The importance of spatial and temporal structure in determining the interplay between plasticity and evolution

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Hoffman and Bridle describe two processes that the framework introduced by Vinton *et al.* (2022) did not explicitly consider. These two processes, reversibility of plastic responses and time lags in sensitivity of responses to the environment, can affect how plasticity impacts evolution. These processes are easily incorporated into our framework by adding stage-structure and lagged environmental drivers. In Vinton *et al.*, when discussing the costs of plasticity, we primarily focused on energetic impacts on fitness, and the role of environmental predictability. Hoffman and Bridle are correct that differential impacts of plasticity across an individual's lifetime may determine its response to different types of environmental change.

In Vinton *et al.*, we take a quantitative genetic approach whereby an individual’s phenotypic trait can be decomposed into a genetic and environmental component. Environmental drivers impact the environmental component of the phenotype (see also Coulson *et al.* 2017). For example, the presence of predators may induce the development of armour in *Daphnia* (Diel *et al.* 2020). Morphological traits such as armour that develop early in life are irreversible. Such irreversible plasticity could impact population dynamics and evolution if there is a cost of having armour in a predator-free environment, a cost to not having it in a predator-rich environment, and/or the presence of predators fluctuates with time. Thus, the expression of armour remains constant at all ages greater than the age at which it was produced. In contrast, other traits are reversible. For instance, in *Drosophila melanogaster*, individuals can reversibly adjust the fluidity of their membranes in response to temperature change (Cooper *et al.* 2014). Such phenotypically plastic reversibility is most likely to impact evolution for long-lived species, or species which experience high intragenerational environmental variation.

Both the reversibility of plasticity and temporal lag between the environmental cue and the plastic response become especially relevant for individuals experiencing high temporal variation, especially in environments with low temporal autocorrelation. For example, *Daphnia* exposed to predator cues produce offspring that develop spines even if the offspring does not experience these cues. Thus, parental and developmental cues can contradict each other and the adaptive anticipatory effects prove maladaptive. Environmental lags such as these are straightforward to incorporate into the framework in Vinton *et al.*. To do so, one must identify the pertinent environmental drivers from previous time steps and link their effects on phenotypic transitions going forward(*e.g.* Evers et al 2021).

Furthermore, spatial structure may impact plasticity’s effect on fitness (Bridle and Hoffmann 2022). If the environment is locally heterogeneous, the organism might experience multiple environments during its lifespan - in this context plasticity will be beneficial. In contrast, if the environment is locally homogenous, individuals may only experience a single type of environment within their home range. Here, there is less opportunity to modify their phenotype.

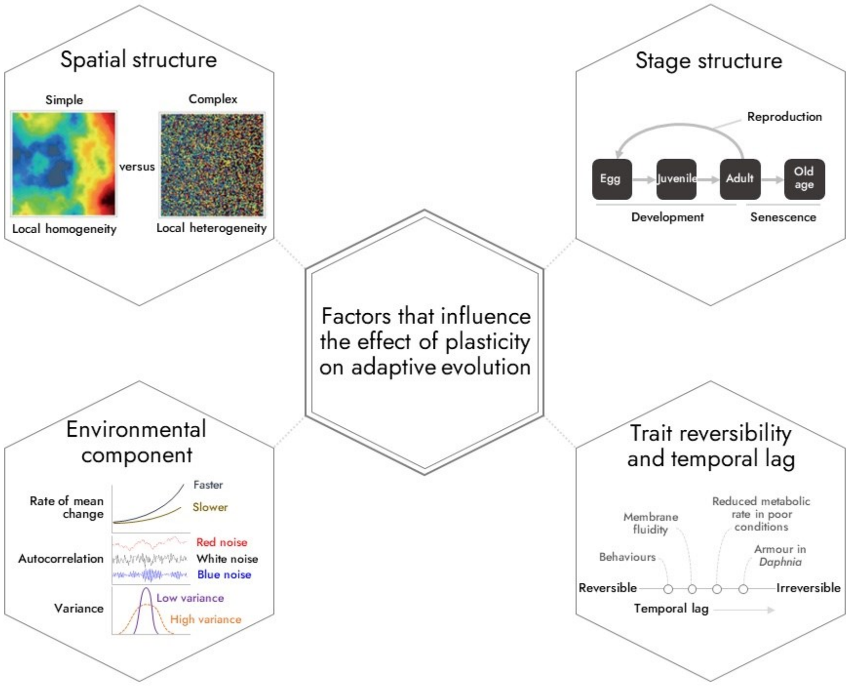
The reversibility and time lags of plasticity can be incorporated into our framework introduced in Vinton et al. via an explicit temporal component. This component accounts for the stage of individuals, as well as other issues that we did not include in depth, such as how the cost of plasticity may be related to the life stage in which it occurs (Figure 1). To incorporate these drivers, we recommend two relevant widely used methods; structured population and individual-based models (IBMs). Structured population models such as integral projection models (IPMs) have the advantage that they quantify all possible transitions between phenotypic traits, even if these transitions are unlikely. These models can also be analysed with the tool box of linear algebra. Specifically, tradeoffs of plasticity within lifecycle stages, or related to a quantitative trait such as body size, can be incorporated to assess the impact of plasticity on population growth rate and evolution(Coulson *et al.* 2017). Moreover, spatial structure similarly can also be incorporated(Jongejans *et al.* 2011). Performing integrated sensitivity analysis would allow us to assess how important specific stages or traits are to population dynamics and evolution while explicitly incorporating lagged trade-offs. The data to construct a model necessary for such analysis is best obtained via experimental manipulations -

or via simulations. In addition to the data recommended in Vinton *et al.,* experimental work will be necessary to parameterise the stage(s) at which individuals are most sensitive to environmental change, as well as at the stage(s) where phenotypic plasticity occurs(Coulson *et al.* 2021).

A limitation of IPMs is that they become computationally demanding when the number of phenotypic traits being tracked becomes large. IBMs may be more appropriate in such cases. A limitation of IBMs, however, is that they only iterate forward a sample of all possible phenotypic transitions, such that each run of the model will produce a different outcome, thus limiting reproducibility. Nonetheless, the algorithms defining IBMs are similar to those used in structured population models. This similarity means that, for low dimensional stage models, insights gained from IPMs and IBMs are equivalent(Ellner *et al.* 2016).

The flexibility of the proposed modelling approaches has been vastly increased in recent years. For instance, IPMs have been expanded to examine the role of plasticity on population growth rate, phenotypic traits, life history traits, and eco-evolutionary dynamics (Coulson *et al.* 2017). An example includes the role of plasticity in great tit (*Parus major*) in hatching date, coupled with shifts in temperature (Simmonds et al 2020). Although reversibility and environmentally lagged variables have not been explicitly incorporated into these approaches, it is a simple step to do so. The conditions under which these processes impact the role of plasticity in adaptive evolution is yet to be investigated, and there will likely be parameter space in which factors such as reversibility and lag time are more or less impactful. We pose the utilisation of the aforementioned well-developed approaches to theoretically and empirically explore the impact of these processes. Ultimately a spatiotemporal framework will lend the ability to connect hypotheses drawn from Vinton *et al.* to real world systems.

Figure 1. Factors that impact the cost of plasticity on individual fitness. In addition to the components discussed in Vinton *et al.* (2022), here we explicitly include the importance of the reversibility and temporal lag of plasticity, spatial structure and stage structure in the impact of plasticity on adaptive evolution. Spatial complexity (top left) depicts the importance of the scale of spatial variability within an individual's home range. Stage structure (top right) depicts the importance of the stage (*e.g.* age, body size) in the potential benefit of plasticity. Trait reversibility and Temporal lag (bottom right) refer to the potential impact of whether plasticity can be reversed, and the time lag between when an individual is sensitive to an environment, and when the plasticity is manifested. Lastly, environmental component (bottom left) refers to the different types of temporal change discussed in Vinton *et al.*, changes in the environmental mean, variation, and temporal autocorrelation.



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Referenced

1) Hoffman, A.A. and Bridle, J. (2023) Vinton et al TREE Response
2) Vinton, A.C. et al. (2022) Plasticity’s role in adaptive evolution depends on environmental change components. Trends in Ecology & Evolution, https://doi.org/10.1016/j.tree.2022.08.008.

3) Coulson, T., et al. (2017). Modeling adaptive and nonadaptive responses of populations to environmental change. *The American Naturalist*, *190*(3), 313-336.

4) Diel, P., *et al.* (2020). Knowing the enemy: inducible defences in freshwater zooplankton. *Diversity*, *12*(4), 147.

5) Cooper, Brandon S., *et al.* "Thermal adaptation of cellular membranes in natural populations of Drosophila melanogaster." *Functional Ecology* 28.4 (2014): 886-894.

6) Evers, S. M., *et al.* (2021). Lagged and dormant season climate better predict plant vital rates than climate during the growing season. *Global Change Biology*, *27*(9), 1927-1941.

7) Bridle, J. and Hoffmann, A.A. (2022) Understanding the biology of species' ranges: when and how does evolution change the rules of ecological engagement? Philosophical Transactions of the Royal Society B 377 (1848), 20210027.

8) Jongejans, E., *et al.* (2011). Importance of individual and environmental variation for invasive species spread: a spatial integral projection model. *Ecology*, *92*(1), 86-97.

9) Coulson, T. *et. al* "Predicting evolution over multiple generations in deteriorating environments using evolutionarily explicit Integral Projection Models." *Evolutionary Applications* 14.10 (2021): 2490-2501.

10) Ellner, S. P., *et al.* (2016). Data-driven modelling of structured populations. *A practical guide to the Integral Projection Model. Cham: Springer*.

11) Simmonds, E. G., *et al.* (2020). Phenological asynchrony: a ticking time-bomb for seemingly stable populations?. *Ecology Letters*, *23*(12), 1766-1775.

12) Hoffmann, A.A. and Bridle, J. (2022) The dangers of irreversibility in an age of increased uncertainty: revisiting plasticity in invertebrates. Oikos 2022 (4), e08715.