

## Plasticity and the costs of incorrect responses

Ary A. Hoffmann, Pest and Environmental Research Group, Bio21 Institute, University of Melbourne, Vic 3010, Australia

Jon Bridle, Department of Genetics, Evolution and Environment, University College London, London WC1E 6BT, UK

Vinton et al [1] raise important issues in understanding plastic responses to climate change, by focusing on whether existing genotypic sensitivities increase or decrease rates of evolutionary response, depending on local environmental variability and the autocorrelation between environmental states. Their perspective emphasizes interactions between environmental variability and predictability when assessing the likelihood and magnitude of evolution under climate change. We point to a framework for further understanding these interactions.

In assessing the role of plasticity and evolution in responding to climate change, specific aspects of the environmental context wherein responses occur need to be considered, e.g. [2-5]. Alongside environmental variance, two fundamental components of plastic responses are their reversibility and the duration of genotypes' sensitivity to environmental cues while assembling plastic responses. Both components are closely tied to development, in that less reversible (but potentially more profound) plastic phenotypic changes are often determined early in development, whereas more reversible changes are often less developmentally constrained but demand greater investment in sensitivity and persistence. We think that such a trade-off between the accuracy and magnitude of plastic responses is critical in determining population persistence as environments become more variable and unpredictable.

From this perspective, the cost of plasticity becomes directly tied to environmental sensing and phenotypic reversibility. Genotypic sensitivity that leads to largely irreversible changes becomes extremely costly if it results in phenotypes with low fitness under future conditions. We stress the importance of understanding the reliability of environmental cues and encoding of plastic responses when assessing costs. Such an approach also considers the demographic cost of inappropriate phenotypic responses, with reducing mean fitness making local adaptation (and the evolution of more appropriate forms of plasticity) more difficult [6].

We argue that the "environmental lag" highlighted by Vinton et al [1] can be further dissected by defining the conditions triggering a plastic response and conditions requiring this response. We think that it helps to have these components of a lag spelt out specifically, providing a clear framework to define the lag (sensing versus response development) and its likely cost (both in terms of inaccurate sensing and the inability for the genotype to revert to a better adapted state). We hope that this integration leads to a rich area of investigation beyond the energetic costs of plasticity. It also directs attention to how components of plastic responses can evolve, either through changes in sensitivity to cues predicting new environmental regimes, or through changes in the physiological machinery and gene networks that make phenotypic responses more reversible.

A plasticity framework that includes reversibility and sensitivity duration also helps in understanding interactions between evolutionary and plastic changes. Some of these will inevitably interact directly and mechanistically. For example, if heat shock resistance of a genotype is controlled by the (reversible) level of expression of heat shock protein (*hsp*) genes, there will likely be some limit beyond which climatically triggered *hsp* expression is no longer independent of fixed changes in *hsp* expression. Such a framework also makes important links with discussions in behavioural ecology

about “genomic reprogramming” [see 7] and the value of non-genetic transmission of information across generations.

A challenge in facing climate change is that the reliability of environmental cues for plastic responses will diminish with time, as genotypes continue to respond to past cues [8]. Such mismatches between plastic responses and local phenotypic optima are often not rapidly reversible. They will require changes in sensitivity early in development to express appropriate phenotypes. Otherwise, organisms may face developmental traps [9] and local extinction as mismatches increase [8]. For example, a warmer period in spring followed by frosts under climate change can result in insect larvae emerging from diapause encountering conditions that prevent them reaching adulthood.

As Vinton et al. [1] note, an important consideration is whether the information collected about plasticity and evolution can be of practical value. Rapid evolution of plasticity could rescue populations and communities from the demographic declines, but this depends on within species' biodiversity [10], and may require forms of sensitivity and reversibility that differ to those favoured in existing habitats [see 11]. In long-lived plants the evolution of plasticity will likely be too slow, and climate effects may only be alleviated by introducing provenances with plastic responses pre-adapted to future climates, a process that requires careful matching [12]. Avoiding the cost of potentially maladaptive plastic responses depends on knowing the cues used by provenances to make environments more predictable, their duration, and the reversibility of phenotypic responses triggered.

In summary, we agree with Vinton et al [1] that a renewed emphasis is needed on those plastic responses critical for the long-term persistence of many populations and species under environmental change. These new ideas can be linked to an existing framework highlighting the costs of environmental mismatches. Together these complementary approaches provide important directions for future research [5].

## References

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