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Morphology, Physiology, Behavior, and Landscape Context Across the Diversity of Insect Dispersal Syndromes

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ABSTRACT

Insect dispersal is often inferred from single traits or single movement measurements, yet realized displacement emerges from interactions among morphology, physiological capacity, behavioral propensity, and environmental opportunity. This scoping review examines how those domains have been studied together or separately and identifies the inferential limits of treating any one of them as a universal dispersal proxy. Peer-reviewed literature published during 2017–2022 was mapped using insect and dispersal terms combined with morphology, physiology, behavior, landscape, and movement-measurement concepts. Evidence was charted by taxon, biological level, setting, focal construct, measurement class, and inference stage. Because source-specific search and selection counts were not available in the documented search record, no numerical screening or inclusion totals are reconstructed. The literature supports a heterogeneous view of dispersal. Wing form and body size can relate to flight performance or movement strategy, but their interpretation changes with environmental context and measurement method. Physiological studies identify energetic, thermal, muscular, endocrine, and transcriptomic correlates of flight-related states, whereas behavioral studies show that sex, reproductive context, social environment, habitat structure, and generation can alter movement propensity. These domains therefore cannot be collapsed into a single trait axis without losing biological and methodological distinctions. The review develops a proposed cross-domain interpretation of insect dispersal syndromes in which trait architecture, physiological state, behavioral decision-making, and landscape opportunity are treated as separable but interacting components. The framework is intended for evidence organization and hypothesis generation, not as a validated predictive model.

Keywords: Insect dispersal, Flight morphology, Physiological capacity, Movement behavior, Landscape connectivity, Dispersal syndrome

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Introduction

Dispersal links individual movement to colonization, gene flow, range dynamics, and persistence, but the term is applied to biologically different events. Across insects, dispersal is increasingly treated as a composite phenotype whose expression depends on organismal traits, environmental context, and sex or life-history state [1-3]. Experimental evolution in *Drosophila* further shows that selection on dispersal can be accompanied by

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coordinated phenotypic and metabolomic change, supporting the possibility of correlated dispersal-associated traits without establishing a universal syndrome [4].

The principal interpretive difficulty is that the evidence base spans different stages of dispersal and different inferential distances from realized movement. Wing morphology describes aspects of aerodynamic configuration; flight-performance assays measure capacity under particular conditions; emigration experiments measure propensity under constrained choices; telemetry and mark-recapture observe portions of realized movement; population-genetic structure integrates movement with successful reproduction across longer temporal scales; and invasion-front spread additionally incorporates demographic processes. Treating these outcomes as interchangeable can obscure where movement is directly observed and where dispersal is inferred.

A second difficulty is that dispersal capacity and dispersal expression need not coincide. An individual may possess flight structures and physiological reserves compatible with movement yet remain within a patch because reproductive state, social context, or habitat conditions suppress departure. Conversely, movement may be initiated under adverse conditions even when energetic or aerodynamic capacity limits its extent. Landscape structure can then alter whether initiated movement becomes successful transfer between suitable patches.

This review therefore asks how morphology, physiological capacity, behavioral propensity, and landscape context jointly structure the diversity of reported insect dispersal syndromes. Its contribution is not a claim that one multidomain syndrome has already been established. Instead, the review develops a proposed evidence architecture that separates trait state, performance capacity, behavioral activation, and environmental realization while retaining taxonomic, sex, life-stage, geographic, temporal, and methodological boundaries. This architecture provides the basis for asking when evidence from one domain can reasonably inform another and when such transfer would constitute overinterpretation.

Materials and Methods

The review followed scoping-review reporting principles because the objective was to map heterogeneous forms of dispersal evidence rather than estimate a pooled intervention or exposure effect [5]. Four linked questions guided charting: which morphological, physiological, behavioral, and landscape variables have been associated with insect dispersal; which measurement classes support those associations; where findings vary by taxon, sex, life stage, environment, or analytical scale; and which cross-domain relationships are directly supported rather than interpretively proposed.

Search logic combined insect taxon terms with dispersal, migration, movement, emigration, immigration, connectivity, or spread. These terms were paired with domain blocks addressing wing and body morphology, flight muscle, energetics, endocrine or molecular state, movement behavior, habitat configuration, matrix structure, topography, climatic conditions, tracking, and connectivity methods. The evidence window was restricted to 2017–2022. PubMed-compatible scholarly searching, publisher and DOI verification, and supplementary citation checking were used in constructing the evidence set.

Database-specific export totals and downstream screening counts were not preserved as verified numerical values. Consistent with an evidence-bounded review, those quantities were therefore not retrospectively inferred from the size of the reference list or reconstructed from later screening decisions. The selection process is consequently reported as a qualitative sequence rather than as artificial numerical arithmetic.

Records were retained when they directly addressed insect dispersal or provided methods necessary for interpreting dispersal evidence. Data charting separated taxon; sex or life stage where reported; laboratory, field, comparative, or modeling setting; focal construct; measurement method or data source; temporal design; reported direction; contradictory or null evidence; methodological limitation; and applicability boundary.

Evidence was then classified according to its inferential position: direct movement observation; behavioral or performance observation; morphological or physiological correlate; population-connectivity inference; and population- or range-spread inference. These classes were not treated as a ranking of biological importance. Rather, they define what each measurement can support without crossing an untested inference boundary.

Results and Discussion

The evidence base was heterogeneous in both organismal coverage and measurement level. Lepidopteran studies were particularly prominent in analyses of wing form, migration, habitat-specific movement, topography,

telemetry, and conservation. *Drosophila* studies contributed experimental-evolution and behavioral evidence, while termites, aphids, dragonflies, and small beetles broadened the physiological, landscape, and biomechanical range represented.

The principal evidence classes also differed markedly in what they measured. Morphological studies focused on wing geometry, body size, or flight-associated structures. Physiological studies examined energetic stress, thermal state, flight-muscle condition, endocrine regulation, or transcriptomic profiles. Behavioral studies addressed emigration, movement propensity, mate finding, and habitat-dependent trajectories. Landscape studies considered matrix cover, topography, resource distribution, climatic variation, and population connectivity.

These differences matter because superficially similar claims about "high dispersal" can originate from fundamentally different observations. A long-winged phenotype, long-duration experimental flight, frequent emigration from a patch, large field displacement, weak population genetic differentiation, and rapid range spread need not describe the same biological process. The mapped evidence therefore supports multidimensional interpretation but does not justify collapsing those measures into a common dispersal score.

Cross-domain evidence was also methodologically asymmetric. Individual studies commonly concentrated on one or two components rather than measuring morphology, physiology, behavior, and landscape response concurrently in the same individuals under field conditions. The cross-domain synthesis developed later is therefore explicitly proposed as an organizational model rather than presented as an empirically validated syndrome classification.

Morphological dispersal traits

Morphology constrains or facilitates flight, but morphological association cannot automatically be translated into realized dispersal. Comparative work on butterfly wings links shape variation with aspects of flight behavior while emphasizing that the functional interpretation of wing form depends on ecological context [6]. Field evidence from dragonflies similarly demonstrates species-specific responses to open and closed landscape cover, showing that realized movement cannot be inferred from an external landscape category without considering the organism interacting with it [7].

Environmental conditions can also alter dispersal-associated morphology. Experimental modification of host-plant conditions under elevated carbon dioxide changed monarch wing morphology, but the morphological response itself did not establish that field dispersal increased [8]. This distinction is critical because environmentally induced variation in wing dimensions may reflect developmental plasticity without demonstrating a corresponding change in movement propensity, transfer success, or population consequence.

Morphology also acquires meaning through demographic context. Conservation research on butterflies emphasizes that movement and demography should be evaluated together because displacement alone does not reveal successful settlement or contribution to population persistence [9]. Experimental flight in *Melitaea cinxia* alters energetic, reproductive, and longevity-related states, indicating that measurement of flight can itself intersect with life-history allocation [10]. Thus, even apparently direct tests of flight capacity should not be treated as behaviorally or physiologically neutral observations.

At larger spatial scales, insect movement research relies on complementary methods because departure, long-distance displacement, arrival, and subsequent reproduction are not captured equally by any single technique [11]. Behavioral decomposition reinforces this point: emigration, movement through the intervening matrix, and immigration or settlement constitute separable components of dispersal [12]. A trait correlated with one component need not predict the others.

The distinction becomes still more important when movement is inferred from population spread. Invasion dynamics combine dispersal with reproduction, survival, density dependence, and environmental conditions, so rates of range expansion cannot be reduced to individual flight ability [13]. Likewise, comparative evidence from butterflies indicates that migration and dispersal can show contrasting relationships with flight morphology and reproductive allocation [14]. Similar external movement phenotypes may therefore arise from different life-history configurations.

The morphological evidence consequently supports a restrained interpretation: wing form, body size, and related flight structures provide information about aerodynamic configuration, developmental allocation, or potential performance, but they do not independently establish realized dispersal. The analytical conflicts that arise when morphological signals are transferred across inference stages are condensed below.

Table 1 shows that the central problem is not which morphological traits have been studied, but what level of dispersal inference each morphological signal can legitimately sustain.

Table 1. Reconciling morphological signals with the dispersal process they can actually support

Morphological association			
Morphology-to-dispersal question	**Wing-shape association**	**Environmentally shifted wing form**	**Species-specific cover response**
Taxonomic or methodological scope	Butterfly comparative evidence	Monarch–host-plant experiment	Dragonfly field movement
Construct measured	Wing geometry linked with flight behavior	Wing morphology under altered plant environment	Movement through open versus closed cover
Observed pattern	Morphology covaries with flight-related function	Morphology changes with developmental environment	Species respond differently to the same cover classes
Dispersal inference supported	Treat as a context-dependent performance correlate	Separate morphological plasticity from movement outcome	Interpret morphology and movement within species context
Uncertainty	Ecological context alters functional meaning	Realized movement is not established by form alone	Landscape permeability is organism-dependent

Performance and realized movement			
Morphology-to-dispersal question	**Flight-stress phenotype**	**Movement–demography coupling**	**Migration–dispersal contrast**
Taxonomic or methodological scope	Experimental butterfly flight	Butterfly conservation studies	Comparative butterfly evidence
Construct measured	Organismal state following imposed flight	Movement interpreted with population processes	Flight morphology and reproductive allocation
Observed pattern	Flight effort intersects with energetic and reproductive condition	Displacement alone does not establish demographic contribution	Different movement strategies can carry contrasting allocation patterns
Dispersal inference supported	Avoid treating performance tests as biologically neutral	Keep movement potential distinct from population consequence	Reject a single morphology-based syndrome label
Uncertainty	Assay conditions can modify the phenotype being interpreted	Survival, settlement, and reproduction intervene	Movement category and life-history state alter interpretation

Physiological capacity

Physiological capacity introduces a state-dependent layer between anatomical structure and expressed movement. Flight structures may exist, but their functional use depends on temperature, energetic condition, muscular state, endocrine regulation, and other physiological constraints. These mechanisms operate at different biological levels and need not covary in a simple direction.

In crickets, cool environmental temperature is associated with changes in dispersal-flight behavior and physiology, demonstrating that flight-related performance can depend on thermal context rather than on morphology alone [15]. This illustrates an important boundary between possessing a flight apparatus and being physiologically able or behaviorally prepared to deploy it under particular environmental conditions.

In the termite *Reticulitermes chinensis*, dispersal flight is accompanied by biochemical, molecular, and morphological changes in flight muscle [16]. Within this species and life-history stage, the evidence supports a coordinated flight-state phenotype. It does not, however, establish that the same combination of muscular or biochemical changes characterizes dispersal across insect orders.

A different trajectory occurs during the transition away from flight. In aphids, nutritional conditions and juvenile-hormone sensitivity participate in flight-muscle degeneration during the dispersal-to-reproduction transition [17]. The structures underlying dispersal capacity can therefore be actively reorganized as life-history priorities change. Physiological state is consequently temporally dynamic rather than a fixed individual attribute.

Transcriptomic evidence adds another level. Genome-wide expression differences associated with migratory state in hoverflies identify molecular pathways correlated with movement-related phenotypes [18]. Such expression

profiles are valuable for identifying candidate processes, but association with migratory state is not equivalent to demonstrating that a particular transcriptomic signature causes movement or represents a generally adaptive mechanism.

Taken together, these studies argue against treating physiological capacity as a scalar variable. The synthesis used here therefore **proposes** three analytically distinct states: latent flight capacity, activated flight physiology, and post-flight physiological reallocation. These categories organize evidence from different levels without implying that insects universally pass through a fixed physiological sequence.

Behavioral propensity

Behavior determines whether available morphological and physiological capacity is expressed as movement. This distinction is evident in a range-expanding invasive insect in which body size relates to flight capacity and flight propensity, illustrating that the ability to fly and the tendency to initiate flight are not necessarily equivalent [19]. A dispersal syndrome based only on capacity can therefore misclassify individuals that possess adequate flight performance but rarely initiate movement.

Dispersal decisions can also depend on social context. Experimental evidence indicates that an individual's propensity to disperse may respond to the behavioral composition of its peers rather than only to its own behavioral type [20]. This finding does not imply that peer effects occur uniformly among insects, but it demonstrates that dispersal propensity can emerge relationally rather than as a fixed individual disposition.

Habitat structure adds another behavioral contingency. In *Drosophila*, dispersal across patchy habitat reflects interaction between genotype and habitat configuration [21]. Genetic differences therefore cannot be interpreted independently of the environmental geometry through which movement is expressed. Reproductive conditions matter as well: mate-finding context can modify sex-biased dispersal and local mate limitation [22], linking departure decisions to the social and reproductive environment.

Field movement studies reinforce the need to identify the behavioral stage being measured. Habitat-specific butterfly behavior alters trajectories across landscapes, and movement models that omit those responses can mischaracterize effective displacement [23]. Topography can also interact with sex, producing sex-biased differences in dispersal across terrain [24]. Within a bivoltine butterfly, dispersal differs between sexes and generations, showing that temporal life-history state can modify movement even within a single species [25].

These findings support a proposed stage-specific distinction among initiation propensity, transfer behavior, and settlement-related response. Sex, reproductive state, social context, habitat structure, and generation are treated as modifiers of these stages rather than as universally directional determinants. This framing helps distinguish apparently conflicting findings that may actually concern different behavioral decisions.

The analytical value of staging becomes clearest when observations with different biological meanings are placed side by side. The following matrix therefore separates what was observed from the behavioral inference that can reasonably follow.

Table 2. Behavioral stages that change the meaning of an insect dispersal observation

Behavioral event	**Inference from the event**		**Where it was observed**	**Validation**	
Behavioral checkpoint	**Observation**	**Meaning for dispersal**	**Focal system**	**Boundary**	**Measurement needed**
Departure and initiation					
Capacity versus initiation	Flight ability compared with flight propensity	Ability does not guarantee departure	Range-expanding insect	Body size and assay context can influence both measures	Measure performance and initiation independently
Socially contingent initiation	Change in movement with peer behavioral composition	Propensity can depend on the social environment	Experimental group context	Peer effects may not transfer among social systems or taxa	Manipulate focal and group phenotype separately
Genotype × habitat response	Dispersal across	Behavioral expression depends	Drosophila in patchy habitat	Experimental patch geometry	Cross genotype with replicated habitat structures

	structured patches	on environmental configuration		limits field transfer	
Search, transfer, and mate finding					
Mate-finding dispersal	Movement under mate limitation	Departure may respond to reproductive opportunity	Sex-specific reproductive context	Sex ratio and local mating conditions alter interpretation	Record mating state and social environment with movement
Habitat-specific transfer	Paths through contrasting habitat types	Matrix behavior alters realized displacement	Butterfly field movement	Habitat classes are species- and scale-dependent	Fit movement models with habitat-specific responses
Topography × sex	Sex-specific movement across terrain	Terrain can constrain or facilitate transfer differently by sex	Butterfly field dispersal	Local relief and species behavior restrict generalization	Replicate sexes across contrasting topographic settings
Generation-dependent propensity					
Generation-dependent propensity	Movement compared across generations	Behavioral state can vary through the season	Bivoltine butterfly	Generation covaries with phenology and environment	Separate generational effects from contemporaneous conditions

Landscape context

Realized dispersal depends not only on whether an insect can and will move, but also on whether the surrounding landscape permits, redirects, or terminates that movement. In agricultural landscapes, set-aside configuration can alter the balance between local abundance and movement, indicating that management features favorable for occupancy are not automatically equivalent to features facilitating transfer [26, 27]. Landscape context therefore acts on realized trajectories rather than simply modifying an intrinsic dispersal coefficient.

Genetic-connectivity evidence adds a longer-term perspective. Alpine landscape barriers can structure connectivity among butterfly populations, but such patterns integrate successful movement and reproduction over time rather than directly recording individual journeys [28]. Climatic context also matters: aphid dispersal responses to temperature can change with precipitation conditions, demonstrating that environmental drivers may interact rather than operate independently [29].

These findings support a distinction between landscape opportunity, which determines accessible pathways and resources, and landscape resistance, which alters the probability that initiated movement reaches another suitable location. Neither construct should be treated as species-independent. Habitat categories, topographic features, climatic states, and resource distributions acquire functional meaning through the sensory, behavioral, and physiological characteristics of the insect encountering them.

The resulting interpretive problem is better expressed as conditional predictions than as a list of landscape variables.

Table 3. Landscape conditions that change when dispersal observations can be generalized

Landscape state			**Generalization boundary**		
Landscape contrast	**System**	**Field signature**	**Condition that changes meaning**	**Consequence for generalization**	**Required test**
Resource opportunity					
Resource-rich versus movement-permissive habitat	Agricultural butterflies	Abundance and movement responses	Management configuration and species behavior differ	High local abundance need not imply high transfer	Measure occupancy and movement separately
Matrix permeability					
Barrier versus permeable matrix	Alpine butterfly populations	Connectivity across landscape structure	Genetic structure integrates reproduction and time	Landscape features can restrict effective connectivity	Pair connectivity inference with direct movement where possible

Climate interaction					
Climatic main effect versus climatic interaction	Aphid flight phenology	Temperature and precipitation responses	Seasonal and regional conditions constrain transferability	Direction of response may change with concurrent climate	Test interacting drivers rather than isolated averages
Opportunity–resistance synthesis					
Proposed opportunity–resistance state	Cross-domain synthesis	Landscape pathways, resources, and constraints	Species, sex, stage, and scale remain explicit	Context determines whether initiated movement becomes realized transfer	Validate within taxa before comparative generalization

Cross-domain dispersal syndromes

Across the reviewed evidence, no single domain is sufficient to describe dispersal. The synthesis therefore proposes a four-component architecture: morphological affordance, physiological readiness, behavioral activation, and landscape realization. These are not sequential necessities in every insect, nor are they assumed to be independent. They are analytical states that clarify where an observed association enters the dispersal process. Morphological affordance describes structures that can enable or constrain flight. Physiological readiness represents the temporary energetic, thermal, muscular, endocrine, or molecular state in which those structures operate. Behavioral activation concerns whether movement is initiated and how transfer decisions are expressed. Landscape realization represents whether external conditions convert initiated movement into displacement, settlement, or longer-term connectivity.

The architecture also makes mismatch scientifically informative. High flight capacity with low departure propensity is not contradictory; it represents capacity without activation. Strong departure behavior coupled with restrictive terrain represents activation without successful landscape realization. Weak population connectivity can arise from restricted transfer, low settlement, or limited reproductive contribution rather than from one identifiable morphological deficit.

Figure 1 therefore represents dispersal syndrome diversity as trajectories through interacting state fields rather than as a single high-to-low dispersal continuum.

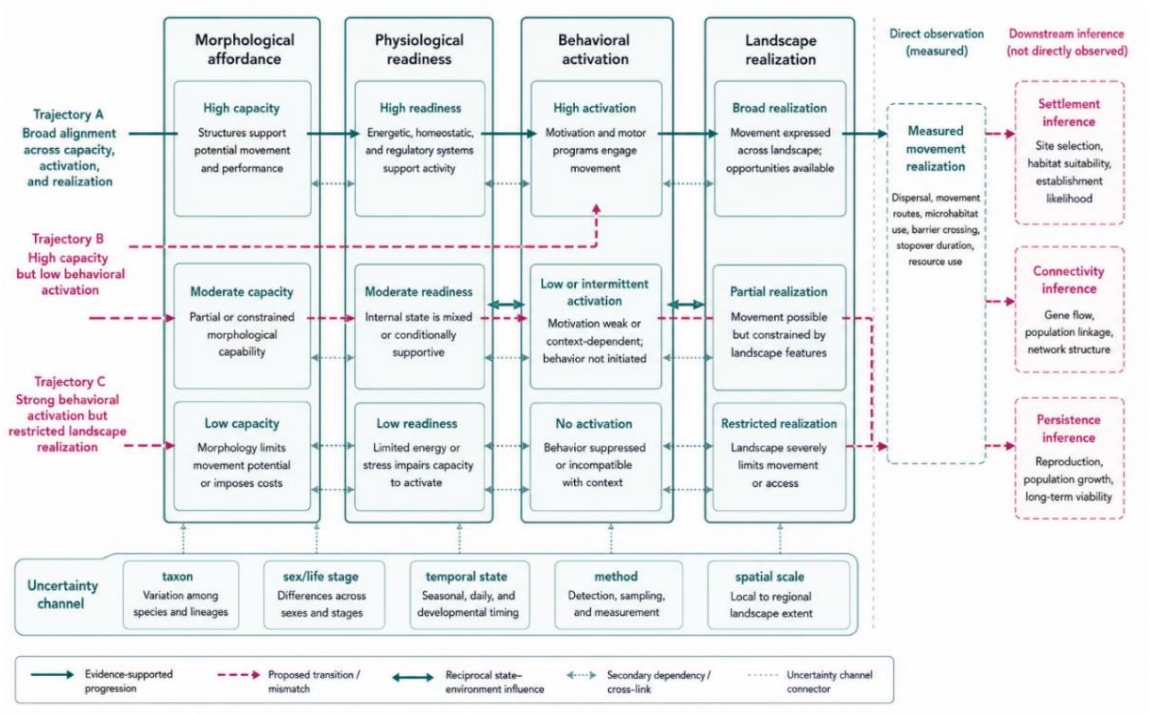


Figure 1. State mismatches that separate dispersal capacity from realized movement

Evidence gaps

The strongest limitation is not simply insufficient evidence, but uneven correspondence among evidence classes. Biomechanical studies can resolve how extreme wing architecture affects flight performance [30] and how small-insect wing morphology relates to aerodynamic efficiency [31], yet these mechanistic advances do not by themselves establish field dispersal, settlement, or demographic consequence.

Measurement can also alter the phenomenon being measured. Tracking devices may influence terrestrial arthropod performance or behavior, requiring explicit evaluation of tag effects before movement estimates are generalized [32]. Isotopic geographic assignment provides another route to reconstruct movement origin, but assignment uncertainty and spatial baselines remain distinct from direct individual tracking [33].

The priority is therefore cross-validation across inference stages rather than accumulation of additional isolated proxies.

Table 4. Evidence gaps that determine whether a dispersal inference can cross biological scales

Capacity or tracking without field realization		
Biomechanics without field realization		
Evidence currently reaches	Wing-performance mechanics	
Flight efficiency interpreted as dispersal success	**INFERENCE AT RISK**	Laboratory performance versus field transfer
Prospective bridge	Couple biomechanical measures with movement observations	
Tracking without device-effect testing		
Evidence currently reaches	Tagged individual movement	
Observed trajectory treated as unaltered behavior	**INFERENCE AT RISK**	Tag burden and behavioral disturbance
Prospective bridge	Include untagged or device-effect controls	
Geographic assignment without direct trajectory		
Evidence currently reaches	Isotope-based origin inference	
Assigned origin treated as continuous tracking	**INFERENCE AT RISK**	Baseline resolution and assignment uncertainty
Prospective bridge	Combine assignment with independent movement evidence	
Proxy and syndrome-level gaps		
Cross-domain proxy substitution		
Evidence currently reaches	Traits, physiology, behavior, connectivity measured separately	
One evidence class used as another	**INFERENCE AT RISK**	Biological level and temporal scale
Prospective bridge	Measure multiple domains in the same individuals or populations	
Proposed syndrome classification without prospective validation		
Evidence currently reaches	Integrative synthesis	
Organizational categories treated as predictive states	**INFERENCE AT RISK**	Taxon and context specificity
Prospective bridge	Test predefined cross-domain predictions prospectively	

The reviewed literature supports a plural rather than unitary conception of insect dispersal. Morphological features can shape potential performance, physiological state can enable or suppress that potential, behavioral context can determine whether movement is initiated, and landscapes can transform the same movement tendency into contrasting realized outcomes. The major analytical error is therefore not choosing the "wrong" dispersal trait, but assuming that measurements taken at different stages of this process answer the same question.

The proposed architecture resolves this problem by retaining boundaries among capacity, activation, realization, and downstream inference. It also accommodates apparent contradictions. A morphology associated with efficient flight may coexist with low emigration; strong emigration may coexist with weak connectivity; and rapid population spread may occur without evidence that every individual has high flight capacity. These are not necessarily inconsistent observations because they occur at different biological and inferential levels.

This interpretation also changes how conservation applications should be framed. Movement-supportive habitat cannot be inferred solely from abundance, and connectivity cannot be interpreted without considering behavioral transfer, settlement, reproduction, and temporal scale. Likewise, physiological and molecular associations may identify candidate mechanisms but should not be promoted directly to adaptive or predictive explanations without appropriate functional and field validation.

Methodological triangulation is therefore central. Direct movement observation, performance assays, morphology, molecular physiology, connectivity inference, and geographic assignment should be treated as complementary evidence classes whose convergence is informative precisely because they are not interchangeable [32]. Where methods disagree, the discrepancy may reveal life-stage change, behavioral switching, environmental constraint, temporal averaging, or measurement disturbance rather than simple error.

The proposed cross-domain dispersal-syndrome architecture should consequently be used as a question-generating framework: which component is being measured, which component is being inferred, what environmental state separates them, and what validation is required before interpretation crosses that boundary? Its value lies in preserving those distinctions while still allowing integrated biological reasoning.

Conclusion

Insect dispersal syndromes are best interpreted as context-dependent combinations of morphology, physiological state, behavioral activation, and landscape realization rather than as fixed trait packages. The proposed architecture organizes these domains without assuming that they are universally coupled or prospectively predictive. Future progress depends on measuring multiple components across the same organisms and environments, validating transitions between evidence classes, and retaining taxonomic, life-stage, sex, temporal, methodological, and spatial boundaries when dispersal inferences are transferred across scales.

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