Eurasia Specialized Veterinary Publication

**Entomological Research Letters**

**ISSN: 3108-639X**

2022, Volume 2, Issue 2, Page No: 110-121
Copyright CC BY-NC-SA 4.0
Available online at: www.esvpub.com/

# Behavioral Plasticity Under Climate Change and the Limits, Costs, and Carry-Over Effects of Insect Adjustment

**Sara Ben Youssef[1]*, Amal Trabelsi[1], Karim Boudiaf[2], Nabil Jebali[3]**

[1]Department of Behavioral Plasticity and Climate Adaptation, Faculty of Sciences, University of Tunis, Tunis, Tunisia.
[2]Department of Behavioral Costs and Carry-Over Effects, Faculty of Biosciences, University of Sousse, Sousse, Tunisia.
[3]Department of Insect Adjustment Under Global Change, Faculty of Life Sciences, University of Sfax, Sfax, Tunisia.

***E-mail** ✉ sara.benyoussef@fst.rnu.tn

## ABSTRACT

Behavioral plasticity is frequently invoked as a means by which insects can buffer rapid climatic change, yet observed adjustment is not equivalent to successful compensation. Behavioral thermoregulation, phenological shifts, movement, and habitat choice can each alter exposure, but their consequences depend on environmental opportunity, life stage, taxon, seasonality, and the persistence of effects beyond the period in which adjustment is observed. We systematically synthesized peer-reviewed evidence published from 2017 through 2022 addressing insect behavioral and timing responses to climatic warming, temperature variability, heat extremes, drought, microclimate, and altered seasonality. Evidence was coded separately for direct behavioral responses, developmental or phenological adjustment, physiological boundaries, spatial redistribution, fitness-related consequences, and cross-stage or cross-season carry-over. Methodological distinctions between active plasticity and passive thermal dependence, laboratory and field inference, immediate and delayed outcomes, and trait change versus population consequence were retained. Evidence indicates substantial heterogeneity rather than a single compensatory response. Thermoregulatory capacity depends on morphology, habitat, thermal opportunity, and performance limits. Phenological advancement can reduce exposure or improve seasonal use, but its demographic consequences can reverse with geography, voltinism, trophic synchrony, or late-season development. Habitat choice and climate tracking are additionally constrained by drought, resource suitability, and landscape structure. Across domains, responses measured as successful in one stage or season may generate later costs. Behavioral plasticity is most defensibly interpreted as conditional adjustment rather than evidence of adaptation. The synthesis supports evaluating insect climate responses through response capacity, environmental accessibility, temporal propagation, and consequence rather than through behavioral change alone.

**Keywords:** Behavioral thermoregulation, Insect phenology, Microclimate, Climate tracking, Carry-over effects, Thermal plasticity

**Received:** 08 November 2022
**Revised:** 22 December 2022
**Accepted:** 24 December 2022

**How to Cite This Article:** Ben Youssef S, Trabelsi A, Boudiaf K, Jebali N. Behavioral Plasticity Under Climate Change and the Limits, Costs, and Carry-Over Effects of Insect Adjustment. Entomol Res Lett. 2022;2(2):110-21.
https://doi.org/10.51847/tI4PHQt4zO

## Introduction

Behavioral plasticity allows organisms to alter activity, location, timing, or resource use without requiring immediate genetic change. Insects are particularly informative because behavioral responses can occur over minutes or hours while developmental and phenological adjustments extend across seasons or generations. Nevertheless, environmentally induced behavioral change is not inherently beneficial: its value depends on

**© 2022 Entomological Research Letters**

whether the response reduces harmful exposure, preserves access to resources, or improves later performance rather than merely changing phenotype or behavior [1].

Recent climate change affects insects through shifts in mean temperature, seasonal timing, extreme events, precipitation regimes, and interactions with host plants, predators, competitors, and landscapes [2]. Temperature extremes deserve separate treatment from gradual mean warming because episodic heat can compress the interval available for compensatory behavior and can create abrupt physiological or demographic consequences [3]. Responses to thermal challenge also operate across interacting physiological and ecological mechanisms, making it inappropriate to interpret an observed behavioral shift independently of the organismal limits within which it occurs [4]. At sufficiently high temperatures, avoidance, acclimation, and other responses may no longer prevent exposure from approaching damaging limits [5].

A second problem is inferential. Phenotypic plasticity can contribute to persistence under environmental change, but an observed plastic response does not itself demonstrate evolutionary adaptation or increased fitness [6]. Plasticity may alter subsequent selection or the rate and direction of evolutionary change, yet these processes remain distinct from the immediate environmentally induced response [7]. Climatic variability further modifies both physiological tolerance and the predictability of environmental cues, meaning that identical mean temperatures can generate different consequences when variability, seasonality, or environmental history differs [8].

This review therefore asks a narrower question than whether insects respond behaviorally to climate change. It examines when behavioral and timing adjustments remain usable, when environmental conditions restrict their deployment, when apparent compensation is associated with biological costs, and when effects propagate into later stages or seasons. The central synthesis developed later in the manuscript is explicitly proposed: insect adjustment is interpreted across four separable dimensions—response capacity, environmental accessibility, temporal propagation, and downstream consequence. These dimensions are not treated as a validated universal model, but as an evidence-bounded way to distinguish behavioral change from successful climatic compensation.

## Materials and Methods

*Protocol, search, eligibility, coding, quality assessment, and synthesis*

The review was organized according to transparent systematic-review reporting principles derived from PRISMA 2020 [9]. Searches were structured around combinations of insect taxon terms, climatic drivers, and adjustment terms including behavioral plasticity, thermoregulation, phenology, habitat choice, movement, dispersal, oviposition, acclimation, carry-over effects, transgenerational effects, costs, limits, diapause, and voltinism. The evidence window was restricted to peer-reviewed publications from 2017 through 2022.

Eligible primary evidence involved insects exposed to temperature, warming, heat extremes, drought, altered seasonality, or relevant microclimatic variation and reported behavioral, developmental-timing, movement, habitat-choice, or downstream performance outcomes. Reviews and methodological papers were retained only when they informed conceptual boundaries, synthesis, or quality assessment. Physiological studies were not treated as behavioral evidence unless they established a plausible limit or downstream consequence relevant to behavioral adjustment.

Coding distinguished direct behavioral observation from inferred movement or occupancy change; behavioral plasticity from thermal performance; and active plastic adjustment from passive temperature-dependent kinetics. This distinction is important because environmentally induced differences measured after thermal exposure can reflect acclimation, ordinary temperature dependence, or both [10]. Phenological studies were additionally evaluated for temporal confounding because shared long-term trends in climate and biological timing can exaggerate climate–phenology relationships when detrending or comparable controls are absent [11].

Quality assessment was therefore domain-based rather than reduced to a single numerical score. Greater interpretive weight was assigned when exposure, life stage, behavioral or phenological endpoint, comparator, and temporal sequence were explicit. Laboratory studies were considered strong for controlled response estimation but were not automatically generalized to field persistence. Landscape or occupancy studies were informative for spatial constraints but were not interpreted as direct observations of individual movement.

Thermal-limit evidence was treated as a boundary on, rather than a substitute for, behavioral plasticity. Meta-analytic evidence indicates that insect thermal limits are plastic but that average plasticity can be modest and heterogeneous among traits and life stages [12]. Seasonal development similarly requires explicit treatment

because a temperature-induced acceleration can alter voltinism, synchrony, or fitness differently depending on when within the annual cycle the response occurs [13].

The review workflow included documented identification, deduplication, title/abstract screening, full-text eligibility assessment, and final inclusion decisions. Searches were conducted across major bibliographic databases using predefined combinations of insect, climate, behavioral, phenological, and adjustment-related terms. After duplicate removal, 1,964 records were screened, 312 articles underwent full-text eligibility assessment, and 144 studies were retained for qualitative synthesis. The included evidence consisted of 118 primary behavioral or phenological studies and 26 contextual or methodological studies. Evidence synthesis was conducted through structured coding of response categories, limits, and inference boundaries.

**Results and Discussion**

*Taxonomic coverage*

The selected evidence was taxonomically uneven. Lepidoptera provided the most recurrent set of examples spanning adult thermoregulation, climatic buffering, phenological timing, microclimate exposure, oviposition, diapause, and cross-stage consequences. In British butterflies, physical and ecological traits were associated with differences in thermoregulatory ability and with population trends, but the observational design does not establish thermoregulation as the causal determinant of population change [14]. Long-term work in *Pieris napi* further illustrates that climatic effects can interact with drought, host-plant dynamics, and thermal buffering rather than acting through temperature alone [15]. Tropical butterfly assemblages also show morphological and behavioral differences among environments, emphasizing that the thermal strategies observed in temperate species cannot simply be generalized across climatic zones [16].

Other orders extend, but do not eliminate, this imbalance. Along tropical mountains, Odonata differed in thermal physiology according to environmental, taxonomic, morphological, and sex-related factors [17]. Bumblebee flight performance showed a nonlinear relationship with temperature under controlled conditions, providing a performance boundary relevant to foraging without directly demonstrating equivalent field reductions in resource acquisition [18]. In the dung beetle *Phanaeus vindex*, experimental changes in both thermal mean and variability altered reproductive behavior, showing that behavioral responses may depend on the statistical structure of temperature exposure rather than mean warming alone [19].

Taken together, the taxonomic evidence supports comparison but not universality. Lepidopteran results offer unusually rich cross-domain continuity, whereas evidence from bees, beetles, dragonflies, damselflies, and grasshoppers often addresses narrower components of the broader adjustment problem. The resulting synthesis therefore preserves taxon, life-stage, sex, and environmental boundaries rather than treating “insects” as a homogeneous response unit.

*Thermoregulatory behavior*

Behavioral thermoregulation can reduce the temperature actually experienced relative to ambient conditions, but its effectiveness depends on both organismal capability and the availability of usable microclimates. In butterflies, thermoregulatory ability varies with physical and ecological traits, indicating that individuals and species differ in how effectively posture, activity timing, or microhabitat use can buffer atmospheric conditions [14]. This variability matters because the same climatic exposure may be behaviorally avoidable for one species but effectively unavoidable for another.

Environmental context modifies that capacity. Long-term evidence from *Pieris napi* links drought, thermal buffering, and host-plant dynamics, suggesting that thermal conditions cannot always be separated from concurrent resource limitation [15]. Tropical butterfly assemblages provide a related caution: morphological and behavioral differences vary across environments, indicating that behavioral cooling or warming strategies are not fixed species-independent properties [16].

Thermal behavior is also bounded by physiology. In tropical Odonata, field body temperatures and thermal traits vary with taxonomy, habitat, morphology, and sex, making simple extrapolation across species problematic [17]. In *Bombus terrestris*, flight performance changes nonlinearly with temperature, so access to a cooler or warmer microhabitat is useful only if the resulting body temperature remains compatible with locomotor performance [18]. Thermal environment can additionally alter reproduction-linked behavior: experimental manipulation of temperature mean and variance changed brood-ball-related behavior in *P. vindex* [19].

These observations support a distinction between thermoregulatory capacity and thermoregulatory opportunity. Capacity concerns the behavioral and physiological repertoire available to an insect; opportunity concerns whether the environment contains accessible thermal states in which that repertoire can be expressed successfully. This distinction is proposed here as an interpretive device, not as an established taxonomic classification. It prevents a common overreach in which demonstrated behavioral flexibility is assumed to provide effective climatic buffering regardless of habitat structure, resource context, or performance limits.

The comparison is clearest when response, setting, and inference boundary are kept separate, as summarized in **Table 1**.

**Table 1.** When thermoregulatory flexibility can and cannot be interpreted as climatic buffering

| Capacity measured | | | Context of expression | Inference | |
|---|---|---|---|---|---|
| **Buffering state** | **Thermal construct** | **Observed climatic response** | **Taxonomic/environmental scope** | **Synthesis consequence** | **Quality limit** |
| **Thermoregulatory capacity** | | | | | |
| **Trait-linked thermal regulation** | Adult thermoregulatory ability and ecological traits | Species differ in capacity to regulate body temperature | Temperate butterflies | Behavioral capacity is heterogeneous | Population associations do not establish causal demographic protection |
| **Drought-modified thermal buffering** | Climatic exposure, phenotype and host-related context | Thermal buffering occurs within interacting drought and resource conditions | Mediterranean butterfly system | Thermal behavior cannot be isolated from ecological context | Multiple environmental pathways covary |
| **Environment-dependent strategy** | | | | | |
| **Environment-dependent behavioral strategy** | Behavioral and morphological thermal responses | Behavioral strategies differ among environmental settings | Tropical butterfly assemblages | Strategy is context dependent | Cross-species field comparisons cannot identify one universal mechanism |
| **Taxon- and sex-conditioned thermal response** | Body temperature and thermal physiological traits | Thermal relationships vary across taxonomic and biological strata | Tropical Odonata | Capacity must retain taxonomic and sex boundaries | Physiological measures are not equivalent to direct behavioral observations |
| **Performance and reproductive realization** | | | | | |
| **Performance-constrained mobility** | Flight performance across temperatures | Locomotor performance is nonlinear across thermal conditions | Bumblebee workers | Access to microclimates is useful only within performance-compatible temperatures | Laboratory flight does not equal field foraging success |
| **Temperature-structure-sensitive reproduction** | Reproduction-linked behavior under altered mean and variability | Behavioral response differs with thermal regime structure | Dung beetle | Mean warming and thermal variability should not be treated interchangeably | Single-species experiment |

*Phenological adjustment*

Phenological responses extend the concept of adjustment from space to time. Temperature-sensitive development can advance emergence, alter generation time, or change the duration of life stages, making developmental rate a major route through which climate modifies seasonal insect activity [20]. Yet earlier is not inherently better. Altered timing can change both direct exposure and interaction timing with resources, predators, or prey [21]. Predator and prey phenologies may therefore shift at different rates, producing mismatch whose direction and consequence depend on the interacting species rather than on a universal expectation of ecological disruption [22]. Comparative evidence reinforces this conditionality. Across temperate butterflies, responses to latitude differ according to ecological traits, demonstrating that phenological sensitivity is not taxonomically uniform [23]. Within species, climatic responses can also differ among populations, while among-species comparisons may conceal local environmental or genetic structure [24]. Montane grasshopper resurveys show that shifts in species-

specific seasonal timing can reorganize phenological overlap within communities, but changes in timing do not translate mechanically into identical abundance responses [25]. Long-term analyses of aphids, butterflies, and moths likewise show spatial and habitat variation in phenological trends [26].

The climatic scale used in analysis is itself consequential. Fine-resolution work in *Pieris napi* demonstrates that meter-scale microclimatic heterogeneity can alter developmental phenology, synchrony, and voltinism [27]. This means regional air-temperature averages may misrepresent the thermal conditions that insects actually experience during development.

More importantly, the demographic meaning of an earlier date can reverse. Modeling in the multivoltine butterfly *Pieris oleracea* showed that earlier phenology can either enable an additional generation or create a developmental trap when late-season individuals fail to complete development successfully [28]. Phenological adjustment therefore has to be evaluated across the remainder of the annual cycle rather than only at the first shifted event.

Carry-over processes add another layer. In the winter moth *Operophtera brumata*, photoperiodic cues can regulate how changes in one stage propagate into subsequent stages, allowing some early phenological displacement to be compensated later in the life cycle [29]. Consequently, a climate-associated change in hatching or emergence does not necessarily propagate unchanged through adulthood. Phenological plasticity should instead be interpreted as a sequence of stage-specific transitions whose direction, compensation, and demographic consequence depend on seasonality, cue structure, and the remaining developmental window.

*Movement and habitat choice*

Movement can alter climatic exposure only when suitable destinations are both identifiable and accessible. Habitat choice therefore differs fundamentally from thermoregulation within an already occupied patch: it depends on resource distributions, landscape permeability, and the correspondence between behavioral preference and environmental quality.

The Glanville fritillary *Melitaea cinxia* illustrates how that correspondence can fail. Narrow oviposition preference that was ordinarily compatible with offspring survival became risky during severe drought because selected sites no longer provided equivalent developmental conditions [30]. The result is not evidence that oviposition preference is generally maladaptive. Rather, it shows that a previously viable behavioral rule can become mismatched when climatic extremes change the relationship between the cue used for choice and the conditions ultimately experienced by offspring.

Climate tracking at larger spatial scales faces a different boundary. Analyses of moth range shifts indicate that unsuitable landscape structure can hamper expansion into climatically favorable areas [31]. These data do not directly observe individual dispersal decisions, but they demonstrate that redistribution cannot be interpreted solely from climatic suitability. A species may possess dispersal capacity yet still encounter landscapes that reduce the probability of successful colonization.

Long-term occupancy change provides complementary evidence. Across butterflies, grasshoppers, and dragonflies in central Europe, climatic warming was associated with consistent occupancy signals, while land use remained an important contextual driver [32]. Occupancy change is an integrated population-level outcome rather than direct behavioral evidence, so it should not be treated as a measurement of movement plasticity itself.

The synthesis therefore separates three movement-related states: choice plasticity, in which organisms alter habitat or oviposition decisions; tracking capacity, in which movement could potentially follow shifting climatic space; and landscape realization, in which successful redistribution depends on suitable habitat actually being reachable. These categories are proposed for interpretation and should not be read as validated behavioral classes.

**Table 2** distinguishes the evidence needed to test these states without converting them into an unsupported score.

**Table 2.** Distinguishing habitat-choice adjustment, climatic tracking, and realized redistribution

| **Cue-based habitat choice** | | | |
|---|---|---|---|
| **Cue-consistent habitat choice** | | | *Evidence-supported distinction* |
| **Behavioral evidence** | Repeated selection of habitat associated with offspring conditions | **Biological setting** | Ovipositing herbivorous insect |
| **Spatial condition** | Resource quality and microclimate may change independently of the cue | | |
| **Choice may be locally viable while environment remains within the historical cue–quality relationship** | | | **Interpretation** |
| **Validation** | Measure both selected habitat and offspring outcome | | |

| | | | |
|---|---|---|---|
| **Climate-induced cue–quality mismatch** | | | *Evidence-supported pattern* |
| **Behavioral evidence** | Preferred oviposition sites no longer confer equivalent offspring survival | **Biological setting** | Butterfly under severe drought |
| **Spatial condition** | Extreme-event severity and host condition | | |
| **Behavioral preference can become maladaptive under extreme conditions** | | | **Interpretation** |
| **Validation** | Test whether preference changes as cue reliability changes | | |
| **Tracking through landscapes** | | | |
| **Potential climate tracking** | | | *Proposed interpretive state* |
| **Behavioral evidence** | Climatically suitable areas occur beyond current distribution | **Biological setting** | Range-shifting insects |
| **Spatial condition** | Individual dispersal capacity is not directly measured by distribution data | | |
| **Movement could contribute to redistribution** | | | **Interpretation** |
| **Validation** | Combine dispersal observations with climatic suitability | | |
| **Landscape-constrained tracking** | | | *Evidence-supported pattern* |
| **Behavioral evidence** | Range expansion is reduced where landscape structure impedes colonization | **Biological setting** | Moths in fragmented or unsuitable landscapes |
| **Spatial condition** | Connectivity and habitat availability | | |
| **Climatic suitability alone does not determine realized shift** | | | **Interpretation** |
| **Validation** | Test colonization across matched climate but contrasting landscape permeability | | |
| **Redistribution and successful adjustment** | | | |
| **Realized occupancy redistribution** | | | *Evidence-supported outcome* |
| **Behavioral evidence** | Long-term changes in occupancy across landscapes | **Biological setting** | Multiple insect taxa over decades |
| **Spatial condition** | Occupancy is not a direct behavioral metric | | |
| **Redistribution integrates climate, land use, demography and movement** | | | **Interpretation** |
| **Validation** | Pair occupancy models with movement or demographic data | | |
| **Successful behavioral adjustment** | | | *Proposed inference rule* |
| **Behavioral evidence** | Choice or movement followed by persistence-compatible conditions | **Biological setting** | Any taxon |
| **Spatial condition** | Benefit cannot be inferred from movement alone | | |
| **Requires both behavioral response and appropriate destination conditions** | | | **Interpretation** |
| **Validation** | Measure post-movement survival, reproduction or population consequence | | |

A standards-based selection-flow figure is presented at this point to separate identification, deduplication, screening, eligibility, and inclusion from the later biological synthesis. The selection process documented the progression from database retrieval and supplementary searching through duplicate removal, screening, full-text assessment, and final inclusion of the evidence base.

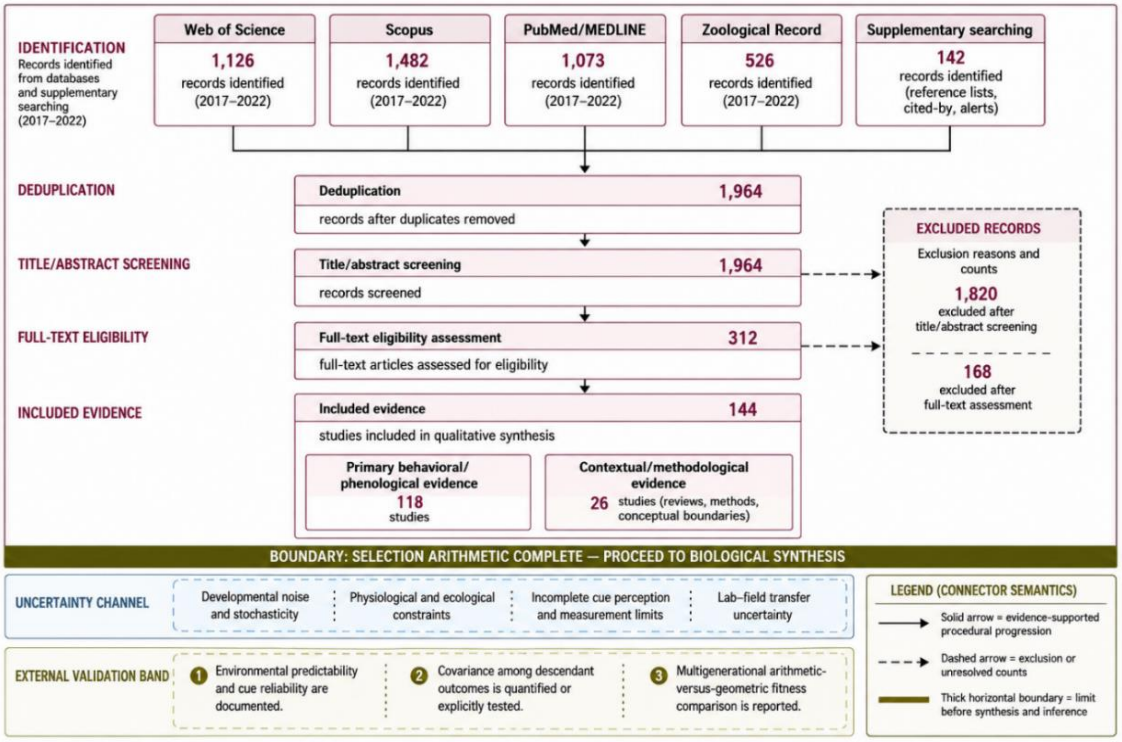



**Figure 1.** Review-flow boundaries that prevent bibliography size from substituting for screening evidence

*Plasticity costs*

Plastic adjustment can reduce immediate climatic exposure while transferring costs to later stages or functions. Experimental heat stress during the egg stage of *Bicyclus anynana* reduced subsequent performance, demonstrating that the biological consequence of thermal exposure may persist after the original stage has ended [33]. Simulated warming in the dragonfly *Erythemis collocata* similarly increased larval mortality, altered emergence timing, and modified adult flight morphology, although altered morphology cannot by itself establish impaired adult behavior [34].

Plasticity also varies with environmental predictability and developmental context. In *Drosophila mojavensis*, within- and transgenerational heat-tolerance responses differed among life stages and climatic regions, cautioning against treating transgenerational plasticity as uniformly beneficial [35]. In diapausing *Pieris napi*, longer and warmer prewinter conditions reduced later performance despite the temporal separation between exposure and post-winter phenotype [36]. Developmental nutrition can further modify metabolic responses to projected warming in *Drosophila melanogaster*, showing that internal condition can alter thermal responsiveness even when the measured outcome is physiological rather than behavioral [37]. Simulated heatwaves also affected reproductive traits differently among *Bombus* species, reinforcing the need to retain species and endpoint boundaries when inferring climatic cost [38].

The relevant cost is therefore not simply the energetic expense of performing a behavior. It includes opportunity loss, altered development, delayed mortality, reproductive impairment, or reduced later performance that becomes visible only when observation extends beyond the initial response.

*Carry-over effects*

Carry-over effects are treated here as consequences of an earlier environmental exposure or adjustment that remain detectable after a life-stage, seasonal, or generational boundary. This definition distinguishes them from simultaneous trade-offs. Photoperiod-sensitive compensation in *Operophtera brumata* shows that an early phenological shift can be modified during later stages rather than transmitted unchanged through the annual cycle [29]. By contrast, egg-stage heat exposure in *B. anynana* produced adverse later-life effects [33], and larval warming in *E. collocata* altered adult phenotype after metamorphosis [34].

The evidence therefore supports several non-equivalent trajectories. Within-generation persistence can connect juvenile exposure to adult performance; seasonal carry-over can link prewinter conditions to post-winter fitness; and transgenerational responses can transmit environmentally conditioned effects between generations [35].

Warmer and longer prewinter periods in *P. napi* illustrate why immediate survival is an insufficient endpoint when costs emerge after diapause [36].

This review proposes that carry-over should be adjudicated by boundary crossed, persistence of effect, and consequence measured, rather than by delay alone. **Table 3** separates those dimensions.

**Table 3.** Distinguishing compensatory, persistent, and delayed-cost carry-over across insect life histories

| Within-season and within-life-cycle | | | |
|---|---|---|---|
| **Temporal carry-over dimension** | **Compensated phenological carry-over** | **Persistent cross-stage effect** | **Metamorphic carry-over** |
| **Boundary crossed** | Annual-cycle moth | Butterfly | Dragonfly |
| **Evidence before and after** | Early-stage timing followed by later photoperiod-sensitive adjustment | Egg heat exposure followed by later performance reduction | Larval warming followed by altered adult morphology |
| **Carry-over reading** | Initial shift need not propagate unchanged | Early stress remains biologically detectable | Pre-adult environment can influence adult phenotype |
| **Discriminating test** | Follow multiple stages through one seasonal cycle | Measure downstream traits after exposure ends | Link adult phenotype to actual performance |
| **Alternative** | Cue availability and stage sensitivity | Species and laboratory context | Morphology does not prove behavioral impairment |
| **Standing** | Evidence-supported | Evidence-supported | Evidence-supported |

| Across generation or winter | | | |
|---|---|---|---|
| **Temporal carry-over dimension** | **Transgenerational carry-over** | **Seasonal delayed cost** | **Carry-over adjudication rule** |
| **Boundary crossed** | Drosophila | Diapausing butterfly | Cross-taxon synthesis |
| **Evidence before and after** | Parental/offspring thermal conditions and heat tolerance | Warm/long prewinter followed by post-winter decline | Boundary crossed + persistence + consequence |
| **Carry-over reading** | Effects may cross generations | Cost can emerge after diapause | Delay alone is insufficient for classification |
| **Discriminating test** | Factor parental and offspring environments | Extend measurement beyond overwintering | Predefine exposure, boundary and later endpoint |
| **Alternative** | Direction depends on stage and climatic history | Laboratory-to-field transfer | Requires explicit temporal sequence |
| **Standing** | Evidence-supported | Evidence-supported | Proposed |

*Evidence for limits*

The evidence indicates several distinct limits rather than a single ceiling on plasticity. First, response capacity itself can be limited: thermal-limit plasticity is detectable across insects but is often modest and heterogeneous [12]. Second, effective behavior requires suitable environmental opportunities; thermoregulation is constrained when accessible microclimates cannot place body temperature within performance-compatible conditions [14]. Third, temporal adjustment can become counterproductive when earlier development produces a late-season developmental trap rather than an additional successful generation [28]. Fourth, behavioral preference may become mismatched with habitat quality during severe drought [30]. Fifth, landscape structure can restrict redistribution even where climates become suitable elsewhere [31]. Finally, delayed effects can make an apparently tolerated exposure costly only after metamorphosis or diapause [33].

These patterns support the proposed distinction in **Table 4** between capacity, access, timing, cue reliability, spatial realization, and delayed-consequence limits.

**Table 4.** Context–mechanism–outcome register for diagnosing limits to insect climatic adjustment

| Capacity and opportunity limits | | |
|---|---|---|
| **Limit-diagnosis dimension** | **Response-capacity limit** | **Thermal-opportunity limit** |
| **Diagnostic observation** | Weak or heterogeneous plastic change | Suitable operative temperatures not always accessible |
| **Biological setting** | Thermal tolerance | Behavioral thermoregulation |
| **Condition limiting inference** | Trait and life stage | Habitat structure |

| | | |
|---|---|---|
| **Meaning for adjustment** | Adjustment magnitude may be insufficient | Capacity requires environmental opportunity |
| **Test implication** | Measure response magnitude, not presence alone | Measure available microclimates with body-temperature response |
| **Standing** | Evidence-supported | Proposed synthesis |

| **Seasonal information limits** | | |
|---|---|---|
| **Limit-diagnosis dimension** | **Seasonal-timing limit** | **Cue-reliability limit** |
| **Diagnostic observation** | Earlier timing produces benefit or developmental trap | Preferred site becomes poor offspring environment |
| **Biological setting** | Multivoltine development | Oviposition under drought |
| **Condition limiting inference** | Geography and voltinism | Extreme drought |
| **Meaning for adjustment** | Direction depends on remaining season | Historical cue–quality relation can fail |
| **Test implication** | Track complete seasonal outcome | Measure preference and offspring consequence jointly |
| **Standing** | Evidence-supported | Evidence-supported |

| **Realization and delayed consequence** | | |
|---|---|---|
| **Limit-diagnosis dimension** | **Spatial-realization limit** | **Delayed-consequence limit** |
| **Diagnostic observation** | Suitable climates separated by poor landscape | Later performance declines after exposure |
| **Biological setting** | Range tracking | Cross-stage/diapause systems |
| **Condition limiting inference** | Connectivity | Life-stage transition |
| **Meaning for adjustment** | Redistribution requires accessible habitat | Immediate tolerance may conceal later cost |
| **Test implication** | Separate climatic suitability from colonization | Extend follow-up beyond exposure period |
| **Standing** | Evidence-supported | Evidence-supported |

The reviewed evidence does not support a binary classification of insect behavior as either plastic or inflexible. A more useful interpretation asks whether an insect can respond, whether the environment provides somewhere or sometime for that response to work, whether consequences persist across biological boundaries, and whether the eventual outcome is favorable.

This synthesis therefore proposes four linked but separable dimensions: response capacity, environmental accessibility, temporal propagation, and downstream consequence. The distinction is analytical rather than mechanistically validated. A butterfly may thermoregulate effectively but lose access to appropriate microclimates; a phenological advance may create either a demographic opportunity or a seasonal trap; an oviposition rule may remain viable until drought breaks the association between cue and offspring habitat; and a thermal exposure may appear tolerated until costs emerge after metamorphosis or diapause.

Laboratory and field evidence consequently answer different questions. Controlled experiments can establish temporal ordering and isolate thermal responses, whereas field and landscape studies reveal environmental heterogeneity, resource coupling, and spatial constraints. Neither scale alone establishes population persistence. Likewise, occupancy change, altered morphology, thermal tolerance, and reproductive physiology should not be relabelled as behavioral adaptation merely because they occur under climate-related exposure.

The principal evidence gap is longitudinal integration. Stronger tests should connect behavioral choice or timing to the environment actually experienced, then follow survival, reproduction, or population consequence across relevant stages and seasons. Such designs would clarify when apparent flexibility is compensatory and when it merely redistributes risk.

*Conservation implications*

Conservation interpretation should therefore focus less on whether a species displays plasticity and more on whether environments retain the opportunities required for useful adjustment. Maintaining heterogeneous microclimates may preserve behavioral options where insects can exploit temperature differences [27]. Landscape

permeability may similarly determine whether climate tracking can be realized rather than merely predicted from climatic envelopes [31].

Monitoring should also extend across life stages when early exposure can produce later costs [33]. Phenological surveillance is most informative when it measures interacting species, seasonal completion, and local microclimate rather than recording a single earlier emergence date [25]. These implications identify priorities for habitat management and monitoring, but the reviewed evidence does not establish that any single intervention will reliably prevent climate-driven insect decline.

## Conclusion

Behavioral plasticity can modify insect exposure to climatic change, but behavioral change alone is an incomplete measure of climatic resilience. Thermoregulation depends on accessible microclimates and performance limits; phenological shifts can produce compensation, mismatch, opportunity, or seasonal traps; movement depends on cue reliability and landscape realization; and thermal effects can persist across developmental, seasonal, or generational boundaries.

The review therefore advances an evidence-bounded interpretation of insect adjustment based on response capacity, environmental accessibility, temporal propagation, and downstream consequence. These dimensions should be treated as a proposed synthesis rather than a validated universal model. Their value lies in preventing the presence of plasticity from being mistaken for successful adaptation and in directing future studies toward the conditions under which adjustment actually persists, fails, or transfers cost to another stage.

**Acknowledgments:** None

**Conflict of Interest:** None

**Financial Support:** None

**Ethics Statement:** None

## References

1. van Baaren J, Candolin U. Plasticity in a changing world: Behavioural responses to human perturbations. Curr Opin Insect Sci. 2018;27:21-5. doi:10.1016/j.cois.2018.02.003
2. Halsch CA, Shapiro AM, Fordyce JA, Nice CC, Thorne JH, Waetjen DP, et al. Insects and recent climate change. Proc Natl Acad Sci U S A. 2021;118(2):e2002543117. doi:10.1073/pnas.2002543117
3. Harvey JA, Heinen R, Gols R, Thakur MP. Climate change-mediated temperature extremes and insects: From outbreaks to breakdowns. Glob Chang Biol. 2020;26(12):6685-701. doi:10.1111/gcb.15377
4. González-Tokman D, Córdoba-Aguilar A, Dáttilo W, Lira-Noriega A, Sánchez-Guillén RA, Villalobos F. Insect responses to heat: Physiological mechanisms, evolution and ecological implications in a warming world. Biol Rev Camb Philos Soc. 2020;95(3):802-21. doi:10.1111/brv.12588
5. Ma CS, Ma G, Pincebourde S. Survive a warming climate: Insect responses to extreme high temperatures. Annu Rev Entomol. 2021;66:163-84. doi:10.1146/annurev-ento-041520-074454
6. Kingsolver JG, Buckley LB. Evolution of plasticity and adaptive responses to climate change along climate gradients. Proc Biol Sci. 2017;284(1860):20170386. doi:10.1098/rspb.2017.0386
7. Gibert P, Debat V, Ghalambor CK. Phenotypic plasticity, global change, and the speed of adaptive evolution. Curr Opin Insect Sci. 2019;35:34-40. doi:10.1016/j.cois.2019.06.007
8. Dillon ME, Lozier JD. Adaptation to the abiotic environment in insects: The influence of variability on ecophysiology and evolutionary genomics. Curr Opin Insect Sci. 2019;36:131-9. doi:10.1016/j.cois.2019.09.003
9. Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: An updated guideline for reporting systematic reviews. BMJ. 2021;372:n71. doi:10.1136/bmj.n71
10. Havird JC, Neuwald JL, Shah AA, Mauro A, Marshall CA, Ghalambor CK. Distinguishing between active plasticity due to thermal acclimation and passive plasticity due to Q10 effects: Why methodology matters. Funct Ecol. 2020;34(5):1015-28. doi:10.1111/1365-2435.13534

11. Iler AM, Inouye DW, Schmidt NM, Høye TT. Detrending phenological time series improves climate-phenology analyses and reveals evidence of plasticity. Ecology. 2017;98(3):647-55. doi:10.1002/ecy.1690
12. Weaving H, Terblanche JS, Pottier P, English S. Meta-analysis reveals weak but pervasive plasticity in insect thermal limits. Nat Commun. 2022;13(1):5292. doi:10.1038/s41467-022-32953-2
13. Buckley LB, Arakaki AJ, Cannistra AF, Kharouba HM, Kingsolver JG. Insect development, thermal plasticity and fitness implications in changing, seasonal environments. Integr Comp Biol. 2017;57(5):988-98. doi:10.1093/icb/icx032
14. Bladon AJ, Lewis M, Bladon EK, Buckton SJ, Corbett S, Ewing SR, et al. How butterflies keep their cool: Physical and ecological traits influence thermoregulatory ability and population trends. J Anim Ecol. 2020;89(11):2440-50. doi:10.1111/1365-2656.13319
15. Carnicer J, Stefanescu C, Vives-Ingla M, López C, Cortizas S, Wheat CW, et al. Phenotypic biomarkers of climatic impacts on declining insect populations: A key role for decadal drought, thermal buffering and amplification effects and host plant dynamics. J Anim Ecol. 2019;88(3):376-91. doi:10.1111/1365-2656.12933
16. Wenda C, Xing S, Nakamura A, Bonebrake TC. Morphological and behavioural differences facilitate tropical butterfly persistence in variable environments. J Anim Ecol. 2021;90(12):2888-900. doi:10.1111/1365-2656.13589
17. Bota-Sierra CA, García-Robledo C, Escobar F, Novelo-Gutiérrez R, Londoño GA. Environment, taxonomy and morphology constrain insect thermal physiology along tropical mountains. Funct Ecol. 2022;36(8):1924-35. doi:10.1111/1365-2435.14083
18. Kenna D, Pawar S, Gill RJ. Thermal flight performance reveals impact of warming on bumblebee foraging potential. Funct Ecol. 2021;35(11):2508-22. doi:10.1111/1365-2435.13887
19. Kirkpatrick WH, Sheldon KS. Experimental increases in temperature mean and variance alter reproductive behaviours in the dung beetle Phanaeus vindex. Biol Lett. 2022;18(7):20220109. doi:10.1098/rsbl.2022.0109
20. Buckley LB. Temperature-sensitive development shapes insect phenological responses to climate change. Curr Opin Insect Sci. 2022;52:100897. doi:10.1016/j.cois.2022.100897
21. Abarca M, Spahn R. Direct and indirect effects of altered temperature regimes and phenological mismatches on insect populations. Curr Opin Insect Sci. 2021;47:67-74. doi:10.1016/j.cois.2021.04.008
22. Damien M, Tougeron K. Prey-predator phenological mismatch under climate change. Curr Opin Insect Sci. 2019;35:60-8. doi:10.1016/j.cois.2019.07.002
23. Faltýnek Fric Z, Rindoš M, Konvička M. Phenology responses of temperate butterflies to latitude depend on ecological traits. Ecol Lett. 2020;23(1):172-80. doi:10.1111/ele.13419
24. Gutiérrez D, Wilson RJ. Intra- and interspecific variation in the responses of insect phenology to climate. J Anim Ecol. 2021;90(1):248-59. doi:10.1111/1365-2656.13348
25. Buckley LB, Graham SI, Nufio CR. Grasshopper species' seasonal timing underlies shifts in phenological overlap in response to climate gradients, variability and change. J Anim Ecol. 2021;90(5):1252-63. doi:10.1111/1365-2656.13451
26. Bell JR, Botham MS, Henrys PA, Leech DI, Pearce-Higgins JW, Shortall CR, et al. Spatial and habitat variation in aphid, butterfly, moth and bird phenologies over the last half century. Glob Chang Biol. 2019;25(6):1982-94. doi:10.1111/gcb.14592
27. Greiser C, von Schmalensee L, Lindestad O, Gotthard K, Lehmann P. Microclimatic variation affects developmental phenology, synchrony and voltinism in an insect population. Funct Ecol. 2022;36(12):3036-48. doi:10.1111/1365-2435.14195
28. Kerr NZ, Wepprich T, Grevstad FS, Dopman EB, Chew FS, Crone EE. Developmental trap or demographic bonanza? Opposing consequences of earlier phenology in a changing climate for a multivoltine butterfly. Glob Chang Biol. 2020;26(4):2014-27. doi:10.1111/gcb.14959
29. Salis L, van den Hoorn E, Beersma DGM, Hut RA, Visser ME. Photoperiodic cues regulate phenological carry-over effects in an herbivorous insect. Funct Ecol. 2018;32(1):171-80. doi:10.1111/1365-2435.12953
30. Salgado AL, DiLeo MF, Saastamoinen M. Narrow oviposition preference of an insect herbivore risks survival under conditions of severe drought. Funct Ecol. 2020;34(7):1358-69. doi:10.1111/1365-2435.13587
31. Hodgson JA, Randle Z, Shortall CR, Oliver TH. Where and why are species' range shifts hampered by unsuitable landscapes? Glob Chang Biol. 2022;28(16):4765-74. doi:10.1111/gcb.16220

32. Engelhardt EK, Biber MF, Dolek M, Fartmann T, Hochkirch A, Leidinger J, et al. Consistent signals of a warming climate in occupancy changes of three insect taxa over 40 years in central Europe. Glob Chang Biol. 2022;28(13):3998-4012. doi:10.1111/gcb.16200
33. Klockmann M, Kleinschmidt F, Fischer K. Carried over: Heat stress in the egg stage reduces subsequent performance in a butterfly. PLoS One. 2017;12(7):e0180968. doi:10.1371/journal.pone.0180968
34. McCauley SJ, Hammond JI, Mabry KE. Simulated climate change increases larval mortality, alters phenology, and affects flight morphology of a dragonfly. Ecosphere. 2018;9(3):e02151. doi:10.1002/ecs2.2151
35. Diaz F, Kuijper B, Hoyle RB, Talamantes N, Coleman JM, Matzkin LM. Environmental predictability drives adaptive within- and transgenerational plasticity of heat tolerance across life stages and climatic regions. Funct Ecol. 2021;35(1):153-66. doi:10.1111/1365-2435.13704
36. Nielsen ME, Lehmann P, Gotthard K. Longer and warmer prewinter periods reduce post-winter fitness in a diapausing insect. Funct Ecol. 2022;36(5):1151-62. doi:10.1111/1365-2435.14037
37. Alton LA, Kutz TC, Bywater CL, Beaman JE, Arnold PA, Mirth CK, et al. Developmental nutrition modulates metabolic responses to projected climate change. Funct Ecol. 2020;34(12):2488-502. doi:10.1111/1365-2435.13663
38. Martinet B, Zambra E, Przybyla K, Lecocq T, Anselmo A, Nonclercq D, et al. Mating under climate change: Impact of simulated heatwaves on the reproduction of model pollinators. Funct Ecol. 2021;35(3):739-52. doi:10.1111/1365-2435.13738