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Traits, Environmental Filters, and Adaptive Responses Underlying Behavioral and Physiological Mechanisms of Insect Urbanization

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ABSTRACT

Urbanization exposes insects to coupled changes in temperature, artificial light, habitat configuration, vegetation, resource distributions, disturbance, and biotic interactions. Yet urban occurrence is often treated as evidence of a coherent "urban-adapted" phenotype even when studies measure different biological levels and provide very different strengths of evolutionary inference. This systematic map organized peer-reviewed insect evidence published from 2017–2025 around urban environmental filters, behavioral traits, physiological traits, plasticity, evolutionary divergence, and persistence-related trait combinations. Publications were coded according to taxon, life stage, environmental exposure, biological level, study setting, response class, and inferential strength. Thirty-three individually verified publications constituted the mapped working evidence set. Source-specific database-export totals were not recoverable; consequently, unavailable upstream retrieval and deduplication counts are reported transparently as not recoverable rather than reconstructed. Evidence indicates substantial heterogeneity among taxa, cities, spatial scales, life stages, and measured outcomes. Urban warming can filter physiological tolerance and sometimes generate evolutionary divergence, but common-garden evidence also demonstrates plasticity without detectable urban evolutionary differentiation. Behavioral timing, foraging, and light responses can alter realized exposure, while local floral resources, habitat structure, microclimate, and lighting may explain responses that a simple urban–rural classification obscures. The mapped literature supports treating insect urbanization as conditional matching among environmental filters, trait states, response mechanisms, and biological consequences rather than as a universal syndrome. Strong claims of adaptation require evidence beyond urban association or phenotypic divergence, particularly where fitness, life-stage, geographic, and genomic validation remain limited.

Keywords: Urban ecology, Insect functional traits, Urban heat island, Behavioral plasticity, Thermal physiology, Urban evolution.

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Introduction

Urbanization restructures insect environments through simultaneously altered climate, land cover, vegetation, resource distributions, disturbance and sensory conditions. Quantitative syntheses generally detect negative average effects of urbanization on terrestrial arthropod diversity, abundance or richness, but they also reveal marked heterogeneity among taxa, response variables and environmental contexts [1–3]. This heterogeneity is not a statistical inconvenience. It is the principal biological problem for interpreting why some insect populations decline, others persist, and still others express altered phenotypes in cities.

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A single "urban-tolerant" trait syndrome is unlikely to resolve that problem. A global comparative analysis found multiple taxon-dependent trait syndromes rather than one general set of characteristics associated with urban occurrence [4]. Consequently, traits such as mobility, body size, heat tolerance, resource breadth or phenological flexibility cannot be interpreted independently of the filter they encounter, the scale at which they are measured, and the biological consequence being inferred.

The distinction becomes especially important when urban differences are described as adaptation. Urban–rural phenotypic or genomic divergence can be consistent with evolutionary change, but local adaptation requires stronger evidence linking heritable divergence to differential performance or fitness in the relevant environment [5]. Reviews of urban bee research likewise show that community-level observations substantially outnumber direct behavioral, physiological and evolutionary tests, leaving major mechanistic gaps [6]. The central problem is therefore inferential: urban occurrence, trait association, plastic response, evolved divergence and adaptive benefit occupy different evidential levels.

This systematic map organizes those levels rather than collapsing them. It asks how environmental filters are represented experimentally and observationally; which behavioral and physiological traits have been linked to urban conditions; when evidence supports plastic versus evolved responses; and which trait combinations are associated with persistence without being prematurely treated as universal adaptive syndromes. The article further proposes that urban insect persistence is most defensibly interpreted through conditional filter–trait–response–consequence matching, with explicit boundaries between observation, mechanism, evolutionary inference and demonstrated fitness consequence.

Materials and Methods

The evidence-mapping procedure followed principles of transparent environmental evidence synthesis and systematic-review reporting [7]. Selection stages and reporting boundaries were additionally informed by PRISMA 2020 principles where they were applicable to identification, eligibility and inclusion [8].

Search logic combined insect or arthropod terms with urban-exposure terms and behavioral, physiological, trait, plasticity, evolutionary and persistence terms. The publication window was restricted to 2017–2025. Urban exposure was defined broadly enough to include explicit urban–rural contrasts, urbanization gradients, urban heat-island conditions, artificial light at night, fragmentation, impervious cover, urban green space and other environmental components directly attributed to urban landscapes. Studies were not coded as demonstrating urban adaptation solely because populations occurred in cities.

Thirty-three peer-reviewed publications were individually verified for bibliographic identity, DOI, evidential relevance and suitability for the mapped domains. Because a source-by-source database export was not retained during the evidence-identification stage, total records retrieved before candidate selection, formal duplicate-removal totals and title/abstract exclusion totals could not be reconstructed. These upstream stages are therefore treated as not recoverable, not as zero. Within the retained evidence set, no duplicate DOI was identified.

Coding separated taxon and species, life stage or sex where reported, study environment, spatial comparison, biological level, focal environmental filter, measured trait, response class and evidential design. Behavioral responses were kept separate from physiological tolerances; organismal performance was kept separate from community occurrence; and common-garden or experimental evidence was distinguished from field association. Plastic responses were coded separately from population-of-origin divergence, while adaptation was reserved for evidence capable of connecting inherited divergence to environment-dependent performance or fitness.

The map was designed as a structured evidence landscape rather than a meta-analysis. No pooled effect estimate, universal trait score or predictive urban-persistence index was calculated. Contradictory, null and context-dependent outcomes were retained because disagreement among studies can reveal life-stage, taxonomic, climatic or methodological boundaries that would be lost by forcing evidence into a single directional classification.

Results and Discussion

The mapped evidence spans several major insect groups but does not represent them evenly. Urban-gradient work includes insects sampled as broad assemblages, Orthoptera, Lepidoptera, Hymenoptera and aquatic insects, with particularly detailed mechanistic evidence available for ants, bees and selected moth or butterfly systems.

Metric choice materially affects apparent urban response. Along urban gradients, insect biomass can decline more strongly than species richness, demonstrating that richness alone may understate changes in ecological quantity [9]. Orthopteran assemblages in Berlin showed reduced diversity and a shift toward relatively mobile species under urbanization [10], whereas butterfly communities exhibited both taxonomic and functional homogenization along an urban gradient [11]. These outcomes describe community filtering, not necessarily within-population evolutionary change.

Even within well-studied pollinators, coarse land-use labels can be weaker predictors than local habitat conditions. Bumblebee occupancy was more strongly related to local floral abundance than to urban–agricultural landscape context in one regional study [12]. Multitrophic work on cavity-nesting bees, wasps and associated organisms likewise showed that urban intensity can affect richness, abundance and performance through different abiotic and biotic pathways [13]. Across four cities in eastern China, climatic and urban variables produced taxon- and site-dependent insect responses rather than a common urban trajectory [14]. Taxonomic coverage therefore supports comparison of recurring filters, but not a rank ordering of insect orders from "urban sensitive" to "urban adapted.".

Urban environmental filters

Treating urbanization as a single exposure obscures the environmental mechanisms insects actually encounter. In urban grasslands, moth diversity reflected combinations of habitat area, management, surrounding land cover and lighting rather than an indivisible effect of "city" status [15]. For the Malaysian giant ant Dinomyrmex gigas, vegetation structure and relative humidity were associated with diurnal foraging activity across fragmented urban forests, illustrating how fine-scale microhabitat can mediate realized conditions within the same broader urban matrix [16].

Artificial light requires similar decomposition. A factorial moth study distinguished diffuse skyglow from direct streetlighting and found that both altered community attributes, with direct lighting producing stronger effects for several responses [17]. Lumping these components into a single light-pollution variable would erase biologically meaningful differences in exposure intensity and sensory context.

Temperature is equally conditional. Experimental work with cavity-dwelling ants showed that thermal tolerance, foraging performance and competitive responses depended on species, population origin and incubation temperature rather than conforming to a single urban-origin effect [18]. Urban heat therefore cannot be interpreted only as selection for higher heat tolerance; it may interact with acclimation capacity, behavioral exposure, cold limitation, life history and species-specific thermal margins.

The completed evidence synthesis consequently requires an environmental-filter vocabulary that distinguishes broad urban classification from the proximal exposure actually measured. The cross-scale grid below compresses that distinction while retaining uncertainty and inference boundaries that prose would otherwise repeat.

Table 1. Separating coarse urban classification from the proximal environmental filters that shape insect exposure and response

Taxonomic with observed basis	Measured construct	Uncertainty within its limit
Composite urban landscape		
Community studies across multiple insect groups **Urban response varies with metric, taxon and locality**	Richness, abundance, biomass, composition	Composite exposure does not identify the active mechanism Use as contextual classification, not as a mechanistic variable
Habitat amount and configuration		
Moths, Orthoptera and other field assemblages **Habitat structure can reorganize diversity and trait composition**	Habitat area, isolation, surrounding land cover, mobility	Correlated urban variables complicate attribution Separate configuration from other urban stressors
Local vegetation and resource environment		
Ants, bees and multitrophic nest communities **Local habitat conditions may outweigh coarse landscape category**	Floral resources, vegetation structure, humidity, nesting context	Effects can be taxon- and season-specific Code proximal resource and microhabitat filters independently
Artificial light environment		

Primarily nocturnal Lepidoptera **Direct and diffuse light can produce distinguishable responses**	Direct streetlight, skyglow, community response	Spectral, spatial and temporal exposure varies Avoid treating all artificial light as one exposure class
Urban thermal environment		
Experimental and field studies of ants and other ectotherms **Responses differ among species, origins and exposure regimes**	Temperature, thermal tolerance, activity or performance	Acclimation and behavior can modify realized temperature Distinguish ambient warming from physiological response
Proposed cross-filter state		
Integrative coding across mapped studies **Multiple filters may jointly define realized urban conditions**	Concurrent exposure to several urban filters	Relative contribution is rarely isolated experimentally Interpret persistence through filter combinations rather than a single urbanity axis

Behavioral traits

Behavior can change the environmental conditions actually experienced by an insect and therefore occupies a different analytical level from habitat classification. In urban and nonurban forest ants, fixed diel activity patterns only partly compensated for thermal differences, indicating that behavioral timing can buffer exposure without eliminating warming effects [19]. Behavioral response should therefore be evaluated by how much it modifies realized exposure, not merely by whether activity differs between habitats.

Urban ant assemblages also differ in when and how they exploit resources. Comparisons of urban and forest ants detected shifts in foraging activity, food-particle preference and biomass removal [20]. Such differences can alter ecological function, but they do not by themselves establish that urban behavior is genetically evolved or that altered foraging improves lifetime fitness.

A stronger evolutionary case arises when urban behavioral divergence persists under controlled comparisons. Urban populations of the moth Yponomeuta cagnagella showed reduced flight-to-light responses together with changes in wing morphology [21]. The association is consistent with evolutionary change in a sensory-behavioral phenotype, while the morphological correlation does not establish that wing form is the sole causal mechanism.

Behavioral evidence therefore spans at least three distinct states: modification of realized environmental exposure, altered resource-use behavior in the field, and population divergence consistent with evolutionary change. These states should not be merged because their inferential requirements differ.

The selection-flow figure is placed here to make equally explicit the evidential boundary of the map itself: the final mapped set is auditable at the retained-publication level, whereas unavailable upstream database totals remain visibly unresolved rather than being converted into artificial precision.

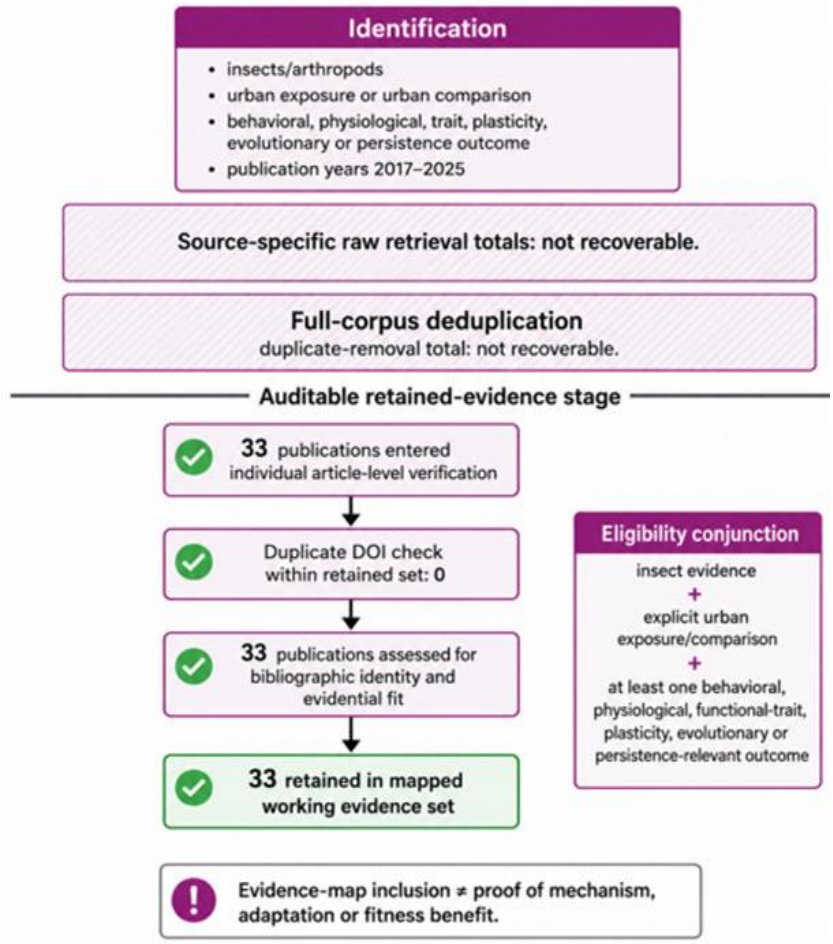


Figure 1. Auditable selection boundary for the urban-insect trait evidence set when upstream database totals are not recoverable

Physiological traits

Physiological traits are often invoked as candidate mechanisms of urban persistence because ectothermic insects experience altered thermal distributions at fine spatial scales. Yet the evidence shows that physiological tolerance should not be interpreted as a single axis running from urban sensitivity to urban adaptation.

In bees sampled across an urban heat-island gradient, critical thermal maxima predicted differential population responses, supporting a role for heat tolerance in filtering species under warmer urban conditions [22]. This result establishes that physiological limits can matter ecologically; it does not establish that critical thermal maximum alone determines persistence.

Ant evidence illustrates the boundary more sharply. In temperate urban and peri-urban parks, species did not show a simple urban elevation in critical thermal maximum, while cold tolerance and activity relationships suggested that cold exposure could remain an important constraint [23]. Thus, an urban heat-island environment need not generate uniformly higher heat tolerance across resident taxa.

Common-garden evidence further separates plasticity from evolutionary divergence. In the cabbage white butterfly Pieris rapae, developmental temperature produced plastic changes in thermal limits, but urban and rural populations did not show detectable evolutionary divergence in those limits [24]. A successful urban population can therefore possess environmentally responsive physiology without demonstrating genetically differentiated thermal adaptation.

The physiological evidence supports three interpretive safeguards. First, the environmental temperature measured at a site is not identical to the thermal exposure realized by an insect because behavior and microhabitat modify exposure. Second, measured tolerance is not equivalent to fitness or population persistence. Third, an urban–rural difference is not required for plastic physiological buffering, while an urban–rural difference alone would still be insufficient to demonstrate local adaptation.

These distinctions are condensed below as conditional inference states rather than as a physiological "success score."

Table 2. When physiological evidence can—and cannot—support inference about insect persistence under urban thermal environments

Permitted interpretation within its limit	Physiological evidence state, discriminating check, and proposed status	Biological setting with observed basis
Physiological limits can contribute to ecological filtering **Predictive contribution may be partial and taxon-specific**	Thermal tolerance predicts urban sensitivity Test alongside resources, behavior and microclimate Evidence-derived	Bee assemblages across urban warming Species-level thermal-limit measurements linked to population response
Urban residence does not require universally higher heat tolerance **Cold limitation, species identity and microhabitat may dominate**	No elevated urban heat tolerance Measure both upper and lower thermal limits Evidence-derived	Temperate urban and peri-urban ants Urban comparison of critical thermal limits
Plastic physiology can occur without evolved urban–rural differentiation **One species and experimental thermal endpoints limit transfer**	Temperature-dependent plasticity without population divergence Replicate across life stages, cities and fitness components Evidence-derived	Urban and rural Pieris rapae in common garden Rearing-temperature response with no detectable origin divergence
Tolerance should be interpreted together with realized exposure **Site temperature can misrepresent body temperature**	Behavioral modification of thermal exposure Couple thermal assays to field exposure measurements Proposed synthesis	Urban ectotherms whose activity changes realized temperature Physiological measurements interpreted with activity or microclimate data
Candidate mechanism, not demonstrated persistence benefit **Trait–fitness mapping may change by stage or environment**	Physiological tolerance linked only indirectly to persistence Add demographic or reciprocal-performance tests Proposed synthesis	Any taxon lacking direct demographic or fitness validation Tolerance difference without survival, reproduction or population-growth evidence
Evidence consistent with inherited differentiation **Does not by itself establish local adaptation**	Population-of-origin difference under controlled conditions Test environment-dependent fitness and genetic basis Proposed inference rule	Urban–rural common-garden comparisons Persistent origin effect after environmental standardization

Plastic versus evolved responses

Urban phenotypes can arise through plasticity, inherited divergence, or both, and the distinction depends on study design. Common-garden work on an aquatic insect detected urban–rural differentiation in thermal-performance curves after environmental standardization [25]. In acorn ants, replicated city comparisons likewise demonstrated evolutionary change in thermal tolerance, but the direction and fitness consequences were not fully parallel among cities [26]. These studies support population-of-origin effects while showing why a single city cannot establish a universal urban evolutionary response.

Field associations remain weaker evidence of evolutionary change. Urbanization was associated with shifts in bumblebee body size and with pollination consequences, but the observational design does not identify whether the morphological pattern was genetically based [27]. By contrast, monitoring combined with common-garden experiments in Lepidoptera identified longer urban flight seasons and evolved differences in seasonal plasticity [28]. Geographic context further modifies inference: life-history responses in Ischnura elegans varied with latitude [29], while Chiasmia clathrata showed replicated urban evolution of increased adult heat tolerance but no corresponding larval divergence [30]. Genomic synthesis in mosquitoes similarly cautions that urban-associated variants can reflect adaptation, exaptation, standing variation, demographic history, or gene flow [31].

The resulting evidence hierarchy is therefore design-based rather than label-based. Plasticity requires an environmentally responsive phenotype; inherited differentiation requires persistence of population-origin effects under controlled conditions; and adaptive inference additionally requires environment-dependent performance or fitness evidence. **Table 3** preserves these boundaries.

Table 3. Evidence states that separate plasticity, inherited divergence and adaptive inference in urban insects

Evidential basis, consequence for inference, and boundary condition	Urban-insect example or context	Test needed next
Plastic response		
Evidence-derived		
Within-population environmental response **Phenotypic flexibility is supported** **Does not establish inherited urban divergence**	Thermal limits responsive to developmental environment	Reciprocal or common-garden population comparison
Persistent origin effect		
Evidence-derived		
Common-garden population effect **Inherited differentiation is consistent with the data** **Fitness advantage remains unresolved**	Urban–rural populations differ after standardization	Environment-specific performance test
Geographic nonparallelism		
Evidence-derived		
Replicated population comparisons **Urban evolution is context dependent** **One city cannot define a universal trajectory**	Thermal responses differ among cities or latitudes	Multi-city replication
Life-stage discordance		
Evidence-derived		
Stage-specific common-garden assays **Evolutionary response can be ontogenetically bounded** **Adult phenotype cannot be transferred to larvae**	Adult divergence occurs without larval divergence	Matched assays across development
Genomic urban association		
Evidence-derived		
Population-genomic evidence **Candidate evolutionary mechanism** **Adaptation, exaptation and demographic structure remain alternatives**	Urban-associated variants or genomic structure	Functional and fitness validation
Adaptive urban response		
Proposed inference rule		
Origin × environment performance evidence **Local adaptation becomes testable** **Trait divergence alone is insufficient**	Inherited difference improves performance in the relevant urban environment	Replicated fitness comparison

Trait combinations associated with urban persistence

Persistence is unlikely to depend on one trait measured at one scale. Flight-related morphology in aquatic beetles varied both among and within species and changed with the landscape scale used to quantify urbanization [32]. Long-term Orthoptera evidence from Rome associated local persistence or extinction with combinations involving mobility, fertility and niche breadth rather than a solitary universal trait [33]. These findings support multivariate, scale-dependent filtering but not a transferable urban-winner formula.

The synthesis developed here therefore treats persistence as an outcome of conditional matching among proximal filters, realized exposure, behavioral adjustment, physiological capacity, life-history state and inherited response. Common-garden studies in an aquatic insect, ants and a moth each detected population-origin differentiation in thermal phenotypes after environmental standardization [25, 26, 30]. This proposed architecture identifies routes to persistence, impairment or unresolved inference; it is not a validated predictive model.

Because the key contribution is the separation of parallel biological lanes and their inference boundaries, **Figure 2** compresses relationships that would be difficult to recover from a list of individual traits.

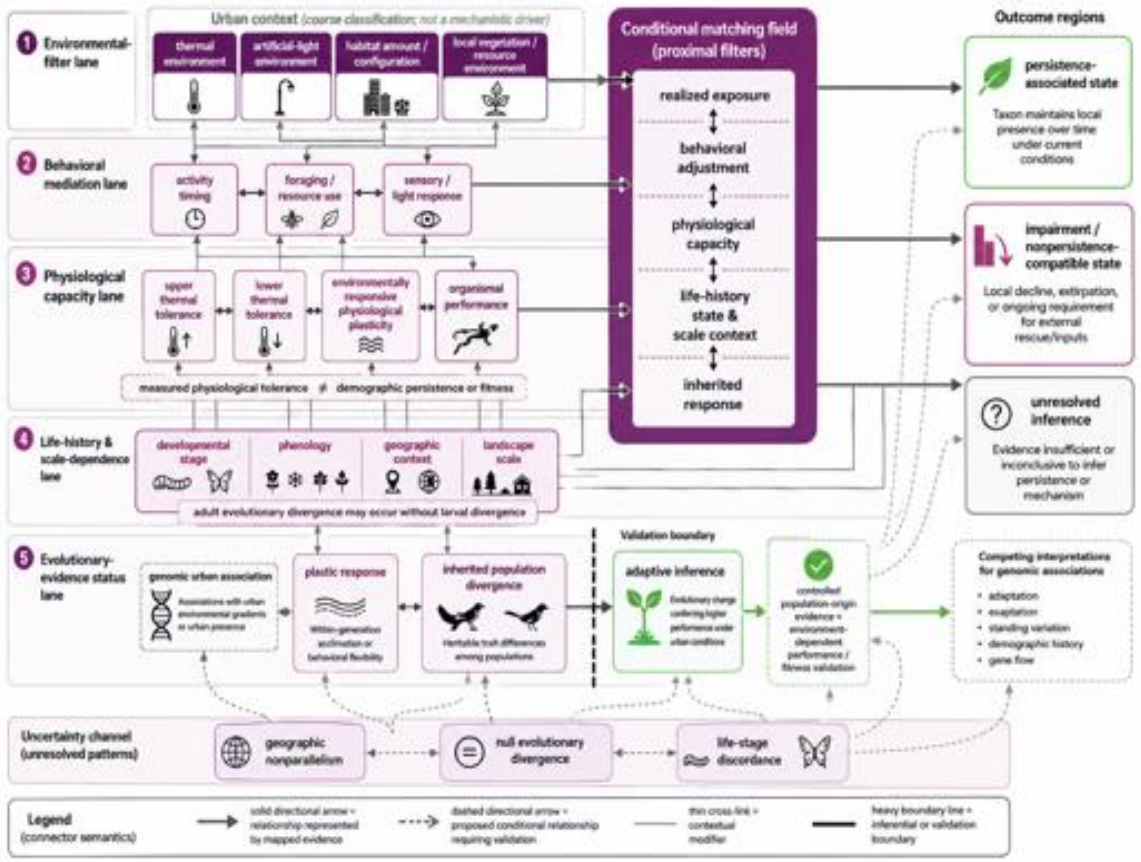


Figure 2. Conditional trait matching separates urban persistence from adaptive inference

Evidence gaps

The evidence landscape remains uneven in taxonomic representation, geography, life stage and inferential strength. Broad synthesis documents substantial heterogeneity and publication bias [3], while urban-bee scholarship shows that community description has outpaced behavioral, physiological and genetic testing [6]. Multicity evidence further demonstrates that climatic context can modify urban insect responses [14]. Apparent consensus can therefore partly reflect concentration on tractable taxa and locations rather than biological universality.

Three gaps are especially consequential: paired measurement of exposure and organismal response, experiments connecting traits to demographic or fitness consequences, and replication across life stages and cities. Evidence conflict should therefore be treated diagnostically rather than removed. **Table 4** specifies which conflicts require different follow-up tests.

Table 4. Evidence conflicts that limit generalization of behavioral and physiological mechanisms of insect urbanization

Interpretation at present, main unresolved boundary, and priority test	Evidence conflict with evidential standing	Biological scope with observed basis
Thermal filtering is taxon and context dependent **Taxon, climate, cold exposure** **Comparable bidirectional thermal assays across cities**	Heat tolerance predicts response vs no urban CTmax increase Evidence-derived	Bees versus temperate ants Different relationships between upper thermal limits and urban occurrence
Urban persistence need not require evolved differentiation **Trait and population sampled**	Plasticity vs inherited divergence Evidence-derived	Butterfly and other common-garden systems

Common garden plus fitness measurement		Environmental responsiveness may occur without origin divergence
Species-level adaptation labels can conceal stage limits **Ontogeny** **Matched developmental assays**	Adult vs juvenile divergence Evidence-derived	Lepidoptera Evolutionary signal present in one stage but absent in another
"Urban" is an incomplete exposure descriptor **Spatial scale and resource distribution** **Hierarchical multiscale exposure designs**	Local resource effect vs coarse urban class Evidence-derived	Pollinators and community studies Proximal habitat variables may outperform urban category
Mechanism or adaptation remains unresolved **Fitness and causality** **Reciprocal performance or functional validation**	Association vs adaptive benefit Proposed reconciliation rule	Trait and genomic studies Urban difference without environment-specific fitness evidence

The mapped evidence does not support a single behavioral or physiological phenotype that defines urban insects. Multiple taxon-dependent trait syndromes have been documented [4], and local floral resources can outperform coarse landscape context for occupancy in some bumblebees [12]. Global heterogeneity is therefore biologically compatible with the proposed filter–trait–response–consequence architecture rather than an obstacle to it.

Behavior and physiology cannot be placed in a simple compensatory hierarchy. Behavioral timing may reduce thermal exposure without fully buffering warming [19]; physiological tolerance can explain differential sensitivity in some assemblages while showing little urban elevation in others [23]; and plastic responses may occur without inherited divergence [24]. Conversely, evolutionary responses can vary among cities [26] or disappear across life stages [30]. Conditional matching is thus more defensible than assuming progressive urban improvement.

Persistence can arise because pre-existing traits fit urban conditions, plasticity alters phenotype, selection shifts trait distributions, or local resources compensate for adverse filters. These routes produce similar observations—continued occurrence—but different evolutionary meanings. Because adaptation requires stronger evidence than urban divergence [5], future studies should pair proximal exposures with behavioral, physiological and demographic measurements and replicate those links across cities and developmental stages.

The proposed architecture is an evidence-organizing device rather than a validated forecasting model. Its value lies in preserving boundaries frequently compressed by urban-ecology terminology: city category versus proximal filter, trait measurement versus organismal consequence, plasticity versus inherited divergence, and evolutionary change versus adaptation. That discipline also makes null results informative rather than treating them as exceptions.

Conclusion

Insect urbanization is best interpreted as a conditional interaction between environmental filters and biological responses rather than as a universal urban-adaptation syndrome. Behavioral adjustment, physiological tolerance, plasticity and inherited divergence can each contribute to persistence, but none is sufficient by itself to establish adaptive benefit. Explicit separation of proximal exposure, trait state, life stage, spatial scale and evidential strength provides a more defensible basis for comparing urban insects across taxa, cities, seasons, and developmental stages and identifying where mechanistic and fitness validation remain necessary.

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