A quantitative framework for evaluating transgenerational phenotypic plasticity under environmental change

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Abstract

Rapid environmental change has intensified interest in inter- and trans-generational phenotypic plasticity (TGP) as a mechanism underlying populations responses to changing environments. Parental environments frequently induce shifts in offspring phenotypes, and it is often implicitly assumed that these generational responses enhance offspring fitness and thus population persistence. However, evidence for phenotypic change alone is insufficient to demonstrate adaptive value, particularly when fitness is inferred from performance proxies rather than survival or reproduction. Here, we argue that a more agnostic null hypothesis is required when evaluating the fitness consequences of TGP: that phenotypic shifts across generations can be neutral, detrimental, and context-dependent, rather than inherently beneficial. We present a quantitative analytical framework that integrates selection analysis into multigenerational experiments to evaluate whether TPG aligns with variation in offspring fitness. This approach does not seek to identify the mechanistic basis of TGP, nor to disentangle plasticity from genetic or epigenetic causation, but instead provides a diagnostic test of whether observed phenotypic shifts are associated with positive, negative, or absent selection. Because the framework requires only individual-level phenotypic and fitness measurements, it can readily be incorporated into existing multigenerational studies spanning a range of study systems, without additional complexity to experimental designs. Integrating selection analysis into studies of TGP provides a tractable and comparable framework for evaluating whether intergenerational responses enhance, constrain, or have no effect on population persistence under environmental change.

Introduction

Climate variability is one of the most ubiquitous forces shaping ecosystems globally. Natural environments change at different time scales, from variation at geological scales to the immediate impacts of weather events. These different rates and magnitudes of change impact the physiology that underlies reproduction, growth, and dispersal of individuals (Baduel et al., 2024; Briscoe et al., 2023; Lema, 2020), and thereby affect population dynamics and communities (Amarasekare, 2024; Herrera Fuchs et al., 2025; Lema et al., 2024). For example, the composition of communities changes in response to current climate warming as more susceptible species are replaced by species more tolerant to warmer temperature (Khaliq et al., 2024). Similarly, drought and storm activity were associated with species turnover in a subtropical forest (Wu et al., 2024). Environmental variation, and anthropogenic climate change in particular, is causing population declines in some species. For example, declines in arctic auks (*Alle alle*) are associated with climate change-induced increases in sea surface temperatures and decreases in sea ice (Jakubas et al., 2024). Population declines may be associated with loss of genetic diversity and thereby further reduce the potential for genetic adaptation to climate change (Aagaard et al., 2022; Zhou et al., 2024). Understanding how organisms respond across generations to such rapid environmental change is therefore central to predicting population persistence under global change.

Many species have evolved mechanisms to respond to environmental change and to reduce or alleviate its potentially negative impacts (McGaughran et al., 2021; Seebacher et al., 2015). Darwinian selection drives genetic adaptation to favour phenotypes that perform best under prevailing environmental conditions and thereby alters population allele frequencies. However, genetic adaptation is slow relative to the potential pace of environmental change. Even rapid evolution takes tens of generations before there are significant phenotypic effects that can render a population more resistant to environmental change (Lescak et al., 2015). The pace of adaptation is therefore too slow to mount effective responses to climate change, except for species with very short generation times.

In addition to genetic adaptation, most if not all organisms have evolved the capacity for phenotypic plasticity, that is the expression of different phenotypes from a single genotype (DeWitt & Scheiner, 2004). Plastic responses are much faster than genetic adaptation, and therefore can be more effective in buffering individuals and populations from rapid environmental variability (Schulte et al., 2011). Inter- and trans-generational phenotypic plasticity describes cases where parental environments influence offspring phenotypes, regardless of the underlying regulatory mechanism (Brass et al., 2021; Chapelle & Silvestre,

2022). Such effects are often associated with epigenetic regulation, including DNA methylation and histone modification (Best et al., 2018; Fellous et al., 2022; Heckwolf et al., 2020, 2020; Loughland et al., 2021; Sävilammi et al., 2021; Skvortsova et al., 2018; Venney et al., 2022), but their mechanistic basis is frequently unresolved, particularly in non-model organisms.

Inter- and trans-generational transmissions (hereon referred to collectively as 'TGP') of environmentally-induced information are often proposed to enable phenotypes to better match prevailing environmental conditions across single or multiple generations, and may influence population dynamics and responses to environmental change (Brass et al., 2021; Chapelle & Silvestre, 2022; Klughammer et al., 2023; Lynch & Kemp, 2014; Stajic & Jansen, 2021). Consequently, TGP has emerged as a prominent mechanism by which populations can respond to rapid environmental change and is has now been documented across flowering plants, marine and freshwater invertebrates, insects, fishes, amphibians, reptiles, birds, and mammals (Byrne et al., 2020; Fellous et al., 2022; Gilbert & Warner, 2026; Matesanz et al., 2022; McGaughran et al., 2021; Rodgers et al., 2015; Schwanz et al., 2020; Signor, 2020). Across these systems, parental and grandparental environments influence offspring development, physiology, morphology, behaviour, and reproduction, making TGP central to predictions of biological responses to climate change.

Despite the taxonomic breadth of evidence for TGP, there remains no general analytical framework for determining whether these transgenerational responses actually enhance offspring fitness or population persistence. Despite their potential to improve resistance and resilience to environmental change, phenotypic effects across generations are not necessarily beneficial. First, parental environments may induce offspring phenotypes that are neutral or detrimental if they do not match the environment experienced by offspring (Beaman et al., 2016; T. DeWitt & Scheiner, 2004; Gibert et al., 2019; Schwanz et al., 2020). Moreover, changes in regulatory states can arise stochastically, independent of environmental cues. For example, spontaneous epimutations and age-related changes in DNA methylation can accumulate over time (Bertucci-Richter et al., 2024; Bogan & Yi, 2024; Han, 2024; Johannes & Schmitz, 2019), generating phenotypic variation that may have neutral or negative fitness consequences.

In a now seminal paper, Gould and Lewontin (1979) argued against the "adaptationist program" that accepted the "near omnipotence of natural selection in forging organic design and fashioning the best among possible worlds". In other words, studies often implicitly assumed that expressed biological traits were the result of selection optimising fitness. However, there are a myriad of stochastic processes, constraints, and historical contingencies that can produce patterns that are not adaptive. A similar bias can arise in studies of TGP.

Environmentally induced TGP are frequently interpreted as adaptive responses to environmental change without explicit tests of fitness consequences. Empirical evidence that such responses enhance fitness under climate change remains limited and context dependent (Byrne et al., 2020; Gilbert & Warner, 2026).

Here we present a quantitative analytical framework that integrates selection analysis into standard multi-generational experimental designs to determine whether parental environment-induced phenotypic shifts align with natural selection acting on offspring fitness. The framework is broadly applicable across taxa and ecosystems, requires only individual-level phenotypic and fitness measurements, and generates comparable estimates of adaptive alignment across studies. Rather than identifying the mechanistic basis of TGP, the framework provides a practical tool for distinguishing beneficial, neutral, and detrimental transgenerational responses under environmental change.

Evaluating the fitness consequences of inter- and trans-generational phenotypic plasticity

There is a growing focus on the potential benefits of "adaptive" TGP as a mechanism by which populations may persist in the face of rapid environmental change (Faraji & Metz, 2026; Harmon & Pfennig, 2021). Rather than relying on selection on standing genetic variation, which typically produces population-level responses only after many generations, parental environments may directly influence offspring phenotypes via regulatory mechanisms that operate across generations (Burggren, 2015; Skvortsova et al., 2018). Such phenotypic changes are often interpreted as adaptive because they can increase offspring performance under environmental conditions that are similar to those experienced by parents, and "buy time" for evolution via genetic adaptation to take place (Chevin et al., 2010). This interpretation rests on the assumption that environmentally-induced phenotypic shifts are aligned with fitness benefits, an assumption that is rarely tested explicitly (Byrne et al., 2020; Gilbert & Warner, 2026; Sánchez-Tójar et al., 2020).

Determining whether TGP is adaptive requires more than demonstrating that parental environments alter offspring phenotypes. Instead, adaptive value depends on whether those phenotypic shifts increase survival or reproductive success in the environment experienced by offspring. TGP is not always beneficial or "adaptive" (DeWitt et al., 1998). For example, moderate heat stress experienced by parents can induce offspring phenotypes that confer increased tolerance to elevated temperatures, whereas more severe or prolonged heat stress can induce DNA methylation patterns that ultimately reduce offspring performance and survival (Murray et al., 2022). In such cases, the direction and magnitude of parental environmental

effects determine whether offspring phenotypes are beneficial, neutral, or detrimental with respect to fitness.

A practical challenge is that many multigenerational studies rely on performance-related traits as proxies for fitness because direct measurements of survival or lifetime reproductive success are often logistically difficult, particularly in long-lived species or field-based studies. Common proxies include offspring size, growth rate, metabolic rate, and locomotor capacity (Donelson et al., 2012; Le Roy et al., 2017; Pettersen et al., 2019). Although biologically informative, these traits may correlate only weakly with fitness, or even trade off against survival or reproduction (**Figure 1**). For example, there may be trade-offs between reproduction and aging or lifespan (Cohen et al., 2020), growth (Larue et al., 2021), resistance to parasitism (Ives et al., 2020), and survival (Cox et al., 2010). Consequently, shifts in offspring phenotype alone cannot be interpreted as evidence that TGP enhances fitness or population persistence. Tests of the adaptive nature of TGP should include estimates of offspring fitness (lifetime reproductive output) or at least major components of fitness (survival, mating success [fertility], or reproductive output) (Burgess & Marshall, 2014; Matesanz et al., 2022).

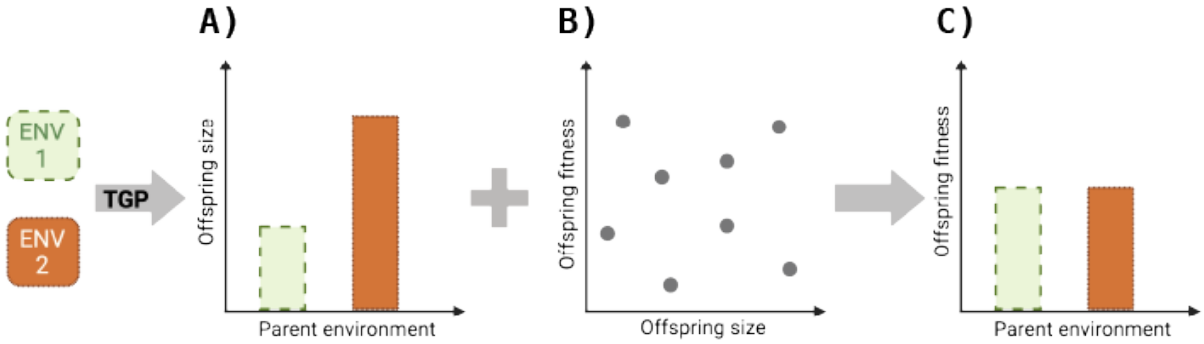

Figure 1. Measures of parental performance, such as offspring size or aerobic scope may not be correlated, or may even trade-off, with actual fitness (that has not been measured). In this hypothetical example, there appears to be adaptive inter-generational plasticity in offspring size: parents reared in Environment 2 ('ENV 2', orange shading) produce larger offspring than parents exposed to Environment 1 ('ENV 1', green shading); **A)**. However, if there is no relationship between offspring fitness and size (**B**) then there will be no fitness benefit of the inter-generational plasticity in size (**C**). It is therefore essential to link measures of offspring fitness (survival and reproductive output) to plastic traits (size in this case) to avoid misinterpreting the adaptive nature of TGP.

Parental environments can even induce phenotypic shifts in offspring that reduce fitness (Marshall & Uller, 2007). For example, chronic paternal stress in mice alters sperm

184 microRNA composition and is associated with altered hypothalamic-pituitary-adrenal axis
185 function in offspring (Rodgers *et al.* 2015). Demonstrating maladaptive TGP therefore requires
186 the same evidence as demonstrating adaptive TGP: an explicit association between offspring
187 phenotype and fitness. In both cases, phenotypic change alone is insufficient.
188 An appropriate null expectation is therefore that environmentally induced phenotypic
189 shifts have no consistent fitness consequences unless demonstrated otherwise. Analogous to
190 genetic drift, we use the term "epigenetic drift" to describe inter- and trans-generational
191 phenotypic variation that arises independently of selection and does not necessarily confer
192 fitness benefits. Such variation may result from ageing, stochastic changes in regulatory states,
193 incomplete transmission of environmental information, or mismatches between parental and
194 offspring environments (Bertucci-Richter et al., 2024; Bogan & Yi, 2024; Han, 2024; Johannes &
195 Schmitz, 2019). Importantly, the concept we describe is not contingent on any specific
196 underlying mechanism (McGuigan et al., 2021). Rather, it provides a parsimonious null
197 hypothesis against which adaptive or maladaptive fitness consequences of TGP can be tested.
198 We present a quantitative analytical framework that integrates selection analysis into
199 standard multigenerational experimental designs (**Figure 2**). The framework links individual-
200 level phenotypic measurements directly to offspring fitness, allowing assessment of whether
201 environmentally induced trait shifts align with natural selection. The framework can be readily
202 incorporated into existing studies because it requires only phenotype and fitness
203 measurements that are often already collected in TGP experiments. A strength of this approach
204 is that it provides metrics that can be compared across taxa and ecosystems to evaluate
205 whether transgenerational responses to environmental change are beneficial, neutral, or
206 detrimental.
207

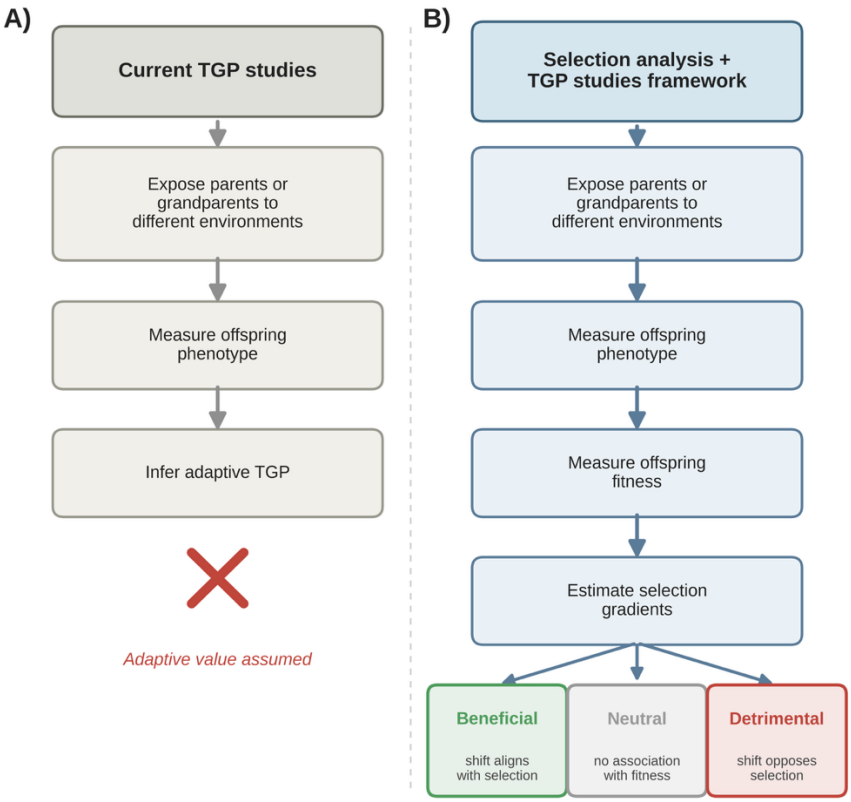

Figure 2. Contrasting workflows for inferences in inter- and trans-generational phenotypic plasticity (TGP) studies. **A)** Current approaches typically expose parents or grandparents to different environments and offspring phenotypes are measured, from which adaptive value is typically inferred directly. Because offspring fitness is not measured, the assumption that phenotypic shifts are adaptive remains untested. **B)** The proposed framework retains the same experimental design but adds measurement of offspring fitness (survival and/or reproductive output) and estimates of selection gradients. Comparing the direction of the parental environment-induced phenotypic shift with the direction of selection allows each response to be classified as beneficial (shift aligns with selection), neutral (no association with fitness), or detrimental (shift opposes selection), providing a diagnostic test of adaptive alignment rather than assumption of it.

Applying a quantitative genetics framework to TGP

To evaluate whether TGP enhances resilience to environmental change, it is necessary to quantify whether phenotypic shifts induced by parental environments align with variation in offspring fitness. We define TGP as beneficial when parental environment-associated trait shifts occur in the same direction as that favoured by selection, detrimental when they oppose

selection, and neutral when no detectable association exists between the shift in offspring trait and offspring fitness (Pettersen et al., 2024).

Selection analysis provides a tractable and comparable framework for estimating the direction and strength of associations between phenotypic variation and fitness (Lande & Arnold, 1983). Although it cannot distinguish phenotypic selection from an evolutionary response to selection (Haldane, 1954), it is well suited as a diagnostic tool for evaluating whether phenotypic shifts are associated with positive, negative, or absent fitness consequences (**Box 1**). Similar approaches have previously been used to study within-generation phenotypic plasticity, for example by regressing plasticity on individual fitness (DeWitt, 1998) or genotype-mean fitness (Arnold et al., 2019). Here, we show how selection analysis can be incorporated into common parent x offspring experiments to generate comparable estimates of fitness alignment across taxa and environmental contexts.

Selection analysis methods

Selection analysis requires paired measurements of individual phenotypes (e.g., morphological, behavioural, or physiological traits) and components of fitness (e.g., lifespan, fecundity, mating success, and reproductive output) within a population (Lande & Arnold, 1983). Fitness components such as survival, reproductive success, or reproductive output can be used to quantify viability, fertility, or fecundity selection, respectively (Pettersen et al., 2020). Data collected in inter- and trans-generational studies are particularly well suited to this framework. In many experiments, parents are exposed to different environmental treatments and variation in offspring performance traits are then measured (see examples below in Box 1, and in Supplementary Material). This experimental design can produce the phenotype-fitness data needed to estimate selection gradients within each combination of parental and offspring environments. However, below we list several methodological considerations that need to be addressed to isolate the effects of parental and offspring environments. Once phenotypic and fitness data have been collected for each environmental combination, the selection landscape can be quantified using the following steps.

1. *Check for multicollinearity among traits*

   Before including multiple traits in a selection analysis, it is important to assess whether these traits are too strongly correlated with one another. If traits are highly correlated, it can be difficult to determine statistically how selection acts on each trait independently. To evaluate this, variance inflation factor (VIF) values should be calculated as $VIF = 1/(1-R^2)$, where R^2 is the coefficient of variation of the regression

between the trait in focus against all other traits that may show collinearity (Zuur et al., 2010). VIF values provide a measure of how much the variance of one trait is inflated by its relationship with other traits. As a rule of thumb,

• A VIF value < 5 generally indicates low multicollinearity, meaning the traits are not overly correlated and can be analysed together.

• A VIF value > 5 suggests high multicollinearity, meaning that it may be difficult to estimate independent selection gradients for each trait (Zuur et al., 2010).

In cases of high multicollinearity, it may be necessary to i) combine correlated traits into composite variables, ii) remove one of the correlated traits, or iii) apply methods designed to handle multicollinearity such as ridge regression or principal component analysis.

2. *Define the environments in which selection will be estimated*

Selection analyses are typically conducted within the ecological contexts in which individuals experience selection. These contexts may represent experimental treatments, environments, or combinations of both. For example, in the zebrafish case study presented here (Pettersen et al., 2024), selection gradients were estimated separately within each parental temperature × parental food × offspring temperature combination. Estimating selection within environments allows the strength and direction of selection to be compared across ecological contexts.

3. *Choose an appropriate fitness measure*

Selection analyses require a measure of individual fitness or a proxy for fitness. Depending on the study system, this may include survival, reproductive output, fertility, or growth to a critical life-history stage. The statistical model used will depend on the distribution of the fitness variable. For example:

• Gaussian models are appropriate for continuous fitness measures such as reproductive output.

• Binomial or logistic models are appropriate for binary fitness measures such as survival (alive - dead) or fertility (reproduce yes or no).

In the zebrafish case study (**Box 1**)**,** offspring fitness was measured as survival to two weeks post-hatching, which was analysed using logistic regression.

4. *Standardise trait values within environments*

To ensure that selection coefficients are comparable across traits, phenotypic traits should be standardised to have a mean of zero and a standard deviation of one. The most common method to do this is by calculating z-scores: $z = (x - \mu) / \sigma$,where x =

individual measurement, μ = population mean and σ = population standard deviation (Quinn & Keough, 2023). This procedure places all traits on the same scale and allows the resulting coefficients to be interpreted as selection acting on one standard deviation change in the trait (Lande & Arnold, 1983).

When selection is estimated within treatments or environments, traits should be standardised within each environment, rather than across the entire dataset. This ensures that trait variation is evaluated relative to the conditions in which selection occurs.

5. *Estimate directional selection gradients using multiple regression*

Directional selection gradients can be estimated using multiple regression models in which fitness is regressed on the standardised traits of interest. Including multiple traits in the same model allows the selection gradient for each trait to be estimated while accounting for covariance among traits. A complete worked example, including extraction and transformation of selection gradients, is provided in **Box 1** and the accompanying Supplementary Material.

6. *Transform logistic regression slopes to selection gradients*

When fitness is measured as a binary variable (e.g., survival), logistic regression coefficients are expressed on the logit scale and therefore cannot be interpreted directly as selection gradients. To obtain average directional selection gradients (β*), these slopes should be transformed using the method described by Janzen and Stern (1998). This transformation rescales logistic slopes to reflect the expected change in relative fitness associated with variation in the trait.

The transformation incorporates:

• the predicted survival probabilities from the fitted model, and

• the mean fitness within the environment.

Applying this transformation yields directional selection gradients that are directly comparable across traits and environments**.** For continuous fitness measures such as reproductive output, clutch size, or seed production, selection gradients can be estimated directly using standard linear regression after trait standardisation and conversion of fitness to relative fitness (Lande & Arnold, 1983). In these cases, transformation of regression coefficients is unnecessary because fitness is already measured on a continuous scale.

7. *Interpret the direction and strength of selection*

   Directional selection gradients indicate whether higher or lower trait values are associated with increased fitness.

   • Positive β* indicates selection favouring higher trait values.

   • Negative β* indicates selection favouring lower trait values.

   • Values with 95% confidence intervals overlapping zero indicate weak or absent directional selection.

   Comparing these selection gradients with observed intergenerational shifts in trait values shows whether plastic responses align with, oppose, or are unrelated to the direction of selection (see Box 1). Beneficial alignment occurs when plastic shifts move trait values in the same direction favoured by selection, whereas mismatch occurs when plastic shifts oppose the direction of selection.

8. *Visualise and interpret selection patterns*

   Selection gradients can be visualised using forest plots or similar graphical approaches that display the magnitude and uncertainty of β* estimates across environments. These visualisations facilitate comparison of the strength and direction of selection across treatments and traits. When combined with estimates of intergenerational trait shifts, these plots provide a clear framework for evaluating whether intergenerational plasticity aligns with selection on fitness.

Discussion

What selection analysis can and cannot show

Selection analysis is not designed to identify the mechanistic basis of intergenerational phenotypic variation. Phenotypic shifts associated with parental environments may arise through genetic, molecular modifications, parental, or environmental pathways, and these mechanisms are not mutually exclusive. Rather than identifying causation, the framework proposed here addresses a different question: whether phenotypic variation associated with parental environments aligns with variation in offspring fitness. This distinction is important because studies of TGP frequently conflate the presence of cross-generational phenotypic change with evidence of adaptive benefit. The selection analysis we propose here therefore complements, rather than replaces, studies seeking to identify underlying mechanisms. For example, experiments using isogenic lines, clonal organisms, allele-frequency monitoring, or direct manipulation of candidate epigenetic pathways can help disentangle the causes of phenotypic variation (McGuigan et al., 2021; Santos et al., 2019). Selection analysis can then be

used alongside these approaches to evaluate whether the resulting phenotypic variation is associated with increased, decreased, or unchanged fitness.

Interpreting fitness alignment across generations

Alignment between TGP and selection in a single generation should not be interpreted as evidence that TGP will necessarily enhance fitness over multiple generations or promote long-term population persistence (Bonduriansky & Day, 2009; Marshall & Uller, 2007). A parental effect that is beneficial in one generation may become neutral or detrimental if environmental conditions change, if selection differs among life stages, or if selection acting on offspring conflicts with selection acting on subsequent adult or parental phenotypes (Burgess & Marshall, 2014; Marshall & Uller, 2007; Uller et al., 2015). The context dependence observed in Box 1 highlights this point: the same parental treatment produced similar phenotypic responses across environments, yet only some of these responses aligned with viability selection. Future studies that quantify fitness across complete life histories and over multiple generations will therefore be important for determining whether fitness alignment is transient or persists over time, and for assessing whether short-term fitness benefits ultimately translate into long-term demographic or evolutionary consequences (Bonduriansky & Day, 2009; Donelson et al., 2018; Marshall & Uller, 2007).

Conclusion

Inter- and transgenerational phenotypic plasticity is increasingly incorporated into predictions of resilience under global change (Byrne et al., 2020; Fellous et al., 2022; Gilbert & Warner, 2026). Yet, phenotypic responses alone cannot determine whether parental effects ultimately enhance or reduce fitness. By explicitly linking offspring phenotype to survival and reproduction, selection analysis provides a practical framework for evaluating whether TGP responses are likely to enhance, constrain, or have little effect on population persistence. Rather than relying on phenotypic change as a proxy for adaptive value, this framework enables researchers to quantify whether parental-environment-induced phenotypic shifts align with natural selection. Because it can be readily incorporated into existing multigenerational experiments using measurements that are often already collected in studies, the approach provides a standardized and broadly applicable method for comparing fitness alignment across taxa and environmental conditions. By shifting focus from detecting TGP responses to evaluating their fitness consequences, this framework provides a practical step towards more robust predictions of resilience of populations to global change.

BOX 1. An example of testing whether intergenerational shifts in development and growth are adaptive

Inter- or trans-generational phenotypic plasticity (TGP) is frequently inferred to be adaptive when parental environments induce shifts in offspring traits linked to performance. In zebrafish (*Danio rerio*), development time and growth rate are commonly used as proxies for early-life success, and both traits are sensitive to parental thermal and nutritional environments (Pettersen et al., 2024). Here, we demonstrate how incorporating a simple selection analysis changes interpretation of TGP in these traits.

Intergenerational shifts in offspring traits

In two parental temperature treatments (24 °C and 30 °C), low parental food availability consistently produced offspring that developed more slowly (longer time to hatching) and exhibited reduced early growth rates, relative to offspring from high-food parents (**Table S1**). These shifts were observed at both offspring rearing temperatures (24 °C and 30 °C), indicating clear evidence of TGP in response to parental environment. Without explicit fitness data, such shifts towards slower development and reduced growth might be interpreted as i) maladaptive consequences of parental nutritional stress, or ii) protective adjustments that enhance survival under stressful conditions because slower growth reduces food requirements. However, trait shifts alone cannot resolve this ambiguity.

Quantifying alignment of TGP with viability selection

To test whether these intergenerational shifts align with fitness, we quantified viability selection by regressing relative survival (to two weeks post-hatching) on standardised measurements of development time and growth rate within each parental x offspring environmental combination. Logistic regression coefficients were transformed following Janzen and Stern (1998) to yield directional selection gradients (β) on a relative fitness scale. Selection gradients revealed that adaptive effects were highly context-dependent (**Table S2**). Strong positive selection on slower development and negative selection on growth occurred only in one environmental combination (parents at 24 °C, low food; offspring at 30 °C). In this case, the direction of TGP - low parental food was associated with slower development and reduced growth - matched increased survival (viability selection), which is consistent with beneficial TGP. In contrast, in most other environments selection was weak or absent, and in one combination (parents at 30 °C, high food; offspring at 24 °C), selection favoured faster development, opposite to the direction of the parental temperature-induced shift. Thus, intergenerational shifts that might be

broadly described as adaptive based on trait patterns alone were only beneficial under specific environmental conditions.

How inference changes

If the analysis had stopped at documenting intergenerational trait shifts only, it might have been concluded that parental thermal and nutritional environments modify offspring development and growth to maximise fitness. However, incorporating explicit estimates of selection demonstrates that adaptive alignment is neither universal nor consistent across environments. Some trait shifts are strongly favoured by selection, others are effectively neutral, and some may oppose the direction favoured by viability (survival). This additional analytical step required only individual-level trait and survival data and does not depend on pedigree information or complex quantitative genetic modelling. Yet it fundamentally alters inference about whether TGP enhances, constrains, or has no effect on offspring fitness. Zebrafish are widely used in TGP and epigenetic studies, including investigations of DNA methylation dynamics (Loughland et al., 2021; Seebacher & Bamford, 2024). This case study illustrates how integrating selection analysis into such designs provides a direct and comparable test of adaptive alignment, strengthening inference about the evolutionary and ecological consequences of TGP under environmental change.

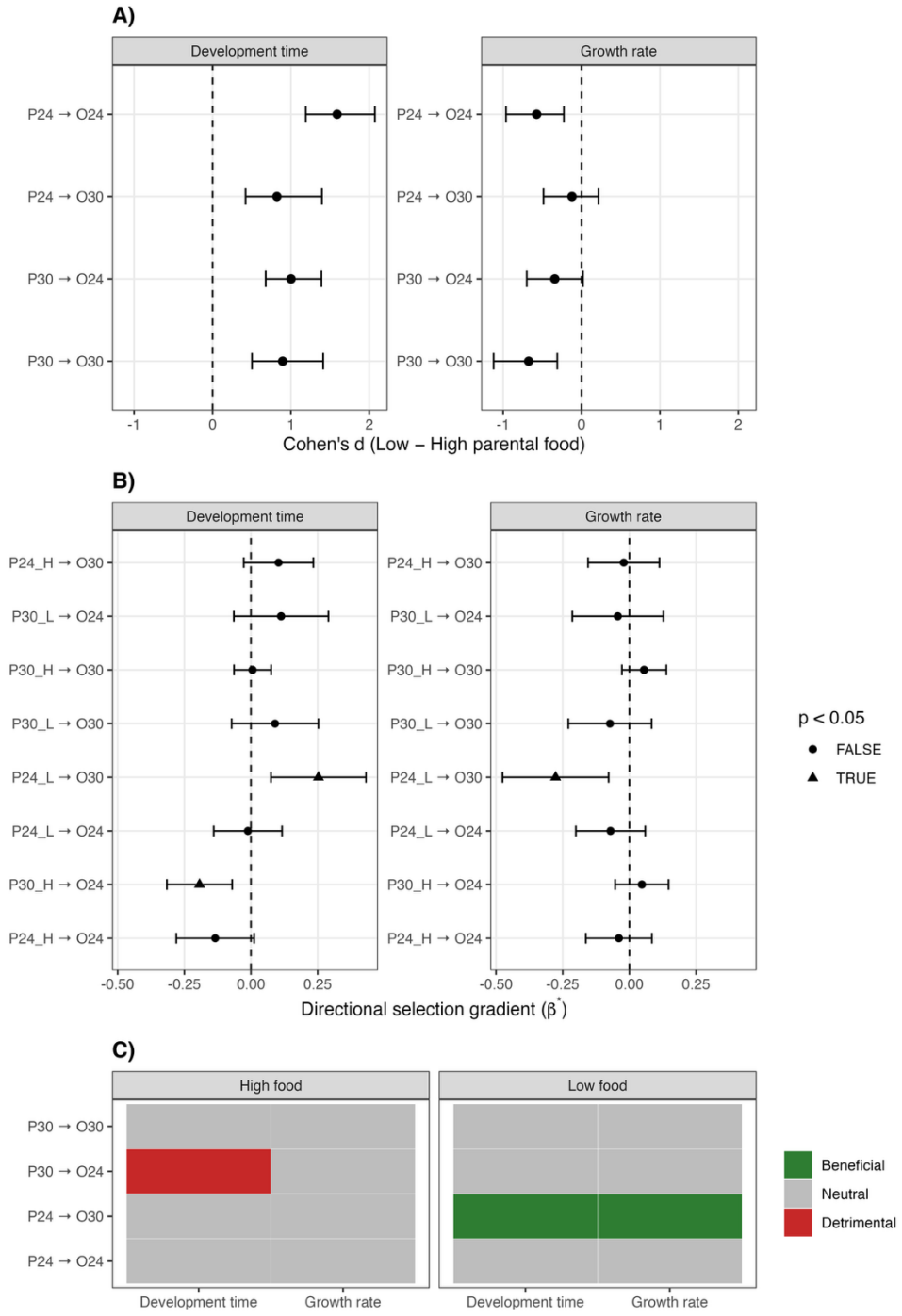

Figure (Box 1). Testing whether intergenerational phenotypic plasticity aligns with viability selection. A) Intergenerational shifts in offspring ("O") development time and growth rate induced by parental ("P") food environment, expressed as standardized mean differences (Cohen's *d*; low – high parental food) with bootstrapped 95% confidence intervals. Positive values indicate increased development time or faster growth under low parental food; negative values indicate faster development or slower growth. **B)** Multivariate directional selection gradients ($\beta*$) estimated from logistic regressions of offspring ("O") survival on standardised

development time and growth rate within each parental ("P") temperature (24 = 24 °C, 30 = 30 °C) × parental food (L = Low, H = High) × offspring temperature (24 = 24 °C, 30 = 30 °C) environment. Error bars show 95% confidence intervals. **C)** Alignment between the direction of intergenerational trait shifts and the direction of viability selection for each parental food environment. Green indicates alignment between plastic shifts and selection, red indicates detrimental, and grey indicates neutral or unclear outcomes where selection gradients overlap zero. Together, these panels illustrate how incorporating selection analysis can change inference about the adaptive value of intergenerational plasticity: although parental environment consistently altered offspring traits (panel A), only some shifts aligned with selection on survival (panels B–C). This workflow demonstrates a practical approach for testing whether intergenerational plasticity enhances offspring fitness under environmental change.

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