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Developmental Plasticity Functions as Environmental Forecasting Only When Early-Life Cues Reliably Predict Adult Conditions

Ravi Kumar[1]*, Neha Sharma[1], Aniket Deshmukh[2], Sanjay Kulkarni[3], Arjun Nair[4]

[1]Department of Developmental Plasticity and Environmental Forecasting, Faculty of Life Sciences, Indian Agricultural Research Institute, New Delhi, India.
[2]Department of Early-Life Cues and Predictive Responses, Faculty of Biosciences, IIT Bombay, Mumbai, India.
[3]Department of Reliable Prediction and Adult Conditions, Faculty of Sciences, Savitribai Phule Pune University, Pune, India.
[4]Department of Adaptive Plasticity and Environmental Signal Reliability, Faculty of Life Sciences, IIT Kharagpur, Kharagpur, India.

***E-mail** ✉ ravi.kumar@iari.res.in

ABSTRACT

Developmental plasticity is often interpreted as an anticipatory adjustment through which early environmental conditions prepare insects for later life. That interpretation is stronger than the observation that developmental environments alter adult phenotypes. For plasticity to function specifically as environmental forecasting, an early-life cue must contain reliable information about a later selective environment, the induced response must persist to the relevant adult stage, its developmental costs must not outweigh subsequent benefits, and adult performance must improve under the condition predicted by the cue. This perspective develops a proposed Cue-Predictiveness Framework that separates these requirements and identifies where forecasting interpretations succeed or fail. Evidence from insect thermal plasticity, photoperiodic polyphenism, coloration, dispersal morphology, physiology, reproduction, and behavior shows that early environments can strongly alter later phenotypes, but these effects are frequently genotype-dependent, trait-specific, reversible, costly, or disconnected from adult fitness. Environmental predictability is therefore treated as a property of cue–future-environment relationships rather than of plastic responses themselves. Full developmental-by-adult environmental comparisons further show that matching environments do not consistently maximize reproductive performance and that developmental optima or persistent developmental damage can provide alternative explanations. The framework consequently distinguishes cue responsiveness, developmental carry-over, adult environmental match, and adaptive forecasting as progressively stronger inferential claims. It predicts that forecasting should be most defensible where cue reliability is high, developmental responses persist to the relevant adult context, response costs remain limited, and matched-environment performance advantages are directly demonstrated.

Keywords: Developmental plasticity, Environmental predictability, Carry-over effects, Thermal reaction norms, Beneficial acclimation, Seasonal polyphenism.

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Introduction

Developmental plasticity allows a single genotype to generate different phenotypes under different environmental conditions, but the evolutionary interpretation of those differences depends on how environments vary. Rate of change, environmental variance, and temporal autocorrelation can have distinct consequences for the value of

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plasticity, so environmental variability should not be treated as a single axis [1]. This distinction becomes especially important when developmental plasticity is described as anticipatory. A juvenile response can only forecast adulthood if the developmental environment contains information about conditions that will later matter to performance or fitness.

In insects, seasonal polyphenism provides one of the clearest ecological settings in which that requirement can be examined. Across tropical butterfly communities, stronger temporal predictability of seasonal climatic variation has been associated with stronger seasonal polyphenism, supporting the expectation that recurrent environmental structure can favor reliable phenotype–season relationships [2]. Yet even persistent effects across life stages do not by themselves establish forecasting. Carry-over effects can arise through several evolutionary and developmental routes, and persistence into adulthood may reflect constraint, allocation history, damage, or state dependence rather than anticipatory preparation [3].

Theory similarly indicates that the evolutionary value of plasticity depends on the relationship between the environment in which information is acquired and the environment in which selection acts. Temporal and spatial covariance can favor different reaction norms, including conditions under which reduced plasticity is expected [4]. Plastic responses may also become less favorable when their costs are substantial, even when environmental states are autocorrelated [5]. Experimental evolution outside insects further demonstrates the methodological importance of manipulating predictability separately from environmental variance: changes in predictability can alter the evolution of plasticity across several biological levels [6]. Such results are not insect-specific evidence, but they reinforce the need to distinguish environmental information structure from response magnitude.

This separation becomes especially important under rapid environmental change. A cue that historically correlated with a later environment may become misleading if climatic, trophic, phenological, or habitat relationships are reorganized. Evolutionary models show that population responses can depend on prior histories of cue reliability and on whether plastic responses operate within or across generations [7]. Thus, an apparently anticipatory phenotype may persist after the informational relationship that once made it useful has weakened.

The central argument developed here is therefore deliberately narrower than the claim that insects show developmental plasticity. The proposed Cue-Predictiveness Framework treats forecasting as a conditional interpretation requiring successive evidence that an early cue is informative, that the induced response reaches the relevant adult stage, that developmental costs are not prohibitive, and that the adult phenotype performs better under the environment predicted by the cue. Failure at any one of these stages weakens a forecasting interpretation without implying that the plastic response itself is biologically unimportant.

Materials and Methods

Cue-predictiveness framework

This article is an evolutionary perspective constructed from the approved theoretical, comparative, mechanistic, experimental, and synthetic literature. No new dataset, meta-analysis, pooled estimate, experimental manipulation, or prospective validation was performed. The analytical procedure was to separate evidence for environmental information from evidence for developmental responsiveness and then from evidence for adult performance.

The first distinction concerns cue sensitivity. Insect thermal limits are plastically responsive across many taxa, but a broad meta-analysis found that mean plastic responses were generally modest and heterogeneous among stages and species [8]. Such evidence establishes that developmental or acclimation environments can influence phenotype, not that the response predicts later selective conditions. The same inferential boundary applies at the genetic level. Developmental temperature reaction norms for body size in Drosophila melanogaster show heritable genetic variation and genotype-by-environment structure [9], demonstrating evolutionary substrate for plasticity without demonstrating that any particular reaction norm is an adaptive forecast.

The proposed Cue-Predictiveness Framework therefore uses six linked questions. First, what environmental variable is detected during development? Second, does that variable statistically predict the adult condition relevant to selection? Third, does the induced phenotype persist to the adult period in which the predicted condition is encountered? Fourth, what developmental or later-life costs accompany the response? Fifth, is adult performance measured under both predicted and alternative environments? Sixth, does the induced phenotype perform better specifically where the early cue predicts that it should?

These questions are not treated as an empirically validated scoring system. They are an inference architecture intended to prevent evidence from one level from being promoted automatically to a stronger level. A molecular pathway can support cue transduction without demonstrating environmental predictiveness; a persistent phenotype can support developmental carry-over without demonstrating adaptive matching; and an adult performance difference can indicate consequence without demonstrating that the developmental cue historically predicted that adult environment. Environmental forecasting is therefore reserved for cases in which information structure and later performance are both supported.

Results and Discussion

Insects respond developmentally to diverse environmental inputs, but the biological meaning of those inputs differs substantially among taxa. In the water strider Gerris buenoi, developmental photoperiod strongly influences adult wing morph, with density contributing additional information. Experimental disruption of insulin-receptor signaling did not support the expected central mechanistic role, showing that a robust environmentally induced phenotype can coexist with uncertainty about the pathway producing it [10]. This is strong evidence of cue responsiveness, but it does not demonstrate that photoperiod predicts the adult dispersal environment sufficiently well to make wing induction an adaptive forecast.

Photoperiod can also modify developmental timing across stages. In the winter moth Operophtera brumata, long-term phenological evidence combined with experimental manipulation indicates that photoperiod contributes to compensation for earlier developmental timing and thereby modifies cross-stage phenological carry-over [11]. Such compensation is compatible with an anticipatory interpretation because photoperiod is seasonally structured, yet the relevant outcome is phenological alignment rather than a direct demonstration of increased lifetime fitness.

Mechanistic studies reinforce the same inferential separation. In planthoppers, environmentally induced phenotypes involve insulin/insulin-like signaling, FoxO and other regulatory pathways, but the connections linking particular ecological stimuli to downstream phenotype remain incompletely resolved [12]. Aphid wing plasticity likewise integrates environmental inputs through endocrine, neural and genetic mechanisms that differ among clones, species and cue contexts [13]. These systems show how early environmental information can be biologically encoded; they do not show that the information necessarily predicts the later selective environment.

Developmental cues may also interact rather than operate independently. In Bicyclus anynana, thermal plasticity of protective wing pigmentation depends not only on developmental temperature but also on food availability and genotype [14]. A reaction norm inferred from temperature alone can therefore misrepresent the phenotype produced when nutritional conditions change simultaneously. This matters for forecasting because natural environments frequently contain correlated or partially independent cues, and an apparently reliable predictor in one ecological setting can become weak when another environmental dimension changes.

The distinction between direct environmental matching and forecasting is illustrated particularly clearly by springbok mantises. In Miomantis caffra, substrate background was the strongest developmental determinant of body coloration, while humidity and temperature contributed additional effects [15]. Because the phenotype responds to the environmental state in which coloration itself is expressed, this represents direct developmental matching more clearly than prediction of a separate future environment. Calling such a response environmental forecasting would require evidence that the early conditions contain information about later camouflage conditions rather than merely inducing coloration appropriate to the present background.

Behavioral and physiological carry-over further demonstrate that developmental effects can propagate without producing equivalent changes at higher biological levels. In treehoppers, developmental temperature altered the thermal sensitivity of courtship activity and signal–preference relationships, yet mating rates were not detectably altered [16]. The result separates change in an intermediate behavioral phenotype from change in a realized reproductive outcome. Similarly, developmental oxygen exposure in Manduca sexta alters later thermoregulatory and flight performance [17], establishing adult physiological consequences without showing that juvenile oxygen conditions predict the adult oxygen environment.

Collectively, these systems support a narrow conclusion. Early-life environmental responsiveness is common enough to provide the mechanistic substrate for forecasting, but cue responsiveness alone is insufficient evidence of forecasting. The developmental environment must be evaluated not only for its capacity to induce a phenotype but also for whether it carries reliable information about the later conditions in which that phenotype will matter.

Environmental autocorrelation

Environmental forecasting requires a relationship through time, and this relationship cannot be inferred from the existence of a reaction norm. Developmental reaction norms themselves may evolve among populations. During the range expansion of Onthophagus taurus, temperature- and nutrition-dependent allometric responses differed among populations, demonstrating that environment-by-environment effects can change over geographic and evolutionary contexts [18]. Such differentiation shows that developmental cue interpretation is evolutionarily labile, but it is not direct evidence of temporal environmental autocorrelation.

Field conditions can also expose a more basic problem: a candidate cue may simply fail to track the ecological variable it is assumed to represent. In sympatric tropical Bicyclus butterflies, local temperature did not reliably predict rainfall in the forest environment examined, complicating interpretations that treat developmental temperature as a universal proxy for seasonal moisture conditions [19]. A developmental response to temperature could therefore be precise and repeatable while remaining poorly informative about the environmental dimension that is actually important later.

The proposed framework accordingly defines cue predictiveness as a property of the statistical relationship between an early-life cue and a later selective environment. Temporal autocorrelation is relevant only to the extent that it preserves information across the developmental interval separating cue perception from adult consequence. Predictiveness may be direct, as when the same environmental variable persists, or indirect, when one variable reliably anticipates another seasonal state. It may also be multivariate, requiring combinations of photoperiod, temperature, nutrition, density, host state, or moisture.

This formulation creates an important boundary. Strong developmental responsiveness cannot compensate for weak environmental predictiveness. Conversely, a highly predictable environment does not guarantee forecasting if insects do not detect the relevant cue, if the induced phenotype is transient, or if developmental costs erase later benefits. Environmental autocorrelation is therefore a necessary contextual condition for many forecasting hypotheses, not a sufficient explanation for developmental plasticity.

Developmental response costs

Even a reliable cue may fail to favor anticipatory plasticity when the developmental response imposes persistent costs. Developmental temperature can alter adult traits in different ways within the same organism. In ladybirds, elevated pupal temperature produced effects on adult thermal performance that were at least partly reversible, whereas effects on immunity and fecundity persisted [20]. A single developmental treatment therefore cannot be assigned one uniform category such as “beneficial acclimation” or “developmental damage”; different adult traits can retain different signatures of the same developmental environment.

Reproductive costs can also become particularly visible under fluctuating developmental stress. In Drosophila melanogaster, fluctuating developmental heat generated adult reproductive consequences that varied among genotypes and measured traits, with substantial evidence of reproductive costs despite context-specific putative benefits [21]. A response that improves one component of performance could therefore still be unfavorable when other reproductive components are considered.

The architecture underlying these consequences is itself variable. Genetic analyses in D. melanogaster show that developmental thermal plasticity and its adult reproductive consequences possess measurable genetic variation [22]. This provides potential for evolutionary change in the magnitude or direction of carry-over effects, but genetic variance alone does not establish that selection has optimized those responses for environmental forecasting.

The proposed framework therefore treats developmental response cost as multidimensional. Costs can be immediate or delayed, reversible or persistent, physiological or reproductive, trait-specific or genotype-dependent. Most importantly, they must be evaluated relative to the adult benefit attributed to forecasting. A reliable cue cannot support an adaptive-forecasting interpretation if the induced developmental response carries costs that equal or exceed the later benefit, although available studies often measure only subsets of lifetime performance.

Because these cost states are difficult to compare in prose without collapsing persistence, reversibility and evolutionary interpretation, the following ledger separates what can be observed from what must still be tested.

Table 1. Developmental response-cost states that alter whether cue-induced plasticity can be interpreted as environmental forecasting

Evidence · Interpretation for forecasting	Limits and uncertainty	Research or test · Evidential standing	Biological setting
Reversible adult performance shift			
Adult response diminishes or changes after later environmental exposure **Developmental carry-over may be temporary and therefore irrelevant to a later selective episode**	Reversibility can differ among traits	Measure persistence through the adult period in which performance matters Evidence-supported distinction	Thermally induced physiological performance
Persistent physiological or reproductive burden			
Adult cost remains after the developmental treatment has ended **A reliable cue may still fail to produce net forecasting benefit**	Lifetime fitness may not be measured	Compare persistent cost with performance under predicted and alternative adult environments Evidence-supported distinction	Thermal development affecting immunity, fecundity or reproductive performance
Genotype-dependent cost			
Different genotypes show different adult consequences under the same developmental treatment **Forecast value may vary within populations rather than characterize a species uniformly**	Genetic covariance and demographic frequencies remain relevant	Estimate genotype-by-development-by-adult-environment interactions Evidence-supported distinction	Developmental thermal reaction norms with genetic heterogeneity
Trait discordance			
Multiple adult traits respond in different directions or differ in reversibility **A single "adaptive" or "maladaptive" label becomes biologically incomplete**	Relative fitness contribution of traits may be unknown	Measure linked performance components within the same individuals or cohorts Evidence-supported distinction	One developmental environment produces beneficial, neutral and costly adult responses across different traits
Cost compensated by matched-environment benefit			
Cost and later benefit are both demonstrated in appropriate environmental comparisons **Forecasting remains plausible when later benefit exceeds relevant costs**	Requires a defined adult performance or fitness endpoint	Use reciprocal or factorial developmental-by-adult environmental tests Proposed inferential state	Developmental response has measurable cost but later improves performance in the predicted adult environment
Cost without demonstrated later benefit			
Adult consequence documented without a specific matched-environment improvement **Forecasting is unsupported even if cue responsiveness is strong**	Unmeasured benefits may remain possible	Avoid adaptive-forecasting language until later performance is tested Proposed inferential state	Developmental response persists or is costly but no matched adult advantage is shown

Because the same developmental exposure can generate reversible performance shifts, persistent reproductive costs and genotype-dependent consequences, a second representation is needed to keep observation, inference and validation requirements visually distinct rather than treating all carry-over as equivalent.

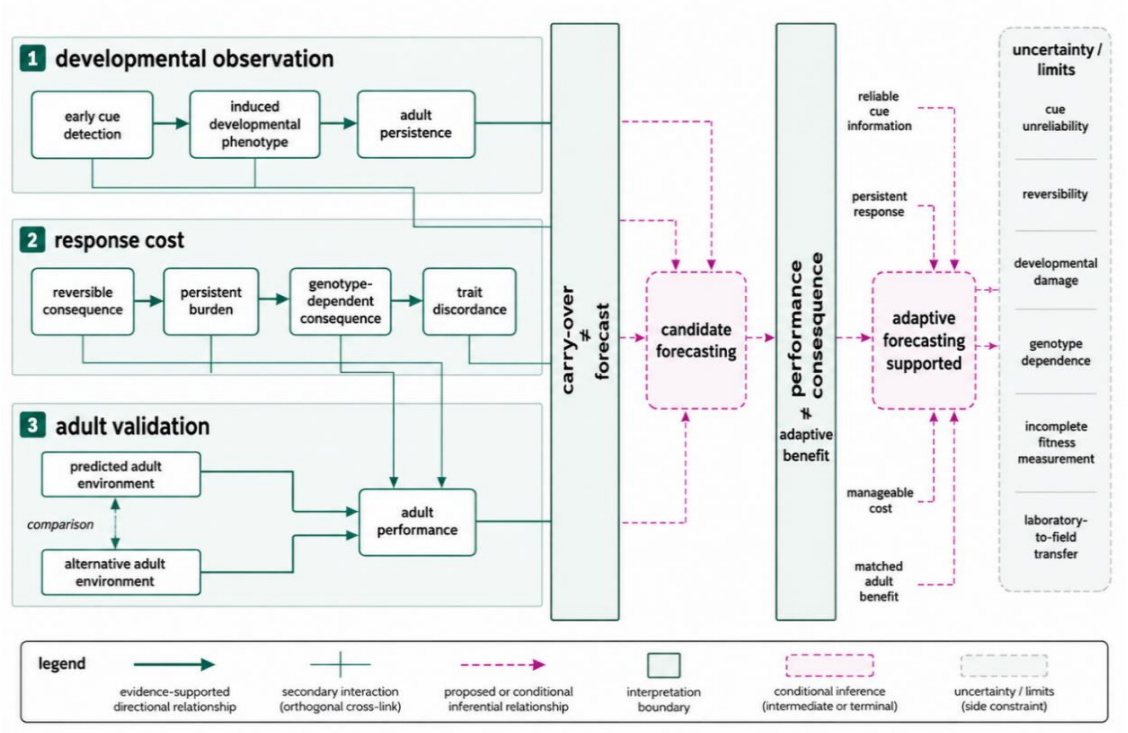


Figure 1. Evidence gates separating developmental carry-over from a defensible forecasting interpretation

Adult environmental match

Environmental forecasting becomes testable only when adult conditions are included explicitly. The strongest designs therefore cross developmental and adult environments rather than comparing adults that share one developmental history. In the seed beetle Callosobruchus maculatus, a full developmental-by-adult thermal design did not support a broad beneficial-acclimation prediction; developmental heat produced particularly important reproductive costs in females, while effects also depended on adult environment and age [23]. Matching developmental and adult temperatures was therefore not equivalent to improved later performance.

A similar problem appears when adult performance is represented across a wider thermal range. In Drosophila melanogaster, developmental temperature reshaped the thermal performance curve for reproduction, but the resulting surface was not reducible to a simple rule in which adults performed best whenever their developmental and adult temperatures matched [24]. Forecasting hypotheses should consequently be evaluated against performance surfaces or complete factorial comparisons where possible, rather than through a binary matched-versus-mismatched label detached from the shape of the underlying reaction norm.

Earlier work in D. melanogaster makes the alternative explanation especially clear. Across developmental and adult temperature combinations, an intermediate developmental temperature generally produced higher reproductive performance than extreme developmental temperatures, even when the adult environment differed [25]. This pattern supports a developmental optimum interpretation rather than a universal beneficial-matching interpretation. The distinction matters because the same observation—poor adult performance after extreme juvenile temperature—can otherwise be described incorrectly as mismatch when it may instead reflect damage accumulated during development.

Persistent developmental costs provide a second alternative. In Drosophila subobscura, high developmental temperature reduced later reproduction despite variation in adult temperature [26]. Adult conditions therefore did not simply reverse the consequences of stressful development. Such results caution against interpreting every developmental-by-adult interaction through environmental forecasting: some patterns are better explained by developmental constraint, irreversible damage, or broadly favorable developmental conditions.

Within the proposed framework, adult environmental match is therefore an empirical comparison rather than a descriptive resemblance between early and later environments. A strong test requires adults originating from different developmental environments to be evaluated across the relevant adult environments, with performance endpoints selected before the adaptive interpretation is made. Evidence for forecasting is strengthened when the phenotype induced by a reliable early cue specifically improves adult performance under the predicted

environment relative to credible alternatives. It is weakened when an intermediate developmental optimum performs broadly well, when developmental damage dominates later performance, or when matched and mismatched environments produce no consistent difference.

These distinctions do not imply that failed beneficial acclimation means developmental plasticity is maladaptive. A plastic response may affect survival, reproduction, behavior, dispersal or physiological tolerance in different ways, and most experiments capture only a subset of those consequences. They do, however, establish a higher evidentiary standard for environmental forecasting: developmental responsiveness and adult carry-over must be connected to the ecological information content of the cue and to direct evidence of later performance under the conditions that the cue purportedly predicted.

Forecast success and failure

Direct performance matching is possible, but the life stage at which it is demonstrated matters. In Tribolium castaneum, reciprocal thermal manipulation during gametogenesis improved sperm and egg performance under corresponding temperatures [27]. This provides a useful benchmark for strong matching evidence, yet it concerns adult reproductive plasticity rather than juvenile developmental forecasting. Timing itself can alter interpretation: in the European corn borer, reproductive consequences of elevated temperature depended on the developmental stage exposed [28]. Plastic responses also need not follow generic stress predictions; in Gryllus firmus, responses to developmental environmental variation were more complex than simple life-history expectations [29]. Forecast success therefore requires convergence between cue reliability and later matched performance, whereas failure can arise through cue decoupling, mistimed induction, developmental damage, or absence of a specific adult advantage.

Adaptive versus maladaptive plasticity

Phenotypic consequence must also be separated from evolutionary consequence. In Telostylinus angusticollis, larval nutrition altered adult competitive and mating phenotypes, but evidence that these changes translated into corresponding changes in selection or reproductive isolation was limited [30]. The proposed framework therefore treats “adaptive,” “maladaptive,” “constrained,” and “unresolved” as evidence states rather than labels inferred from phenotype direction. Unexpected plasticity is not automatically maladaptive, and failure to demonstrate beneficial matching is not evidence of harm.

Table 2 resolves this classification problem by separating observations from the additional evidence required for evolutionary interpretation.

Table 2. Evidence states for distinguishing adaptive forecasting from maladaptive or unresolved developmental plasticity

State	Associated dimensions	State	Associated dimensions
Supported forecasting		**Responsive but unresolved**	
Adult consequence · Interpretation boundary	Benefit under predicted condition Benefit must exceed relevant response costs	**Adult consequence · Interpretation boundary**	Consequence absent, partial, or unmeasured Responsiveness alone is insufficient
Decisive test · Evidential standing	Factorial or reciprocal performance test with field-relevant cue structure Proposed classification	**Decisive test · Evidential standing**	Measure cue–future correlation and adult performance Proposed classification
Cue requirement · Evidence	Early cue demonstrably predicts adult condition Persistent induced phenotype plus matched adult advantage	**Cue requirement · Evidence**	Predictiveness unknown Developmental phenotype changes
Constrained carry-over		**Potentially maladaptive response**	
Adult consequence · Interpretation boundary	Cost or altered performance across adult environments Persistence can reflect damage or allocation history	**Adult consequence · Interpretation boundary**	Demonstrated disadvantage Unexpected phenotype alone is insufficient
Decisive test · Evidential standing	Separate developmental optimum from environment-specific benefit Proposed classification	**Decisive test · Evidential standing**	Compare fitness across predicted and alternative environments Proposed classification

Cue requirement · Evidence	Cue may be reliable or unreliable Persistent developmental effect	**Cue requirement · Evidence**	Cue is misleading, obsolete, or response is inappropriate Induced phenotype performs worse in the relevant later environment

These states form a trade-off space rather than a one-dimensional adaptive–maladaptive continuum, because information quality, persistence, cost, and adult performance can vary independently**. Figure 2** is therefore needed to preserve combinations that a categorical taxonomy cannot display without implying a false ranking.

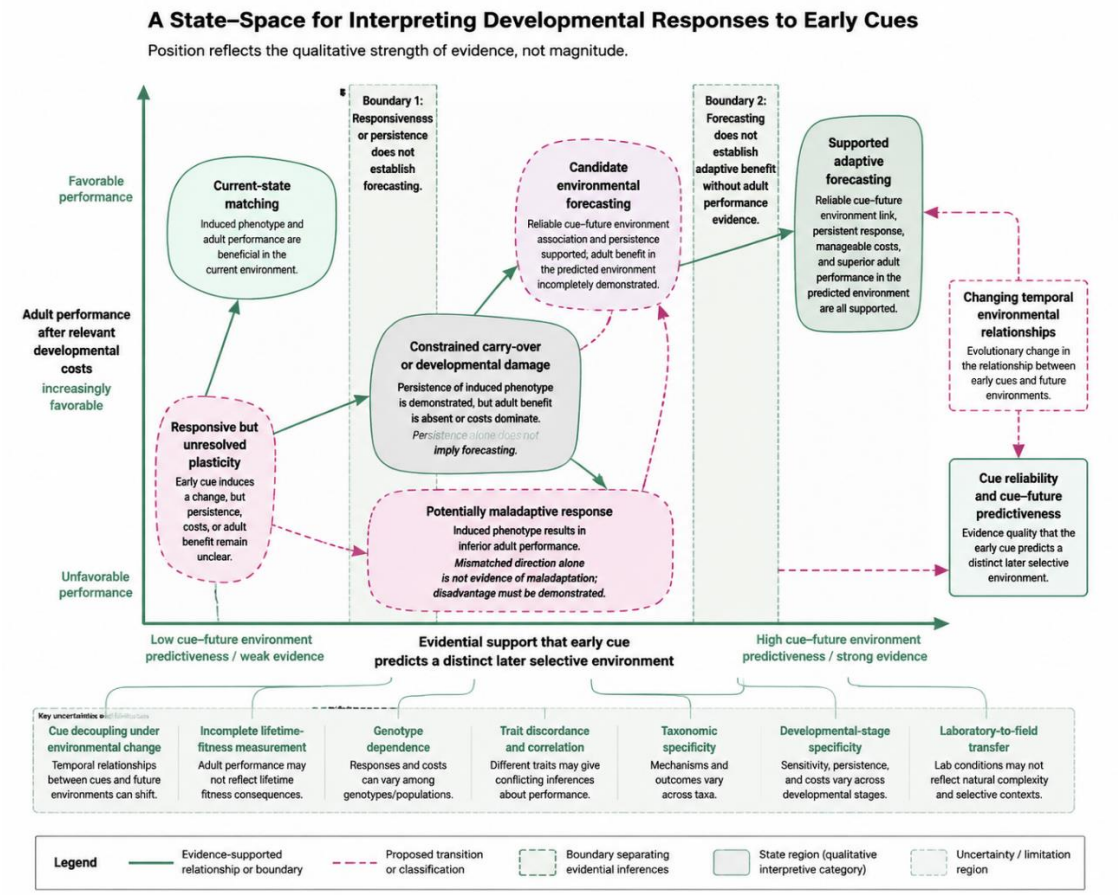


Figure 2. State-space boundaries governing evolutionary interpretation of developmental plasticity

Evolutionary predictions

The framework predicts stronger anticipatory plasticity where cue–adult correlations remain reliable and response costs are limited, while weakened correlations should favor reduced plasticity, alternative cues, or greater reliance on other strategies. Genotype- and population-specific reaction norms further predict that forecasting capacity should not be assumed uniform within species. Longitudinal field studies should therefore pair measurements of cue structure with reciprocal adult-performance tests rather than infer forecasting from reaction norms alone.

The evidence supports widespread developmental responsiveness but not a general rule of beneficial developmental–adult matching. Several factorial thermal studies fail to support simple matching as a universal explanation [23–25], while persistent, trait-specific and genetically variable costs further complicate adult outcomes [20–22]. Positive matching effects can occur, but stage, trait, taxon and ecological information structure determine what they establish.

The proposed Cue-Predictiveness Framework therefore narrows the inference. Mechanistic resolution, phenotypic persistence, and adult performance are complementary evidence classes, not substitutes for one another. Its principal limitation is that many supporting experiments are laboratory based and measure selected performance components rather than lifetime fitness. Validation requires taxonomically broader field studies that quantify temporal cue–environment relationships and test induced phenotypes across realistic adult environments.

Conclusion

Developmental plasticity functions as environmental forecasting only under restricted evidentiary conditions. An early cue must reliably anticipate a later selective environment, its induced response must persist to the relevant stage, costs must remain compatible with benefit, and matched adult performance must be demonstrated. Separating these conditions prevents responsiveness, carry-over, damage, current-state matching, and adaptive forecasting from being treated as equivalent evolutionary explanations.

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