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Behavioral Heat Avoidance Can Scale from Individual Thermoregulation to Population Persistence and Geographic Range Stability

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ABSTRACT

Rising thermal exposure does not act on insects only through ambient climate. Fine-scale thermal heterogeneity, behavioral repositioning, and the timing of activity jointly determine realized exposure, yet these individual-level processes are often interpreted too quickly as evidence of demographic or range-level resilience. This article develops a proposed Cross-Scale Thermal Buffering Model that separates seven inferential stages: availability of usable microclimates, detection of thermal heterogeneity, behavioral avoidance, reduction of realized heat load, preservation of performance, net demographic consequences after activity-time costs, and eventual implications for population persistence and geographic range stability. The framework organizes evidence without treating any complete cross-scale pathway as validated. Evidence across aphids, ants, treehoppers, butterflies, *Drosophila*, and odonates shows that thermoregulatory behavior can reduce exposure or redistribute activity, but benefits are contingent. Heat escape may require abandonment of profitable sites, warming can exceed behavioral compensation, survival can improve without reproductive rescue, and physiological acclimation or habitat heterogeneity can independently alter thermal outcomes. The framework therefore treats behavioral buffering as sufficient for higher-level stability only when exposure reduction remains biologically meaningful after opportunity costs and when preserved functions propagate into vital rates and spatial persistence. It predicts that failures can occur at any transition, making population and range consequences conditional rather than inevitable.

Keywords: Behavioral thermoregulation, Thermal refugia, Microclimate, Activity-time trade-offs, Demographic buffering, Range stability

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Introduction

Thermal vulnerability is often evaluated from climatic exposure or physiological tolerance, but the evidence base itself is uneven. Butterfly temperature research remains biased toward particular regions, taxa, and adult stages, limiting unqualified generalization across Insecta [1]. At the same time, insects experience temperature at spatial scales far finer than conventional macroclimatic measurements, so local geometry, radiation, and shelter can either buffer or intensify operative thermal conditions [2]. Temperature extremes can then propagate through physiology, behavior, species interactions, and population processes, but their consequences are strongly context dependent rather than uniformly catastrophic [3]. These observations create an inferential problem: the climatic temperature experienced by a landscape is not identical to the thermal exposure experienced by an insect, and reduced exposure is not identical to demographic protection.

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Direct studies illustrate why each transition must be separated. Experimental manipulation of microhabitat conditions altered the activity responses of insect assemblages under heat, showing that spatial configuration can change the biological expression of thermal stress [4]. Among cereal aphids, heat-avoidance temperature was associated more closely with thermal sensitivity than with critical thermal maximum, indicating that behavioral withdrawal and physiological tolerance represent distinct dimensions of thermal response [5]. Avoidance itself can also be costly: aphids that leave heated host plants reduce direct thermal exposure but may incur relocation, feeding, and demographic penalties [6]. Behavioral thermoregulation therefore cannot be treated as a binary protective trait. Its value depends on what is avoided, what ecological opportunity is surrendered, and whether the resulting body-temperature change protects functions relevant to persistence.

Field evidence further limits simple scaling. Urban ants used microhabitats non-randomly but did not fully compensate behaviorally for warmer sites or times of day [7]. In a plant-feeding treehopper, thermoregulation improved survival under heat while failing to preserve reproduction, demonstrating that different fitness components can respond differently [8]. Across British butterflies, thermoregulatory ability varied among species and was associated with physical and ecological traits as well as population trends, but such associations do not establish that thermoregulation caused those trends [9]. The central contribution here is therefore a proposed cross-scale framework that asks not whether insects avoid heat, but when avoidance remains effective as inference moves from body temperature to performance, activity budgets, vital rates, population persistence, and ultimately geographic stability.

Materials and Methods

This article uses a conceptual synthesis rather than a new experimental dataset. The proposed Cross-Scale Thermal Buffering Model was constructed by preserving the measurement and inferential boundaries represented in the selected evidence. First, thermal exposure is treated as organism-relevant heat load rather than as weather-station air temperature alone. Microclimate measurement must account for the physical environment experienced by the organism, because radiation, convection, humidity, and microsite geometry can make standard air temperature a poor proxy for operative exposure [10]. Accordingly, the model begins with the availability and accessibility of thermally distinct microsites, not with regional mean temperature.

Second, cross-scale propagation is treated as a sequence of conditional transitions rather than a single causal arrow. Process-explicit range modelling emphasizes that demographic, physiological, dispersal, and biotic processes must be matched to the forecasting question and that greater mechanistic detail does not automatically guarantee predictive accuracy [11]. The framework therefore distinguishes exposure reduction, biological performance, demographic consequences, and spatial persistence as separate analytical levels. A relationship documented at one level is not promoted to the next unless the intervening requirement is independently plausible or supported.

Third, behavioral mitigation is incorporated as one possible modifier of distributional responses rather than as a presumption of range rescue. In insect distribution research, microclimate, thermoregulation, and other mitigation responses can alter projected exposure and potential distributions [12]. The proposed model extends that insight by requiring explicit accounting of behavioral opportunity costs and demographic sufficiency before any range-level inference is made. Thus, the model is an organizing architecture for evidence and testable propositions, not a fitted forecasting model or an empirically validated mechanism.

Results and Discussion

Behavioral heat avoidance requires more than environmental heterogeneity; insects must encounter thermal contrasts that are both detectable and ecologically usable. Evidence from tropical butterflies shows that thermal buffering and upper thermal tolerance can operate as alternative response dimensions rather than covarying positively across species [13]. This distinction matters because an insect that remains cool through microsite choice may not require the same physiological margin as one that tolerates higher body temperatures. In the proposed framework, microhabitat detection therefore precedes avoidance and is analytically distinct from tolerance.

Broad geographic assumptions are also unreliable. Standardized comparisons of neotropical and temperate butterflies did not reveal a consistent regional difference in thermoregulatory ability or mechanism [14].

Consequently, climatic-zone labels cannot substitute for direct information about local thermal heterogeneity, morphology, behavior, and available shelter. The framework treats detection as context dependent: a potentially cool refuge has no buffering value if it is inaccessible, cannot be discriminated from surrounding habitat, or conflicts with essential resources.

Field observations in Mediterranean butterflies provide evidence that local habitat structure can matter under warming. During hotter conditions, butterfly occurrence shifted toward features associated with cooler conditions, including wetter, shadier, or higher microhabitats [15]. These patterns support the existence of behaviorally relevant thermal heterogeneity, but they do not demonstrate that the shifts preserved reproduction, population growth, or long-term occupancy. Microhabitat detection is therefore a necessary but insufficient condition for higher-level buffering.

Behavioral avoidance

Once thermal heterogeneity is detectable, avoidance depends on decision thresholds and movement capacity. In aphids, heat-avoidance temperature tracked thermal sensitivity more closely than critical thermal maximum [5], showing that behavioral withdrawal can begin well before physiological failure. Avoidance should therefore be represented as a state-dependent decision boundary rather than as a direct readout of lethal tolerance.

The response is also constrained by what movement costs. Leaving a hot host can reduce immediate exposure while increasing the probability of losing access to food or suitable habitat, and those costs can alter demographic performance [6]. This creates a central distinction between thermal effectiveness and ecological profitability: a behavior may successfully cool the body while still reducing net performance. For sessile, immature, or host-bound stages, the relevant constraint may be even stronger because locomotor escape is limited or impossible.

Field evidence from urban ants shows another boundary. Workers avoided some nonpreferred thermal conditions, yet behavior did not fully offset spatial and diel warming [7]. The proposed model therefore includes a finite behavioral compensation envelope: avoidance can reduce realized exposure only while suitable refuges remain accessible within the insect's movement, sensory, and temporal constraints. That envelope is conceptual rather than numerically specified, and it is expected to vary among taxa, stages, sexes, and environments.

Performance preservation

The next inference step asks whether reduced exposure actually preserves functions that matter biologically. Experimental heating showed that microhabitat configuration can modify insect activity responses [4], supporting the idea that behaviorally accessible thermal structure can maintain activity under some conditions. Activity, however, is an intermediate endpoint. It cannot by itself establish preserved feeding, mating, fecundity, or survival.

This distinction is demonstrated directly by the treehopper system in which thermoregulation enhanced survival but did not rescue reproduction [8]. A cooler body temperature can therefore prevent one form of damage while leaving another fitness component impaired. In the proposed framework, performance preservation is decomposed into endpoint-specific outcomes rather than summarized as “benefit.” A transition toward demographic buffering requires that the particular functions limiting population replacement are maintained, not merely that acute mortality declines.

Butterfly field studies add interspecific heterogeneity. Thermoregulatory ability varies among species and is associated with morphology and ecological traits [9]. Such variation can plausibly change how much protection is obtained from the same thermal landscape, but the associations do not establish a universal mechanism linking thermoregulation to population trends. The framework therefore treats morphology, ecology, and thermal strategy as moderators of performance preservation rather than as deterministic predictors.

Activity-time costs

Heat avoidance competes for time as well as space. In tropical forest butterflies, habitat disturbance was associated with shifts in activity patterns rather than a uniform reduction in activity [16]. This distinction is important because behavioral buffering may preserve total activity while moving it into different hours or microsites, or it may compress the usable activity window enough to reduce feeding, courtship, oviposition, or movement opportunities. The ecological cost is therefore not captured by body temperature alone.

Weather-dependent movement modelling provides a second constraint. In the meadow brown butterfly, weather altered flight and inactivity and consequently changed predicted movement behavior [17]. A thermally safe

interval can thus become ecologically expensive if it coincides with reduced locomotor opportunity, while favorable thermal windows may enhance both safety and movement. The proposed framework treats this as an activity-time budget in which cooling behavior competes with other functions for finite suitable periods. Importantly, it does not assume that every activity shift is caused by heat or that reduced movement necessarily lowers fitness; those links require direct testing in the focal taxon and environment.

Because these costs arise through qualitatively different routes, prose alone obscures where evidence ends and new inference begins. The coverage-and-gap map below separates observed activity-time states from the proposed cross-scale interpretations they motivate.

Table 1. When thermal safety consumes ecological time: coverage and gaps in activity-window costs relevant to behavioral heat avoidance

Activity-time mechanism	Exposure setting	Behavioral evidence	Opportunity cost	Ecological boundary	Field test	Evidence state
Direct heat avoidance and disturbance redistribution						
Heat-driven host abandonment	Host-bound herbivorous insect	Movement away from a heated feeding site with subsequent demographic consequences	Cooling can reduce exposure while sacrificing feeding-site continuity	Depends on host distribution, mobility, and recovery of feeding access	Measure both body-temperature benefit and post-escape resource reacquisition	Evidence-supported pattern
Disturbance-linked activity redistribution	Adult tropical butterflies	Changes in timing or location of activity across disturbed habitats	Thermal or structural change may reallocate activity rather than simply suppress it	Disturbance effects are not uniquely attributable to heat	Pair microclimate records with individual activity budgets and resource use	Evidence-supported pattern
Weather-gated movement and biologically idle cooling						
Weather-gated movement opportunity	Mobile adult butterfly	Flight and inactivity vary with weather conditions	Safe thermal periods may differ from periods suitable for dispersal or foraging	One-species movement model; movement is not equivalent to reproductive success	Connect weather-dependent movement with realized resource acquisition or dispersal outcome	Evidence-supported pattern
Cooling-safe but biologically idle interval	Cross-taxon conceptual state	Reduced heat exposure accompanied by reduced feeding, mating, oviposition, or movement opportunity	Thermal protection may fail to preserve net performance	Requires endpoint-specific measurements; not directly established as a universal state	Quantify the fraction of safe time that remains usable for limiting activities	**Proposed synthesis**
Compressed usable window						
Compressed usable activity window	Cross-scale conceptual state	Repeated exclusion of hot periods from otherwise suitable daily or seasonal time	Small acute benefits could accumulate into chronic opportunity costs	Magnitude depends on season length, life stage, and resource phenology	Test cumulative effects on vital rates rather than only acute survival	**Proposed synthesis**

The same evidence can be organized more efficiently as a mechanism-and-boundary map because activity-time costs arise simultaneously from refuge use, movement constraints, and endpoint-specific performance. **Figure 1** therefore distinguishes relationships supported at the behavioral scale from proposed transitions toward demographic consequences.

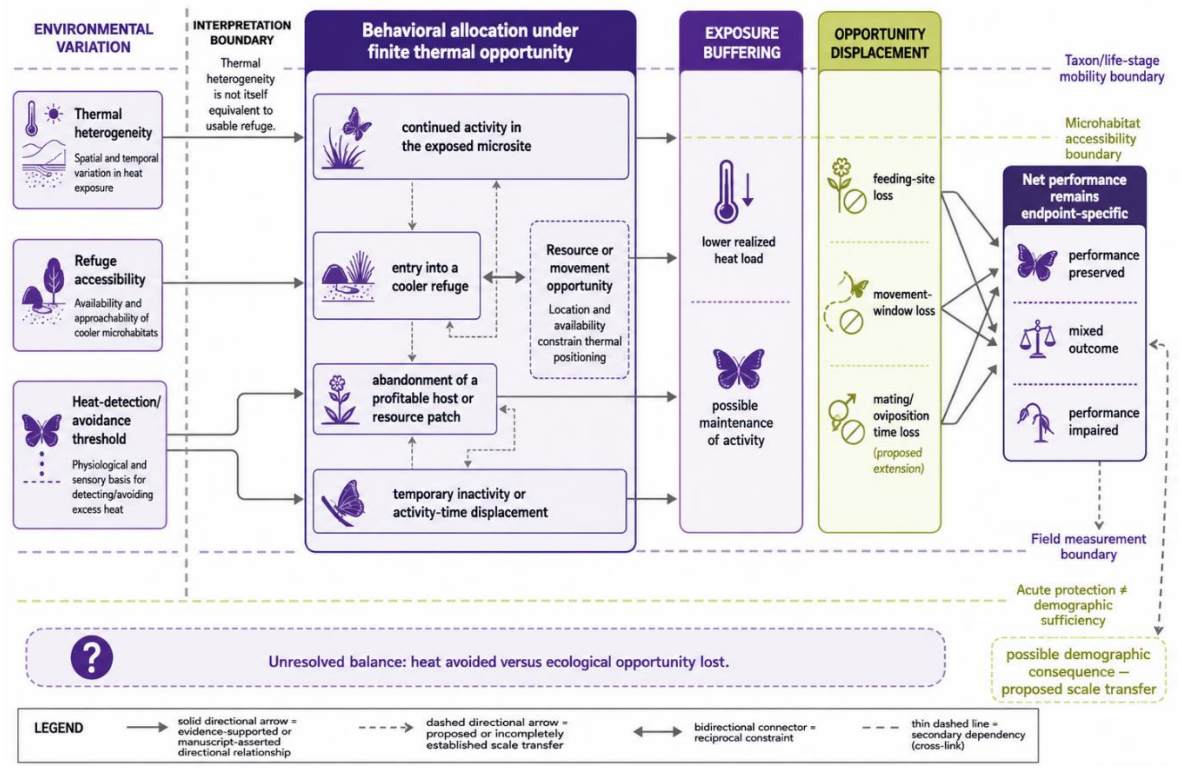


Figure 1. Thermal refuge use under a finite activity budget: where exposure buffering becomes an opportunity-cost problem

Demographic consequences

Behavioral cooling acquires demographic meaning only when it changes survival, development, reproduction, or recruitment after its ecological costs are included. The aphid evidence provides a direct warning against assuming that escape is automatically beneficial: leaving a hot host can reduce exposure while altering resource access and demographic performance [6]. In the proposed model, demographic buffering therefore depends on the net balance between thermal protection and the vital-rate costs created by relocation, inactivity, or missed resource use.

Population consequences can also be dominated by stressors that behavior does not remove. In *Pieris napi*, combinations of extreme heat and resource limitation were associated with negative modeled population rates under severe climatic regimes [18]. This evidence does not test behavioral rescue; instead, it shows why the framework must represent compound environmental load. A thermally successful behavior may still be demographically insufficient when drought, host scarcity, or other constraints limit recruitment.

Physiology provides an additional, analytically separate route. Warm acclimation reduced modeled heat-mortality sensitivity across four *Drosophila* species [19]. Because acclimation can modify mortality risk independently of movement, demographic outcomes cannot be assigned to behavior when physiological state is unmeasured. The proposed framework consequently treats behavior, acclimation, and environmental refuge quality as interacting but non-interchangeable contributors to realized demographic exposure.

Population persistence

Population persistence requires more than preventing acute deaths. The treehopper example shows that survival can be improved while reproduction remains impaired [8], so persistence cannot be inferred from short-term survival protection alone. In the proposed framework, behavioral buffering becomes demographically sufficient only when the vital rates limiting replacement remain compatible with continued local occupancy across the relevant sequence of thermal events.

Compound climatic regimes add another failure route. Negative population rates modeled for *P. napi* under extreme heat and resource scarcity [18] indicate that repeated or coincident stresses can overwhelm protection that might be adequate during isolated heat exposure. Persistence should therefore be evaluated across event frequency, recovery intervals, resource conditions, and life stages rather than from a single refuge-use episode.

Landscape heterogeneity can nevertheless alter the temporal expression of climatic change. Across 120 mountain transects, butterfly communities showed delayed climate tracking where habitat and microclimatic heterogeneity contributed to local buffering, although colonization barriers remained an alternative explanation [20]. Such delay is compatible with local persistence but does not demonstrate that individual heat avoidance caused it. The framework accordingly distinguishes persistence-compatible buffering from proven behavioral rescue.

The adjudication problem is clearest when the same outward pattern—continued occupancy—can arise through different processes. **Table 2** separates those persistence states so that apparent stability is not automatically attributed to behavioral thermoregulation.

Table 2. Continued occupancy is not a single mechanism: adjudicating population persistence under thermal buffering

Occupancy pattern	Population setting	Demographic signal	Persistence mechanism	Critical alternative	Threshold test and state
Partial or compound-stress buffering					
Survival buffered, reproduction impaired	Heat-exposed reproductive insects	Lower mortality with persistent reproductive loss	Acute protection may not sustain replacement	Fitness components respond differently	Measure survival and reproduction across repeated heat events Evidence-supported pattern
Compound-stress demographic decline	Populations exposed to heat plus resource limitation	Negative population rate under severe combined regimes	Thermal buffering may be insufficient when another limiting factor remains	Resource scarcity and event sequence	Link individual thermal responses to stage-specific vital rates under compound stress Evidence-supported pattern
Delayed or merely apparent stability					
Delayed community climate tracking	Heterogeneous mountain landscapes	Local assemblages lag regional climatic change	Microclimate may contribute to persistence-compatible delay	Colonization barriers can generate similar patterns	Combine individual refuge use, demographic turnover, and colonization data Evidence-supported association
Apparent stability without demonstrated buffering	Any occupied site or stable census	Continued occurrence without individual-to-demographic linkage	Persistence mechanism remains unresolved	Dispersal, immigration, acclimation, habitat heterogeneity, or time lag	Test competing mechanisms before assigning behavioral causation **Proposed adjudication rule**
Demographically sufficient buffering					
Demographically sufficient buffering	Cross-scale inference state	Thermal avoidance preserves the vital rates limiting local replacement	Behavioral buffering could contribute to persistence	Must survive repeated-event and life-stage tests	Demonstrate exposure reduction, preserved limiting vital rates, and sustained occupancy in the same system **Proposed synthesis**

The population-level evidence is better represented as a layered architecture than as a direct individual-to-range arrow. **Figure 2** separates exposure, performance, vital rates, occupancy, and spatial inference while keeping competing persistence mechanisms visible.

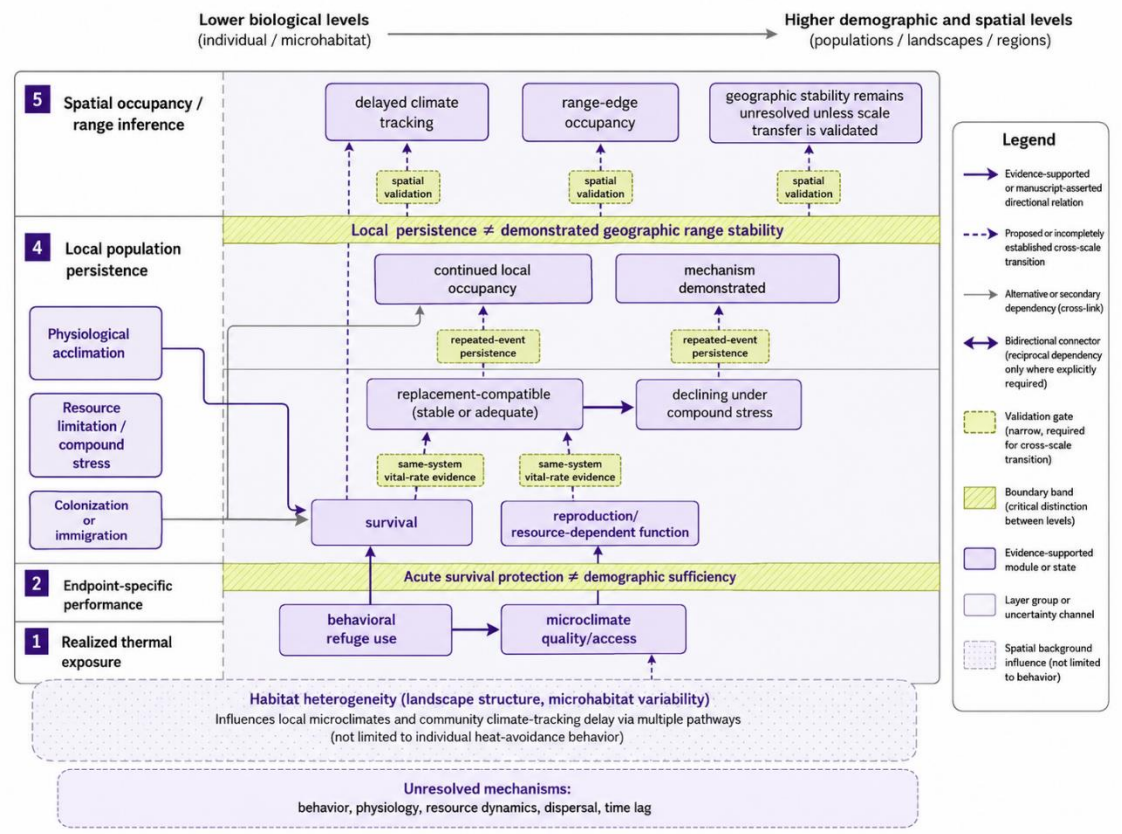


Figure 2. The persistence threshold between local thermal buffering and geographic stability

Geographic range consequences

Range-level inference requires another change of scale. Comparative evidence across 119 butterfly species indicates that thermal physiology does not map simply onto contemporary warm range boundaries, abundance responses, or phenological exposure [21]. Thermal tolerance can matter, but its geographic consequence is filtered through when and where extremes occur, which life stages are exposed, and whether populations can access suitable microclimates. A measured individual trait therefore should not be treated as a direct range-stability predictor.

Community structure introduces a related interpretive problem. In tropical Odonata, high temperature and habitat disturbance affected taxonomic and functional dimensions differently [22]. Consequently, apparent stability in richness or occurrence can coexist with restructuring of traits or ecological composition. For this framework, "range stability" must specify the entity and timescale being considered: persistence of a focal population, maintenance of occupancy, stable range boundaries, and stable community composition are not interchangeable outcomes.

Proxy traits also require caution. In Sulawesi swallowtails, expected elevation-related differences in thermoregulatory morphological traits were weak or unsupported [23]. Museum-derived morphology can therefore inform hypotheses about thermal vulnerability but cannot demonstrate behavioral regulation or geographic buffering. The proposed range component requires direct linkage among realized exposure, demographic performance, movement or colonization, and occupancy before behavioral heat avoidance is invoked as an explanation for stable geographic limits.

Limits of behavioral buffering

Behavior is intrinsically unavailable or constrained during some stages and ecological situations. Temperature-sensitive development shapes insect phenological responses [24], meaning that eggs, larvae, pupae, or otherwise mobility-limited stages may experience thermal regimes that adult refuge use cannot offset. Seasonal shifts in development can also change the timing of exposure and resource matching. Adult behavioral evidence should therefore not be extrapolated across the life cycle without stage-specific measurements.

Even among mobile adults, morphology and behavior interact with environmental structure. Field and biophysical work on tropical butterflies at a range boundary indicates that different morphological and behavioral strategies can facilitate persistence in variable environments [25]. This supports treating behavior as one contributor to environmental persistence, but not as a universal explanation for warm-edge stability.

The proposed framework consequently recognizes five recurrent failure classes: unavailable or inaccessible refuges; avoidance capacity exceeded by thermal conditions; protection of survival but not limiting functions such as reproduction; cumulative opportunity costs that reduce vital rates; and failure of locally adequate buffering to propagate through dispersal and spatial dynamics. Physiological acclimation, immigration, habitat heterogeneity, resource availability, and time-lagged responses remain alternative or complementary processes. Demonstrating behavioral buffering therefore requires identifying which link is operating rather than inferring mechanism from continued occurrence.

The principal implication of this framework is that behavioral heat avoidance should be evaluated by cross-scale sufficiency, not by the presence of thermoregulatory behavior alone. Escape from heat can reduce exposure while imposing demographic costs [6], and survival protection can coexist with reproductive impairment [8]. At still higher levels, population rates can become negative under compound heat and resource stress [18]. Together, these findings motivate—but do not empirically validate—the proposed rule that every transition must preserve the biological quantity that limits the next level.

Microclimatic heterogeneity is similarly double-edged. Fine-scale conditions can buffer macroclimatic exposure [2], and heterogeneous mountain landscapes can contribute to delayed butterfly community tracking [20]. Yet comparative evidence shows that simple thermal traits alone do not consistently explain range outcomes [21]. Refugia may therefore create time, reduce exposure, or slow local change without providing permanent climatic security. The duration and accessibility of buffering are as important as its instantaneous magnitude.

This distinction changes the conservation question. Observed shifts toward cooler habitat features [15] identify candidate refuge structure, while weather-dependent movement shows that access to those structures and movement among patches can itself be constrained [17]. Landscape heterogeneity may further slow climate tracking [20]. These observations justify testing refuge accessibility, continuity, resource compatibility, and demographic adequacy; they do not establish that protecting a particular refuge will stabilize a population or range.

Validation should accordingly couple organism-relevant microclimate measurement with behavioral observation, endpoint-specific performance, stage-specific vital rates, and spatial dynamics. Operative exposure should be measured rather than inferred solely from coarse air temperature [10], and process-explicit models should be chosen according to the processes and applications they are capable of representing [11]. Finally, taxonomic and life-stage gaps in the thermal literature [1] mean that validation should deliberately extend beyond adult butterflies and a small set of well-studied terrestrial insects. A convincing test would follow the same population across scales rather than assembling a causal narrative from different taxa at each transition.

Conclusion

Behavioral heat avoidance can reduce the thermal exposure experienced by insects, but its ecological significance depends on what happens after the animal moves or changes activity. The proposed Cross-Scale Thermal Buffering Model separates refuge availability and detection, avoidance, realized exposure, performance preservation, activity-time costs, demographic sufficiency, population persistence, and geographic consequences. This separation prevents short-term cooling, survival, or continued occupancy from being interpreted automatically as population or range stability.

The framework identifies behavioral buffering as a conditional contributor rather than a universal rescue mechanism. Its strongest future test is therefore cross-scale and within-system: demonstrate that accessible refuges change realized exposure, that the change preserves limiting biological functions after opportunity costs, that those effects protect relevant vital rates across repeated thermal events and life stages, and that the resulting demographic response contributes to sustained occupancy at the spatial scale of interest. Until those links are demonstrated together, behavioral heat avoidance should be treated as a potentially important component of thermal resilience whose demographic and geographic consequences remain context dependent.

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