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Mechanisms, Constraints, and Ecological Consequences of Insect Phenological Plasticity Under Increasing Climate Variability

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ABSTRACT

Climate variability is changing the timing of insect development, diapause, emergence, flight, and species interactions, but phenological responses cannot be interpreted reliably as simple advances under warming. This systematic review synthesizes evidence published from 2017–2023 to distinguish environmental cues from biological responses, phenotypic plasticity from evolutionary differentiation, and altered timing from ecological consequence. Temperature-sensitive development can translate thermal exposure into seasonal timing, yet realized responses depend on microclimate, nonlinear developmental performance, latitude, ecological traits, life stage, and interacting species. Photoperiod provides a comparatively stable seasonal cue, but its phenological effects depend on temperature-sensitive diapause induction and endocrine or circadian mechanisms whose generality varies among taxa. Across the evidence base, the magnitude and direction of phenological plasticity are conditional rather than uniform. Warming can advance, delay, desynchronize, or alter voltinism, while ecological consequences depend on whether interacting organisms shift concordantly and whether altered overlap affects performance or population dynamics. We therefore propose an inference hierarchy separating climatic exposure, cue processing, phenotypic timing, interaction overlap, organismal performance, and population consequence. This distinction limits overinterpretation of phenological shifts as automatically adaptive responses to climate change.

Keywords: Insect phenology, Developmental plasticity, Thermal cues, Photoperiodism, Diapause, Phenological mismatch

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Introduction

Phenology is often summarized as the calendar timing of recurrent biological events, yet insect phenology is generated by multiple processes operating before an event is observed. Environmental cues must first be encountered, integrated and translated through developmental, physiological or behavioral systems before emergence, migration, diapause termination or adult activity becomes visible. Mechanistic syntheses therefore distinguish changes in environmental cues from changes in cue sensitivity and from changes in the biological processes that generate phenological timing [1]. This distinction is especially important under climate change because broad analyses show substantial variation in phenological responses among animal taxa and regions rather than a universal shift in one direction [2].

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Temperature-sensitive development provides a direct route through which climatic conditions can alter insect seasonal timing, but the relationship is rarely equivalent to a fixed number of days advanced per unit warming [3]. Weather anomalies can influence insect timing independently of long-term climatic means, emphasizing that short-lived thermal departures may be biologically important even where average conditions change slowly [4]. In butterflies, thermal responsiveness also differs within and among species, showing that the same climatic exposure need not generate the same phenological response across populations or ecological contexts [5].

The central interpretive problem is therefore not whether insects respond to changing climate, but how to distinguish several inference levels that are frequently collapsed: environmental exposure, cue perception, developmental or diapause response, measured phenological change, altered synchrony with interacting species, and eventual performance or population effects. In this review, phenological plasticity refers specifically to environmentally induced variation in timing expressed without assuming underlying genetic change. It is kept separate from acclimation, genetically differentiated seasonal programs, and adaptive evolution. We further distinguish phenological change from ecological benefit: earlier or later timing is not inherently advantageous, and altered synchrony does not necessarily imply reduced fitness or population decline.

The review evaluates evidence across thermal and photoperiodic cue systems, variation in plasticity magnitude, physiological and genetic constraints, and ecological consequences. Its principal contribution is a proposed inferential hierarchy for interpreting phenological responses under increasing climate variability. The hierarchy is not treated as an empirically validated universal model; rather, it organizes where existing evidence supports direct mechanism, where only association is demonstrated, and where ecological inference requires additional validation.

Materials and Methods

The review was structured according to contemporary systematic-review reporting principles, including explicit eligibility criteria, staged screening logic, and separation of identification, screening, eligibility and inclusion decisions [6]. The evidence window was restricted to peer-reviewed literature published from 2017 through 2023. Search logic combined insect or taxonomic terms with phenology, emergence, seasonal timing, diapause, voltinism and developmental timing, together with terms for temperature, climate variability, photoperiod, plasticity, microclimate, mismatch, physiology and genetic mechanisms.

Eligible biological studies had to address insect seasonal timing directly or examine a mechanistic process sufficiently close to phenology to inform interpretation of cue response, diapause, developmental timing, plasticity magnitude, or ecological synchrony. Reviews were retained when they supplied mechanistic, methodological or conceptual boundaries not replaceable by a single empirical study. Studies addressing climate change without a timing-related response, or seasonal observations without interpretable phenological content, were excluded from biological synthesis.

Historical occurrence and natural-history collection data were treated as observational phenological evidence rather than as standardized developmental experiments. Such records can support seasonal inference but require explicit attention to sampling date, effort, geographic coverage and collection biases [7]. This distinction is important because adult occurrence dates may reflect both developmental timing and detectability. Odonate collection data, for example, demonstrate that flight timing can be associated with temperature, precipitation and photoperiod, but do not by themselves identify a single causal developmental pathway [8].

For each eligible source, coding distinguished taxon, life stage where reported, study setting, environmental driver, measured phenophase, evidence type, level of biological organization, direction of response, contradictory or null findings, and limits on transferability. Quality appraisal was qualitative and design-specific rather than converted into a synthetic numerical score. Particular attention was given to microclimate representation, temporal resolution, experimental manipulation versus association, laboratory-to-field transfer, taxonomic breadth, and whether ecological consequences were measured directly or inferred from altered timing.

Results and Discussion

The evidence base was methodologically heterogeneous. Some studies measured emergence, adult flight or voltinism from long-term field or collection records; others experimentally manipulated temperature, quantified developmental reaction norms, tested diapause responses to combined cues, or perturbed endocrine and circadian

mechanisms. This heterogeneity is analytically important because the same term—phenological response—can refer to different biological levels.

Regional comparisons demonstrate substantial geographic variation in both insect phenology and the relationship between phenology and temperature [9]. Consequently, a single regional thermal coefficient cannot be assumed to represent the response of the same taxon elsewhere. Long-term Lepidoptera analyses likewise show that shifts in seasonal timing and geographic range can occur together but are not interchangeable dimensions of climate response [10]. Phenological movement in time therefore cannot be used as a proxy for spatial redistribution, population persistence or adaptive capacity.

The strongest evidence for immediate cue-response processes came from thermal-development and diapause studies, whereas ecological consequences were typically more conditional because they depended on interacting taxa, alternative resources, population regulation and the particular phenophases compared. This distribution motivated separate treatment of thermal cues, photoperiodic cues, plasticity magnitude, mechanistic constraints and ecological consequences.

Thermal cues

Temperature can modify insect phenology through development-rate changes, but the predictive value of thermal response depends on how accurately biologically experienced temperatures are represented. In *Pieris napi*, developmental performance measured under constant laboratory temperatures predicted development across naturally variable microclimates when nonlinear thermal responses were incorporated [11]. The result supports laboratory-to-field transfer in that system, but not the assumption that coarse climatic means are sufficient.

Fine-scale exposure can substantially modify seasonal outcomes. In the same butterfly system, microclimatic variation altered developmental phenology, synchrony and voltinism, demonstrating that nearby individuals can experience different developmental calendars despite occupying the same broader climate region [12]. Such results make microclimate an inference boundary between meteorological warming and organismal exposure.

Warming also does not guarantee earlier activity. A field experiment on a bee pollinator found delayed phenology together with reduced body mass, fat content and survival under experimental warming [13]. This counterexample is important because it separates the direction of temperature change from the direction of phenological change. Comparative butterfly data provide an additional boundary: responses to latitude depend on ecological traits, so geographic gradients cannot be interpreted as interchangeable temperature experiments [14].

Plastic responses may nevertheless align with selection in particular systems. In damselflies, phenotypic plasticity was aligned with phenological adaptation across micro- and macroevolutionary scales [15]. The result supports the possibility of concordance between plastic and evolutionary responses, but it does not justify defining plasticity itself as adaptive. Interaction context creates a further complication. Simulated warming in the *Rhagoletis* system produced asymmetric changes in life-history timing among interacting insects, illustrating how the same thermal perturbation can generate different phenological outcomes in linked species [16].

Taken together, thermal evidence supports a conditional sequence: experienced temperature → developmental-rate response → phenological expression, with microclimate, nonlinear performance, ecological traits and species identity altering each transition. The evidence does not support a universal rule in which higher temperature produces a proportional advance.

Because these distinctions are difficult to compare in prose alone, **Table 1** adjudicates what can—and cannot—be inferred from major thermal evidence states.

Table 1. Thermal evidence states that separate climatic exposure from phenological inference

Taxonomic or methodological scope · Main evidence pattern	Measured construct · Uncertainty or quality limitation	Synthesis consequence
Laboratory thermal performance translated to field exposure		
Butterfly developmental system **Nonlinear thermal performance can predict field timing when realistic exposure is represented**	Development time across temperature regimes Transfer demonstrated in a restricted taxonomic system	Laboratory response is informative only when exposure modelling is biologically credible
Fine-scale microclimate divergence		
Field butterfly population	Developmental timing, synchrony, voltinism	Regional climate means can obscure biologically relevant variation

Nearby thermal environments produce different seasonal outcomes	Spatial microclimate measurements may not capture all behavioural exposure	
Experimental warming with delayed timing		
Field pollinator experiment **Warming can delay phenology while reducing performance**	Emergence timing and condition Species- and site-specific response	Direction of warming does not determine direction of phenological shift
Trait-dependent geographic response		
Comparative butterflies **Phenological relationships vary with ecological traits**	Seasonal timing across latitude Latitude combines multiple environmental gradients	Geographic pattern is not equivalent to isolated temperature causation
Plasticity aligned with selected timing		
Damselfly comparative/experimental evidence **Plastic response can align with selection**	Plastic and evolved phenological responses Alignment is context-specific	Plasticity and adaptation must remain analytically separate
Asymmetric response among interacting insects		
Experimental host-associated system **Linked taxa can shift unequally**	Life-history timing under simulated warming Experimental conditions simplify future field climates	Interaction mismatch can arise without identical thermal sensitivity

Photoperiodic cues

Photoperiod differs from temperature because day length follows a predictable astronomical cycle even while climatic conditions become more variable. Insects can therefore use photoperiod as a seasonal timing signal, particularly in diapause, but photoperiodic control is not independent of physiology. Circadian and seasonal timing systems contribute to diapause regulation, although their mechanistic integration differs among taxa and remains incompletely resolved [17].

Environmental regulation of insect development also involves coordinated responsiveness and robustness rather than unlimited reaction to external conditions [18]. This is relevant to phenology because photoperiod may constrain the degree to which temperature can shift seasonal timing. In migratory locusts, embryonic diapause induction depends interactively on photoperiod and temperature rather than on either cue in isolation [19]. Similarly, modelling across populations of *Apolygus lucorum* showed that combined temperature–photoperiod responses vary geographically [20]. These findings indicate that apparent thermal plasticity can partly reflect the photoperiodic context in which temperatures are experienced.

Functional studies provide narrower mechanistic resolution. In the cabbage beetle *Colaphellus bowringi*, ecdysone deficiency promoted preparation for photoperiodic reproductive diapause, demonstrating an endocrine contribution to seasonal-state regulation [21]. In *Bombyx mori*, disruption of positive and negative elements of the circadian clock interfered with photoperiodic diapause induction [22]. Such experiments provide direct evidence for mechanistic components within particular species, but they do not establish that the same pathway determines climatic phenology across insect orders.

The resulting interpretation is that photoperiod can act as a seasonal boundary condition on temperature-sensitive development. Under novel climatic combinations, temperature may increasingly indicate conditions that are inconsistent with historically reliable day-length cues. Whether this produces stronger plasticity, constrained response or maladaptive timing depends on species-specific cue integration and life-history architecture.

Plasticity magnitude

Phenological plasticity cannot be represented adequately by the direction of change alone. Its magnitude depends on the environmental range examined, the phenophase measured, the temporal and spatial scale of exposure, and the biological unit under comparison. Climatic variation and functional traits predict substantial differences in bee phenology, illustrating that even within one broad functional group, seasonal responsiveness is heterogeneous [23].

Three dimensions are therefore required to interpret magnitude. First, response amplitude describes how much timing changes across an environmental contrast. Second, response consistency asks whether the direction is retained across locations, years or life stages. Third, ecological translation asks whether the observed timing

difference changes synchrony, performance or population processes. These dimensions constitute a proposed interpretive classification rather than a standardized empirical score.

Magnitude can also be misestimated when environmental exposure is poorly represented. A large shift relative to regional mean temperature may actually reflect microclimatic divergence, whereas a small shift may indicate either genuine constraint or an inappropriate environmental predictor. Likewise, concordance between plastic and selected phenology in one taxon cannot be generalized to imply adaptive plasticity elsewhere.

Table 2 distinguishes these states without converting plasticity into an unsupported ranking system.

Table 2. Proposed state-and-response ledger for interpreting phenological plasticity magnitude

Plasticity magnitude state	Article-specific dimension	Scientific content
High response amplitude	**Biological context · Evidence basis · Biological setting · Evidence**	Strong timing shift across environmental contrast Large within-population change in measured phenophase
	Interpretation	Strong environmental sensitivity is plausible
	Boundary condition	May depend on exposure range or nonlinear development
	Research or test · Status · Evidential standing	Test across realistic microclimates and multiple years Proposed interpretive state
Low response amplitude	**Biological context · Evidence basis · Biological setting · Evidence**	Small measured timing change Weak phenological displacement despite environmental variation
	Interpretation	Could indicate constraint, buffering or poor predictor choice
	Boundary condition	Cannot distinguish mechanisms without physiological evidence
	Research or test · Status · Evidential standing	Measure experienced rather than ambient environment Proposed interpretive state
Directionally consistent response	**Biological context · Evidence basis · Biological setting · Evidence**	Similar shift across settings Repeated advance or delay
	Interpretation	Greater generality of cue-response relationship is plausible
	Boundary condition	Consistency does not establish fitness benefit
	Research or test · Status · Evidential standing	Replicate across populations and life stages Proposed interpretive state
Directionally discordant response	**Biological context · Evidence basis · Biological setting · Evidence**	Advance in some contexts, delay in others Sign reversal among sites, years or taxa
	Interpretation	Interaction terms or alternative cues are likely important
	Boundary condition	Averaging may erase biologically meaningful heterogeneity
	Research or test · Status · Evidential standing	Model cue interactions explicitly Proposed interpretive state
Large timing shift without ecological translation	**Biological context · Evidence basis · Biological setting · Evidence**	Pronounced phenological movement but stable performance or overlap Timing changes without demonstrated downstream effect
	Interpretation	Phenological plasticity is present, ecological consequence uncertain
	Boundary condition	Trait response must not substitute for fitness inference
	Research or test · Status · Evidential standing	Measure interaction overlap and demographic endpoints Proposed interpretive state
Moderate shift with strong interaction consequence	**Biological context · Evidence basis · Biological setting · Evidence**	Limited timing change creates large relative change between species Small phenological displacement alters synchrony
	Interpretation	Ecological importance depends on relative rather than absolute timing

	Boundary condition	Requires matched phenophase data from interacting taxa
	Research or test · Status · Evidential standing	Test coupled reaction norms of interacting species Proposed interpretive state

Phenological responsiveness is bounded by biological architecture as well as environmental exposure. Diapause traits can evolve rapidly among geographically differentiated populations, as demonstrated during range expansion of *Aedes albopictus* [24]. Such genetically based divergence must be distinguished from within-generation plasticity because similar seasonal phenotypes can arise through different processes. In *Drosophila melanogaster*, diapause-associated variation also has a complex spatial and temporal genetic basis, arguing against simple attribution of seasonal timing to a single locus or pathway [25].

Functional and evolutionary genetics therefore address different questions: the former identifies components capable of modifying seasonal states, whereas the latter asks how variation is maintained or differentiated among populations [26]. Together with the endocrine and circadian evidence discussed above, these studies indicate that plasticity can be physiologically constrained even when thermal conditions favour a timing shift.

Table 3 separates mechanisms that generate seasonal responsiveness from boundaries that restrict what can be inferred from them.

Table 3. Mechanism–boundary distinctions governing physiological and genetic limits on phenological response

Constraint or mechanism	Dimension	Scientific content	Dimension	Scientific content
Genetically differentiated diapause	**Biological context · Evidential basis · Biological setting · Evidence**	Geographic populations Population-level divergence in seasonal traits	**Principal boundary · Required test · Principal limit**	Must not be labelled immediate plasticity Common-environment and multigeneration comparison
	Phenological interpretation	Similar timing can reflect evolved differentiation		
Polygenic seasonal architecture	**Biological context · Evidential basis · Biological setting · Evidence**	Population genomic context Multiple spatially and temporally variable genetic signals	**Principal boundary · Required test · Principal limit**	Association does not identify a universal causal locus Functional validation across populations
	Phenological interpretation	Seasonal response may have distributed genetic control		
Endocrine state regulation	**Biological context · Evidential basis · Biological setting · Evidence**	Diapause-capable insects Experimental perturbation of hormonal signalling	**Principal boundary · Required test · Principal limit**	Species-specific mechanism Couple endocrine manipulation to field-relevant timing
	Phenological interpretation	Internal state can constrain environmental responsiveness		
Circadian/photoperiodic machinery	**Biological context · Evidential basis · Biological setting · Evidence**	Photoperiod-sensitive development Functional disruption of clock components	**Principal boundary · Required test · Principal limit**	Mechanism may differ among orders Cross-taxon functional comparison
	Phenological interpretation	Seasonal timing can depend on cue-processing architecture		
Cue–genotype interaction	**Biological context · Evidential basis · Biological setting · Evidence**	Proposed synthesis across evidence classes Environmentally expressed timing within genetically structured systems	**Principal boundary · Required test · Principal limit**	Phenotype alone cannot identify the generating process Reaction norms across replicated genotypes and environments

	Phenological interpretation	Observed phenology can combine plastic and inherited components

Ecological mismatch and population consequences

Phenological change becomes ecologically consequential only when it modifies the timing of interactions and when altered interactions affect performance or population processes. Temperature can act directly on insects while simultaneously changing relative timing among hosts, prey, predators, parasitoids or mutualists [27]. Consequently, mismatch is better treated as a relationship between phenophases than as a property of one species. Community context can modify that relationship. Experimental and modelling work with host–parasitoid systems shows that alternative community pathways can buffer or redirect consequences expected from pairwise mismatch [28]. In butterfly–host-plant interactions, spring temperature altered synchrony, demonstrating that relative phenology is sensitive to the responses of both partners rather than the insect alone [29].

Importantly, altered timing does not guarantee demographic harm. A long-term sycamore–aphid–parasitoid study found phenological changes without the straightforward population decline expected from a simple mismatch model, with population regulation providing an important interpretive boundary [30]. Plant–pollinator analyses likewise indicate that warming can sometimes increase temporal overlap rather than reduce it [31]. Changes in alpine bumble-bee communities were not completely explained by phenological mismatch, reinforcing the need to retain alternative ecological drivers [32].

Phenological sensitivity can nevertheless alter ecological exposure. Historical plant–herbivore analyses linked temperature-sensitive phenology with herbivory patterns [33], whereas experimental warming in an eastern spruce budworm system improved host synchrony and insect performance under the conditions studied [34]. Thus, both detrimental and favourable outcomes are possible, and neither direction should be inferred from timing alone.

The principal interpretive difficulty is deciding when a measured timing shift constitutes meaningful mismatch and when that mismatch can legitimately be extended to performance or population consequence. **Figure 1** triages these inference transitions explicitly.

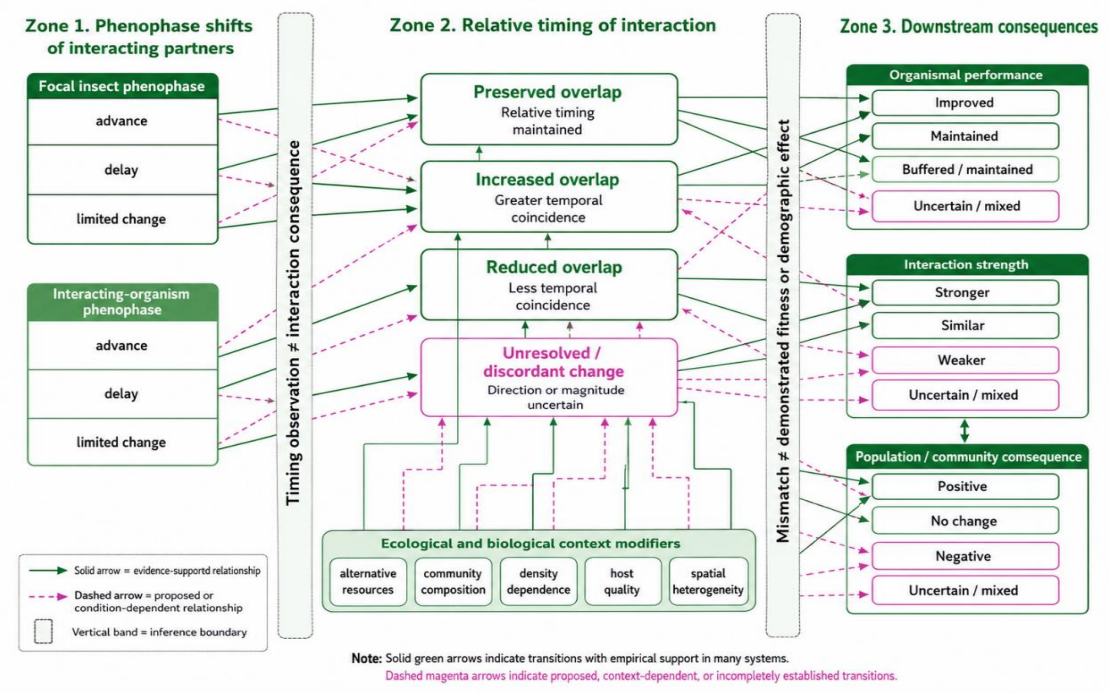


Figure 1. Phenological discordance branches among altered overlap, ecological buffering, performance change, and demographic consequence

The evidence supports a hierarchical interpretation of insect phenological plasticity rather than a universal warming-response rule. Thermal exposure can alter development, but microclimate and nonlinear performance

determine what temperature an organism effectively experiences. Photoperiod and diapause systems can further constrain thermal responsiveness, while genetic differentiation can generate seasonal differences that superficially resemble plasticity. At the ecological level, the relevant variable becomes relative timing between interacting organisms rather than the absolute phenology of either species.

We therefore propose six inference levels: climatic exposure → cue integration → phenotypic timing → interaction overlap → organismal performance → population or community consequence. Evidence at one level does not automatically validate the next. Weather–phenology associations do not alone identify mechanism [4]; validated developmental thermal models remain taxonomically bounded [11]; concordance between plasticity and selection does not establish that all plasticity is adaptive [15]; and community context can substantially alter the ecological effects of mismatch [28]. Long-term population evidence further shows that altered relative timing may be buffered rather than translated directly into demographic decline [30]. Community change likewise may involve mechanisms additional to phenological discordance [32].

Table 4 converts this hierarchy into a cross-scale evidence grid that makes the principal inference boundaries explicit.

Table 4. Cross-scale evidence grid for deciding how far a phenological observation can support ecological inference

Inference level	Climatic exposure	Cue integration	Phenotypic timing	Interaction overlap	Organismal performance	Population/community consequence
Typical observable	Ambient or microclimatic temperature, weather anomaly, photoperiod	Developmental, endocrine or photoperiodic response	Emergence, flight, diapause termination, voltinism	Relative timing of consumer–resource or antagonist phenophases	Survival, condition, development or reproductive performance	Abundance, persistence, interaction structure
Permitted interpretation · Principal competing explanation	Environmental conditions capable of influencing timing Behavioural or microhabitat buffering	Biological processing of seasonal information Alternative cue combinations	Realized seasonal phenotype Population differentiation or sampling bias	Potential synchrony or mismatch Alternative resources and spatial overlap	Individual-level consequence Density dependence and compensation	Higher-level ecological outcome Habitat change, range shifts, community turnover
Major boundary · Validation needed	Ambient conditions may differ from experienced exposure Organism-relevant exposure measurement	Mechanism may be species- or stage-specific Functional and cross-context tests	Timing alone does not identify plastic versus genetic origin Repeated reaction norms/common environment	Overlap is not equivalent to performance Direct interaction measurements	Individual effects need not scale to populations Demographic linkage	Multiple simultaneous drivers Long-term multicausal analysis

Knowledge gaps

Future work should prioritize environmental variability rather than climatic means alone, particularly sequences of extremes and fluctuating microclimates. Photoperiod–temperature combinations deserve greater attention because historically correlated cues may become increasingly discordant. Stage- and sex-specific reaction norms are also needed to determine whether adult occurrence records represent developmental plasticity or only one component of seasonal expression.

Mechanistic studies should connect endocrine, circadian and genetic processes to field phenology without assuming cross-taxon generality. Long-term studies should measure interacting phenophases together and extend beyond synchrony to performance, reproduction and population dynamics. Laboratory-derived thermal models require independent field validation, while tropical, low-latitude and taxonomically underrepresented systems remain particularly important for testing whether conclusions drawn largely from temperate insects transfer across climatic regimes.

Finally, distinguishing plasticity from rapid evolutionary change requires replicated genotypes, populations and environments rather than phenological trajectories alone. The proposed inference hierarchy should therefore be treated as a testable organizational scheme, not as a validated predictive model.

Conclusion

Insect phenological responses to increasing climate variability arise from interacting thermal exposure, photoperiodic regulation, developmental physiology, genetic architecture and ecological context. Their direction and magnitude are neither uniform nor automatically adaptive. A phenological shift becomes ecologically meaningful only when the successive transitions from cue exposure to interaction timing, performance and population consequence are demonstrated. Preserving these inference boundaries provides a more defensible basis for interpreting insect seasonal change under increasingly variable climates.

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