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Perceptual Range, Movement Motivation, Matrix Cost, and Connectivity Jointly Determine Insect Dispersal Success in Fragmented Landscapes

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ABSTRACT

Landscape connectivity is frequently represented as a property of habitat arrangement, yet insects encounter fragmentation through sensory, behavioral, and survival processes that are not captured by geometry alone. A structurally connected landscape can remain functionally difficult to cross, whereas some altered landscapes can retain realized connectivity for mobile taxa. Approach: This framework decomposes dispersal success into linked components: perceptual range, departure motivation, matrix resistance, movement mortality, patch detectability, and the distinction between structural and functional connectivity. Evidence is interpreted at the level at which it was measured, separating direct movement observations from trait proxies, genetic exchange, community responses, and modeled outcomes. Synthesis: The framework proposes that dispersal success emerges from sequential but interacting filters. An insect must leave a source context, traverse a matrix at acceptable cost, survive exposure, detect or encounter a suitable destination, and convert landscape opportunity into realized movement. High performance in one component cannot automatically compensate for failure in another. Taxon, sex, life stage, resource distribution, experience, spatial scale, and measurement method can shift each filter. Implications: Connectivity management should therefore diagnose which component constrains movement rather than assuming that increasing structural linkage alone will improve dispersal. The framework is a testable synthesis, not a validated predictive model, and requires comparative field validation across insect taxa and landscape contexts.

Keywords: Insect dispersal, Perceptual range, Matrix resistance, Movement ecology, Functional connectivity, Habitat fragmentation.

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Introduction

Fragmented landscapes are often described through patch area, isolation, corridors, or resistance surfaces, but those descriptors do not by themselves establish whether an insect can complete dispersal. Monarch research illustrates why: extensive mobility can connect habitat elements across agricultural landscapes, yet movement remains contingent on the spatial distribution of resources and other landscape-scale pressures [1]. Across 25 butterfly species, diffusion-like movement showed a negative association with local density, whereas several other

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movement metrics did not, demonstrating that even closely related movement descriptors are not interchangeable predictors of population pattern [2].

The inferential problem becomes sharper when geometric connectivity is compared with realized movement. Experimental-landscape work showed that network metrics differ in how well they represent observed insect transfers, making biological validation necessary rather than optional [3]. Conversely, two insect pollinators retained substantial genetic connectivity across a human-altered landscape, providing a counterexample to the assumption that visible fragmentation necessarily produces functional isolation [4]. Connectivity therefore describes different phenomena depending on whether it is inferred from map geometry, individual trajectories, successful reproduction, genetic exchange, community composition, or interaction networks.

A second problem is that matrix "quality" is often compressed into a single resistance concept. Spatial modeling has separated the probability of entering or traversing matrix habitat from survival within it and found that improving matrix survival can have stronger regional consequences than increasing permeability alone under modeled fragmentation scenarios [5]. This distinction does not establish a universal insect response, but it identifies a critical analytical error: movement opportunity and movement survival are not the same process.

This article develops a proposed landscape-ecology framework in which dispersal success is jointly conditioned by perception, motivation, matrix cost, mortality, destination detection, and realized connectivity. The contribution is not a universal dispersal equation. It is an inference structure for preventing one evidence class from being substituted for another and for identifying where apparently connected landscapes may fail biologically, or apparently fragmented landscapes may retain function.

Materials and Methods

Connectivity components

The framework was constructed by decomposing dispersal into components that can, in principle, be measured independently and then linked without collapsing measurement levels. Perceptual evidence was treated as information about detection or orientation; movement trajectories as evidence of realized path choice; telemetry as a measurement system with explicit localization uncertainty; genetic structure as time-integrated evidence of reproductive exchange; and landscape simulations as conditional tests of mechanisms rather than direct observations.

This separation is supported by behavioral work showing that patch distance, matrix type, and previous experience can alter habitat perception and flight behavior in Heliconius butterflies [6]. It is also supported by field telemetry of breeding female monarchs, in which habitat quality and resource density altered movement and space use [7]. Those studies measure organismal responses directly but remain bounded by species, sex, season, and landscape context.

Movement measurement itself introduces another inference layer. VHF telemetry has been used to reconstruct monarch flight paths across heterogeneous landscapes [8], while automated multi-antenna telemetry demonstrates that locations can be estimated repeatedly but with method-specific uncertainty that must be calibrated [9]. Accordingly, this framework treats "movement" as an observed or estimated trajectory only when the evidence warrants that level of inference. Morphological traits, community occupancy, genetic differentiation, and modeled connectivity are retained as distinct proxies or downstream outcomes rather than relabeled as direct dispersal.

The analytical unit is therefore a component state rather than a universal species score. Relationships supported directly by the literature are distinguished from the article's proposed links among components. No numerical weights, thresholds, or compensation rules are assigned because the evidence does not establish transferable values across taxa or landscapes.

Results and Discussion

Perceptual range

Perceptual range defines the spatial scale over which environmental information can alter orientation or target choice; it should not be treated as a fixed radius around an insect. Experiments with greater fritillaries showed that habitat targeting weakened with increasing distance, indicating a graded detection process rather than a universal categorical threshold [10]. The relevant outcome was behavioral targeting under specified experimental conditions, not proof that the same distance governs routine dispersal in every matrix.

Resource identity adds another boundary. Female monarch experiments showed finite and resource-dependent detection of common milkweed and flowering nectar resources [11]. A disperser may therefore detect one biologically relevant cue while failing to detect another at the same spatial separation. This matters because "patch detectability" can be overestimated when habitat is represented as a visually homogeneous polygon even though insects respond to particular host, nectar, mate, microclimatic, or structural cues.

The proposed interpretation is that perceptual range is a conditional filter on connectivity opportunity. Distance, cue strength, matrix structure, previous experience, sensory modality, and behavioral state may jointly determine whether a destination enters the animal's actionable information field. The evidence currently justifies the direction of this argument more strongly than any general numerical threshold. Perceptual range should thus enter landscape models as context-dependent where possible, and transfer across species, sexes, life stages, or cue classes should require validation.

Departure motivation

Dispersal cannot occur merely because a destination is detectable. Individuals must also enter a behavioral state in which leaving the current patch is preferable to remaining. Mark–recapture evidence from three threatened butterflies documented long-distance movements and density-dependent dispersal, showing that emigration and immigration can change with population context rather than behaving as fixed species constants [12]. Density dependence, however, should not be generalized beyond the taxa and conditions in which it was measured.

Habitat quality can pull movement in the opposite direction. In agricultural set-aside strips, butterfly abundance and measured movement did not respond as interchangeable outcomes; resource-enhanced habitat could support abundance without producing equivalent changes in all flight-path characteristics [13]. Thus, a patch that is locally favorable may increase residence even when the surrounding landscape is structurally permeable.

Dispersal-related traits also carry demographic boundaries. In Hamadryas februa, associations between habitat amount and flight-related morphology differed between males and females [14]. Morphological differences are not direct measures of successful dispersal, but they warn against assigning one movement propensity to an entire species. The framework therefore treats departure motivation as a state-dependent probability influenced by density, resource conditions, sex, reproductive context, and potentially experience. It is conceptually distinct from locomotor capacity: an insect may be capable of crossing a matrix yet not initiate the movement.

Matrix resistance

Matrix resistance is commonly represented as the energetic, behavioral, or ecological cost of moving through non-habitat, but direct and indirect evidence show that its meaning depends on the endpoint measured. Population-genetic analyses of two alpine butterflies identified the Central Alps as a major barrier separating western and eastern population groups [15]. Such genetic discontinuity supports restricted effective exchange across a large landscape feature, but it does not reveal the precise routes, failed crossings, or mortality events that produced the pattern.

Landscape-genetic work on the soil-feeding termite Embiratermes neotenicus likewise linked changing forest landscapes and geographic features with population differentiation across Suriname and French Guiana [16]. The taxon and movement biology are very different from butterflies, underscoring that a "matrix" is organism-specific: open agricultural land, mountain systems, degraded forest, rivers, and host-poor habitat cannot be assigned a common biological cost without evidence.

The proposed framework therefore partitions matrix resistance into costs affecting entry, movement speed or path tortuosity, exposure duration, energetic expenditure, and eventual survival, while keeping those mechanisms separate unless a study measures them directly. Genetic differentiation can indicate restricted effective connectivity; it cannot by itself identify which matrix-cost mechanism was responsible.

Movement mortality

The mortality component asks a narrower question than resistance: conditional on an insect entering the matrix, does it survive long enough to reach a destination and contribute to realized connectivity? This distinction is essential because a permeable matrix can invite movement while still imposing substantial exposure, whereas a behaviorally avoided matrix may generate little direct mortality simply because few individuals enter it. The modeled comparison between permeability and survival demonstrates why these quantities should not be merged [5].

Landscape-change simulations for woodland invertebrates further show that functional and genetic connectivity can respond differently to tree loss and pre-emptive felling scenarios [17]. These outputs are conditional on model structure and parameterization, so they do not establish field mortality rates. They do, however, show that altered movement opportunity can propagate differently to downstream connectivity measures.

Direct mortality during dispersal remains difficult to estimate because disappearance from telemetry, recapture, or genetic datasets has multiple explanations. A lost signal is not a death, failure to recapture is not proof of mortality, and genetic absence can reflect reproductive failure or sampling limitations. Telemetry can reconstruct trajectories [8], but localization and detection error remain measurement constraints [9]. Movement mortality should therefore be estimated with designs that distinguish confirmed death, censored observation, emigration beyond the sampling frame, temporary signal loss, and successful but undetected arrival.

To prevent matrix entry, exposure, and mortality from being interpreted as the same process, the following ledger separates observable states from the inferences they permit.

Table 1. Distinguishing movement-mortality states from matrix entry and dispersal failure

Verified arrival, death, or observation loss			
Entry with documented survival to destination			*Evidence-defined state*
Trajectory setting	Tracked disperser crossing non-habitat		
Fate evidence	Continuous or sufficiently resolved trajectory ending in verified arrival		
Matrix was traversable and survived for that individual under those conditions			**Meaning for dispersal success**
Observation boundary	Arrival does not establish reproduction or population contribution	**Required test**	Link tracking to post-arrival fate when effective dispersal is the endpoint
Entry followed by confirmed death			*Evidence-defined state*
Trajectory setting	Individually monitored movement		
Fate evidence	Direct recovery or unambiguous mortality observation		
Mortality, not merely resistance, terminated the dispersal attempt			**Meaning for dispersal success**
Observation boundary	Cause of death may remain uncertain	**Required test**	Record exposure duration, matrix features, and cause where defensible
Entry followed by loss of observation			*Evidence-defined state*
Trajectory setting	Telemetry or mark–recapture study		
Fate evidence	Signal loss, censoring, or non-recapture		
Outcome is unresolved; mortality cannot be assumed			**Meaning for dispersal success**
Observation boundary	Emigration, equipment failure, missed detection, or death are alternatives	**Required test**	Use censoring-aware designs and independent detection where possible
Entry probability versus survival			
High entry probability with low survival			*Proposed diagnostic state*
Trajectory setting	Matrix-management scenario		
Fate evidence	Separate estimates or modeled parameters for permeability and survival		
Structural or behavioral permeability can coexist with a strong mortality filter			**Meaning for dispersal success**
Observation boundary	Empirical prevalence is taxon- and context-dependent	**Required test**	Manipulate permeability and survival separately
Low entry probability with high conditional survival			*Proposed diagnostic state*
Trajectory setting	Avoided but physically traversable matrix		
Fate evidence	Few entries but low mortality among verified entrants		
Resistance is primarily pre-entry or behavioral rather than lethal			**Meaning for dispersal success**
Observation boundary	Small entrant samples can obscure mortality	**Required test**	Separate reluctance to enter from consequences after entry
Downstream connectivity without direct fate			
Downstream connectivity decline without observed deaths			*Proposed inference guardrail*
Trajectory setting	Genetic, demographic, or modeled endpoint		
Fate evidence	Reduced functional or genetic connectivity		
Mortality is only one candidate explanation			**Meaning for dispersal success**

Observation boundary	Reproductive failure, route choice, detection, or demographic change may generate the same endpoint	**Required test**	Do not attribute mechanism without direct movement-fate evidence

Mortality risk is expressed along a moving trajectory rather than as a single patch attribute. **Figure 1** therefore separates entry, exposure, observation loss, verified survival, and downstream inference so that structurally similar outcomes are not assigned the same biological mechanism.

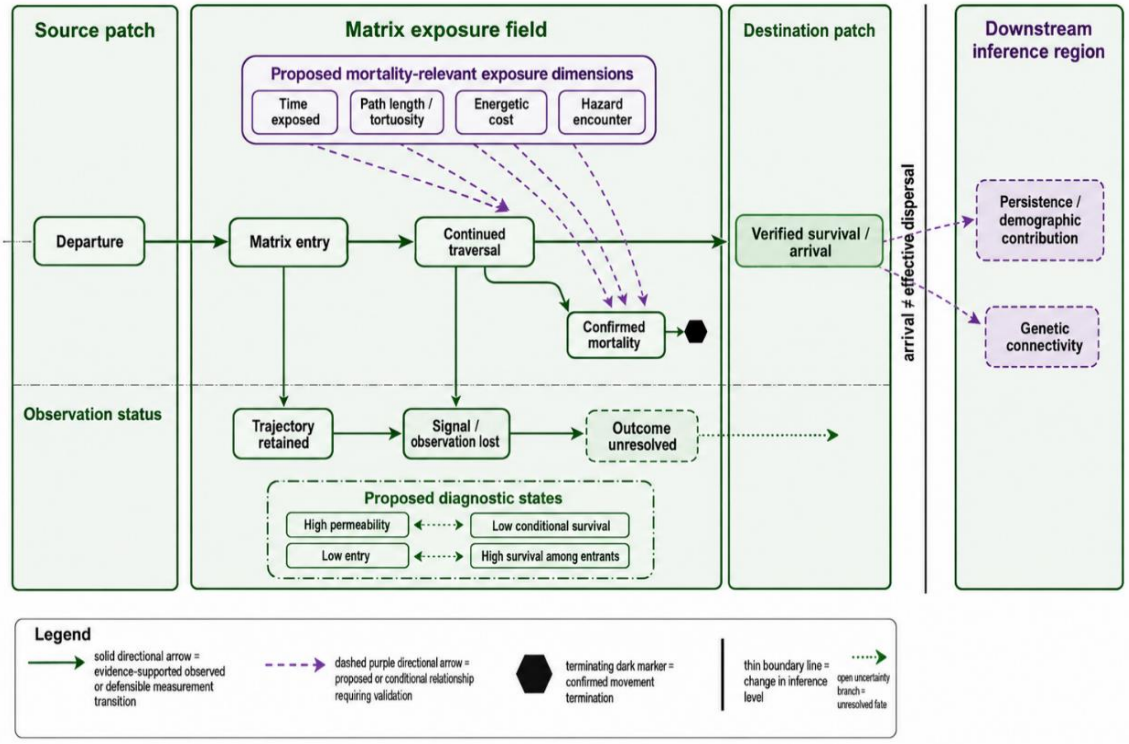


Figure 1. Where a disperser is lost: separating matrix entry, traversal exposure, observation failure, and true movement mortality

Patch detectability

Detectability is distinct from perceptual capacity because a sensory system with adequate range still requires a destination to emit discriminable and biologically relevant cues. Greater fritillaries showed distance-dependent habitat targeting [10], whereas female monarchs responded differently to milkweed and nectar resources [11]. In Heliconius, matrix context and previous experience further altered habitat perception [6]. Thus, destination detection should be interpreted as an interaction among sensory range, cue identity, matrix interference, prior experience, and behavioral state.

The framework therefore distinguishes potentially detectable habitat from behaviorally detected destination habitat. Resource-rich patches may modify movement and space use [7], but resource abundance does not demonstrate that distant dispersers can locate those patches. Management maps that classify patches solely by habitat quality may consequently overestimate functional accessibility when cue detection has not been measured.

Structural versus functional connectivity

Structural connectivity describes spatial opportunity: distances, corridors, stepping stones, habitat amount, or modeled resistance between patches. Functional connectivity concerns biological realization of those opportunities through movement, colonization, reproduction, genetic exchange, or other organism-dependent outcomes. Grassland-fragment assemblages show that connectivity and fragment size can jointly structure arthropod species composition [18], but community composition is not a direct measurement of individual movement.

Likewise, small grassland fragments can retain substantial arthropod functional diversity when landscape connectivity is favorable [19]. Fragmentation responses are nevertheless taxon-dependent: plant and insect-

pollinator communities in coastal dune slacks responded differently to patch configuration [20]. At still another level, green infrastructure can influence restoration of pollination networks [21], while restored plant–pollinator associations have shown strong relationships with surrounding landscape connectivity [22]. These endpoints capture different ecological consequences and should not be treated as interchangeable measures of dispersal.

The key inference problem is therefore not whether one landscape is "connected," but which connectivity state has actually been demonstrated and at what biological level. The distinction is summarized below because the evidential boundaries are easier to recover comparatively than from repeated narrative qualifications.

Table 2. Evidence transitions that separate mapped connectivity from biologically realized insect connectivity

Opportunity		**Biological realization**		**Cross-level verification**	
Connectivity level	**Biological level**	**Observable evidence**	**Inference allowed**	**Validation**	**Boundary preventing overreach**
Mapped and modeled opportunity					
Structural proximity	Landscape geometry	Patch distance, configuration, corridor continuity	Movement opportunity may exist	Compare with observed movement	Geometry does not establish organismal use
Modeled functional pathway	Individual or population model	Resistance surface, network or movement simulation	Candidate routes or relative accessibility	Test against independent field movement	Output depends on parameterization and assumed behavior
Realized individual movement					
Realized individual movement	Individual	Telemetry, tracking, mark–recapture transition	A route was traversed by observed individuals	Follow post-arrival fate	Traversal does not establish reproduction
Emergent population, community, and genetic signals					
Community connectivity signal	Community	Composition, occupancy or functional-diversity pattern	Landscape context is associated with assemblage structure	Link assemblage response to colonization processes	Community pattern has multiple demographic causes
Interaction-network connectivity	Community/network	Pollination or other interaction network	Landscape structure corresponds to ecological interaction continuity	Separate movement, visitation and functional transfer	Interaction observation is not equivalent to dispersal
Effective genetic connectivity	Population /genetic	Kinship, gene flow or population structure	Reproductive exchange has occurred over an integrated period	Combine genetics with contemporary movement data	Current routes and individual movement events remain unresolved
Agreement and disagreement among levels					
Cross-level agreement	Multiple levels	Concordant structural, movement and downstream evidence	Stronger support for realized connectivity	Replicate across landscapes and demographic states	Agreement remains taxon-, time- and scale-specific
Cross-level disagreement	Multiple levels	Structural and biological indicators diverge	A component between opportunity and realization may be limiting	Diagnose perception, departure, matrix exposure and destination detection	The limiting mechanism cannot be inferred automatically

Because the evidence classes form nested but non-equivalent levels, **Figure 2** places structural opportunity, individual realization, population consequences, and ecological-network evidence in separate analytical bands rather than along one undifferentiated connectivity axis.

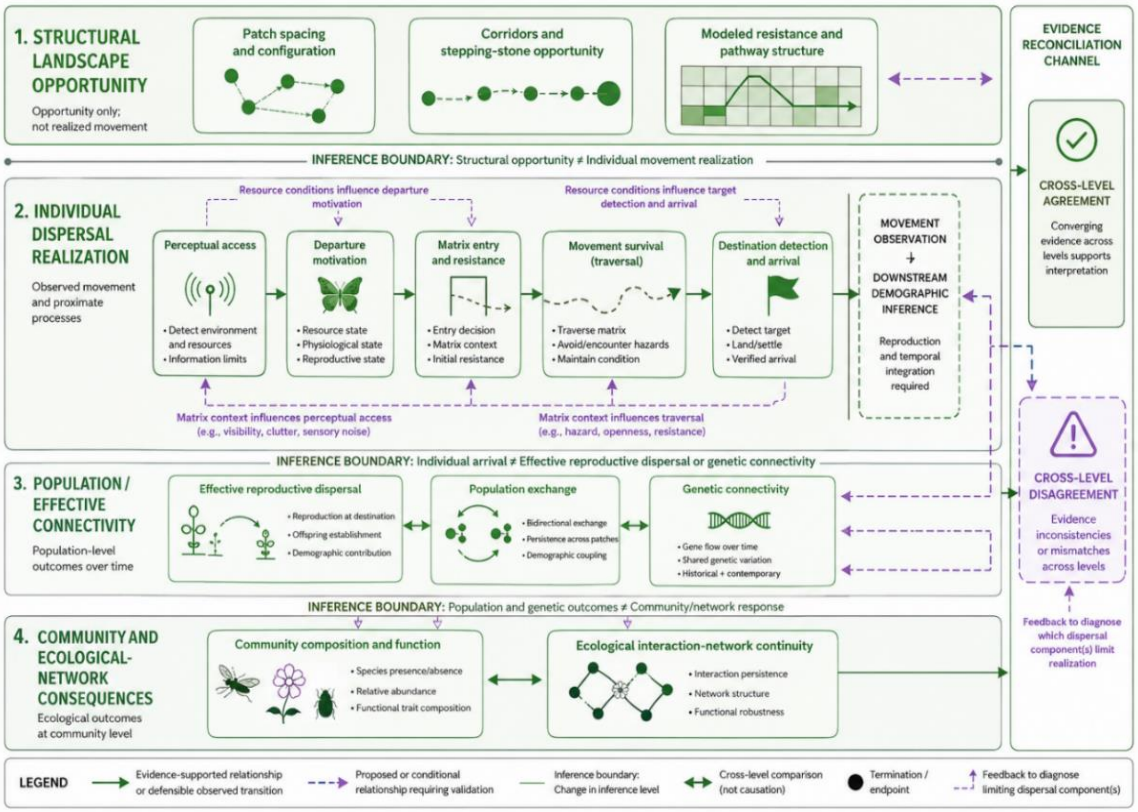


Figure 2. When connectivity indicators disagree: reconciling landscape opportunity, realized movement, and downstream biological evidence

Integrated dispersal-success model

The synthesis proposed here treats successful dispersal as the outcome of conditionally linked filters rather than a single resistance value. Genetic reconstruction of Glanville fritillary families demonstrates that effective between-patch dispersal can be inferred from reproductive relationships, while remaining distinct from direct trajectory observation [23]. Comparative work also shows that closely related butterflies can exhibit markedly different demographic and genetic landscape structures [24], limiting parameter transfer even between congeners. Resource-tracking strategy provides another source of heterogeneity: contrasting Curculio species show different genetic population structures in expanding forests [25]. At broader agroecosystem scale, natural-habitat connectivity and management can affect pest gene flow and natural-enemy communities differently [26].

The proposed model therefore represents dispersal success as requiring sufficient performance across perception, motivation, matrix traversal, survival, and target acquisition before downstream effective connectivity can occur. It deliberately assigns no universal weights or thresholds. A component may constrain another, and compensation is possible only where empirical validation demonstrates it.

Management implications

Connectivity interventions should begin by diagnosing the limiting component. Restoration evidence indicates that dispersal-constrained arthropods can remain underrepresented in highly fragmented restoration settings even when habitat is being re-established [27]. Increasing habitat amount without addressing isolation or matrix conditions may therefore fail to restore taxa with limited movement capacity.

Functional interpretation also depends on what is measured. Flower-visitation and pollen-transport metanetworks can produce different pictures of bee–plant connectivity [28]. Consequently, corridor success should not be inferred solely from occupancy, visitation, or structural linkage when the intended conservation endpoint is successful movement, reproduction, or ecological function.

Management evaluation should combine appropriately scaled structural measures with organism-level or downstream biological evidence and should state explicitly which connectivity component the intervention is expected to modify.

The framework resolves a recurring ambiguity in fragmented-landscape ecology: the same word, connectivity, is used for opportunity, behavior, successful passage, reproduction, gene flow, assemblage structure, and ecological interaction. The cited evidence shows that these layers can correspond, but it also contains clear cases of decoupling. Movement metrics do not uniformly predict density [2]; increased local abundance need not imply altered movement [13]; and substantial genetic connectivity can persist across modified landscapes [4].

The framework therefore predicts no universal effect of fragmentation. Instead, it proposes that identical structural configurations can produce different biological outcomes because perceptual ability, motivational state, matrix cost, mortality risk, resource detectability, sex, species biology, and temporal context modify realization. Long-term Glanville fritillary dynamics further show that spatial synchrony in environmental conditions can propagate into metapopulation synchrony [29], reminding us that connectivity operates within changing temporal as well as spatial environments.

Several limits remain. Much direct perceptual and telemetry evidence comes from butterflies, particularly monarchs, whereas termite, weevil, pollinator, community and genetic studies operate at different inferential scales. Laboratory or release experiments may not reproduce natural dispersal motivation, while genetic endpoints integrate movement and reproduction over longer periods. The proposed component structure therefore requires prospective testing using designs that measure multiple components simultaneously and test whether cross-level predictions improve over structural connectivity alone.

Conclusion

Insect dispersal success cannot be reduced safely to patch spacing or a single landscape-resistance surface. Perception, departure motivation, matrix traversal, survival, destination detection and downstream functional connectivity represent distinct but interacting filters. The proposed framework makes these filters explicit so that evidence from movement, genetics, communities and ecological networks is interpreted at the biological level actually measured. Its value lies in identifying where connectivity inference can fail and in specifying what must be measured next; its predictive generality remains to be established across taxa,

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