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Rapid Environmental Change Alters Which Developmental Effects Persist, Are Compensated, or Become Irreversible Across Metamorphosis

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ABSTRACT

Rapid environmental change can modify insect development long before adult phenotype is measured, yet cross-stage consequences are often interpreted with an overly simple persistence-versus-recovery distinction. This article develops a proposed mechanistic framework for classifying developmental effects according to whether an exposed–reference difference dissipates, is functionally compensated, remains persistent, or becomes damage-consistent across metamorphosis. The framework treats the classification unit as a focal trait observed at a defined developmental stage and post-exposure horizon rather than assigning a single state to the whole organism. This distinction is necessary because thermal tolerance, immunity, morphology, behavior, metabolism, infection susceptibility, reproduction, and survival can show different trajectories after the same developmental exposure. Metamorphosis is therefore treated as a transformation boundary that can attenuate, reveal, redistribute, or preserve earlier effects rather than as an obligatory physiological reset. Environmental change is represented through magnitude, duration, variability, repetition, interacting stressors, and recovery opportunity, while timing relative to metamorphosis defines a separate source of conditionality. The framework further distinguishes molecular persistence from demonstrated organismal mechanism and plasticity from adaptive benefit. It predicts that persistence and compensation should be understood as trait-specific state trajectories whose interpretation depends on exposure architecture, developmental timing, ecological context, and the observation window. These propositions require prospective cross-stage validation and should not be read as universal laws across insect taxa.

Keywords: Carry-over effects, Developmental plasticity, Metamorphosis, Thermal stress, Cross-stage persistence, Compensatory response.

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Introduction

Rapid environmental change exposes insects to thermal, nutritional, hydric, chemical, and biotic conditions that may shift within a single life cycle. Because thermal tolerance, plasticity, microhabitat use, and exposure regimes differ among developmental stages, the biological meaning of an environmental perturbation depends partly on where it intersects ontogeny [1]. Yet much of the literature still asks whether an early-life effect “carries over” into adulthood as though persistence were a binary property. Carry-over theory instead concerns dependencies

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between earlier environments and later phenotypes, and does not imply that such dependencies are necessarily adaptive or fitness-enhancing [2].

Metamorphosis intensifies this inferential problem. In holometabolous insects, extensive endocrine, cellular, and tissue reorganization separates juvenile and adult phenotypes, but that reorganization is not equivalent to erasure of developmental history [3]. The relevant question is therefore not whether metamorphosis resets the organism, but which components of an earlier environmental effect are attenuated, reconfigured, preserved, or expressed later. A broad synthesis of developmental thermal plasticity found substantial heterogeneity in persistence across ontogeny, showing that persistence cannot safely be assumed from an early response alone [4]. At the same time, insect thermal-limit plasticity is generally weak in magnitude and differs among stages, limiting any assumption that plastic adjustment automatically offsets environmental deterioration [5].

Heterogeneity also occurs below the level of insect order. Developmental temperature can alter life-history, energetic, and molecular traits differently among populations of the same mosquito species, while leaving some thermal traits comparatively unchanged [6]. Thus, an exposed insect cannot be assigned one global state such as "recovered" or "damaged" when different adult traits follow different trajectories.

The central contribution here is a proposed cross-stage state classification for the inferential problem encoded in these observations. Four outcomes are distinguished at the level of a focal trait: reversible effects, compensable effects, persistent effects, and irreversible or damage-consistent effects. These categories are not assumed to be mutually exclusive across the organism. A single individual may show compensation in one functional domain, persistence in another, and reproductive damage in a third. The framework also separates environmental rate and temporal architecture from exposure magnitude, and treats developmental distance from metamorphosis as a distinct moderator. Its purpose is not to supply a validated prediction rule, but to organize evidence into testable cross-stage trajectories while preserving taxonomic, life-stage, environmental, and methodological boundaries.

Materials and Methods

This article is a mechanistic framework rather than a systematic review or meta-analysis. Evidence was organized around studies and syntheses that directly informed cross-stage developmental state, recovery, compensation, persistence, damage, exposure timing, or temporal environmental structure. The classification unit was defined as a focal phenotype measured after a specified developmental exposure and evaluated at a specified later observation horizon. This trait-by-stage-by-time unit prevents a single measurement, such as adult body size or survival, from standing in for organism-wide developmental condition.

Exposure was treated as multidimensional. Temperature and nutrition can interact non-additively, cold stress can cross-talk with other environmental pressures, and fluctuating regimes can create alternating injury and recovery opportunities; consequently, stressor identity, magnitude, duration, sequence, co-occurrence, and recovery interval were retained as separate descriptors rather than collapsed into a single stress score [7-9]. Molecular observations were coded as a distinct evidential layer. Environmentally responsive DNA methylation, histone modification, noncoding RNA, and related processes may contribute to persistent developmental regulation, but such associations do not by themselves establish causal mediation, adaptive memory, or transgenerational inheritance [10].

The proposed state definitions use the exposed–reference difference as an inferential object. A reversible effect is one for which that difference declines substantially or disappears during an appropriate recovery interval. A compensable effect is one in which focal function is restored or maintained through another developmental or physiological response, while costs in other traits remain possible. A persistent effect is a measurable cross-stage displacement retained at a defined later horizon without implying permanence. "Irreversible damage" is reserved for the strongest evidence: failure to recover across an adequate biological interval, persistence through a relevant lifetime window, or demonstrated structural or functional loss for which reversal has been directly excluded. When those conditions are not met, the more conservative label is damage-consistent persistence. This hierarchy is explicitly proposed and is intended to prevent finite-time observations from being converted into claims of biological permanence.

Results and Discussion

Direct evidence shows that early environmental effects can weaken after metamorphosis, but reversibility is usually trait-specific. In the ladybird Harmonia axyridis, pupal temperature altered multiple adult traits, yet some thermal-performance effects diminished after emergence while other immune and reproductive consequences were retained [11]. The appropriate inference is therefore not that the insect "recovered," but that particular response dimensions showed a declining exposed–reference difference.

Recovery can also depend on when and how strongly stress occurs. Experimental heatwaves in Tribolium castaneum produced life-stage- and severity-dependent mortality and fertility consequences, with post-exposure recovery differing among endpoints [12]. Such designs show why a recovery interval is itself part of the phenotype: an effect recorded immediately after stress may be transient, whereas persistence after sufficient recovery supports a different classification.

Reversibility need not be passive. In a seasonal herbivorous insect, photoperiodic information modified phenological carry-over generated by prior environmental conditions [13]. Later cues can therefore partially offset earlier developmental displacement. Conversely, salinity exposure in the rock-pool mosquito Aedes mariae altered behavioral plasticity and weakened coupling between larval and pupal size-related traits [14]. This latter pattern does not demonstrate adult recovery, but it illustrates that cross-stage relationships can be reorganized before adulthood. Reversible effects should consequently be defined by observed trajectory change, not by an assumption that metamorphosis erases earlier history.

Compensable effects

Compensation differs from reversibility because the original perturbation may remain biologically consequential even when focal performance is maintained. Larval diet in black soldier flies altered thermal tolerance and preference in stage- and sex-dependent ways, showing that nutritional history need not map uniformly onto later thermal phenotype [15]. An attenuated adult response may therefore reflect developmental reallocation or trait-specific buffering rather than disappearance of the original effect.

The distinction becomes clearer when multiple traits are measured. In Hyles lineata, larval nutrition altered growth–immunity allocation and produced region-specific changes in adult morphology [16]. Maintenance of one function can therefore coexist with redistribution of resources or latent cost elsewhere. Under the proposed classification, compensation requires evidence that a focal function is restored or maintained, but it does not authorize a claim of whole-organism recovery.

Measurement choice can itself create apparent compensation. In Aedes albopictus, larval diet and temperature affected development and adult traits, while alternative morphometric proxies were not interchangeable predictors of adult longevity [17]. A single size metric could therefore conceal continued physiological or life-history differences. More broadly, a meta-analysis comparing constant and fluctuating temperatures at the same mean found limited general differences in plastic responses [18]. Environmental variability should thus be tested as a moderator rather than assumed to increase compensatory capacity. Compensation is best treated as a multivariate and context-dependent state, not as restoration of one convenient endpoint.

Persistent effects

Persistent effects are cross-stage differences that remain detectable at a defined later horizon, but persistence alone does not establish irreversibility. Larval heat stress in Drosophila melanogaster altered adult behavior, metabolism, and expression of candidate regulatory genes after metamorphosis [19]. These results demonstrate retention of developmental history across several adult domains, while the implicated molecular pathways remain hypotheses for mediation rather than proven causal mechanisms.

Persistence can also differ by sex or social phenotype. Simulated pupal heat stress in native stingless bees produced adult effects on morphology, immunity, behavior, or longevity-related traits that differed among workers, gynes, and males [20]. Such heterogeneity makes sex and caste part of the state definition rather than nuisance variation. It also prevents extrapolation from an adult worker endpoint to colony performance or population persistence.

Some developmental effects are not merely retained but become more visible after metamorphosis. In a damselfly, combined larval pollutant and food stress produced survival-related consequences that strengthened during and especially after metamorphosis [21]. This pattern is important because it contradicts a simple attenuation model: metamorphic reorganization can reveal or amplify latent costs in particular contexts. Ecological history can also carry over into adult functional susceptibility. In mosquitoes, larval competition altered subsequent arboviral

infection measures in adults, although effects depended on mosquito–virus combination and infection should not be equated with demonstrated transmission [22]. Persistence therefore spans physiological, behavioral, ecological, and infection-related phenotypes, but its interpretation must remain tied to the trait actually measured.

Irreversible damage

The strongest cross-stage claims arise when later function remains impaired despite opportunities for acclimation or recovery. Developmental warming in Aedes aegypti increased critical thermal maximum while reducing fertility, demonstrating that an apparently beneficial shift in thermal tolerance can coexist with reproductive cost [23]. This dissociation is central to the proposed framework: persistence or compensation in one trait cannot be used to infer net developmental benefit.

Longitudinal evidence provides a stronger basis for inferring damage than a single adult snapshot. In a damselfly, larval pesticide exposure generated effects on female lifetime fitness whose magnitude depended on hatching phenology [24]. Lifetime follow-up strengthens the case that a developmental perturbation was not merely transient, but the timing dependence also shows why irreversibility cannot be assigned independently of developmental context.

Sublethal heat further exposes the limitations of mortality-centered classification. Experimental heatwaves can reduce male reproductive output without corresponding lifetime survival costs, while stage-specific high-temperature exposure in Tuta absoluta alters development and reproductive traits in ways that depend on when exposure occurs [25, 26]. These studies support a functional definition of damage that includes reproduction and development rather than mortality alone, while only the latter directly concerns developmental-stage exposure.

Accordingly, the framework uses “irreversible” conservatively. Persistence at one adult time point is insufficient. High-confidence irreversibility requires a biologically adequate recovery window, lifetime evidence, or a demonstrated loss that cannot recover under the studied conditions. Otherwise, “damage-consistent persistence” is the more defensible term. This distinction is especially important under rapid environmental change, where apparent recovery in tolerance, size, or survival may coexist with delayed reproductive, immune, metabolic, or ecological costs that emerge only later.

Environmental rate of change

Environmental change is often represented by its magnitude: maximum temperature, minimum temperature, pollutant concentration, or nutritional deficit. For cross-stage inference, however, the rate and temporal architecture of change are equally consequential because biological injury and recovery accumulate through time. In Drosophila suzukii, thermal limits for reproduction and survival depended strongly on exposure duration, with reproductive impairment occurring under conditions less extreme than those producing lethal failure [27]. A short pulse and a prolonged episode at the same nominal temperature therefore cannot be treated as equivalent developmental exposures.

This distinction matters because survival may remain apparently intact while reproductive function deteriorates. Broader synthesis of heatwave effects identifies reproductive costs that can remain cryptic when mortality is the dominant endpoint [28]. The proposed framework therefore separates exposure magnitude from duration and separates both from the phenotype used to classify outcome. An adult surviving developmental heat cannot be considered compensated solely because mortality was avoided.

Repetition adds another temporal dimension. In Mythimna separata, short high-temperature exposures produced reproductive consequences that varied with exposed life stage and exposure frequency [29]. Repeated episodes may allow recovery between pulses, repeatedly interrupt recovery, or accumulate injury, depending on spacing and the biological process measured. These possibilities cannot be inferred from peak temperature alone. Likewise, the limited average difference between constant and fluctuating temperatures reported across ectotherms [18] cautions against treating variability itself as inherently beneficial or harmful. Much available evidence concerns particular forms of fluctuation, especially regular thermal cycles, rather than every kind of rapid environmental variability.

Accordingly, environmental rate of change is defined here as a proposed multidimensional exposure property comprising duration, repetition, interval between events, variability around the mean, directional speed of change, and coincidence with other stressors or recovery opportunities. These components should not be collapsed into a numerical severity score without empirical justification. Their role is inferential: they identify why two exposures with similar means or extrema may generate different cross-stage state trajectories. Rate also interacts with

measurement horizon. A phenotype measured immediately after a pulse may indicate injury, whereas the same phenotype after recovery may indicate reversibility, residual persistence, or damage-consistent failure to recover. Because identical peak conditions can represent biologically different developmental histories, **Table 1** reconciles the temporal dimensions that must remain distinct when interpreting cross-stage outcomes.

Table 1. Environmental tempo states that change the interpretation of cross-metamorphic developmental effects

Biological with observed basis	Principal limit	Discriminating check
Duration accumulation		
Evidence-supported distinction		
Longer exposure can impair reproduction at conditions below those associated with lethal failure **A surviving individual may still enter a persistent or damage-consistent reproductive state**	Thermal duration functions are species-, stage-, and endpoint-specific	Compare multiple durations at matched intensity and follow both survival and reproduction
Repetition and recovery spacing		
Evidence-supported distinction; state consequence proposed		
Repeated pulses can differ from a single event even when peak conditions are similar **Inter-event recovery may favor reversibility; insufficient recovery may permit cumulative persistence**	Pulse frequency, recovery physiology, and stage determine direction	Manipulate pulse number and inter-pulse interval independently
Variability around the mean		
Evidence-supported boundary		
Fluctuating conditions do not show a uniform advantage over constant conditions with the same mean **Variability cannot be assigned a priori to compensation or damage**	Existing syntheses are dominated by particular fluctuation regimes and ectotherm groups	Test irregular and directional variability rather than only regular cycles
Directional environmental speed		
Proposed		
Rapid movement toward stressful conditions may shorten the time available for developmental adjustment **Faster change is predicted to shift some traits from compensation toward persistence or damage-consistent states**	Direct comparative tests of rate independent of magnitude remain sparse	Hold endpoints constant while manipulating the speed of environmental change
Coincident drivers and recovery opportunities		
Evidence-supported distinction; integrative interpretation proposed		
Temperature, nutrition, contaminants, competition, or other pressures can overlap or alternate **The same focal exposure may yield different states depending on co-stress and recovery context**	Interaction signs are not universally additive or synergistic	Use factorial cross-stage designs and record recovery opportunity explicitly

The reconciliation in **Table 1** implies a multilevel architecture rather than a single stress-severity axis. **Figure 1** therefore separates temporal exposure structure, biological processing, the metamorphic boundary, and trait-specific post-metamorphic states while retaining uncertainty and evidence-status boundaries.

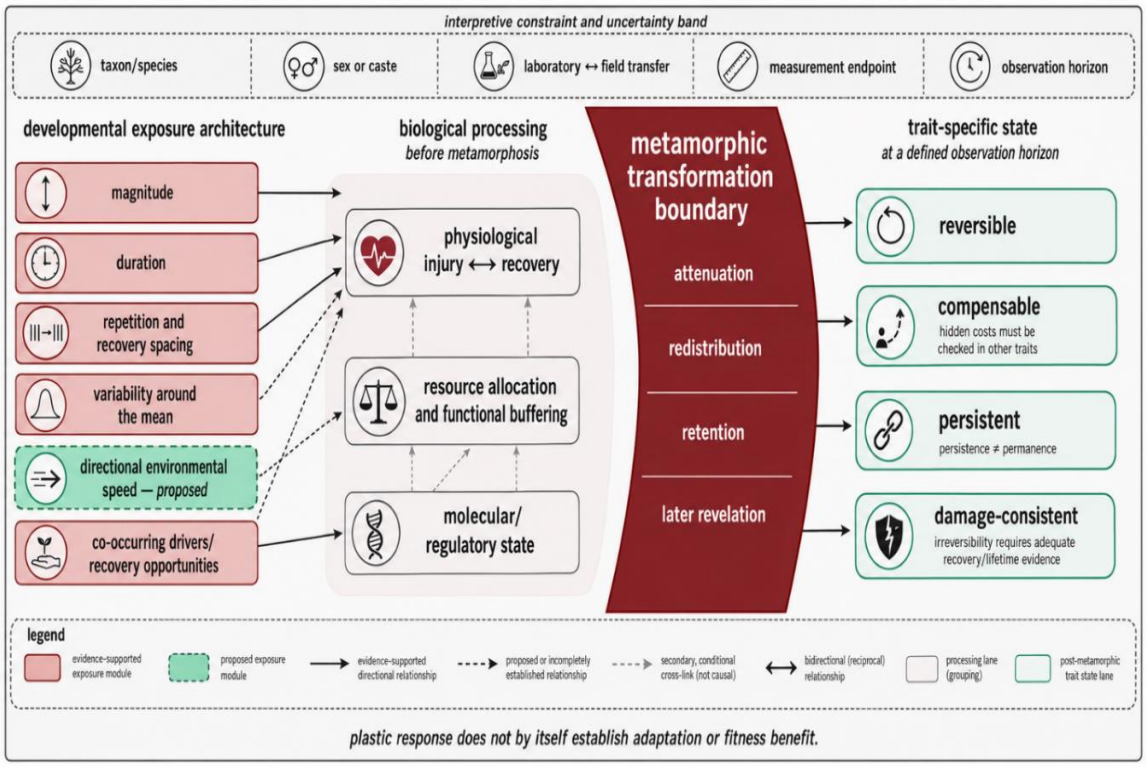


Figure 1. Environmental tempo reconciles divergent cross-metamorphic trajectories of recovery, compensation, persistence, and damage

Timing relative to metamorphosis

Temporal exposure architecture is incomplete without developmental position. Elevated temperature in the European corn borer produces reproductive consequences that depend on the developmental period experiencing warming [30]. This stage dependence means that chronological duration alone cannot identify biological exposure: the same number of hours can intersect tissue growth, terminal juvenile differentiation, pupal reorganization, or adult reproductive maturation.

Evidence also indicates that repeated heat exposure, life-stage identity, and interacting life cycles jointly alter thermal consequences [29-31]. In host–parasitoid systems, for example, a heat event may affect each partner differently because their vulnerable stages do not necessarily coincide. Developmental timing is therefore relational as well as organismal. A perturbation close to metamorphosis may also encounter a physiology unlike that of an earlier juvenile. Across ontogeny in Bicyclus anynana, heat resistance varies with developmental stage and body size, demonstrating that stage-specific structural and physiological constraints can bound thermal responses [32].

The framework therefore treats distance from metamorphosis as a proposed moderator rather than a universal scalar predictor. Proximity to metamorphosis could increase persistence when insufficient time remains for recovery before reorganization, decrease persistence when metamorphic remodeling removes the affected state, or reveal latent effects when developmental demands expose prior resource or tissue deficits. Which trajectory occurs should depend on the focal trait, tissue, driver, stage, and recovery opportunity. Direct comparative tests that manipulate the same exposure at graded distances from metamorphosis while following identical traits across the transition are still needed before any general distance function can be claimed.

Predictive persistence–compensation model

The proposed predictive persistence–compensation model treats the post-metamorphic state of a focal trait as conditional on four linked domains: the initial developmental displacement, temporal exposure architecture, developmental position relative to metamorphosis, and the biological capacity for recovery or reallocation. Ecological context modifies each domain. In Aedes albopictus, temperature changes the consequences of larval competition for later phenotype, demonstrating that carry-over cannot be predicted from one environmental driver independently of the conditions in which it operates [33].

Metamorphosis is represented as a transformation operator, not a binary reset. In the wood tiger moth Arctia plantaginis, pre-metamorphic responses do not map uniformly onto post-metamorphic phenotype, supporting partial decoupling between life stages [34]. The model therefore permits four broad transformations of an exposed–reference difference: attenuation, functional offset, retention, and damage-consistent retention. These correspond to reversible, compensable, persistent, and irreversible/damage-consistent classifications, but the mapping is performed separately for each trait. Multiple states can coexist within one individual.

Prediction must also be bounded by ecological transfer. Field heatwave effects on crop–pest dynamics depend on insect ontogeny and host-plant resistance, illustrating that developmental stage and biotic context can modify outcomes outside simplified thermal assays [35]. Consequently, the model does not assign fixed coefficients or universal transition probabilities. Instead, it generates qualitative, testable expectations. Persistence should become more plausible when exposure is prolonged or repeated without adequate recovery, when the affected trait survives metamorphic reorganization, or when latent costs are exposed by later developmental demands. Compensation should become more plausible when later cues or resource reallocation restore focal function, but only if correlated traits are measured sufficiently to exclude hidden costs. Reversibility requires demonstrated decline of the focal difference, and high-confidence irreversibility requires evidence extending beyond a convenient adult sampling point.

A further boundary concerns classification stability across observation horizons. A trajectory may move from apparent persistence to reversibility if recovery is slow, or from apparent compensation to damage-consistent persistence if later reproduction reveals a deferred cost. State assignment should therefore be revisable as follow-up extends rather than treated as a permanent label generated at first adult measurement. This temporal updating is a proposed feature of the framework and should be tested explicitly with repeated post-metamorphic measurements rather than inferred retrospectively from separate cohorts.

The model also separates prediction from mechanism. A persistent adult phenotype may be compatible with altered metabolic state, resource allocation, endocrine regulation, tissue injury, or molecular regulation, but phenomenological persistence does not identify which mechanism produced it. Conversely, molecular persistence does not establish organismal damage or adaptation. Validation should therefore combine longitudinal phenotype measurement with mechanism-specific assays rather than infer one level from another.

Prospective testing would require factorial manipulation of exposure intensity and temporal architecture at multiple developmental positions, repeated measurement after metamorphosis, and more than one organismal endpoint. Where feasible, sex, caste, population, and ecological context should be crossed with exposure rather than treated as residual variation. The model succeeds only if these inputs improve out-of-sample classification of trait trajectories relative to simpler alternatives; no such predictive performance is claimed here.

The proposed framework changes the unit of interpretation from “the insect” to a trait-specific developmental trajectory. This resolves an otherwise recurrent contradiction: the same developmental exposure can apparently be reversible, beneficial, persistent, and damaging depending on which adult endpoint is examined. Ladybird thermal traits can recover while immunity or fecundity remains altered [11], and developmental warming can raise mosquito heat tolerance while reducing fertility [23]. These are not mutually exclusive study outcomes. They are evidence that organism-wide labels obscure the multivariate structure of cross-stage response.

A second implication is that compensation should not be inferred from restored morphology, tolerance, or survival alone. Nutritional history can redistribute growth and immune investment [16], and alternative body-size proxies can relate differently to adult longevity [17]. The practical consequence is methodological: cross-stage studies need endpoint panels chosen to detect hidden costs, not merely repeated measurements of the easiest trait. Reproductive performance, immunity, behavior, metabolism, and ecological function may reveal costs that gross survival or size does not.

Environmental temporal structure provides a third source of reconciliation. Duration alters reproductive and lethal limits [27], repetition interacts with exposed stage [29], and broad evidence does not support a simple assumption that fluctuation is always more consequential than a constant environment of equivalent mean [18]. “Rapid environmental change” should therefore not be operationalized solely as an extreme endpoint. Rate, duration, repetition, recovery spacing, and predictability describe different biological challenges and may push the same trait toward different state trajectories.

Metamorphosis itself should likewise be interpreted neither as an impermeable boundary nor as passive continuity. Persistent behavioral and metabolic effects after larval stress [19], amplification of combined stress after metamorphosis [21], and partial pre-/post-metamorphic decoupling [34] collectively support a transformation

view. The mechanisms behind those transformations, however, are unlikely to be uniform across tissues or taxa. Molecular marks, endocrine regulation, energetic state, structural injury, and ecological carry-over require independent evidence rather than being collapsed into a single developmental-memory mechanism.

Several boundaries limit generalization. Much of the direct evidence comes from Diptera, Lepidoptera, Coleoptera, Hymenoptera, and Odonata, with individual studies often centered on one species, laboratory population, sex, or caste. Population-specific thermal responses in Aedes albopictus [6] and caste- and sex-dependent responses in stingless bees [20] demonstrate that heterogeneity exists even before comparisons among orders. Laboratory thermal exposures can also miss biotic context that alters field outcomes [35]. The framework is therefore intended as an organizing hypothesis for comparative testing, not a universal insect rule.

The proposed distinction between persistence and irreversibility is particularly important. A significant adult difference establishes persistence only for the interval observed. Irreversibility requires either adequately demonstrated failure of recovery, lifetime persistence, or a nonrecoverable functional loss under the conditions studied. Phenology-dependent lifetime pesticide effects [24] provide stronger evidence than a single adult snapshot, yet even lifetime consequences can remain conditional on developmental context. This calibrated terminology prevents strong mechanistic conclusions from being built on insufficient temporal sampling.

Validation should focus on longitudinal, multivariate, cross-stage experiments. The same focal traits should be measured before metamorphosis, soon after emergence, and following defined recovery intervals; exposure magnitude and temporal structure should be manipulated independently; and developmental position should be varied without changing the outcome definition. Mechanistic assays should be linked to those trajectories rather than substituted for them. Field or semifield replication is needed where ecological interactions plausibly alter state transitions. Such designs would test whether the proposed categories improve explanation and prediction, where boundaries between them are continuous, and whether the same trajectory rules recur across distantly related insect lineages.

Conclusion

Rapid environmental change does not leave a single cross-metamorphic signature. Developmental effects can fade, be functionally offset, persist, or remain damage-consistent, and these states can coexist among traits within the same individual. The proposed framework therefore classifies a focal phenotype at a defined developmental exposure and observation horizon rather than assigning recovery or damage to the organism globally. Environmental tempo and timing relative to metamorphosis supply complementary axes for explaining why similar exposure magnitudes produce different later outcomes. Metamorphosis is treated as a transformation boundary capable of attenuation, redistribution, retention, or revelation of prior effects. The framework remains a testable synthesis rather than a validated predictive mechanism, and its transfer across taxa, sexes, ecological settings, and biological levels requires longitudinal multivariate evidence.

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