their reversibility, while increasing their magnitude. These tradeoffs dictate the costs and effectiveness of plasticity in buffering environmental variation. In particular, plastic responses to narrow developmental or environmental windows increase fitness costs when predicted environmental challenges do not materialise, or when the environment changes in unpredictable ways. We then explore the converse idea that increasing trait reversibility depends on extending the period for which genotypes are sensitive to the environment, but also narrows the range of plastic phenotypes that can be generated. Considering these findings together, we would expect that the costs, benefits and constraints of reversible versus irreversible plasticity affect the rate and magnitude of adaptive responses to rapidly changing and novel environments. However, such predictions have rarely been tested or included in theoretical models. Identifying this knowledge gap leads us to propose new research directions to provide a deeper understanding of the evolution of plasticity in invertebrates and other organisms. We illustrate these possible directions through examples of *Drosophila* adapting to thermal stress.

Keywords: climate change, *Drosophila*, environmental sensitivity, predictability, variation

Introduction

Plasticity can be defined as the extent to which a genotype produces different phenotypes under different environmental conditions (Bradshaw 1965). Such environmental sensitivity is typically represented as a continuous change in a given phenotype along an environmental gradient (a 'reaction norm'). Plastic responses are adaptive

within the range of environmental conditions where they generate a phenotype closer to the optimum phenotype than would be produced by the same genotype without plasticity (Schmalhausen 1949, Bradshaw 1965, Schlichting 1986). The phenotypes created by such plastic responses of genotypes are determined by a wide variety of traits that have evolved sensitivity to some aspect of an environment.

Genotypic variation in sensitivity can be characterised by the rate of response to an environmental change (the norm of reaction) which differs among the genotypes as depicted by the slopes in Fig. 1. A second source of variation among genotypes is the level of phenotypic variability expressed by a genotype in a particular environment (Fig. 1, genotype 1 and 3 are less variable in E1 and E5 than genotype 2). Another key aspect of plastic responses is that they can generate either an immediate phenotypic change which can benefit a genotype, or they can initiate and guide the production of phenotypes intended to increase fitness in future environments. However, such priming of the phenotype to regulate a genotype's future exposure to the environment is not well captured in Fig. 1. This is because when determining whether the future plastic responses of genotypes have a high fitness, the key challenge is not how variable environments are, it is how reliably future environments can be predicted based on current environments, and whether the phenotypes produced to match these environments will have high fitness. For insects and other invertebrates, appropriate phenotypes range from the prolonged diapause essential for life at high latitudes and elevations, to acclimation responses countering stressful conditions that might last a few hours or days (Colinet et al. 2015), or to even more rapid and reversible thermal responses that allow invertebrates to warm up or

cool down more rapidly than ambient temperature changes (Abram et al. 2017).

Various factors constrain the evolution of particular forms of plasticity, including phylogenetic history, allometric relationships, environmental covariances, low genetic variation and/or the direct costs of producing the plastic response (Schlichting and Pigliucci 1998). Plastic responses will also be restricted by the metabolic cost of reacting to the environment, the cost of gathering information about the environment, tradeoffs with other forms of plasticity and the future cost of any mismatches with the environment resulting from making inappropriate responses (Hoffmann and Parsons 1991, Auld et al. 2010, Sgro et al. 2016). Taken together, these constraints confine species to regions of environmental space and time that can be made predictable (and survivable) by the evolution of appropriate forms of genotypic sensitivity. If such evolutionary constraints to plasticity did not exist, more species might be expected to have geographical distributions covering large regions of ecological parameter space, within which clines in genotypic sensitivity to these environments allowed fitness to be maintained. Understanding the evolution of plasticity is therefore fundamental to how species interact with environments (and with each other), as well as how quickly new forms of adaptive plasticity can evolve (Bridle and van Rensburg 2020). The risk of generating inappropriate phenotypic responses based on existing forms of genotypic sensitivity is now particularly important given organisms are increasingly experiencing novel environments and communities, and increasingly variable environmental conditions due to rapid global change (Kirtman et al. 2013).

Unfortunately, the factors that constrain the evolution of plasticity are difficult to define and measure (Auld et al.
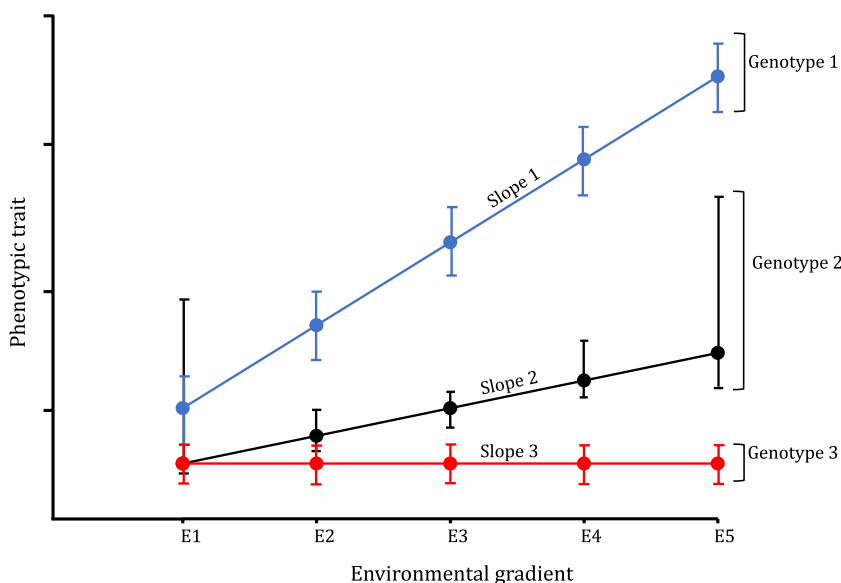

Figure 1. Defining plasticity as changes in a continuous trait along a set of environments that form a gradient. The plasticity of three designated genotypes (1–3) is characterized by the slopes of lines across the gradient, with steeper slopes representing genotypes with greater environmental sensitivity (producing GxE interactions). Genotypes may also differ in the level of phenotypic variability produced in some environments, so genotype 2 is more variable in environments E1 and E5 than the other genotypes.

2010). However, two key concepts are central to the physiological and behavioural processes underpinning plasticity: the risk of being sensitive to environmental cues that sometimes fail to predict future environments (sensitivity costs, related to cue informativeness); and the cost where the mismatches between phenotype and environment generated by such inappropriate sensitivity cannot be reversed (irreversibility costs). Irreversibility describes the extent to which being sensitive to environmental variation at a given point of development (or the need to be sensitive for extended periods) commits genotypes to a pathway of development, so narrowing their range of future phenotypes, and increasingly restricting them to a given range of environmental conditions, albeit ones that have been previously faced (Burggren 2019). Apart from producing the wrong phenotype at the wrong time, there are likely to be additional energetic and structural costs of possessing mechanisms to sense changes in the environment and of being able to produce reversible phenotypes.

To bring these different ideas from the literature together, we have incorporated them into a triangle that links the different types of costs (irreversibility, sensitivity and production costs) to form three points in a triangle (Fig. 2) that constrain the range of phenotypes accessible to genotypes for plastic responses. Increased production costs of maintaining reversibility make it likely that reversible phenotypes will be outperformed by irreversible phenotypes, provided the future environment, and a genotype's exposure to it, can be made predictable (from an organism's point of view) through the use of appropriate environmental cues. However, when defining production costs, it is

important to separate the cost of generating and maintaining a phenotype with a given level of reversibility from the fitness value of the plastic response itself in a given environment, which is easier to define (Callahan et al. 2008). Importantly, the production and response costs need to be considered within the context of the natural environment, where they may vary considerably. For example, the costs of cold acclimation – a reversible form of plasticity – are substantial when they are expressed under hot conditions in *Drosophila* but small under milder conditions (Kristensen et al. 2008).

The costs of plasticity therefore depend on the predictability of the environment and the extent to which traits need to change to match the changing environment. Understanding where and when environmental predictability can be increased (i.e. environments 'smoothed') by the agency of genotypes will become increasingly crucial in determining the local abundance of species, given anthropogenic change typically increases the variance and decreases the predictability of local environmental conditions, while also reducing the range of suitable habitats accessible through dispersal or the timing of key life stages (phenology). This environmental smoothing process may involve genotypes either: 1) moving in space and time to where or when their phenotypes will be at highest fitness, or; 2) creating phenotypes that make them invulnerable to those aspects of the environment that remain unpredictable. Having discussed the different types of costs of plasticity, we summarise in Box 1 future research directions that can help to understand the limits of plasticity in contributing to adaptation to ongoing environmental change.
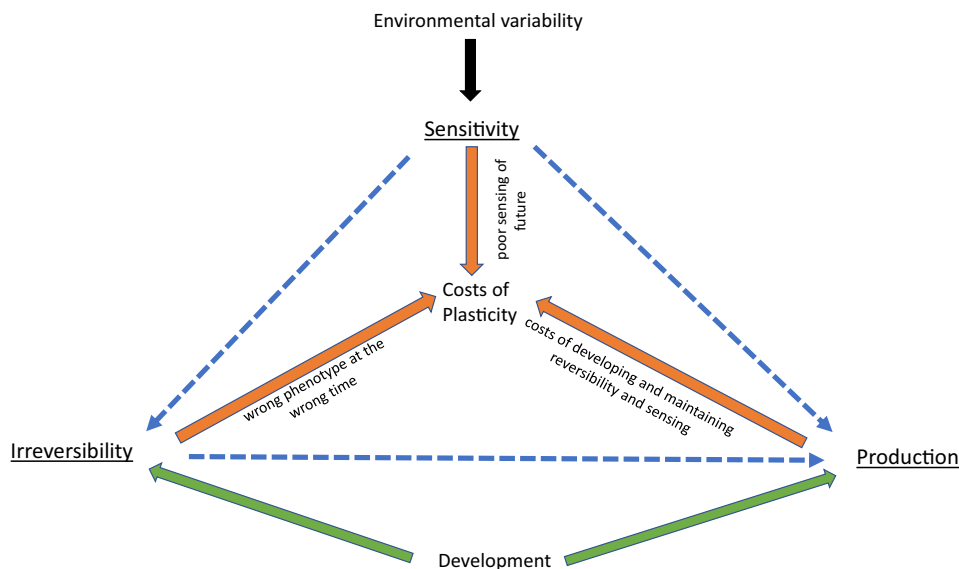

Figure 2. Three cornerstones determining plasticity variation and their costs: sensitivity, irreversibility and production. Costs reflect interactions among these cornerstones, based on producing the wrong phenotype at the wrong time (due to inappropriate cues being sensed to predict future environments (sensitivity costs), and the inability to revert to a phenotype with a higher fitness (irreversibility costs), as well as the cost of producing (and maintaining) the machinery to accurately sense the environment and revert phenotypes (production costs). Green arrows indicate the importance of developmental processes in production and irreversibility. Blue arrows indicate the direction of connections between processes.

Measuring adaptive plasticity

The evolution of adaptive plasticity is often easiest to identify in comparisons at large geographical scales that encompass a range of climatic conditions. Perhaps the most straightforward plastic phenotype to interpret in this manner is diapause, where genotypes that induce diapause in response to a particular set of environmental conditions become more frequent in areas where only individuals whose diapause has been triggered will survive extremes. The changing photoperiod requirements for triggering diapause in pitcher plant mosquitoes along an environmental gradient (Bradshaw and Holzapfel 2001) represents one example.

Where future conditions are unclear, it is often difficult to demonstrate experimentally that plasticity is adaptive in populations. For example, in laboratory tests of the 'beneficial acclimation' hypothesis, populations exposed to different environments are reciprocally swapped to see if there is increased fitness in their home environment (Huey et al. 1999). However, the outcomes of such experiments often fail to match predictions (Wilson and Franklin 2002, Kristensen et al. 2012). This is probably because the natural environments to which organisms become (ultimately) adapted through their plastic responses are different from those used by the experimenter. Instead, the adaptive value of plastic responses triggered at moderately high versus intermediate temperatures may be that these temperatures precede even more extreme conditions (Wilson and Franklin 2002). In other words, when temperatures increase, organisms may be responding to the likelihood temperatures will continue to increase in the future. With extreme conditions becoming more common in coming decades, such responses will be increasingly critical for population persistence.

The fact that many plastic responses attempt to prepare genotypes for future environmental conditions highlights a key challenge in testing the fitness benefit of plastic responses. To demonstrate adaptive plasticity, it is not sufficient to measure a phenotypic state across a given set of environments (Fig. 1), even if this phenotype is relevant to fitness. Instead, we need to show that genotypes can phenotypically match a changing optimum, at the lowest possible production cost, in ways which may include displacement of the genotype in space (mobility) as well as in time (phenology) to limit their exposure to environments where they can both survive and be appropriately sensitive to the environment. In other words, plasticity needs to include the ways that genotypes choose to inhabit environments within which they can create appropriate (high fitness) phenotypes.

Accounting for this mobility of genotypes in space and time is especially challenging in an experimental setting where organisms are necessarily limited in their movement, and where efforts are often made to reduce spatial variation in the environment. When exposed to a changing set of environments that vary in their predictability, adaptive plasticity will be achieved by genotypes evolving sensitivity to the subset of existing environmental cues that are best correlated with the future local environment to change their phenotypes, unless favourable environments are accessible in space through their physical movement (e.g. in the case of short-distance habitat preference, or long-distance periodic migration), or by a combination of these mechanisms. In this way, the sensitivity of genotypes to the environment – and the extent to which they can moderate their exposure to it (so minimising the phenotypic shift required) – fundamentally alters the patterns of environmental variation in time and space that genotypes experience (Nadeau et al. 2017). However, the evolution of genotypes with appropriate sensitivity to engineer their exposure to the environment, instead of making phenotypes that are suitable for all conditions, depends on the degree of autocorrelation in environments in time and space – i.e. whether a combination of cues at a given moment or place can predict future or spatially distant environments (Burgess and Marshall 2014).

The challenge of past environments for plasticity evolution

Over ecological timescales, genotypes are also constrained by past selection affecting the ways that such sensitivities can evolve, particularly if there are tradeoffs with sensitivities in historical environments. For instance, reaction norms may have evolved in environments that are strongly seasonal and highly predictable to an organism across years and across generations (Varpe 2017). High environmental predictability is likely to reduce standing genetic variation in environmentally sensitive pathways, increasing the streamlining and integration of these pathways by selection for pleiotropy and epistatic interactions, which may then constrain future evolutionary trajectories. For example, the ability of *Bicyclus anynana* butterflies to predict seasonal variation accurately to produce polyphenism (discrete seasonal phenotypes) probably explains the remarkably low genetic variation in plasticity in the transcriptome of this species (Oostra et al. 2018). By contrast, in the Glanville fritillary butterfly, high levels of genetic variation in larval plasticity are observed, probably because the optimum plastic response has historically varied from year to year due to spatial and temporal environmental heterogeneity that has made the environment unpredictable across even a few generations (Verspagen et al. 2020).

Beyond these effects of environmental variation on levels and forms of genetic variation within species, constraints also extend deeper into evolutionary history. Phylogenetic constraints persist across genera or families, in the form of genomic architecture, or where the structure of developmental pathways allows only a small subset of genes to be modified by mutation (Maeso et al. 2012).

Genotypic exposure to future environments through sensitivity and reversibility

Alleles that increase 1) the duration of sensitivity to the environment of a trait, and 2) the degree of reversibility in this

trait after this sensitivity is expressed, should increase the predictability of an organism's environment in time and space. For sexual invertebrates, success in predicting future environments and making appropriate phenotypes may also reduce the diversity of genotypes that are available for mating, so increasing the predictability of a given allele's future genomic environments.

Component 1) is determined by the period of an organism's lifetime when a given trait is sensitive to environmental variation. This duration of sensitivity can range from a short period early in development (trait change irreversible), to the entire life cycle (trait change largely reversible) and can also include the genotype's parental or grandparental generation (Fawcett and Frankenhuis 2015, Uller et al. 2015). Sensitivity and reversibility therefore need to be considered within the context of the sex, age and developmental stage of an organism that influence environmental sensing and the subsequent or ongoing phenotypic responses (Bowler and Terblanche 2008, Fischer and Karl 2010, Zhang et al. 2015a).

Appropriate plastic responses typically make a genotype's environment more predictable in time and space. By adjusting phenotypes plastically with sufficient speed and degree, in an appropriate direction, and for sufficiently long, a genotype invests in sensitivity and in maintaining sufficient reversibility to reduce the impact of exposure to an unexpected environmental change on fitness. Such investment in 'smoothing' the environment includes acclimation, but also 'niche construction', for example by increasing parental care and provisioning, oviposition preference, search behaviour, habitat preference and dispersal, or seasonal diapause and subsequent emergence. Similarly, environmental smoothing through plasticity includes sensitivity to indirect cues of predator activity (e.g. the abundance of predator waste products in the environment, or the alarm calls of other prey species), or to the growth of primary producers (e.g. bud burst or flowering, as used by invertebrate herbivores and pollinators), increasing the predictability of future attack or food supply.

Environmental sensitivity evolves in form and duration as a continuum

Sensitivity costs (Fig. 2) arise when genotypes are either too sensitive to an environmental cue that becomes uninformative, not sensitive enough to another (newly informative) one, or are overwhelmed by multiple conflicting cues as opposed to mutually consistent cues (Donaldson-Matasci et al. 2010) meaning that appropriate cues cannot be identified. These costs may arise within the same developmental stage, or for the later adult stage. For a given trait, genotypes may be sensitive only for a short period (e.g. at fertilization; at fourth instar; during morphogenesis, or at a given day of the year), leading to irreversible phenotypic changes, or they could remain sensitive for their entire lifetime (e.g. through foraging behaviour, habitat preference), leading to mostly reversible changes (Fawcett

and Frankenhuis 2015). For example, the evolution of specialised (and costly) sense organs, and/or cognition, allows sensitivity to a great complexity of environmental cues simultaneously, and represents a large investment in an extended period of environmental sensitivity and phenotypic plasticity (Niven and Laughlin 2008). This increases the capacity of organisms to cope with continual unpredictability. By contrast, less investment in sensory or cognitive apparatus is expected to evolve where environmental changes are highly predictable for an organism, even if they are substantial. Such adaptive plasticity is observed in intertidal invertebrates, whose survival depends on extreme physiological and behavioural responses to changes in temperature, salinity, oxygen content and biotic conditions during tidal changes. This diurnal variation is typically greater in magnitude than the average changes in these conditions that constrain the latitudinal ranges of intertidal species. However, at a given locality, changes due to tides are highly predictable for an organism, meaning phenotypic responses can be initiated before the onset of environmental stress, and involve irreversible commitment to an altered phenotype, albeit for a relatively short (diurnal) duration (Stillman and Somero 2000). As the environment becomes increasingly unpredictable, or provides cues that vary in reliability, information from the environment may need to be continually integrated to produce plastic responses with a high fitness. For example, if early bud burst occurs across only a few host plants, it may be too early for overwintering herbivores to initiate egg production because rare bud burst is an unreliable cue. Nevertheless, invertebrates might still evolve to respond to unreliable cues if the fitness benefits of responding to reliable cues are much smaller. For instance, aphids are found on leaf surfaces that provide only small feeding benefits because they thereby avoid large but unpredictable fitness costs associated with predation and abiotic stresses (Yin et al. 2021).

Different levels of sensitivity of given traits to the environment (i.e. the level of phenotypic change effected) can be plotted against the narrowness of the time windows within which they are activated relative to the active period of an organism (Fig. 3). Such variation in sensitivity, based on the period during which plastic responses are possible, is well-known in studies of seasonal adaptation (Varpe 2017). As described above, many irreversible phenotypes are characterised by early and narrow durations of sensitivity. For example, diapause is switched on by conditions encountered during egg laying or seed maturation, or at particular larval instars, but cannot be activated outside these times. Similarly, developmental acclimation and polyphenism (which also increase stress resistance) typically operate within a narrow time window of sensitivity (Moran 1992). By contrast, hardening to increase stress resistance is widespread across cells and maintained throughout the lifetime of an organism if it is mediated through processes like (costly) heat shock protein production, allowing continual and moderated responses to a stress that is difficult to predict (Jaattela 1999).
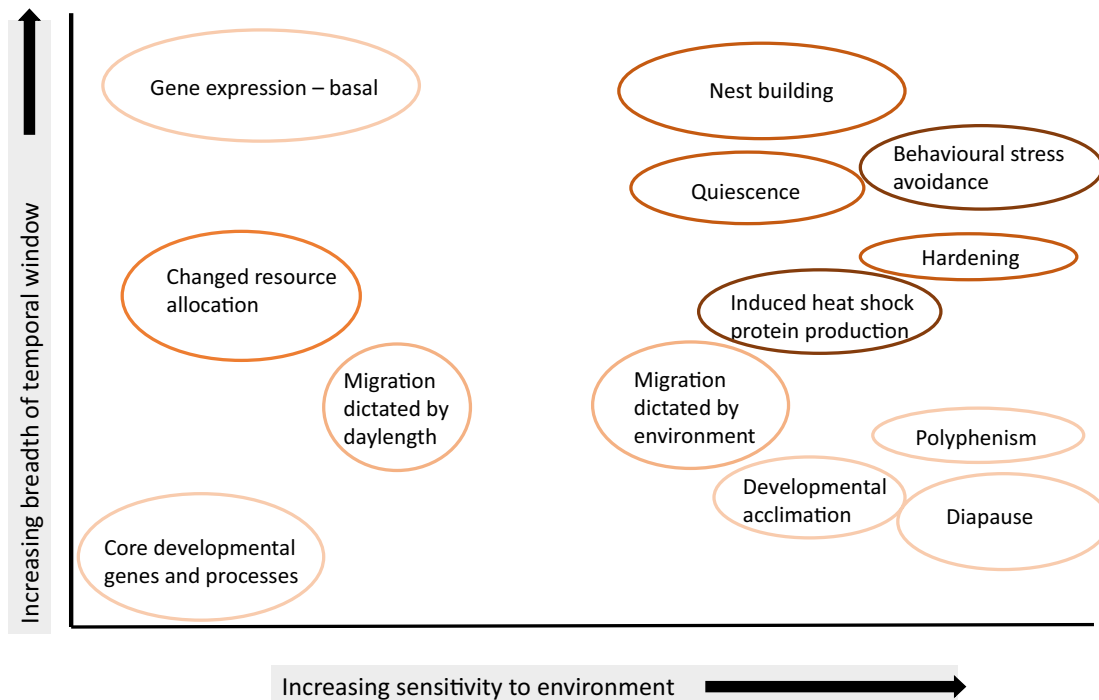
Figure 3. The environmental sensitivity of some traits tentatively mapped against the extent to which plastic responses depend on a particular temporal window of sensitivity (relative to the length of the organism's life). The space where some of these traits sit (such as migration) will be quite variable depending on how responsive they are to environmental conditions. Colour of ovals indicate the relative reversibility of traits (dark = more reversible). Traits determined early in development, often under a narrow developmental window, tend to have low reversibility (core processes, diapause, polyphenism, developmental acclimation). Other processes can change rapidly during a day (behavioural stress avoidance, induction of heat shock protein production), while still others like quiescence and hardening can take a while to be triggered.

Trait reversibility also represents a continuum

The continuum of reversibility shown in Fig. 4 emphasises the variety of responses that contribute to the environmental sensitivity of a genotype (Fischer and Karl 2010), and the idea that periods and timings of sensitivity can be predicted depending on the nature of environmental variation and the fitness consequences of different phenotypes (Fawcett and Frankenhuis 2015).

Some forms of plasticity are easily reversible, but demand continual environmental sensitivity – like variation in body colour in some cephalopods, and reptiles where rapid colour changes occur due to the availability of multiple pigments in the skin (Williams et al. 2019). Other plastic responses like diapause and polyphenism have narrow environmental windows and are largely irreversible once they have followed a particular developmental trajectory (Fig. 3, 4). Yet other plastic responses may be partially reversible, depending on life stage; for example, *Bicyclus* butterflies developing at low temperatures produce larger eggs even at higher temperatures initially; eventually however, high laying temperature effects predominate, resulting in smaller eggs (Fischer et al. 2003). And still other plastic responses are dependent on both reversible and irreversible changes; for instance, acclimation is often seen as a reversible change, but the extent to which an

organism can acclimate can depend on developmental conditions (Beaman et al. 2016).

Behavioural phenotypic change is a rapid and a highly reversible form of plasticity, and allows a genotype to rapidly alter its exposure to environmental variation (e.g. a reduction in prey encounter rate, or a change in their defences), by moving to a more suitable environment, changing its foraging strategy, or its responses to conspecifics. Even for such individual behaviour, however, there is a degree of irreversibility (Sih 2004, Ghalambor et al. 2010). For example, nest building will buffer genotypes from future extreme climatic events and predation risk, and may be prompted by environmental cues that correlate with future privations. However, nest building represents a substantial investment of time and energy that is not easily or instantly reversible. We have therefore included it in the partially reversible category in Fig. 4.

Plastic responses are expected to become less and less reversible as developmental processes are fundamentally altered (Snell-Rood et al. 2018). For example, polyphenism in many insects involves a switch early in development that locks genotypes into particular developmental pathways. This switch relies on a high level of sensitivity to other environmental cues early on (Moran 1992). For example, polyphenism in butterflies can be triggered by temperature, photoperiod (Richard et al. 2019) or a combination of these variables (Nijhout 1999). Many other irreversible phenotypes
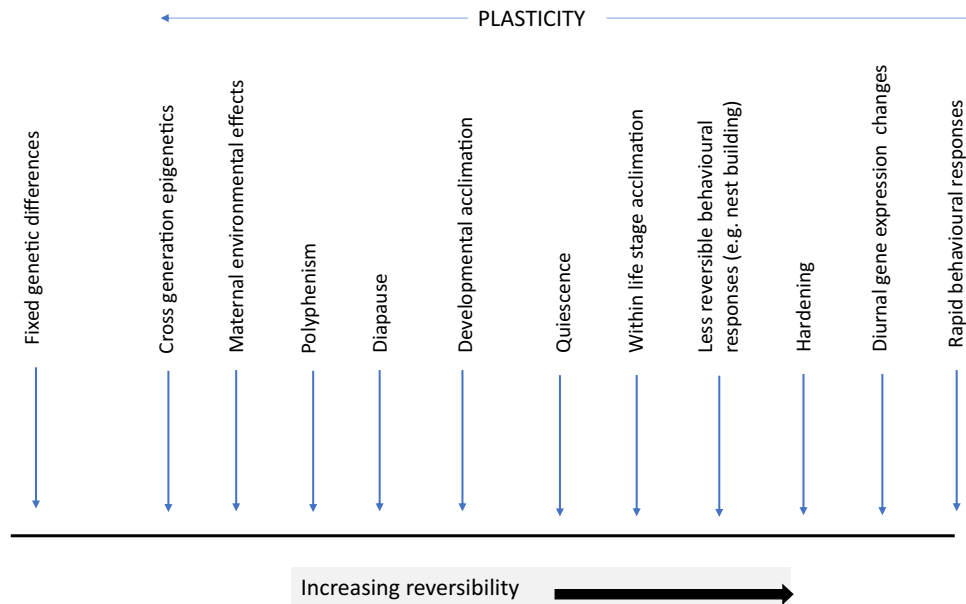
Figure 4. A continuum of plastic components for a given genotype decreasing in levels of reversibility from dynamic behaviour responses to fixed (non-plastic) effects. The continuum includes cross generation effects triggered by the environment including maternal environmental effects (where the phenotypes of the offspring are influenced by the maternal environment) and epigenetic changes (which may persist for several generations). Other forms of plasticity are discussed in the text.

are initiated within certain windows in development (e.g. diapause, colour morphs and anti-predator responses) (Riessen and Sprules 1990, Forsman et al. 2007). Changes as a result of such a short period of plasticity can be locked in for even longer if there are epigenetic effects that last across one or more generations, such as polyphenism in insects (Richard et al. 2019). Where environments are inherently unpredictable for an organism, or where making predictions about future environments requires integrating information from many cues (Botero et al. 2015), trait shifts that are irreversible should therefore favour extended delays before committing to a phenotype. At the same time, any such delays are likely to be metabolically costly, as well as developmentally difficult, given the reduction in totipotency of many cell lineages and insect castes observed with age (Zhang et al. 2015a, Wu et al. 2017).

While the reversibility and environmental sensitivity of plastic phenotypes often vary among traits, levels of reversibility for the same trait can vary among species. Body colour is an instructive example because plastic responses can vary from being completely reversible to completely irreversible across species, as well as varying throughout an individual's lifetime (Duarte et al. 2017). For instance, while wing pigmentation in Lepidoptera is generally irreversible, in grasshoppers it can be either: irreversible (where it forms a useful taxonomic character); fixed early in development (depending on juvenile background); determined by the background or temperatures to which early stages are exposed (Hochkirch et al. 2008, Valverde and Schielzeth 2015); or even (in the case of the alpine grasshopper, *Kosciuscola tristis*), completely reversible with temperature, in that male mountain grasshoppers are able to change colour overnight

(Umbers 2011). Such a continuum of responses provides an opportunity for empirical tests of the production costs associated with the maintenance of reversible plastic phenotypes.

Irreversible change is potentially cheaper and larger than reversible change in phenotype

Theoretical models often assume that the phenotypic space accessible via irreversible and reversible sensitivity (and their developmental production costs) is similar (Botero et al. 2015). However, there may be functional constraints on what types of plastic responses can evolve in each case. These are dictated by the mechanisms underlying the plastic responses. For example, increasing desiccation resistance in insects typically involves decreasing the rate of water loss. This can be achieved by building a protective cuticular hydrocarbon layer or by down-regulating loss of water through spiracles, both of which can be plastic (Arcaz et al. 2016). However, while the latter is highly reversible, the former is much less so and the creation and removal of cuticular hydrocarbons involves an irreversible cost. Similarly, body size in *Drosophila* can be achieved by the rate of targeted growth early on as larvae (defined by the rate of cell proliferation, and the growth of imaginal discs), or be modified during larval growth by adjusting the length of the larval period in response to environmental conditions (Hyun 2018). However, an increased rate of cell proliferation has to happen early on in development, meaning the larvae are committed to a particular adult size early on. By contrast, modifying larval duration – although it demands extended durations of sensitivity – allows the slowing or

acceleration of development when larval environments (and perhaps the ensuing adult environments) change unpredictably. Such active slowing of metabolic rates to reduce rates of larval development may prevent environmental mismatch along latitudinal gradients (Lindestad et al. 2020). Therefore, although the capacity for development rates to be modified within individuals at a given latitude may be critical for adaptation to climate change, it may come at a high metabolic price. Such modifications to plastic strategies may impose unexpected extra costs on organisms as they adapt to decreases in the predictability of future environmental regimes (Box 1).

In addition, for most irreversible plastic changes, we suspect that the phenotypic change possible will be greater than for reversible changes, for example where the deep diapause triggered early in development increases resistance to stressful conditions (Cheng et al. 2018) and allows genotypes to evade predators (Pijanowska and Stolpe 1996). We also suspect that a greater range of phenotypes will be accessible to a given genotype (at least initially) if there is no need to maintain the capacity to revert to former phenotypes. Many phenotypic responses are only possible if they are triggered early in development, and even rapid phenotypic responses may need to be primed early in development. For instance, immunity production in butterfly larvae often involves priming at early instars (Saastamoinen et al. 2013), or even via the mother prior to or at oviposition, requiring a metabolic commitment to a particular form of immunity in the larvae, which may extend development time, either by increasing the period of larval vulnerability, or by reducing adult body size and therefore adult reproductive success (Woestmann and Saastamoinen 2016).

Environmental predictability and reversibility

An invertebrate may evade an extended period of unpredictable stress entirely, for example by entering diapause early, and before the onset of such conditions (Tarazona et al. 2017). However, if unpredictable conditions for an organism cannot be avoided, the cost of committing to a given phenotype depends directly on environmental variation and can be very high where future environments cannot be predicted by an organism, even when many cues are integrated (Fig. 5).

Where environments are largely unpredictable for an organism, models often focus on the fact that genotypes with a lower variance in fitness at the cost of a lower arithmetic mean fitness (i.e. genotypes with a higher geometric mean fitness) should be favoured, which can be achieved by an increase in trait variance (diversified risk spreading) or a phenotype that reduces risk (conservative risk spreading) (Simons 2011). There is an extensive theoretical and conceptual literature on conditions promoting these 'bet-hedging' strategies (Seger 1987, Philippi and Seger 1989) and some of the models that have been developed around diversified risk spreading in invertebrates specifically incorporate a comparison of reversible versus non-reversible phenotypes such as diapause and
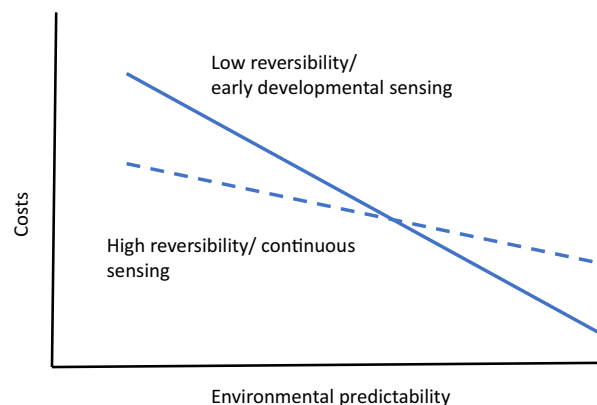

Figure 5. Assumed association between costs of reversibility/sensitivity and environmental predictability. When plastic changes are less reversible, the cost increases as environments become unpredictable. Reduced environmental predictability may generate a mismatch between the environment and the optimal phenotype, increasing costs of irreversible phenotypes relative to those of reversible plastic changes, which are otherwise more costly to maintain in highly predictable environments. This is because they require a longer duration of genotypic sensitivity to the environment and are likely to be limited to smaller changes in phenotype than commitment to a given phenotype early in development.

polyphenism (examples in Hopper 1999). However empirical evidence relevant to the hypotheses generated by the models has proven difficult to collect (Simons 2011).

A different approach to bet-hedging advocated here is to focus on reversibility and environmental sensitivity rather than on how specific sets of phenotypes affect geometric fitness. By considering genotypes that vary in reversibility and sensitivity, our focus is not so much on whether particular phenotypes differ in arithmetic or geometric mean fitness across a set of environments, but about the potential of a phenotype with an optimal level of reversibility to emerge given limits and costs to the extent and speed at which an organism can sense and adjust to an environment. Such an approach means that, when characterising the fitness costs of plastic responses, the predictability of an environment for an organism needs to be considered alongside the reversibility of any plastic response, and therefore the fitness advantage of maintaining phenotypic reversibility despite its increased production cost. As predictability increases, the costs of low reversibility are reduced, and the benefits of a short period of high sensitivity (and associated specialist pathways and structures) are increased (Fig. 5). For instance, earth mites that enter a deep irreversible summer diapause, and that then emerge in predictably favourable cool autumn conditions gain a fitness advantage over earth mites entering a more reversible quiescent state which is less resistant to hot summer conditions (Cheng et al. 2018). By contrast however the more reversible form has an advantage where conditions are sporadically (and less predictably) favourable (Cheng et al. 2018).

By contrast, although maintaining reversibility may only be possible for a narrow range of phenotypes (and may demand extensive and prolonged sensory investment),

reversible phenotypes remain an essential strategy for dealing with future aspects of the environment that are impenetrably unpredictable for an organism, and where the costs of making the wrong response are high (e.g. in detecting predation risk). We believe that such a tradeoff between reversibility and the magnitude of phenotypic change is fundamental in the evolution of plasticity. Such a tradeoff is also likely to become greater as organisms live longer. For example, starvation conditions in insects can be countered by the immediate mobilisation of (easily replaced) carbohydrates, proteins and other endogenous reserves. However, long-term survival in the absence of food may depend on the (less reversible) use of fats accumulated early in development or through the dramatic changes in metabolism possible through diapause (Zhang et al. 2019). Similarly, in social insects, greater caste specialisation is associated with reduced reversibility, as demonstrated by the final determination of larval caste early in development in honey bees, compared to retaining the capacity for workers to become queens throughout much of their life as in *Polistes* wasps (English et al. 2015).

Models have been developed that address the relationship between reversibility and the extent to which organisms can predict an environment (Gabriel et al. 2005, Frankenhuis and Panchanathan 2011, Botero et al. 2015), and which have implications for life history evolution. For instance, Botero et al. (2015) simulate reversible versus irreversible plasticity and suggest that the cost of environmental mismatch should lead to reduced sensitivity of irreversible forms of phenotypic change (i.e. shallower than expected reaction norms), to minimise the risk of overshooting the optimum phenotype, albeit with an inevitable cost of increased phenotypic variance around the (eventual) optimum for that environment (Botero et al. 2015). By contrast, a strategy of continual phenotypic adjustment (i.e. reversibility in key traits by maintaining a long duration of sensitivity) in unpredictable environments should reduce the risk of phenotypic mismatch with the environment growing over time, so increasing fitness at later life stages, and therefore lifespan (Ratikainen and Kokko 2019). Organisms living in environments that are highly predictable for the organism should therefore evolve (more cheaply produced, and greater in magnitude) irreversible plasticity, generating genotypes whose fitness declines more quickly with age, as phenotypic mismatch increases, especially beyond reproductive age.

The fitness of genotypes will depend on how well their phenotypes match future environments, particularly when phenotypic responses have to develop in early life stages, even when the adult environment is not certain. Costs of mismatches between environments of development and adulthood are common. For example, female seed beetles raised at low temperatures have a low hatch rate when their eggs are raised at high temperatures (Stillwell and Fox 2005). In *Daphnia*, the morphological structures and carapace alterations needed to increase stiffness and that reduce the susceptibility of adults to predators (Kruppert et al. 2017) can only be produced within an early developmental window when carapace development takes place, but will be unnecessary

(and costly) in ponds where predators disappear. Similarly, larval investment in toxicity and aposematic coloration in Lepidoptera, which is energetically costly and leads to an irreversible cost in terms of adult body size, will only provide a benefit in future environments that have an abundance of visual and (ideally) experienced predators (Mappes et al. 2005). Alternatively, early instar commitments by larvae to increased immunity in response to plant alarm signals may increase the relative fitness of genotypes, but they may also reduce fitness if the host plant fails to attract parasitoids and predators to attack the larvae (Howe and Jander 2008).

Predicting patterns in plasticity in changing environments

We believe that a richer understanding of plastic adaptation to environmental change emerges when the evolution of adaptive plasticity incorporates: 1) the notions of reversibility, sensitivity and their interactions with the environment to make phenotypes that match future optima, and 2) the idea that genotypic sensitivity evolves to allow environmental variation to be smoothed by reducing the exposure of alleles to periods of low food availability, inclement climate and antagonistic biotic interactions. An understanding of plasticity therefore requires investigations that extend well beyond the reaction norms depicted in Fig. 1. Specific hypotheses can be developed (described in Box 1) by integrating these fundamental aspects of plasticity that extend beyond the metabolic or functional/structural costs associated with producing plastic responses, and their immediate fitness effects. Environmental sensitivity needs to be considered across different timescales and along a response continuum that includes (Fig. 4): 1) epigenetic changes that influence gene expression and persist across many generations; 2) maternal effects including behavioural modifications (e.g. oviposition choice, juvenile feeding) that influence offspring environments; 3) environmental effects that act across generations (e.g. parental nutritional stress, exposure to stress); 4) developmental acclimation depending on juvenile environment which may be mostly irreversible, extending to; 5) reversible changes (such as individual behaviour, or movement), which act predominately within generations and can be rapidly altered. Fixed genetic changes are then placed at the first extreme of this continuum, as ways of modifying genotypic sensitivity that persist for the duration of each allele's lifespan.

To understand costs arising from the irreversibility of phenotypic plasticity, the developmental processes, nature of environmental variability, ways that the environment is sensed (and for how long), and the genetic variation underlying these different components of plasticity all need to be considered (Fawcett and Frankenhuis 2015, Ørsted et al. 2018). For example, for a species that breeds once a year after it reaches sexual maturity, environmental variability mainly consists of diurnal variation and seasonal variation. These routine patterns of environmental variation can be met by a combination of reversible and irreversible changes to phenotypes to match

Box 1. Predictions for the reversibility and sensitivity of plasticity under different environmental regimes

1) If an environment changes daily in a repeatable manner, and there is a large cost of maintaining the local optimum in both environments, the optimal state will involve high reversibility, provided conditions can be sensed and optima matched through reversible phenotypes that involve relatively low production cost (e.g. movement, physiological shifts involving hardening, increased vigilance or immunity).

2) Under seasonal or diurnal environments that are predictable for an organism, limits to reversibility will become increasingly evident (or ecological niches narrower) where conditions become extreme and reversible phenotypes can no longer reliably match both local optima. For example, limits to the geographical distribution of intertidal organisms will be set where the magnitude of temperature variation at high/low tides exceeds critical limits. At such critical limits, seasonally triggered, less reversible phenotypes will evolve such as diapausing stages, and a high degree of sensitivity, or integration of plasticity pathways (Varpe 2017). Although reversible phenotypic states for sedentary organisms might suffice in years where conditions are not too severe, an occasional poor year would eliminate all individuals expressing such a phenotype. Geographical range limits, and limits to local adaptation, will therefore be determined by the thresholds where reversible phenotypes become too costly for organisms to persist at a given location.

3) Under directional environmental change (e.g. a changing climate), less reversible forms of plasticity that are initiated by a short period of sensitivity will evolve as there are limits to what reversible changes can achieve to maintain fitness. Conversely, if irreversible changes create phenotypes that start to have low fitness under directional environmental change (e.g. low temperature dormancy in a warming climate (Footitt et al. 2018)), or directional environmental change reduces predictability, more reversible changes may be selected, unless an irreversible change allows a genotype to escape an unpredictable period such as through the insertion of a diapause step (Tarazona et al. 2017).

4) Given 3) above, where irreversible forms of plasticity do evolve, they increase the cost of moving to an unpredictable environment and reduce the environmental tolerance of genotypes if existing environments become less predictable for an organism. This will favour reduced movement of alleles or individuals into novel environments, populations or genomes, perhaps through the evolution of habitat choice (and investment in high mobility), and assortative mating. Irreversibility therefore leads to ecological and phenotypic specialisation (to increase environmental predictability), which in turn allows even more irreversible forms of plasticity to be favoured. This 'snowballing' of irreversible forms of plasticity has parallels with the loss of plasticity associated with genetic assimilation (Waddington 1961).

5) The maximum size of a plastic change in a phenotype that is possible decreases with increasing reversibility. This hypothesis is supported by studies of cold resistance in many insects where cold resistance in programmed diapause stages is particularly high. This applies to *Drosophila melanogaster* (Anduaga et al. 2018) in the absence of diapause, both reversible (hardening) and irreversible (developmental acclimation) components also contribute to cold resistance at the adult stage (Colinet and Hoffmann 2012), leading to similar levels of resistance (Kristensen et al. 2012).

the conditions. Individuals enter diapause (a periodic irreversible change) in response to environmental cues that accurately predict future climatic conditions and respond to unpredictable cues like sudden shifts in temperature and humidity in a way that allows their metabolic rates (reversible change) to be matched to unexpected changes in climatic conditions.

When a univoltine invertebrate encounters extreme conditions that exceed the prevailing diurnal and seasonal environments, ongoing reversible and irreversible phenotypic responses may be insufficient and may lead to inappropriate (maladaptive) responses. For example, unusually high temperatures at night when an insect's repair response is reduced may cause damage and an inability to counter future heat stress (Zhang et al. 2015b). Similarly, intertidal anemones suffer loss of zooxanthellae, and high mortality when (unpredictable) summer downpours flood rockpools that usually become predictably more saline high on the tide line until the ocean returns (Agrawal et al. 1999).

Although rapidly reversible changes and continual environmental sensitivity (e.g. behavioural responses) can protect against unexpected extremes, irreversible states cannot

and require investment in phenotypes that allow genotypes to survive rare extremes and phenotypic mismatches (e.g. thicker cuticles in anemones). The risks of irreversible plasticity should therefore also increase when mostly predictable conditions start to include more frequent extremes, and as the magnitude of those extremes increases. Episodes of intense selection that occur under extreme conditions may therefore leave a substantial ecological footprint. This may be why extreme events often determine insect geographic range limits (Overgaard et al. 2014), even though their importance will often be hard to detect based on existing relationships between species' abundance and the environment.

A case study: *Drosophila* dealing with cold conditions

We have highlighted how the above framework can lead to testable hypotheses about plastic responses that go beyond the characterization of plastic changes, placing them within an environmental and developmental context that reflects the

multiple costs and benefits to plasticity as outlined in Fig. 2, and its likely evolution and consequences for life history variation. We now give an example of how existing information might be interpreted within such a framework, and where opportunities might arise for testing novel hypotheses by considering the case of plastic responses to thermal extremes in *Drosophila* (mostly *Drosophila melanogaster*) which has been investigated for many years both within a lab context and to a lesser extent in a field context.

Drosophila melanogaster adults show increased resistance to cold extremes following plastic changes triggered by exposure to different temperatures at various life stages. These include being cultured at different temperatures at the larval stage ('developmental acclimation'), being held at different temperatures within a life stage ('acclimation') and being exposed to a short non-lethal cold period ('hardening'). All of these plastic responses have cumulative effects on cold resistance (Colinet and Hoffmann 2012). In addition, reproductive diapause in adult females triggered by cold conditions increases cold resistance (Schmidt and Paaby 2008). These changes vary in their degree of reversibility (hardening being the most reversible, and diapause/developmental acclimation the least reversible).

A combination of these effects no doubt helps *D. melanogaster* overwinter in cool temperate environments, which occurs at the adult stage rather than immature stages (Mitrovski and Hoffmann 2001). Field studies with released adults that were acclimated developmentally or within the adult stage indicate particularly large fitness benefits under cool conditions following developmental acclimation (Kristensen et al. 2008), suggesting that irreversible plastic changes have a larger impact than reversible changes. However, there are costs that depend on temperature conditions experienced in an environment. Costs under warm conditions were particularly evident in flies developmentally acclimated to cool conditions, suggesting that a non-reversible change triggered in the larval stage could result in a very large reduction in fitness if the environment experienced at the adult stage is warm rather than cold. On the other hand, reversible hardening had a much lower cost under warmer conditions. Likewise, high temperature hardening benefited adults under hot conditions but with a relatively low cost under cool conditions (Kristensen et al. 2008). The costs and benefits of irreversible plasticity therefore clearly depend on the predictability of the thermal environment. It is the sensitivity of early developmental stages to cold conditions (and at the appropriate time and for the appropriate duration) that dictate whether these costs are also expressed in the warm environment.

Apart from these costs associated with acclimation, there will also be costs associated with entering reproductive diapause at the wrong time, because females will then stop offspring production – a response that cannot be easily reversed once triggered (Saunders and Gilbert 1990). For this reason, the incidence of diapause induction shows a strong genetically determined latitudinal pattern, being common in high latitude populations but not in low latitude populations. This allows females to survive cold conditions at high latitudes (Schmidt and Paaby 2008) but presumably ensures that females at low latitudes continue to produce offspring if occasional cold conditions are encountered. An evolutionary shift is therefore likely to have resulted in low latitude populations that avoid the (mismatch) costs of diapause associated with the production of a phenotype with a low reversibility that might be triggered due to inaccurate environmental sensing. However, in contrast to these findings for diapause, developmental acclimation is of a similar magnitude in populations across a wide latitudinal gradient (Hoffmann et al. 2005) even if there are likely to be few benefits to developmental acclimation in relatively constant tropical conditions. Perhaps evolutionary constraints restrict the development of latitudinal variation in this plastic response despite its potentially very large cost under warm environments.

Examination of the above patterns supports some of the predictions about the evolution of plasticity that we outline in Box 1. They suggest that developmental acclimation and reproductive diapause are likely to have evolved because of the very high costs involved in failing to survive particularly cold conditions (prediction 2). They also suggest that under warmer conditions there may be a loss of reproductive diapause, perhaps in favour of cold hardening responses (prediction 3), although consequences for developmental acclimation are harder to predict since this trait appears fixed in populations. Comparative studies can be used to test the prediction that plastic changes with low reversibility predominate in *Drosophila* from regions at high latitudes whereas high reversibility responses predominate in species from tropical areas. Surprisingly, comparisons undertaken to date suggest that both tropical and widespread species show relatively similar hardening and developmental acclimation responses (Overgaard et al. 2011). It would be interesting to extend this to species that are restricted to environments with strong seasonality.

Although we have focussed on resistance to cold extremes, responses to other climatic factors, particularly heat and aridity, as well as to exposure to critical biotic interactions such as with parasitoids or host plants, can also be considered from the perspectives outlined in this paper, allowing tests of how adaptive divergence interacts with the evolution of plasticity, and how limits to adaptive plasticity may lead to ecological specialisation and speciation. For instance, for desiccation resistance there is an apparent conundrum in accounting for the relatively higher hardening ability of tropical species compared to widespread species, even though the latter are more frequently exposed to arid conditions (Kellermann et al. 2018). Desiccation resistance is thought to be an important trait limiting the distribution of *Drosophila* species because of the strong association between basal desiccation resistance and *Drosophila* species distributions (Kellermann et al. 2012). Perhaps widespread species rely on less reversible forms of plasticity to increase desiccation resistance, even though this might be more costly when there is an environmental mismatch, generating narrow ecological distributions in the tropics.

Concluding remarks

The evolution of genotypic sensitivity to the environment, either producing different phenotypes or affecting an organism's exposure to environments in space or time (through mobility or phenology), is fundamental to determining how alleles vary in fitness (and frequency) across the environments experienced during an organism's lifetime. However, discussions about how organisms respond to environmental change typically consider genetic (non-plastic) and plastic shifts as dichotomous responses that may interact (Stillwell and Fox 2005, Sgro et al. 2016) through the genetic control of plastic responses (Scheiner 1993). Rather than splitting phenotypic variation into plastic and non-plastic components, a given phenotype may instead be viewed as the result of genotypic sensitivity to some aspect of the environment (or a lack of it). The dichotomy ignores the two fundamental aspects of plasticity that are described in Fig. 2, and ignores environmental predictability.

In this perspective, we have emphasized ways in which different forms of plasticity, and their role in future evolutionary responses, are expected to evolve under different forms of environmental variability. In doing so, we hoped to provide a richer perspective on plasticity, and in particular under what conditions plasticity can increase the predictability of the environment from the organism's point of view, and that of the alleles that it transports between genomes and environments. Many of these ideas considering environmental sensitivity and reversibility are not new. Neither is the idea that historical forms of environmental variability shape current sensitivities to environmental change (Nadeau et al. 2017). However, we think that tests of plasticity evolution should focus more on the costs of different states of reversibility within the context of environmental predictability as experienced by the organism. More focus is also needed on the restricted phenotypic space within which reversibility is possible, and whether the evolution of reversibility limits the ability of species to evolve in response to a new novel set of environmental conditions. By contrast, a fundamentally unpredictable environment for a given organism demands an adaptable phenotype that continually adjusts to environmental variability, monitors the costs of such adjustments to maximise fitness, and often demands wholesale movement to environments in time and space that match the genotype's range of possible phenotypes. Alternatively, organisms can develop irreversible but highly resilient phenotypes whose environment – in effect – is highly predictable from their perspective. However, such strategies also involve associated costs such as extended development time or periods of parental care and vulnerability.

Testing when and where genotypes generate such reversible phenotypes, compared to phenotypes that are determined early in development, requires experimental designs that can track trait changes across time and with different induction periods (Nyamukondiwa et al. 2010). Similarly, experiments that manipulate levels of environmental predictability, or actively reverse expected environmental trends, and test their effect on genotype fitness (Tarazona et al. 2017), could quantify when and where different plastic strategies are likely to evolve (Box 1). Understanding the limits to the evolution of adaptive plasticity, and how the magnitude of its buffering effect is constrained by environmental predictability, is particularly important as organisms and communities experience increasingly novel and more unpredictable environmental regimes due to climate change and biodiversity loss. Such environmental change may lead to abrupt declines in the fitness of invertebrate populations that could once rely on irreversible (and low cost) forms of plastic adjustment.

Speculations

In writing this perspective, we've been struck by the wide-ranging views of researchers on what plasticity encompasses, whether it deserves special focus, and the extent to which issues around its evolution have already been solved. It has also struck us that those who think most deeply about plasticity often find it the most challenging – confirming Roald Dahl's advice that 'You should never, never doubt something that no one is sure of.'

A fundamental challenge in thinking about plasticity is that the environments that alleles and genotypes experience during their lifetimes is shaped by the phenotypes they create, as well as where they place these phenotypes (and their offspring) in space (dispersal), and in time (phenology). Their environment is also shaped by the decisions other phenotypes in their community make. Ultimately, selection favours behaviours that make the environment more predictable, especially where phenotypes demand high levels of irreversible investment.

These considerations make the environmental variance that alleles experience dynamic and difficult to measure. However, understanding how plasticity determines environmental exposure is critical at a time when many organisms are experiencing entirely novel environmental regimes. As our own societies are increasingly demonstrating, without rapid adaption to these new realities, existing forms of plasticity seem unlikely to guarantee population persistence.

Author contributions

Ary A. Hoffmann: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Jon Bridle**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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