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Stage-Specific Vulnerability, Carry-Over Effects, and Recovery Across Insect Life Cycles Exposed to Thermal Extremes

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ABSTRACT

Thermal extremes can affect insects at any developmental stage, but vulnerability is often inferred from a single exposure period, endpoint, or observation time. Such inference is problematic because mortality, developmental disruption, reproductive impairment, physiological injury, carry-over effects, and post-stress recovery can have different thermal sensitivities. This systematic review evaluates evidence published from 2017–2025 on stage-specific responses of insects to extreme or stressful heat and cold, with particular attention to whether effects remain confined to the exposed stage, persist into later stages, or change during recovery and repeated exposure. Across the evidence base, no developmental stage emerges as universally most vulnerable. Instead, apparent vulnerability depends jointly on thermal intensity, duration, fluctuation or repetition, the biological endpoint measured, developmental timing, sex, genotype or population, and environmental context. Embryonic and juvenile exposures can produce delayed consequences after metamorphosis, whereas pupal exposures may generate adult traits with contrasting reversibility. Adults frequently show reproductive effects at thermal exposures that do not cause equivalent mortality, and repeated events can produce cumulative rather than compensatory responses. Cold acclimation and post-heat recovery further demonstrate that tolerance measured immediately after stress is not equivalent to long-term restoration of performance. We therefore propose that insect thermal vulnerability should be interpreted as a stage–exposure–response–time problem rather than as a fixed property of a life stage. This framework preserves distinctions among immediate injury, cross-stage carry-over, recovery, and repeated-exposure history while identifying major taxonomic, laboratory-to-field, and mechanistic limitations in the current evidence.

Keywords: Thermal extremes, Life-stage vulnerability, Carry-over effects, Thermal recovery, Developmental plasticity, Insect reproduction

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Introduction

Thermal vulnerability in insects is frequently summarized through upper or lower thermal limits, survival after acute exposure, or performance measured within one developmental stage. These metrics are useful but incomplete because thermal responses vary ontogenetically and because plastic changes in critical thermal limits are generally modest rather than uniformly protective across taxa and stages [1]. Experimental and comparative evidence further indicates that apparent vulnerability depends on the endpoint used, the developmental stage exposed, and the temporal structure of the thermal event [2–4]. Consequently, a stage that survives an extreme exposure cannot automatically be classified as resistant if development, reproduction, or later-life performance is impaired.

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This distinction becomes especially important when thermal injury is expressed after the original exposure has ended. Developmental warming can reduce juvenile survival while simultaneously altering adult reproductive performance, producing demographic components that differ in both timing and direction [5]. Thermal exposure is also not determined solely by ambient temperature. Microhabitat structure can substantially modify insect activity and realized heat stress [6], while experimental heatwaves can produce stage-dependent fertility impairment whose recovery depends on both the exposed stage and the time elapsed after stress [7]. These observations make a simple ranking of eggs, juveniles, pupae, and adults biologically inadequate.

Stage specificity also extends below the whole-organism level. Larval and adult *Drosophila melanogaster* exposed to cold can show distinct transcriptional and functionally relevant responses [8]. Molecular divergence, however, does not by itself establish that one stage is more evolutionarily adapted, nor does expression change demonstrate improved fitness. The inferential problem is therefore multilevel: thermal extremes can alter survival, development, reproduction, physiology, behavior, and molecular state, but these effects need not be concordant.

This review addresses that problem by organizing evidence around three linked questions. First, which life stages show direct vulnerability during extreme or stressful thermal exposure? Second, when does an effect persist, disappear, reverse, or re-emerge after development proceeds to another stage? Third, how should recovery be interpreted when different traits normalize at different rates or when subsequent thermal exposures occur before restoration is complete? The central contribution is an evidence-bounded synthesis in which thermal vulnerability is treated as conditional on exposed stage, exposure profile, response domain, and observation horizon. The synthesis does not assume a universally most vulnerable stage, equate acclimation with adaptation, or treat laboratory tolerance as a direct proxy for field persistence.

Materials and Methods

The review was organized in accordance with PRISMA reporting principles [9]. The approved search record specified a search date of 25 August 2026 and combined insect, thermal-extreme, developmental-stage, carry-over, recovery, survival, development, fertility, and performance terms. The core logic combined insect or taxonomic identifiers with terms including “heat wave,” “heat stress,” “extreme heat,” “cold stress,” “cold shock,” “cold acclimation,” “winter warming,” egg, embryo, larva, nymph, juvenile, pupa, adult, carry-over, recovery, repeated exposure, mortality, development, fecundity, reproduction, performance, and thermal tolerance. Supplementary bibliographic verification used DOI and publisher records.

Eligibility was restricted to peer-reviewed journal articles published from 2017 through 2025 that provided directly interpretable evidence relevant to thermal exposure and at least one developmental, physiological, reproductive, behavioral, survival, or cross-stage outcome in insects. Studies were retained when the exposed life stage could be identified and when the thermal treatment or environmental contrast was sufficiently explicit to distinguish the exposure from an unspecified background-temperature effect. Developmental-temperature experiments were interpreted conservatively: a temperature treatment was not automatically described as a climatic extreme when the original study instead addressed developmental plasticity, thermal reaction norms, or chronic warming.

Life stages were coded as embryo or egg, juvenile, pupa, or adult. “Juvenile” included larval and nymphal stages because complete and incomplete metamorphosis do not share a homologous pupal state. Pupal evidence was therefore treated as specific to holometabolous insects rather than as a universal developmental category. Sex was retained where reported because male and female reproductive responses can differ markedly under thermal stress.

Exposure classification preserved thermal intensity, duration, temporal fluctuation, repetition, and developmental timing as separate dimensions. This avoided treating a short acute heat pulse, a multiday heatwave, chronic developmental warming, cold acclimation, and anomalous winter warming as interchangeable thermal doses. Outcomes were classified separately as survival or mortality, development, reproduction, behavior or activity, physiological performance, and molecular response. Cross-stage carry-over required an outcome measured after development had proceeded beyond the originally exposed stage. Recovery required an explicit post-exposure observation period or repeated measurement rather than survival alone.

Quality interpretation emphasized whether exposure conditions, developmental stage, comparator, endpoint, timing, and relevant environmental context were recoverable from the study. No numerical certainty score was constructed because heterogeneous experimental designs do not justify a common quantitative quality scale.

Particular attention was given to laboratory-to-field transfer, taxonomic concentration, unmeasured interacting stressors, and the distinction between molecular association and organismal consequence.

The retained review record did not preserve an auditable source-by-source export, deduplication history, or screening arithmetic. Numerical identification, exclusion, and inclusion counts therefore cannot be reported without fabrication. For the same reason, no review-flow numbers are introduced in the text or exhibits below.

Results and Discussion

Embryonic exposure can influence both immediate survival and later performance, but its consequences depend strongly on seasonal and developmental context. In diapausing *Aedes albopictus*, altered fall duration and winter heatwave exposure produced carry-over effects that extended beyond overwinter survival into post-diapause performance [10]. Importantly, the direction of response was not reducible to a single "warming is harmful" interpretation: a thermal episode could affect immediate survival and later performance differently, showing that embryonic vulnerability during dormancy is temporally structured.

Direct developmental heat exposure likewise provides evidence that embryonic injury can remain detectable after the exposed stage has ended. In *Bicyclus anynana*, heat stress during the egg stage reduced subsequent performance, demonstrating that metamorphosis does not necessarily erase an early thermal history [11]. This result supports the existence of embryonic carry-over but does not establish that all egg-stage heat exposure produces persistent adult damage; persistence depends on the trait and experimental regime measured.

Cold exposure further shows that stage ranking is contingent on the physiological endpoint. In *Acanthoscelides obtectus*, cold tolerance differed among eggs, larval stages, pupae, and adults, while cold acclimation improved survival under tested conditions without eliminating stage differences [12]. Supercooling-point responses did not fully mirror survival responses, illustrating why one physiological measurement cannot substitute automatically for organismal cold tolerance.

Multistage heat experiments in *Ophraella communa* similarly showed that short high-temperature exposure affected life-history traits differently among developmental stages [13]. The resulting evidence supports stage dependence but not a fixed ordering that can be transferred across species. Taken together, embryonic studies show three analytically distinct possibilities: direct mortality during exposure, delayed impairment after development proceeds, and context-dependent modification through diapause or acclimation. These forms of vulnerability should not be collapsed into a single egg-stage thermal limit.

Juveniles

Juvenile stages often dominate discussions of thermal vulnerability because larvae and nymphs are actively growing, acquiring resources, and constructing tissues that later stages inherit. Yet juvenile responses vary substantially with exposure intensity, ontogenetic timing, resource environment, and the outcome observed.

In the solitary bee *Osmia lignaria*, high-intensity heatwaves increased larval mortality and delayed development, whereas lower-intensity exposure produced weaker effects; heatwave duration did not explain mortality as strongly as temperature intensity in that design [14]. The result demonstrates that duration and intensity should remain separate descriptors rather than being combined into an undifferentiated measure of "heat exposure."

Field evidence adds an ontogenetic dimension. Experimental heatwaves imposed on Colorado potato beetles affected survival and development most strongly when exposure occurred during the neonate stage, whereas later-stage heatwaves produced limited detectable effects in the same system [15]. Host-plant resistance also modified responses, meaning that the apparent juvenile thermal phenotype was partly embedded in the plant environment rather than being an autonomous insect trait. This finding argues against transferring laboratory temperature thresholds directly to crop systems without accounting for host context.

Population origin can further change the consequences of developmental temperature. In *Aedes albopictus*, developmental thermal regimes altered juvenile viability, development, adult body size, energetic traits, longevity, and gene expression in population-specific ways, while not every adult thermal-response trait changed significantly [16]. The study therefore supports developmental plasticity and population heterogeneity but not the stronger conclusion that exposure to a particular developmental temperature constitutes a universally adaptive response to climatic extremes.

Nutrition is another major modifier. Larval temperature and diet jointly influenced development and adult traits in *A. albopictus*, and commonly used body-size proxies did not produce equivalent inferences about later

longevity [17]. This matters for thermal carry-over studies because an apparently temperature-mediated adult outcome may also reflect altered resource acquisition during juvenile growth. The direction of the downstream effect can consequently depend on which morphological proxy or pathway is measured.

Reproduction provides one of the clearest examples of delayed juvenile vulnerability. Developmental heat stress in *Drosophila suzukii* reduced later adult fertility and altered reproductive characteristics, with important differences between male and female responses [18]. Such effects show why adult reproductive performance should be retained even when the research question begins with juvenile thermal exposure. Conversely, later outcomes need not always be negative. Multistressor experiments in *Ischnura elegans* showed that warming effects depended on predator context and population, with cross-stage consequences changing according to the environmental combination experienced [19]. Thermal exposure therefore cannot always be interpreted independently of concurrent ecological stressors.

Finally, the temporal variance of temperature can matter alongside its mean. In *Spodoptera frugiperda*, temperature fluctuations interacted with mean temperature to influence life-history traits [20]. A constant laboratory treatment and a fluctuating regime with a similar mean may therefore produce biologically different juvenile histories.

These studies resolve a question that prose alone obscures: juvenile vulnerability is not one response but a set of context-dependent states linking the exposure regime to immediate development and later performance. The principal distinctions are summarized in **Table 1.**

Table 1. Juvenile thermal vulnerability depends on how exposure context is translated into developmental and later-life outcomes

Uncertainty within its limit	Juvenile evidence state	Taxonomic with observed basis
Species-specific larval physiology; mortality response did not establish a universal duration effect **Thermal intensity and duration should remain separately coded**	Heatwave-intensity state	Solitary-bee larvae under diel heatwave treatments Mortality and development time High-intensity exposure increased mortality and delayed development more clearly than lower-intensity exposure
Crop host altered responses; one field system **Ontogenetic timing and host environment jointly define realized juvenile vulnerability**	Early-ontogeny field state	Neonate and later Colorado potato beetle stages on contrasting host plants Survival, growth, development, later survival Earlier juvenile exposure produced stronger detectable effects than later-stage exposure
Not every developmental treatment represents an extreme event; several adult traits were unchanged **Population identity should be retained instead of averaging developmental responses**	Population-dependent developmental state	Mosquito populations reared across developmental temperatures Viability, development, adult morphology, longevity, reserves, molecular response Developmental temperature affected multiple later traits, with population-specific patterns
Resource limitation confounds temperature-only interpretations **Juvenile thermal carry-over should be separated from nutritional mediation**	Resource-mediated carry-over state	Mosquito larvae differing in diet and temperature Development, pupal mass, wing size, adult longevity, immune-associated traits Temperature and diet jointly shaped juvenile and adult outcomes; size proxies were not interchangeable
Laboratory pest model; reproductive endpoints differed **Survival through development does not establish adult functional recovery**	Reproductive carry-over state	Juvenile drosophilids exposed to developmental heat Adult fertility and reproductive condition Juvenile heat produced later reproductive impairment, with sex-dependent expression
Thermal effect cannot be isolated from the ecological interaction **Context-sensitive carry-over should be preserved rather than averaged**	Multi-stressor state	Damselfly populations exposed to warming and predator context Survival, development, emergence phenotype Warming effects changed with population and predator treatment

Single-species laboratory setting **Thermal variance is an exposure dimension, not measurement noise**	Fluctuating-temperature state	Lepidopteran pest exposed to different thermal means and amplitudes Life-history traits across development Mean temperature and fluctuation interacted

Note: "Synthesis consequence" denotes an interpretation constructed in this review from the reported evidence; it is not an experimentally validated universal rule.

Pupae

Pupae occupy a distinctive position in holometabolous insects because the exposure occurs during extensive tissue remodeling while the measured consequences may appear only after adult emergence. The evidence does not support treating this stage as either a complete physiological reset or an inevitably fragile bottleneck.

In *Harmonia axyridis*, pupal temperature altered adult thermal performance, immune-related traits, and fecundity, but the persistence of these effects differed among response domains [21]. Some thermal-performance effects were reversible after emergence, whereas immune and reproductive consequences showed greater persistence. Recovery of one adult trait therefore cannot be used as evidence that the organism has returned globally to its pre-exposure state.

Male reproductive development provides another example of unequal carry-over. Developmental heat stress in *D. melanogaster* disrupted spermatogenesis and reduced fertility, with sensitivity and subsequent recovery depending on when exposure occurred [22]. This supports the existence of developmental windows of reproductive vulnerability without implying that every heat exposure causes permanent sterility.

Thermal history can also modify later tolerance rather than simply reduce performance. In *Tenebrio molitor*, pupal developmental temperature and adult acclimation temperature influenced subsequent heat and cold tolerance [23]. Not all cold-tolerance outcomes responded identically to pupal history, emphasizing that conditioning effects remain endpoint dependent. Acclimation in this context should be interpreted as phenotypic plasticity rather than evidence of evolutionary adaptation.

At more severe temperatures, survival through metamorphosis itself becomes vulnerable. In *Tuta absoluta*, high-temperature exposure at egg and pupal stages reduced hatching or adult emergence and could shorten adult longevity among individuals that survived development [24]. This illustrates the distinction between direct stage mortality and latent cost among survivors.

Mild stress may produce still another pattern. In geographically distinct populations of *Grapholita molesta*, sublethal pupal heat reduced adult fecundity while increasing adult heat resistance or longevity in some comparisons [25]. Such mixed responses should not be summarized as either beneficial acclimation or simple damage because the sign of the effect depends on the adult trait used to define performance.

Across these pupal studies, three response classes therefore coexist: persistent impairment, reversible adult change, and cross-domain trade-offs. This stage is particularly informative because metamorphic survival can conceal functional damage that becomes visible only after adult emergence.

Adults

Adult thermal vulnerability is especially difficult to infer from survival because reproduction, gamete function, metabolic state, and realized field exposure may respond at temperatures that leave adults alive. In *Drosophila melanogaster*, reproductive responses to heat differed between sexes and among developmental windows affecting gametogenesis [26]. Male reproductive function was particularly sensitive in the tested system, but this does not establish a universal male-biased response across insects.

The importance of exposure history becomes clearer when stress is repeated. Stage-specific and cumulative heat treatments in *D. melanogaster* produced reproductive outcomes whose magnitude depended on sex and on when thermal stress occurred [27]. Adult exposure therefore cannot always be interpreted independently of developmental history.

Direct gamete-mediated consequences have also been demonstrated. Experimental heatwaves in *Tribolium castaneum* impaired sperm function and reproductive success and produced effects detectable in descendants [28]. These results establish intergenerational consequences in that experimental system but do not justify a universal epigenetic or transgenerational mechanism.

Taxonomic variation further limits generalization. Simulated heatwaves altered reproductive traits in model bumblebees, but responses differed among species [29]. At another ecological extreme, repeated heat exposure in the sub-Antarctic fly *Anatalanta aptera* reduced reproductive success even though broad metabolomic

separation among treatments was comparatively weak [30]. Organismal impairment therefore need not be accompanied by an equally conspicuous global molecular signature.

Field exposure adds another boundary. Foraging *Bombus impatiens* carrying larger pollen loads attained higher thoracic temperatures under natural conditions [31]. Such data demonstrate that workload can alter realized thermal exposure, but they do not independently establish downstream reproductive or population effects. Conversely, adult reproductive impairment can sometimes recover over extended periods: *Monochamus alternatus* regained reproductive function during post-heat observation, alongside changes involving heat-shock-associated proteins [32]. The molecular associations are compatible with recovery mechanisms but do not demonstrate that a single HSP pathway causes the recovered phenotype.

The adult evidence is therefore best interpreted as a coverage-and-gap problem rather than as a single adult tolerance threshold. **Table 2** distinguishes the response domains for which adult thermal vulnerability is directly observable from those for which inference remains conditional.

Table 2. Adult thermal vulnerability is resolved differently by reproductive, molecular, and realized-exposure evidence

Boundary and decisive check	Observable basis and warranted reading	Adult evidence pattern linked with biological context
One taxon cannot define an insect-wide sex ranking	Fertility, spermatogenesis, oogenesis	Sex- and gametogenesis-dependent sensitivity
Compare homologous reproductive endpoints across orders	Reproductive vulnerability depends on sex and developmental timing	Adult and developing reproductive systems
Exposure episodes cannot always be treated as independent	Fertility and reproductive performance	Cumulative thermal-history response
Use sequential rather than single-event experiments	Present adult state partly reflects earlier exposure history	Adults with prior developmental or repeated heat exposure
Mechanism and persistence across generations remain taxon specific	Sperm function, reproductive success, offspring response	Gamete-mediated descendant effect
Separate direct gamete injury from heritable mechanisms	Adult heat can extend biological consequences beyond the exposed individual	Heat-exposed adult males
Laboratory heatwaves may not reproduce nest or field microclimates	Reproductive traits under simulated heatwaves	Species-specific pollinator response
Couple reproductive assays with realized body temperature	Closely related taxa need not share a reproductive threshold	Adult bumblebees
Absence of a broad molecular signature is not evidence of absent mechanism	Reproductive output and metabolomic profile	Cross-level discordance
Link targeted physiology to functional outcomes	Organismal impairment may occur without strong global molecular separation	Adult sub-Antarctic fly
Worker temperature does not establish colony-level consequence	Thoracic temperature and pollen load	Realized-exposure modification
Integrate microclimate, workload, and downstream fitness traits	Behavioral workload can raise experienced heat load	Foraging worker bumblebees
Molecular association does not prove causal recovery pathway	Reproductive recovery and protein associations	Long-horizon recovery
Measure repeated recovery trajectories and functional restoration	Adult fertility can improve after exposure	Heat-exposed adult beetles

Cross-stage carry-over

Carry-over is most informative when the phenotype measured after thermal exposure cannot be explained solely by the condition of the currently observed stage. Repeated juvenile and adult heat exposure in male *D. melanogaster* produced cumulative fertility impairment, and some outcomes remained depressed or became more evident during the nominal recovery period [33]. Thus, elapsed time after exposure should not automatically be interpreted as recovery.

In *Culex pipiens pallens*, sporadic extreme heat imposed during larval or adult stages produced stage- and sex-dependent responses, while larval exposure could influence subsequent adult male reproductive performance [34]. The authors' terminology concerning thermal adaptation should not be interpreted as evidence of evolutionary adaptation; the experiment directly establishes phenotypic response and carry-over under the tested thermal histories.

Genetic background can further modify cross-stage effects. Developmental thermal reaction norms across *D. melanogaster* genotypes were associated with later adult reproductive outcomes and genetic variation [35]. These data demonstrate genotype-dependent developmental plasticity but do not prove that candidate loci constitute adaptations to natural thermal extremes.

Across the broader evidence set, early thermal histories can remain detectable after the exposed stage has ended [10, 11, 15]. Persistence, however, should not be assumed whenever an early exposure occurred. The review therefore distinguishes cross-stage carry-over from simple sequential measurement: a later phenotype qualifies as carry-over only when the study design links it to an earlier exposure while preserving plausible alternative influences such as nutrition, population origin, sex, or subsequent thermal experience.

Table 3 adjudicates the principal interpretations that can otherwise be conflated under the term carry-over.

Table 3. Cross-stage thermal carry-over requires distinguishing persistence, accumulation, trade-off, and context dependence

Biological context	Evidential basis linked with test needed to strengthen inference	Interpretation within its limit
	Persistent delayed impairment ***Evidence-supported category***	
Early-stage exposure followed by reduced later performance	Later fertility, survival, development, or adult function Repeated measurements through the intervening transition	Earlier thermal history remains biologically detectable Later environment may modify expression
	Cumulative sequential impairment ***Evidence-supported category***	
Thermal stress experienced in more than one stage	Stronger or persistent reproductive loss after repeated exposure Compare single-stage and combined-stage treatments	Thermal history can accumulate rather than reset Non-additive interactions cannot be inferred without factorial designs
	Cross-domain trade-off ***Evidence-supported category***	
Surviving insects show opposite directions among adult traits	Greater tolerance or longevity with lower fecundity, or reversible and persistent traits together Measure multiple adult performance domains simultaneously	Carry-over need not have one net sign Net fitness consequence remains unresolved
	Context-modified carry-over ***Evidence-supported category***	
Temperature interacts with diet, host, predator context, population, or genotype	Direction or magnitude differs among contexts Factorial manipulation of thermal and contextual variables	Carry-over is conditional rather than fixed Modifier may be causal, correlated, or stage specific
	Apparent reset ***Proposed interpretive state***	
No later effect detected after an earlier exposure	Later measured endpoint returns toward control state Longitudinal multi-domain recovery assay	Lack of persistence is possible for that endpoint Unmeasured domains may remain altered

Recovery and repeated exposure

Recovery should be treated as a trajectory rather than as a binary label. Experimental studies show that post-stress responses can diverge among traits: mortality, fertility, thermal performance, immunity, and reproduction do not necessarily normalize on the same schedule [7, 21, 33]. Consequently, an insect that survives and restores one functional endpoint cannot automatically be described as fully recovered.

Cold exposure adds an important counterpoint to the predominantly heat-centered evidence. In *Plodia interpunctella*, cold acclimation altered supercooling-related physiology, antioxidant responses, development, and reproduction in stage-dependent ways [36]. These changes demonstrate acclimatory plasticity under the tested conditions; they do not establish that pre-exposure to cold is universally beneficial or evolutionarily adaptive.

Timing within seasonal dormancy also determines later effects. Simulated winter warming in diapausing *Choristoneura fumiferana* produced outcomes that depended on when warming occurred, with later survival not necessarily mirrored by immediate performance measures [37]. Thermal history therefore contains temporal information that cannot be represented adequately by maximum temperature alone.

Repeated heat experiments provide an analogous principle. A second exposure can arrive before reproductive or physiological restoration is complete, so the response to that event may depend on residual effects from the first. In some experiments the resulting phenotype is cumulative damage; in others, prior exposure is associated with altered subsequent tolerance. These alternatives should remain analytically separate unless the experimental design directly distinguishes conditioning from injury.

The synthesis developed here therefore uses four temporal states: acute response, post-exposure recovery, persistent carry-over, and re-exposure before or after recovery. These states are proposed organizational categories rather than experimentally validated universal phases. They separate what was measured from what would otherwise be inferred about restoration.

This distinction is sufficiently multidimensional that prose alone obscures the temporal logic. **Figure 1** therefore represents recovery as several parallel biological trajectories rather than a single arrow returning an insect to baseline.

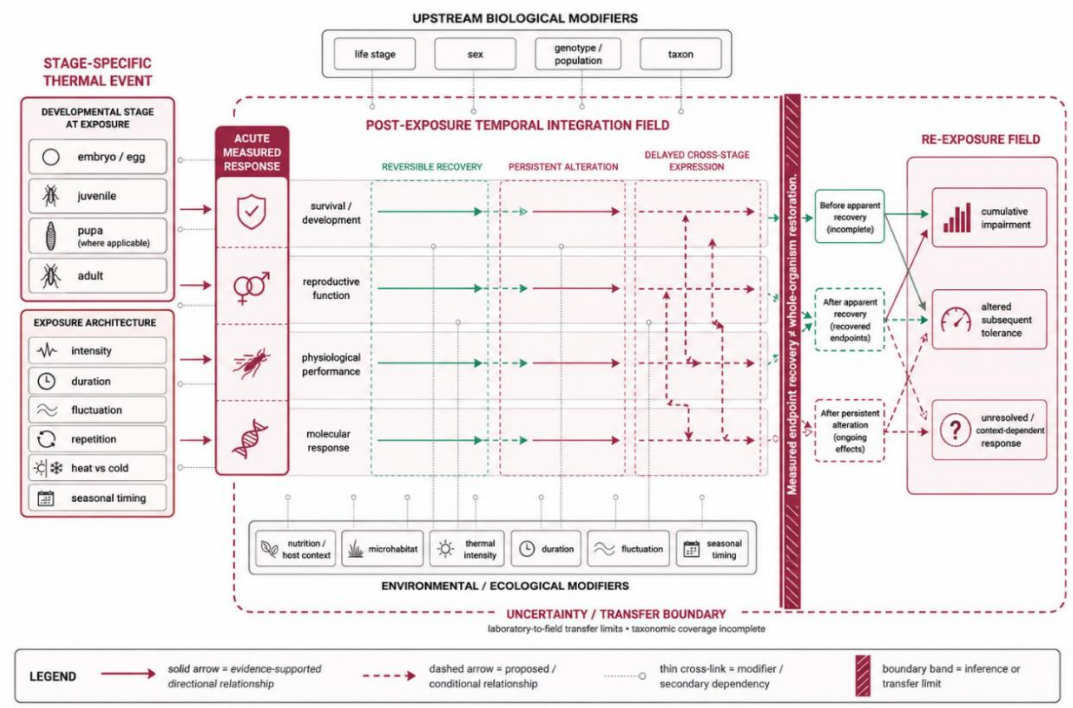


Figure 1. Thermal-history integration separates reversible recovery, persistent carry-over, and cumulative re-exposure across insect life stages

Stage-specific vulnerability synthesis

Across the evidence base, developmental stage is an important determinant of thermal outcome, but it is not an adequate stand-alone definition of vulnerability. Embryonic exposure can persist into later life; juveniles can experience strong mortality, developmental delay, or reproductive carry-over; pupal stress can yield reversible and persistent adult phenotypes; and adults can retain high survival while reproductive function deteriorates. Cold acclimation and winter warming add further evidence that direction and persistence depend on timing and measured domain.

The synthesis therefore rejects a universal ordinal ranking of embryo, juvenile, pupa, and adult. Instead, this review proposes a stage–exposure–response–time interpretation. "Stage" identifies the developmental state exposed. "Exposure" retains intensity, duration, variability, repetition, and seasonal timing. "Response" identifies whether the endpoint is survival, development, reproduction, physiology, behavior, or molecular state. "Time" specifies whether the observation is immediate, post-exposure, after metamorphosis, or following re-exposure. Under this scheme, vulnerability is strongest only relative to a specified combination of those dimensions. A stage may be resistant when judged by acute mortality but vulnerable when judged by later fertility. Likewise, a transient molecular or thermal-performance response may recover while reproductive or immune consequences persist. **Table 4** records these distinct states without converting them into an unsupported vulnerability score.

Table 4. A stage–exposure–response–time ledger prevents incompatible thermal outcomes from being ranked as one vulnerability metric

Interpretation within its limit	Biological basis with observed basis	Required next test
Acute stage failure ***Evidence-supported***		
Direct vulnerability of the exposed stage under the tested regime **Does not establish delayed effects among survivors**	Exposure produces mortality or immediate developmental disruption Survival, emergence, development	Follow survivors into subsequent stages
Surviving but functionally impaired ***Evidence-supported***		
Survival-based tolerance underestimates functional vulnerability **Functional impairment may or may not alter population dynamics**	Mortality is limited but reproduction or performance declines Fertility, fecundity, gamete function, activity	Couple survival with reproductive and performance endpoints
Delayed cross-stage vulnerability ***Evidence-supported***		
Thermal history persists beyond the exposed stage **Later environment and resource history can modify expression**	Earlier exposure is associated with a later phenotype Adult reproduction, longevity, emergence, performance	Longitudinal factorial experiments
Trait-specific recovery ***Evidence-supported***		
Recovery is domain specific **Return of one trait is not whole-organism restoration**	One endpoint returns toward control while another remains altered Thermal performance, immunity, reproduction, physiology	Repeated multi-domain measurements
Cumulative thermal-history state ***Evidence-supported***		
Re-exposure may interact with unresolved earlier effects **Conditioning and accumulated injury require experimental separation**	Repeated or sequential exposure changes later response Fertility, survival, physiological tolerance	Single-event versus repeated-event factorial design
Context-conditioned vulnerability ***Evidence-supported***		
Stage ranking is conditional **Modifier may operate at exposure or response stage**	Stage effect changes with host, diet, predator, population, genotype, sex, or microhabitat Heterogeneous response across contexts	Explicit moderator manipulation
Stage–exposure–response–time state ***Proposed synthesis***		
Vulnerability is defined relative to developmental state, exposure architecture, endpoint, and observation horizon **Not a validated predictive score**	Multiple dimensions interpreted jointly Combination of the above	Prospective cross-taxon testing

The reviewed evidence indicates that the central question is not simply which insect life stage is most thermally vulnerable. Such a ranking changes when mortality is replaced by development, fertility, adult performance, physiological function, or delayed carry-over as the criterion. Exposure duration and thermal variability further change the apparent boundary, and interactions with host quality, nutrition, predators, microhabitat, sex, genotype, and population can alter both direction and magnitude.

Reproductive endpoints are particularly important because they can reveal damage at thermal exposures that produce comparatively little mortality. This does not mean reproduction is universally the most temperature-sensitive trait; rather, it demonstrates why survival alone is insufficient for evaluating biological consequences. Similarly, delayed adult impairment after egg, larval, or pupal exposure establishes that successful metamorphosis does not necessarily erase developmental thermal history.

The opposite overinterpretation must also be avoided. Carry-over is not inevitable. Some traits recover, some appear unchanged, and prior exposure can occasionally be associated with increased later thermal tolerance. Such responses should not automatically be called beneficial adaptation. Acclimation, developmental plasticity, conditioning, injury, selection, and evolutionary adaptation require different evidential standards.

A second major limitation concerns biological scale. Transcriptomic, proteomic, antioxidant, and metabolomic studies identify response pathways or candidate mechanisms, but molecular responses do not substitute for organismal performance. The reverse is also true: absence of a broad molecular signature does not show that a functional effect lacks a mechanism. Stronger future designs should connect molecular measurements to specific tissues and functional endpoints over the same post-exposure trajectory.

Laboratory-to-field transfer remains another important boundary. Controlled experiments establish stage-specific causal responses to defined thermal treatments more readily than field studies, but natural insects experience body temperatures shaped by microhabitat, host plants, workload, behavior, seasonality, and thermal fluctuation. Combining controlled stage-specific experiments with measurements of realized field temperature is therefore necessary before laboratory thresholds are interpreted as ecological limits.

Taxonomic coverage also constrains generalization. Mechanistic and recovery evidence is concentrated in a relatively small collection of drosophilids, mosquitoes, stored-product beetles, crop pests, and pollinators. Hemimetabolous insects, tropical field populations, cold-adapted taxa, and species with unusual diapause or developmental schedules remain less consistently represented. A universal stage ranking would therefore risk converting sampling structure into biological generality.

The proposed stage–exposure–response–time interpretation offers a way to preserve this heterogeneity without abandoning synthesis. It predicts neither a fixed vulnerable stage nor a universal recovery trajectory. Instead, it specifies what must be measured before such claims are made: the stage experiencing the event, the temporal architecture of exposure, the biological domain assessed, and the observation horizon. Prospective validation should expose multiple stages of the same species to comparable thermal histories, follow survivors across metamorphosis, measure several functional domains, and repeat the design across contrasting taxa and realistic microclimates.

Conclusion

Thermal vulnerability across insect life cycles is not a fixed property of embryos, juveniles, pupae, or adults. It emerges from the interaction between developmental state, exposure architecture, biological endpoint, and the time at which consequences are measured. Early-life thermal effects can persist after metamorphosis, adult reproduction can fail despite survival, recovery can differ among traits, and repeated exposure can accumulate before restoration is complete. The proposed stage–exposure–response–time synthesis therefore provides an evidence-bounded way to distinguish acute injury, carry-over, recovery, and re-exposure without implying a universal stage ranking. Its broader validity will depend on longitudinal, multi-endpoint, taxonomically broader experiments conducted under thermal regimes that better represent realized field exposure.

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