Eurasia Specialized Veterinary Publication

Entomological Research Letters

ISSN: 3108-639X

2023, Volume 3, Issue 1, Page No: 44-55
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Available online at: www.esvpub.com/

Insect Phenology Emerges from Interactions Among Developmental Thresholds, Dormancy Decisions, and Seasonal Resource Availability

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ABSTRACT

Insect phenology is commonly represented as the calendar expression of temperature-dependent development, yet seasonal timing is generated by several biologically distinct processes that need not respond to environmental change in parallel. Developmental progression depends on stage-specific thermal responses; dormancy can interrupt otherwise permissive development through photoperiodic, thermal, and internally regulated decisions; and successful seasonal activity additionally requires that external resources and internal energetic state remain compatible with developmental demand. These components operate on different temporal scales and differ in the reliability of the cues governing them. This article develops a proposed phenological-component architecture that treats developmental thresholds, dormancy entry and exit, resource timing, and cue reliability as interacting but analytically separable determinants of insect seasonal timing. The framework distinguishes physiological readiness from calendar occurrence, dormancy state from simple developmental delay, external resource availability from stored energetic capacity, and an environmental cue from the future condition that the cue predicts. It further proposes that phenological outcomes emerge when these components converge, rather than from any component acting as a universally dominant clock. This view accommodates apparently conflicting responses to warming, including advancement, delay, altered voltinism, prolonged or shortened seasonal activity, and variable trophic synchrony. The architecture is intended as a hypothesis-generating synthesis rather than a validated forecasting model. Its transfer requires explicit attention to life stage, population, latitude, microclimate, resource ecology, cue regime, and the distinction between laboratory responses and field phenology.

Keywords: Insect phenology, Developmental thresholds, Diapause, photoperiod, Seasonal resources, Cue reliability

Received: 01 February 2023
Revised: 04 April 2023
Accepted: 07 April 2023

How to Cite This Article: Hassan L, Khalaf O, Jaber R, Mostafa R. Insect Phenology Emerges from Interactions Among Developmental Thresholds, Dormancy Decisions, and Seasonal Resource Availability. Entomol Res Lett. 2023;3(1):44-55. https://doi.org/10.51847/pJ0Prinv93

Introduction

Phenology records when biological events occur, but an observed emergence date, flight period, diapause transition, or generation boundary is the endpoint of several processes rather than a direct measurement of a single seasonal clock. Temperature-sensitive development can generate substantial variation in insect timing, and differences in developmental sensitivity help explain why phenological responses vary among populations, stages, species, and locations [1]. Dormancy adds a qualitatively different control because diapause is a regulated

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developmental state rather than simply slow development under unfavorable conditions [2]. Consequently, identical accumulated thermal exposure can produce different calendar outcomes when individuals differ in whether development is permitted to proceed.

Timing is also relational. A phenological shift matters ecologically when the timing of an insect changes relative to a resource, antagonist, mutualist, or another life-history requirement. Phenological mismatch therefore concerns the relative timing between interacting biological demands and opportunities, not merely whether one species becomes earlier or later [3]. In insects, altered thermal regimes may act directly through physiological stress and development while also acting indirectly through host quality, trophic timing, or natural-enemy activity; those pathways can differ in direction and magnitude [4]. A temperature-only representation may consequently fit one developmental interval yet fail to explain whether the resulting life stage occurs in a biologically usable seasonal environment.

The inferential problem is thus not whether temperature, dormancy, or resources affect insect phenology. Each is well supported in appropriate systems. The unresolved problem is how to organize them without treating distinct processes as interchangeable predictors. A developmental threshold describes conditions under which development can progress; a dormancy decision describes whether developmental progression is suspended or resumed; resource timing describes whether the requirements of the resulting stage can be met; and cue reliability describes how well an organism's information about season predicts those future conditions.

This article therefore proposes that insect phenology should be interpreted as an emergent property of interactions among these components. The proposed architecture is deliberately non-additive: it does not assign universal weights or scores to temperature, photoperiod, dormancy, or resources. Instead, it asks which component constrains timing in a particular life stage, population, and environment, whether the relevant cues remain informative, and where one component can override or decouple another. This distinction is especially important under environmental change because developmental acceleration does not necessarily imply earlier ecological opportunity, and altered seasonal conditions need not shift dormancy, resources, and development at identical rates.

Materials and Methods

Phenological component decomposition

A conceptual phenological-component decomposition was used to separate processes that are often combined when seasonal timing is represented by a single date or degree-day total. The unit of interpretation was not the calendar date itself but the biological transition producing that date. Four components were distinguished: developmental progression, dormancy state transitions, resource compatibility, and cue reliability. A fifth analytical dimension—scale—was applied across all four components to preserve differences among developmental stage, individual physiological state, population, microhabitat, and geographic setting.

Developmental progression was treated as a temperature-sensitive process only within the domain in which the relevant thermal response is biologically appropriate. Experiments with *Pieris napi* show that development measured under constant temperatures can predict development in naturally variable thermal environments when nonlinear thermal responses and realistic microclimate variation are represented [5]. This supports mechanistic transfer under specified conditions rather than a general assumption that laboratory degree-day relationships automatically reproduce field phenology. Field-based work further shows that microclimatic variation can alter development timing, synchrony, and voltinism within an insect population [6]. Accordingly, coarse environmental temperature and experienced developmental temperature were kept conceptually separate.

Life stage was likewise retained rather than averaged away. Thermal sensitivity can differ across ontogeny, while the evidence needed to compare stages is itself uneven among taxa and endpoints [7]. The decomposition therefore does not assume that a threshold estimated for eggs, larvae, pupae, or adults is transferable to another stage.

Dormancy was classified separately from thermal development because entry, maintenance, and termination can involve different environmental signals and physiological states. Resource compatibility was defined at two levels: availability of the external seasonal resource required by the active stage and availability of internal reserves accumulated before periods of restricted acquisition. Cue reliability was defined as the correspondence between a perceived seasonal signal and the later environmental condition for which that signal is informative. These definitions provide the analytical basis for interpreting the evidence below; they do not constitute empirically validated universal state variables.

Results and Discussion

Thermal development models are attractive because temperature frequently changes developmental rate in predictable ways. The limitation is not the existence of thermal dependence but the interpretation of a threshold outside the conditions in which it was estimated. In *P. napi*, models derived from constant-temperature development performed well under naturally variable microclimates when nonlinear responses and realistic temporal variation were retained [5]. This indicates that controlled thermal measurements can be ecologically informative, while also showing why transfer depends on representing the temperature actually experienced by the insect.

Spatial scale changes that exposure. Microclimatic heterogeneity can shift the timing of development and influence synchrony and the number of generations potentially completed within a season [6]. A weather-station temperature therefore cannot be assumed to correspond to the thermal history of insects occupying different host surfaces, vegetation strata, orientations, or sheltered microhabitats. Developmental threshold estimation and phenological forecasting are separate inferential steps.

Ontogeny creates a second boundary. Temperature sensitivity is not necessarily conserved across the insect life cycle [7]. An egg-to-adult developmental total can conceal a stage that is disproportionately sensitive to temperature, while a stage-specific estimate can omit carry-through consequences for later timing. The biologically relevant question is therefore not simply whether a thermal threshold exists, but which developmental transition it describes.

These observations support a proposed distinction between a developmental-permission threshold and a phenological-realization condition. The first concerns whether temperature permits development at a particular stage; the second concerns whether all other state requirements allow that development to generate the observed seasonal event. Temperature-sensitive development remains a central component of insect phenology [1], but developmental acceleration alone does not establish that diapause has ended, that a resource is available, or that the resulting stage will be synchronized with its ecological context.

Dormancy entry and exit

Dormancy changes the meaning of developmental temperature because organisms in diapause do not simply follow the same developmental trajectory at a slower rate. Across univoltine and semivoltine insects, diapause can occupy different life stages and can structure seasonal or multi-year life cycles in markedly different ways [8]. Its placement within the life cycle must therefore be known before thermal accumulation is interpreted as progress toward a phenological event.

Entry itself commonly depends on more than one signal. In *Apolygus lucorum*, experimentally measured diapause induction varied jointly with photoperiod, temperature, and latitude, demonstrating that one fixed day-length rule would not reproduce all population responses [9]. In the migratory locust, embryonic diapause depends on cue exposure distributed across generations and stages: parental photoperiod and the subsequent thermal environment of eggs contribute differently to induction and termination [10]. These systems show why “the diapause threshold” can conceal both the identity of the responsive stage and the temporal location of cue perception.

Mechanistic evidence also demonstrates integration rather than a purely external switch. In female *Drosophila melanogaster*, EYES ABSENT and TIMELESS participate in the integration of seasonal photoperiodic and thermal information [11]. Subsequent work linked seasonal cue processing to the circadian system and pigment-dispersing factor, with downstream physiological responses involving both EYES ABSENT-dependent and additional pathways [12]. In *Bombyx mori*, disruption of positive or negative circadian-clock components altered appropriate photoperiodic induction of maternal diapause programming [13]. These studies establish specific molecular relationships in particular insect systems; they do not justify a universal molecular pathway for insect diapause.

Population history further changes seasonal interpretation. During climate-associated range expansion of *Lasiommata megera*, northern populations differed from southern populations in photoperiodic responses, although the pattern was not identical in an isolated population [14]. Thus, geographical position cannot substitute automatically for the reaction norm actually expressed by a population.

For interpretation, the important distinction is between entry competence, diapause commitment, maintenance, and exit competence. These states may be informed by different signals and may occur in different tissues, stages,

or generations. **Table 1** organizes those distinctions because a single prose description can otherwise make biologically different dormancy transitions appear equivalent.

Table 1. Dormancy transitions require different evidence: a context–mechanism–outcome register for interpreting seasonal entry and exit

	Regulated event		Seasonal calibration	Validation	
Dormancy transition	**Cue-processing evidence**	**Phenological effect**	**Seasonal context**	**Experiment across the transition**	**Uncertainty**
Entry					
Photoperiod-conditioned entry	Reaction of diapause incidence to day length	Calendar timing can be gated before temperature becomes developmentally limiting	Population- and latitude-dependent seasonal insects	Estimate population-specific reaction norms under realistic seasonal trajectories	Critical responses need not transfer among populations
Thermal modulation of entry	Diapause response across combined temperature and light regimes	Thermal exposure may strengthen, weaken, or override a photoperiodic tendency	Species in which temperature modifies photoperiodic response	Cross factorial temperature × photoperiod designs	Direction and magnitude are taxon- and regime-specific
Cross-stage and clock-linked processing					
Cross-stage cue integration	Cue applied in one stage; dormancy expressed in another	The phenological decision may precede the stage in which arrest is observed	Maternal or parental cue perception with offspring diapause expression	Track cue exposure and response across generations/stages	Adult and embryonic environments must not be conflated
Circadian-linked seasonal processing	Molecular perturbation plus seasonal physiological response	Photoperiodic information can be transduced through defined timing machinery	Systems with experimentally implicated clock components	Replicate across taxa and separate clock effects from downstream state effects	Molecular architecture demonstrated in one taxon is not universal
Population calibration					
Population-specific seasonal calibration	Common-environment differences in seasonal reaction norms	Identical calendar or day length can encode different seasonal decisions	Populations spanning latitudinal or range-front environments	Compare multiple populations rather than infer from latitude alone	Geographic patterns may contain local exceptions
Exit competence					
Exit competence	Resumption under permissive thermal/seasonal conditions	Ending dormancy is distinct from subsequent developmental rate	Post-diapause or terminating dormant stage	Measure state transition separately from post-transition development	Termination cue and post-diapause development may be experimentally confounded

Note: The categories organize evidence-supported distinctions but do not constitute universal diapause stages or numerical decision thresholds. Their use as a common interpretive register is proposed here.

Resource timing

Phenological opportunity begins only when the conditions required by the active stage are available. For trophically dependent insects, external resource timing can therefore change the consequence of a developmental shift even when the insect's own development is accurately predicted. Mismatch is fundamentally relational: advancement of an insect is neither beneficial nor detrimental by itself unless the timing of its biological demands is considered relative to the relevant resource or interaction partner [3]. Temperature can additionally alter host quality and trophic interactions in directions that are not uniform among systems [4].

Resources also have an internal temporal dimension. Nutritional state can influence diapause-related responses, but evidence does not support treating “more stored energy” as a universal switch controlling dormancy. A synthesis of insect nutritional status and diapause distinguishes chronic nutritional conditions, acute deprivation, diapause entry, and diapause duration, emphasizing that effects vary with context and that several proposed

relationships remain insufficiently tested [15]. Once overwintering begins, stored lipids are nevertheless a major energetic resource in many insects, and reserve acquisition, use, and postwinter condition can connect autumnal resource history with spring performance [16].

The timing of acquisition and expenditure can therefore matter independently of the calendar date at which dormancy is observed. Experimental work on diapausing *P. napi* showed that longer and warmer prewinter conditions increased energetic expenditure and produced postwinter consequences, demonstrating that the thermal history before winter can alter the state carried through dormancy [17]. In *Culex pipiens pipiens*, experimental microbiome reduction impaired diapause-associated lipid accumulation and survival while ovarian arrest remained evident [18]. Dormancy status and energetic preparedness can thus become partially decoupled.

The proposed synthesis is a resource-compatibility boundary: phenological realization requires not only developmental and dormancy permission but sufficient correspondence between stage-specific demand, external resource opportunity, and internal physiological reserves. This is not a universal energetic threshold. It is a boundary for interpretation, especially where insects can reach an apparently appropriate seasonal state while carrying inadequate reserves or encountering an altered external resource window.

Figure 1 shows that resource timing links environmental opportunity, developmental state, dormancy, and stored physiological capacity across different scales; representing those relations as a single chronological sequence would incorrectly imply that each always follows the previous one.

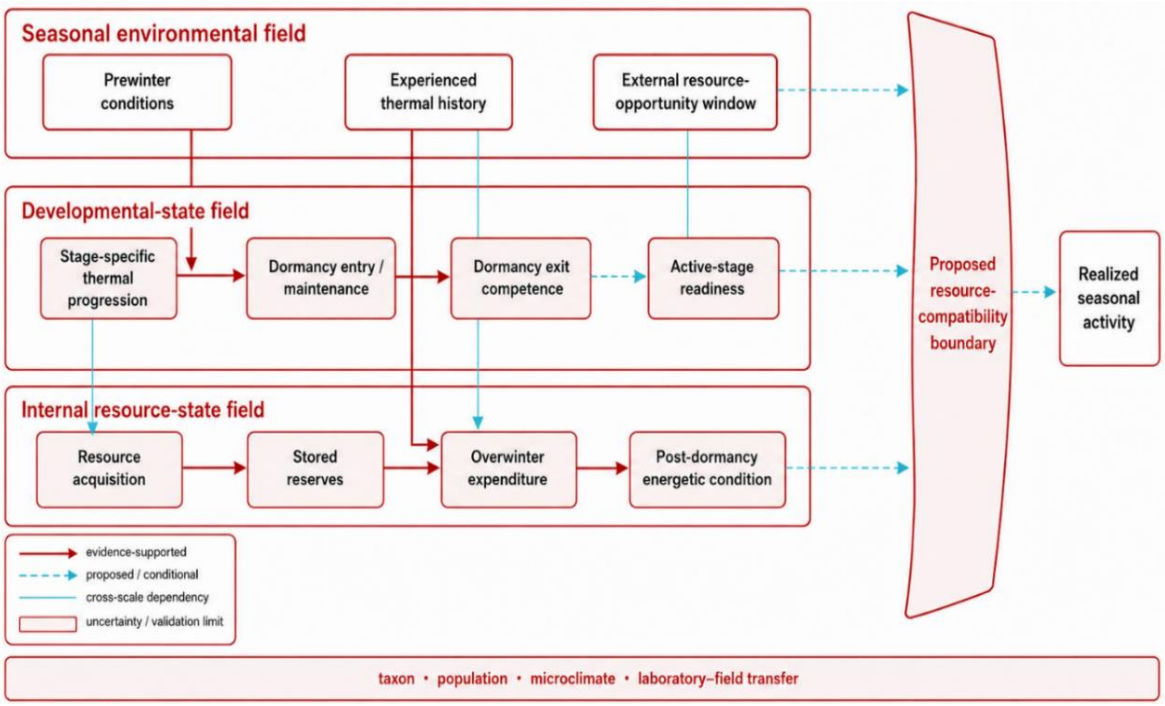


Figure 1. Resource windows and physiological reserves create separate seasonal boundaries around developmental readiness

Cue reliability

A seasonal cue should not be equated with the environmental condition to which the organism ultimately responds. Photoperiod is highly regular astronomically, but biological reliability concerns whether a given photoperiodic signal continues to predict the temperature, resource state, or seasonal interval for which the response is useful. This distinction becomes especially important when different environmental dimensions change at different rates. Even the form of photoperiod exposure matters. Daily increasing or decreasing photoperiod altered developmental and stress-related traits in four *Drosophila* species, but both the number of responsive traits and the direction of responses differed among species and traits [19]. Thus, day length is not a universal instruction with a uniform organismal output. Experimental cue reliability must consider whether the organism experiences a fixed photoperiod, a directional seasonal trajectory, or another temporal structure.

Human alteration can change cue exposure without changing astronomical season. In female *Culex pipiens*, dim artificial light at night under short-day conditions reduced normal diapause-associated characteristics and

permitted reproductive activity [20]. This demonstrates a concrete route by which an otherwise seasonally informative light regime can be modified at the organismal level. It does not imply that all insects respond similarly to light pollution.

Temperature can also alter how a photoperiodic cue is expressed. Across geographically distributed strains of *Drosophila montana*, the temperature above which normal photoperiodic regulation of reproductive diapause was disrupted varied with latitude and covaried with photoperiodic characteristics [21]. Cue interpretation therefore depends on population-specific reaction norms rather than photoperiod alone.

The consequence becomes clear in phenological forecasting. For the introduced psyllid *Aphalara itadori*, a model combining experimentally determined photoperiodic diapause responses with temperature-dependent development produced geographic predictions of attempted voltinism and mismatch that differed substantially from degree-day expectations alone [22]. The relevant principle is not that this particular model transfers to other insects, but that thermal opportunity and photoperiodic permission can encode different seasonal information.

Temperature itself has an observation-scale problem. Fine-scale insect microclimates may differ substantially from the climate variables typically supplied to ecological models, and some microhabitats can buffer whereas others can magnify background thermal conditions [23]. Winter further illustrates why a nominal cue–season relationship cannot be presumed stable: changing mean temperatures, extremes, snow cover, and seasonal duration can alter overwintering conditions in different combinations, while spring phenological responses remain heterogeneous [24].

The proposed framework therefore treats cue reliability as a relationship, not an intrinsic property of "temperature" or "photoperiod." A cue is reliable only with respect to a specified future state, population, developmental decision, and environmental context. **Table 2** maps where current evidence directly links cues to responses and where inference to future resource or fitness conditions remains incomplete.

Table 2. When a seasonal signal is informative—and when it is not: coverage and gaps in cue reliability

Astronomical and conditionally expressed cues			
Cue-reliability dimension	**Directional photoperiod**	**Artificially altered light signal**	**Temperature-dependent photoperiodic expression**
Observed cue relationship	Trait responses under increasing, decreasing, and constant light schedules	Diapause-associated and reproductive traits under short days with night lighting	Joint photoperiodic and temperature response curves
Phenological meaning	Organisms may respond to seasonal trajectory, not only absolute day length	Perceived photoperiod can diverge from astronomical photoperiod	The same day length can have different effects at different temperatures and latitudes
Taxonomic setting	Multiple Drosophila species	Temperate female Culex mosquitoes	Geographic Drosophila montana populations
Coverage gap	Responses are species- and trait-specific	Field intensity, timing, spectral composition, and taxonomic transfer	Reaction norms may change among populations and environments
Required test	Compare realistic directional light regimes across taxa and life stages	Couple field light exposure with seasonal state measurements	Estimate joint rather than single-cue reaction surfaces

Discordant and changing environments			
Cue-reliability dimension	**Thermal–photoperiodic disagreement**	**Microclimatic cue mismatch**	**Changing winter cue environment**
Observed cue relationship	Development model combined with experimentally measured diapause response	Fine-scale thermal exposure differing from coarse climate	Shifts in temperature regime, snow cover, and seasonal duration
Phenological meaning	Thermal opportunity can imply an extra generation while photoperiodic state prevents it	Modeled "temperature cue" may not equal experienced temperature	Historical cue–condition associations may change without a single directional response
Taxonomic setting	Short-day diapausing introduced insect	Small insects occupying heterogeneous microhabitats	Temperate overwintering insects

Coverage gap	Transfer depends on the species' actual dormancy architecture	Sparse measurements at organism-relevant scales	Demographic and evolutionary consequences remain taxon-dependent
Required test	Validate combined models against field life-cycle transitions	Resolve exposure at the relevant body-size and microhabitat scale	Link winter cue history, diapause transitions, spring timing, and subsequent performance

Note: "Cue reliability" is used here as a proposed relational classification. The table does not rank cues, assign reliability scores, or imply that any signal is universally reliable or unreliable.

Interaction among thermal, photoperiodic, and resource signals

Thermal development, photoperiodic regulation, and resource timing should not be interpreted as independent additive predictors. Their biological roles differ: temperature can regulate developmental rate, photoperiod can gate entry into or release from a seasonal developmental program, and resources determine whether a developmentally available stage encounters a usable ecological opportunity. The consequence of changing one component therefore depends on the states of the others.

Community context illustrates this conditionality. In experimental *Drosophila*–parasitoid systems, warming shortened the period during which hosts were susceptible, yet alternative host species extended temporal overlap and sustained interactions across a broader range of phenological shifts. Warming simultaneously reduced parasitoid performance, showing that additional resource pathways could buffer temporal mismatch without eliminating direct thermal effects [25]. Phenological correspondence can similarly change at a community scale: climate-associated changes in alpine bumble-bee communities involved both altered bee activity and changing floral-resource relationships, while species turnover further complicated a simple insect-versus-resource interpretation [26].

Within a single species, apparently greater thermal opportunity can also have opposing consequences. Photothermal and demographic modelling of *Pieris oleracea* indicated that earlier seasonal development could permit an additional completed generation in some environments but initiate a final generation that could not complete development before seasonal deterioration elsewhere [27]. The distinction depends on the remaining seasonal window and diapause regulation, not on developmental acceleration alone.

The proposed synthesis therefore treats thermal accumulation as developmental opportunity, photoperiodic or dormancy regulation as seasonal permission, and resource state as ecological compatibility. None is assigned a universal hierarchy. A component becomes limiting only in relation to the current developmental state and the other components operating at that time.

Emergent phenological architecture

The evidence assembled above supports a proposed emergent phenological architecture in which observed timing is the realized outcome of several partially independent states. The architecture distinguishes developmental readiness, dormancy permission, cue reliability, resource compatibility, remaining seasonal opportunity, and the timing of interacting organisms. These states can converge or become discordant.

Five interpretive states are proposed. In a concordant state, thermal development, dormancy status, and resource timing permit the same seasonal transition. In a constraint-dominant state, one component prevents realization despite permissive values in others—for example, adequate thermal accumulation while photoperiod maintains diapause. In a cue-discordant state, environmental signals point toward different seasonal responses. In a compensated state, shifts in separate components reduce rather than magnify temporal separation. Finally, an interaction-exposed state occurs when internal developmental timing is realized but becomes ecologically consequential because the resource, host, prey, predator, parasitoid, or mutualist follows a different trajectory. These categories are analytical constructs, not mutually exhaustive biological classes or validated predictive states.

This architecture also separates phenological occurrence from demographic consequence. Combined photoperiod–temperature models already demonstrate that potential thermal generations and attempted generations can diverge [22], while demographic modelling shows that an apparently similar extension of seasonal development may produce either completion or a developmental trap [27]. Consequently, observed advancement is insufficient by itself to infer benefit, cost, adaptation, or population growth.

The alternative interpretations are most efficiently distinguished as an adjudication problem rather than as a list of climatic drivers.

Table 3. Adjudicating identical calendar shifts produced by different phenological architectures

Concordance and constraint			
Concordant state			
Seasonal configuration	Developmental readiness, dormancy permission and resource opportunity shift compatibly		
Calendar signature	Parallel stage and environmental timing		
Seasonal transition is jointly permissive			**Architecture-specific interpretation**
Boundary	Concordance may be temporary or population-specific	**Observation needed**	Track all component states through the same seasonal interval
Constraint-dominant state			
Seasonal configuration	One component remains restrictive while others are permissive		
Calendar signature	Development proceeds toward a transition that is not realized		
The restrictive component, not accumulated warmth alone, governs timing			**Architecture-specific interpretation**
Boundary	Identity of the limiting component may change among stages	**Observation needed**	Manipulate the candidate constraint independently
Discordance and compensation			
Cue-discordant state			
Seasonal configuration	Thermal and photoperiodic or resource signals imply different seasonal responses		
Calendar signature	Divergent cue trajectories or response curves		
Historical cue–condition correspondence may be weakened			**Architecture-specific interpretation**
Boundary	Discordance does not establish maladaptation	**Observation needed**	Measure perceived cue and subsequent environmental state separately
Compensated state			
Seasonal configuration	Component shifts partly offset one another		
Calendar signature	Relative timing remains stable or becomes closer despite environmental change		
Warming need not increase mismatch			**Architecture-specific interpretation**
Boundary	Compensation may conceal physiological costs	**Observation needed**	Measure both synchrony and component-specific performance
Interaction and seasonal completion			
Interaction-exposed state			
Seasonal configuration	Insect timing is realized but partner timing diverges		
Calendar signature	Reduced overlap with a necessary interacting stage or resource		
Phenological change acquires ecological consequence			**Architecture-specific interpretation**
Boundary	Pairwise mismatch may be altered by community alternatives	**Observation needed**	Quantify interaction strength and alternative-resource availability
Seasonal-completion boundary			
Seasonal configuration	Development begins under permissive conditions but remaining season is insufficient		
Calendar signature	Late-stage development extends toward seasonal deterioration		
Additional thermal opportunity can become a developmental trap			**Architecture-specific interpretation**

Boundary	Outcome depends on population, latitude and diapause reaction norm	**Observation needed**	Couple phenology with stage-specific demography

Note: The state labels and adjudication scheme are proposed synthesis. They carry no numerical score, imply no universal ordering, and require taxon- and population-specific validation.

Figure 2 integrates these states because the central argument depends on the relative timing of parallel signals and biological states rather than on a linear sequence of causal boxes.

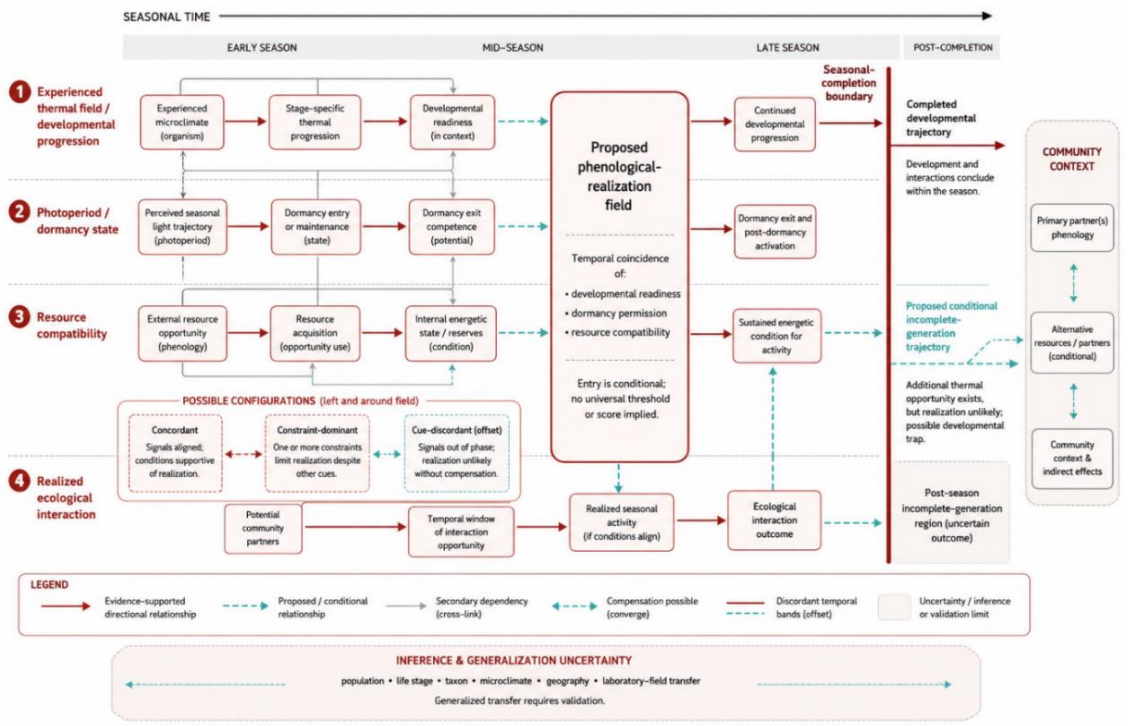


Figure 2. Seasonal timing is realized within a moving field of developmental permission, dormancy gating, and resource compatibility

Mismatch predictions

Phenological mismatch should therefore be predicted from relative component responses rather than from warming direction alone. Trophic reviews show that differential changes in seasonal activity can alter overlap among prey, predators, hosts, and parasitoids, but the ecological consequences remain interaction-specific [28]. The proposed architecture predicts greatest mismatch potential where interacting organisms depend on cues that change differently, where a dormancy gate prevents tracking of thermal conditions, or where resource phenology shifts independently of consumer development.

The opposite outcome is also possible. In controlled spruce–budworm–spruce systems, warming counteracted a defoliation-induced timing difference and increased herbivore–plant synchrony [29]. Thus, warming is not intrinsically a mismatch-generating force. Long-term comparisons across species interactions likewise show that synchrony has changed substantially in recent decades without a consistent global direction of change [30].

Three further predictions follow from the proposed framework. First, temperature-only forecasts should perform worst where photoperiodic regulation imposes a strong seasonal gate. Second, extension of thermal opportunity should generate different demographic outcomes depending on whether the final initiated generation can cross the seasonal-completion boundary [27]. Third, alternative resources may buffer loss of overlap in a focal pair while direct thermal effects on one partner persist [25]. Each prediction requires system-specific testing and should not be read as a universal response rule.

The central argument is that insect phenology is not a single temperature-driven trait but an observed outcome assembled from partially independent processes. Temperature-sensitive development remains indispensable, yet its seasonal expression depends on developmental stage and experienced microclimate [1]. Diapause can interrupt that progression through regulated entry, maintenance, and termination states [2]. Resource timing determines

whether an otherwise ready stage encounters ecological opportunity, while cue reliability determines whether signals such as photoperiod or temperature continue to anticipate the conditions for which seasonal responses are expressed.

This formulation helps explain why identical directional shifts need not have identical biological meanings. Earlier occurrence can reflect accelerated development, altered dormancy timing, changed resource correspondence, or combinations of these. Even a correctly predicted emergence date does not by itself establish improved performance or population benefit. Phenological mismatch similarly requires specification of the interacting stages and resources rather than simple comparison of annual dates [3].

The proposed architecture is intentionally bounded. Much mechanistic evidence comes from a limited set of temperate insects, including dipteran, lepidopteran, hemipteran, and orthopteran systems. Population reaction norms can differ geographically, and organism-experienced microclimates can depart markedly from coarse climatic records [23]. Laboratory manipulations are particularly valuable for identifying thermal and photoperiodic responses, but transfer to natural phenology requires realistic fluctuating exposures and independent field validation. Community context adds another limit because a pairwise mismatch can be buffered or amplified by alternative hosts, competitors, or direct physiological effects [25].

Validation should therefore measure the components simultaneously rather than infer them from a final calendar event. Stage-resolved studies should pair organism-relevant temperature histories with changing photoperiod, explicit diapause state, resource phenology or quality, internal energetic state where relevant, and realized interaction timing. Replication across populations and latitudes is necessary before a reaction norm is treated as geographically transferable. Demographic consequences should then be measured separately from timing itself because the same phenological advancement can correspond to successful additional development or failure to complete the season [27]. Finally, comparative tests should allow both increasing and decreasing synchrony because long-term interaction data do not support a universal directional expectation [30].

Conclusion

Insect seasonal timing is most defensibly interpreted as an emergent state produced by developmental opportunity, dormancy permission, resource compatibility, and the reliability of seasonal information. Separating these components prevents thermal acceleration from being mistaken for realized phenological opportunity and prevents phenological change from being equated automatically with mismatch, adaptation, or demographic benefit. The proposed architecture provides a testable way to identify which component constrains a seasonal transition, when environmental signals become discordant, and why warming can increase, decrease, or leave ecological synchrony comparatively unchanged. Its value depends on validation across stages, populations, taxa, microclimates, and interacting species rather than on assuming a universal insect seasonal clock.

Acknowledgments: None

Conflict of Interest: None

Financial Support: None

Ethics Statement: None

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