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How Variable Environments Reshape Development from Egg to Imago Through Life-History Reaction Norms in Insects

Hans Müller[1]*, Anna Schmidt[1], Thomas Weber[2]

[1]Department of Phenotypic Plasticity and Reaction Norms, Faculty of Life Sciences, University of Bonn, Bonn, Germany.
[2]Department of Insect Development and Environmental Response, Faculty of Biosciences, LMU Munich, Munich, Germany.

***E-mail** ✉ hans.mueller@uni-bonn.de

ABSTRACT

Insect development occurs as a sequence of stage-specific responses rather than as a single, continuous reaction to environment. Yet developmental plasticity is often interpreted from one stage, one trait, or one thermal mean, obscuring how environmental history, fluctuation, and metamorphic transitions reshape later phenotypes. This theoretical framework integrates evidence from egg, immature, metamorphic, and adult phases to distinguish stage-specific reaction norms, cross-stage carry-over, compensation, and environmentally conditioned state transitions. The framework treats environmental variation as a distribution through time, characterized not only by mean conditions but also by amplitude, predictability, timing, sequence, and co-occurring drivers. It further separates plasticity from adaptation, mechanistic response from fitness consequence, and laboratory reaction norms from field generalization. Evidence shows that developmental temperature can leave persistent adult effects, that identical environmental regimes may produce different responses among life stages and species, and that fluctuating conditions cannot always be represented by their mean. Cross-stage effects are selective rather than universal: larval microbial, nutritional, thermal, or toxicological histories may alter some adult traits, whereas later developmental transitions can attenuate, redirect, or compensate earlier effects. The article therefore advances a proposed egg-to-imago reaction-norm architecture in which phenotypic outcome depends on the ordered interaction among stage identity, environmental history, transition constraints, and subsequent exposure. The framework is intended as a testable organizing model, not as an empirically validated universal mechanism.

Keywords: Developmental plasticity, Reaction norms, Metamorphosis, Carry-over effects, Thermal variability, Phenotypic compensation

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Introduction

Environmental effects on insect development are commonly summarized as responses of a trait to a temperature, diet, photoperiod, or stressor, but such summaries can hide the fact that developmental systems vary in both plasticity and robustness. Environmental regulation of growth, maturation, and life-history traits arises from stage-specific developmental processes whose sensitivity is neither uniform nor necessarily persistent across ontogeny [1]. Consequently, an insect exposed to the same nominal environment at two different life stages need not occupy the same physiological or developmental state.

Thermal biology makes this problem especially visible. Thermal performance curves and limits can differ among ontogenetic stages and among fitness-related traits, so one reaction norm cannot safely represent the complete life cycle [2]. The problem is not only stage specificity. Theory also predicts that temporal variance around a mean

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environment can alter the evolutionarily favored thermal phenotype under seasonal conditions, indicating that environmental distributions may matter independently of their averages [3]. In natural settings, extreme heat is likewise experienced as temporally structured episodes embedded within fluctuating backgrounds rather than as a constant treatment [4].

A further inferential problem is that developmental response, acclimation, and adaptation are often conflated. Estimates of acclimation can depend strongly on assay design, thermal history, and the trait used to quantify response; a plastic shift therefore does not by itself establish evolutionary benefit or climate adaptation [5]. The present article addresses this gap by treating development from egg to imago as a sequence of linked but non-equivalent reaction norms. Its central contribution is a proposed theoretical architecture that separates stage-specific response from cross-stage dependence, distinguishes persistence from compensation, and treats metamorphic transitions as biologically active boundaries rather than neutral connectors.

Conceptual scope and reaction-norm construction

The framework was constructed as a synthesis of experimental, comparative, mechanistic, and theoretical evidence relevant to environmental response across insect development. Reaction norms are treated here as mappings between an environmental state or history and a measured phenotype within a defined life stage. Environmental state is therefore not restricted to a scalar mean. Where the evidence permits, it includes fluctuation amplitude, timing, sequence, predictability, and interaction with nonthermal drivers.

Developmental history is included because early thermal conditions can leave measurable effects on later thermal tolerance. In *Drosophila melanogaster*, developmental temperature produced persistent changes in adult upper thermal limits, although the magnitude and expression of those effects depended on population and subsequent conditions [6]. Stage identity is included as a separate axis because aphid nymphal instars and adults exposed to broadly similar thermal conditions nevertheless differed in thermal performance and hardening responses [7]. These studies justify treating stage as a state variable rather than assuming that a single species-level reaction norm applies throughout ontogeny.

The construction also distinguishes constant from fluctuating environments with equal or similar means. Developmental and adult thermal fluctuations can affect lower and upper critical limits differently, and the response can change after transfer to a new adult regime [8]. Across five *Drosophila* species, developmental fluctuations around a common mean altered development time while effects on viability and wing size were more heterogeneous [9]. Thus, variance is represented as a biologically relevant property rather than as noise around a mean.

Finally, reaction-norm shape is not imposed as linear. Adult acclimation experiments show that lower thermal limits can follow nonlinear reaction norms and that fitted shape depends on acclimation regime [10]. The framework therefore permits stage-specific nonlinear responses, discontinuities at transitions, and history-dependent shifts without assigning any of them universal status. These are conceptual allowances grounded in observed heterogeneity, not assumptions that every insect exhibits each form.

Results and Discussion

The approved evidence indicates that developmental environment can alter later performance without supporting a universal “matching-environment” advantage. In *D. melanogaster*, reproductive performance was often maximized after an intermediate developmental temperature rather than when developmental and adult temperatures matched, which is more consistent with favorable-development effects than with a general beneficial-acclimation rule [11]. This distinction is important because a reaction norm may describe plasticity accurately while still failing to predict fitness advantage across subsequent environments.

Evolutionary potential is also uneven across thermal traits. In the invasive ladybird *Harmonia axyridis*, critical thermal limits showed heritable variation, whereas substantial portions of broader thermal-performance variation had limited heritability [12]. Plastic response and capacity for evolutionary tracking must therefore remain separate dimensions of the framework.

Temporal structure further modifies developmental exposure. Reviews of extreme high temperature emphasize that insects experience heat events within naturally variable microclimates, so laboratory constant-temperature treatments may omit biologically relevant timing and recovery intervals [13]. Direct experiments in *Manduca sexta* reinforce this point: the number and developmental timing of larval heat waves altered survival, growth, and

developmental outcomes, showing that equal categories of "heat exposure" are not necessarily equivalent when imposed at different ontogenetic positions [14]. Environmental variation across development is therefore best represented as an ordered exposure history rather than a stage-independent average.

Stage-specific reaction norms

Stage-specific reaction norms describe how the same environmental dimension can have different phenotypic meanings depending on when it is encountered. Environmental predictability is one such modifier. In *Drosophila mojavensis*, within- and transgenerational heat-tolerance responses varied among climatic regions and life stages, linking plasticity patterns to environmental predictability without establishing that all observed responses were adaptively optimal [15]. The appropriate inference is therefore conditional: predictability can shape the form or expression of plastic response, but its evolutionary significance must be tested independently.

Body size illustrates a second boundary. Comparative analyses of British Odonata show heterogeneous temperature–body-size relationships among taxa and life-history contexts [16]. This variability argues against treating warmer development as producing a universal direction of size change across insects. Stage duration, growth trajectory, resource environment, and lineage-specific life history can all alter the observed phenotype.

Stage-specific responses are also multidimensional. In *Aedes albopictus*, larval temperature and competition interacted to influence later survival and fecundity, demonstrating that a larval reaction norm can depend on both abiotic and biotic context and can extend into adulthood [17]. In male *Aedes aegypti*, larval diet and temperature jointly affected development, energy reserves, and thermal tolerance, whereas not every adult performance component shifted in parallel [18]. Accordingly, the proposed framework treats each stage-specific reaction norm as a vector of trait responses rather than as a single value, and it does not assume that correlated developmental outputs remain coupled after transition to the next stage.

Cross-stage dependence and developmental compensation

Cross-stage dependence occurs when the phenotype expressed at one stage depends partly on environmental states encountered earlier. The evidence shows that such dependence is selective. Defined larval bacterial environments in *Aedes aegypti* produced variation in several adult traits, including body size and immune- or vector-related phenotypes, but did not uniformly alter all adult outcomes [19]. Metamorphosis therefore cannot be treated either as a complete reset or as a guarantee that every larval effect persists.

Longitudinal evidence also shows that persistence can depend on developmental timing. In *Coenagrion puella*, the effect of larval pesticide exposure on female lifetime fitness depended strongly on egg-hatching phenology under seminatural conditions [20]. This interaction indicates that an early exposure can be amplified, attenuated, or rendered consequential only within particular developmental schedules. Cross-stage dependence is thus conditional on the state in which a later transition is reached.

Metamorphic transitions provide a mechanistic boundary for this interpretation. In *Leptinotarsa decemlineata*, ecdysone-receptor isoforms had distinct roles in successful larval–pupal–adult transition, and disruption of receptor function impaired normal ecdysis [21]. More broadly, insect metamorphosis is coordinated through interorgan signaling that integrates nutritional, growth, and endocrine information rather than through a passive temporal switch [22]. These findings justify representing metamorphosis as an active state-transition boundary, but they do not establish that endocrine signaling is the universal mechanism of environmental carry-over.

The present synthesis therefore distinguishes several cross-stage states: persistent carry-over, selective carry-over, context-dependent amplification, attenuation, compensation, and transition gating. These categories are proposed analytical states rather than empirically validated universal classes. They are useful because they separate what is observed—a later phenotype depends on earlier conditions—from stronger claims about mechanism, adaptive value, or inevitability.

Because prose alone obscures the distinction between an observed cross-stage dependence and the inference that may legitimately be drawn from it, the state-and-response ledger below separates observable patterns from interpretation, boundary conditions, and the experiments needed to distinguish competing explanations.

Table 1. Cross-stage developmental states separating persistence, selective transmission, compensation, and transition constraints

Biological setting · Evidence	Interpretation for life-history reaction norms · Limits and uncertainty	Research or test · Evidential standing

Persistent carry-over		
Developmental thermal history extending into an adult phenotype **Adult trait remains shifted after earlier exposure**	The later-stage reaction norm retains information from a prior developmental state Persistence may depend on population, trait, and subsequent environment	Re-measure the same trait after standardized transfer to distinguish persistence from contemporaneous acclimation Evidence-supported pattern; proposed state label
Selective carry-over		
Larval biotic, nutritional, or thermal conditions affecting only some adult traits **Some adult phenotypes change while others remain comparatively stable**	Environmental history is trait-specific rather than organism-wide A null response in one trait does not demonstrate absence of carry-over in another	Track multiple adult traits from the same developmental cohort Evidence-supported pattern; proposed state label
Context-dependent amplification		
Early exposure interacts with later temperature, competition, or developmental timing **A later effect increases or appears only under a particular subsequent condition**	The later-stage reaction norm depends on prior-state × current-state interaction Cannot be established from single-environment comparisons	Use factorial environmental sequences rather than isolated-stage treatments Evidence-supported pattern; proposed state label
Attenuation		
An earlier effect weakens after transition or subsequent exposure **A difference present early becomes smaller or undetectable later**	Later-stage processes partially overwrite developmental history Apparent loss may result from insensitive or mismatched trait measurement	Apply repeated stage-resolved assays across the transition Proposed synthesis grounded in observed history dependence
Developmental compensation		
Later timing or phenotype counteracts an earlier displacement **An initial developmental shift is reduced by a later-stage response**	Whole-life outcome cannot be predicted by simply summing stage-specific deviations Compensation may be incomplete, cue-specific, or nonadaptive	Test whether the later response restores phenotype, timing, or fitness rather than merely reversing direction Evidence-supported pattern; proposed state label
Transition gating		
Metamorphic regulatory processes constrain whether earlier effects can be expressed after stage change **Cross-stage outcome changes at a hormonally coordinated developmental transition**	Metamorphosis functions as an active boundary between stage-specific reaction norms Known endocrine mechanisms do not explain all forms of environmental carry-over	Combine stage-resolved phenotyping with mechanistic assays at transition points Mechanistically supported boundary; proposed integrative role

Egg-to-imago integrated reaction-norm model

The proposed model treats the developing insect as stage-specific phenotype–environment mappings connected by state transitions. Phenotype at each stage is conditioned by current environment, the preceding state, and retained environmental history; transition can preserve, filter, amplify, or compensate these effects. The formulation is conceptual: no common effect coefficient is assumed across taxa, stages, or traits.

Body size illustrates why whole-life outcome cannot be inferred from a single developmental slope. Warmer developmental conditions are often associated with reduced size at maturity, but several physiological and allocation explanations for this temperature–size relationship remain plausible and their relative importance differs among systems [23]. Accordingly, adult size is treated as an endpoint emerging from growth, developmental duration, resource state, and stage transitions rather than an inevitable function of temperature.

An external-generalization boundary is equally necessary. Across 121 insect species from 12 orders, altitudinal body-size patterns did not consistently reproduce laboratory, seasonal, or latitudinal temperature–size expectations [24]. Altitude covaries with oxygen, season length, voltinism, dispersal opportunity, and other ecological dimensions; field gradients therefore cannot be read as direct experimental temperature reaction norms. The model therefore separates within-stage response, cross-stage propagation, and field association.

Egg-stage timing provides a complementary example of compensation. In the winter moth, experimentally and longitudinally examined photoperiodic cues allowed later phenological stages to compensate for shifts associated

with egg hatching [25]. This demonstrates that an early displacement need not propagate monotonically through the life cycle. It does not establish that compensation is complete, beneficial, or general across insects. In the proposed architecture, egg, immature, metamorphic, and adult states are therefore linked by conditional transitions rather than fixed carry-over arrows.

Three properties follow. Reaction norms are stage-indexed; histories are path-dependent; and whole-life phenotype is non-additive because later responses can modify earlier effects. An explicit boundary separates observed trait change from inferred fitness, population, or evolutionary consequence.

A reaction-norm trajectory can therefore be represented conceptually as a sequence of conditional mappings rather than a continuous curve. For an environmental driver E, stage-specific phenotype Ps is interpreted as a function of the current exposure distribution, developmental state, and retained history Hs. History is updated at transitions rather than assumed to pass unchanged. This distinction matters because two adults experiencing the same immediate environment can differ if they arrived there through different larval temperatures, resource regimes, microbial contexts, or developmental schedules. Conversely, two early histories can converge on similar adult phenotypes if later responses compensate them. The model therefore separates trajectory convergence from absence of developmental effects: identical endpoints do not demonstrate identical developmental pathways.

The same logic applies to multiple traits. Thermal tolerance, body size, development time, energetic state, phenology, and reproductive performance need not move in parallel. A cross-stage effect can be evident in one trait and absent in another without logical contradiction. The proposed architecture consequently uses phenotype-response vectors and does not infer an organism-wide state from a single assay. It also distinguishes a developmental endpoint from a fitness endpoint. A smaller adult, faster development, or shifted thermal limit is not intrinsically beneficial or detrimental unless performance or fitness consequences are measured in the relevant ecological setting.

Evidence density is also asymmetric. Egg-stage evidence chiefly informs phenological entry conditions, whereas larval and adult studies provide richer trait-level measurements; metamorphic evidence is mechanistically informative but narrower taxonomically. The architecture therefore displays unequal empirical depth rather than implying that every transition has been studied equivalently. This asymmetry is itself a validation target: future whole-life experiments should measure comparable traits before and after each transition.

The figure is needed because these trajectories cannot be represented faithfully as a single linear sequence: it separates within-stage reaction fields from cross-stage memory, compensation, transition gating, and the external field-generalization boundary.

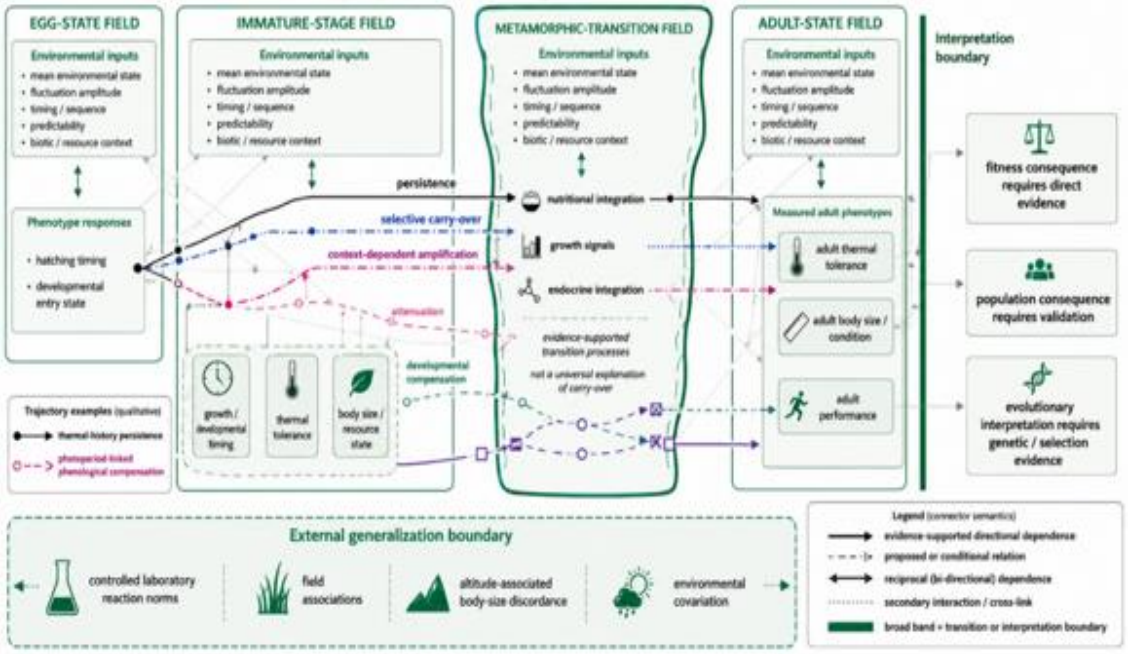


Figure 1. Environmental-history trajectories across stage-specific reaction fields and metamorphic boundaries

Predicted phenotypic outcomes under stable versus fluctuating conditions

The framework predicts stable–fluctuating differences only conditionally. "Stable" denotes low temporal variation, not favorability; "fluctuating" denotes temporal variation, not stress. Outcomes depend on nonlinear reaction norms, sensitive-stage timing, interacting resource or biotic conditions, and cue predictability.

Semi-field evidence illustrates why downstream outcomes cannot be inferred from temperature alone. Urban, suburban, and rural larval environments altered selected life-history and vector-related traits of *Aedes albopictus*, and effects varied with season, yet infectiousness itself was not uniformly different among environmental treatments [26]. Thus, an environmental history can alter adult phenotype without producing a parallel change in every higher-level consequence.

Heat-response mechanisms create another boundary. Insects deploy multiple physiological responses to high temperature, but evidence for molecular or physiological response should not be converted automatically into evidence of evolutionary adaptation [27]. Under stable conditions, the proposed model expects phenotypes to reflect the local position and shape of a stage-specific reaction norm. Under fluctuating conditions, it expects deviations from constant-mean outcomes when nonlinear responses, event timing, recovery, or cross-stage history matter. These are theoretical expectations, not universal forecasts.

Predictability adds a separate axis. Work on parasitoids and their hosts emphasizes that predictable and unpredictable thermal variation can favor different plasticity or diversified-response expectations [28]. The framework therefore distinguishes fluctuation magnitude from informational predictability and does not label variable phenotypes as bet-hedging without direct evolutionary evidence.

Several competing outcomes follow from this construction. When fluctuations remain within an approximately linear portion of a stage-specific reaction norm and recovery is rapid, a constant treatment near the same mean may approximate the average phenotype. When exposures cross nonlinear regions or biological thresholds, however, equivalent means can conceal disproportionate effects. If a brief event occurs during a sensitive developmental interval, event timing may dominate cumulative duration; if it occurs after the sensitive window, an apparently similar exposure may have little detectable carry-over. These alternatives should be tested rather than embedded as assumptions.

Cross-stage history also yields contrasting predictions. Persistent carry-over predicts that differences generated earlier remain detectable after later environments are standardized. Attenuation predicts progressive reduction of that difference. Compensation predicts that a later-stage response moves the phenotype toward a common endpoint, whereas context-dependent amplification predicts divergence under particular subsequent conditions. None of these patterns alone establishes adaptation. The relevant comparison is not simply whether the adult phenotype changed, but whether the sequence of environmental states explains variance beyond current conditions and whether any resulting performance difference is measured under ecologically appropriate circumstances.

The mechanism–boundary matrix is required to keep these predictions from collapsing into the unsupported contrast "stable good, fluctuating bad"; it identifies what must be observed before a proposed outcome can be distinguished from competing explanations.

Table 2. Conditional phenotypic expectations when environmental variance is separated from mean state, timing, and predictability

Focal environmental scenario	Required evidence · Proposed phenotypic interpretation	Principal limit or competing explanation · Research or test	Evidential standing · Biological setting
Stable environment within a favorable response range	Repeated phenotype under low temporal variance Trait expression should approximate the local stage-specific reaction norm	Stability does not establish optimality or fitness benefit Compare multiple mean states before interpreting "stable" as favorable	Proposed expectation A defined stage and trait
Stable environment near a nonlinear limit	Trait response near a curve shoulder or critical region Small mean shifts may produce disproportionate phenotype change even without fluctuation	Apparent sensitivity may be assay- or trait-specific Estimate reaction-norm shape rather than extrapolating linearly	Proposed expectation grounded in nonlinear responses Thermally sensitive stage
Fluctuation around an equivalent mean	Constant and fluctuating treatments with comparable means	Divergence depends on amplitude, duration, recovery, and trait	Evidence-supported pattern; proposed generalization

	Outcome may diverge from constant-mean phenotype	Use matched-mean fluctuation experiments with stage-resolved outcomes	Developmental thermal exposure
Stage-targeted extreme event	Event timing and developmental state recorded Consequence may differ according to ontogenetic timing	Equal thermal dose need not imply equal biological dose Cross event timing with stage identity and subsequent performance	Evidence-supported pattern; proposed state formulation Egg, immature, transition, or adult stage
Predictable fluctuation	Evidence that cues precede or reliably covary with later conditions Cued plasticity may alter later phenotype	Plasticity is not proof of adaptive matching Test cue reliability and fitness consequences separately	Proposed expectation Recurrent environmental sequence
Unpredictable fluctuation	Replicated histories and among-individual responses Diversified or reduced cue-dependent responses may be favored theoretically	Bet-hedging requires evolutionary evidence, not variance alone Measure among-individual variance, inheritance, and fitness across environments	Proposed theoretical expectation Variable sequence with weak cue reliability
Multidriver fluctuation	Factorial or realistic combined exposures Cross-stage outcome may reflect interactions rather than a single driver	Driver covariance can mimic direct effects Manipulate drivers independently where possible and validate in field conditions	Evidence-supported premise; proposed integrative prediction Temperature with diet, competition, microbes, or habitat context

The proposed architecture changes the unit of interpretation from an isolated stage–trait response to an ordered developmental trajectory. Developmental regulation is heterogeneous across traits [1], and thermal sensitivity differs across ontogeny [2]. A whole-life framework must therefore retain stage identity instead of averaging it away.

The evidence also rejects two symmetric simplifications: that metamorphosis erases developmental history and that early-life effects necessarily persist. Developmental and adult thermal regimes can modify one another [8]. Cross-metamorphic pesticide effects can depend on hatching phenology [20]. Photoperiodic responses can compensate an earlier timing displacement [25]. These patterns motivate the proposed categories of persistence, attenuation, amplification, compensation, and transition gating, which are organizational rather than exhaustive states.

A second implication concerns competing developmental hypotheses. The favorable developmental temperature observed for reproduction in *D. melanogaster* does not support a universal matching-environment rule [11]. Larval temperature and competition in *A. albopictus* likewise produced conditional later outcomes [17]. Consequently, "matching," "silver-spoon," and carry-over interpretations should be treated as alternatives whose support depends on the measured phenotype, subsequent environment, and fitness evidence.

Three failure modes are especially important. First, stage substitution occurs when an easily measured adult trait is used as a proxy for larval or whole-life sensitivity. Such substitution can miss stage-specific vulnerability. Second, mean-environment substitution occurs when a fluctuating history is represented by its arithmetic mean despite nonlinear or timing-sensitive responses. Third, endpoint substitution occurs when an adult morphological or physiological difference is interpreted as a fitness consequence. The framework is designed to make these substitutions visible rather than to assign them correction factors.

Empirical tests should manipulate environmental sequences, not only isolated environments. Factorial designs can compare early and late exposures under a common adult assay environment and measure multiple traits across transitions. Where manipulation is impossible, longitudinal field observations should resolve developmental timing and microenvironment rather than regional climate means. Mechanistic assays are most informative when paired with trajectory data, because endocrine or molecular responses can identify transition processes without establishing downstream ecological consequences. Validation should include hemimetabolous and holometabolous insects; the strength and location of developmental boundaries remain empirical questions.

The largest limitation is uneven evidence coverage. Thermal studies dominate, larval and adult stages are better represented than eggs, and mechanistic metamorphosis research is taxonomically narrower than the ecological literature. Acclimation estimates themselves are method-sensitive [5]. Field transfer presents another constraint:

altitudinal size patterns diverge from simple laboratory expectations [24]. Validation therefore requires longitudinal multistage experiments, factorial environmental sequences, multiple phenotypes within cohorts, and field tests preserving realistic covariance among drivers. Alternative trajectories should be compared rather than testing only whether early exposure leaves any adult effect.

Ecological and evolutionary implications

Stage-structured environmental responses could alter ecological timing and vulnerability without implying evolutionary adaptation. Seasonal thermal variance can change modeled evolutionary optima [3], whereas empirical quantitative-genetic work shows that thermal traits differ in available heritable variation [12]. Phenotypic responsiveness and evolutionary potential must therefore remain distinct.

Extreme events may also matter because they intersect particular developmental stages. Field-oriented synthesis emphasizes realistic heat variability [13], and larval heat-wave experiments show timing-sensitive outcomes [14]. Climate exposure should consequently be indexed to developmental calendars rather than represented only by annual or seasonal means.

Generalization across taxa and environments requires similar caution. Odonate temperature–size relationships are heterogeneous [16], and broad altitudinal comparisons reveal strong departures from a simple temperature-size expectation [24]. Urban mosquito experiments further show that environmental context can propagate into selected adult traits without uniform downstream effects [26]. Geographic transferability should therefore be treated as conditional on species, life history, environmental covariance, and measured trait.

Finally, environmental predictability may influence the evolutionary relevance of plasticity. Stage- and region-dependent heat responses in *D. mojavensis* provide empirical context [15], while parasitoid–host theory distinguishes predictable plasticity from responses expected under unpredictability [28]. The framework treats these as hypotheses for comparative testing, not evidence that fluctuating environments universally select for plasticity or bet-hedging.

Conclusion

Insect development is better represented as a sequence of connected reaction norms than as one phenotype–environment relationship stretched from egg to imago. The proposed architecture combines stage-specific sensitivity, ordered environmental history, selective carry-over, compensation, and metamorphic transition constraints while preserving a boundary between measured phenotype and fitness or evolutionary interpretation. Stable and fluctuating environments are distinguished by temporal structure rather than by presumed quality, and predictable variation is separated from unpredictability. The framework is intentionally non-universal: its components require validation across taxa, sexes, developmental modes, environmental drivers, and field contexts. Its principal value is to convert heterogeneous evidence into explicit, testable alternatives about when developmental history persists, when later stages reshape it, and when whole-life outcomes cannot be inferred from any single stage.

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