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Signal Production, Detection, and Behavioral Meaning Across the Ecological Diversity of Insect Chemical Communication

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ABSTRACT

Chemical communication in insects is often described as if signal production, environmental transmission, detection, neural processing, and behavioral response formed one continuous and self-evident causal chain. Evidence across insect taxa instead shows that each transition has distinct biological constraints and distinct evidential requirements. This integrative review examines how chemical signals are generated, released into heterogeneous environments, detected by peripheral chemosensory systems, and transformed by higher-order neural processing before contributing to behavior. The synthesis emphasizes three recurring sources of interpretive error: inferring behavioral meaning from receptor responsiveness, generalizing laboratory signal delivery to natural odor landscapes, and treating context-dependent responses as fixed properties of compounds. A proposed inferential architecture therefore separates production, environmental availability, peripheral detectability, neural interpretation, and behavioral use while retaining taxonomic, life-stage, environmental, and methodological boundaries. This separation clarifies why the same chemical can participate in different ecological relationships and why similar behavioral outcomes can emerge from different sensory-processing routes. The resulting framework is intended as an evidence-bounded guide for integrating molecular, neurobiological, behavioral, and ecological studies rather than as a universal mechanistic model.

Keywords: Pheromone biosynthesis, Olfactory receptors, Odor plumes, Neural processing, Behavioral context, Semiochemical ecology

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Introduction

Chemical communication connects biochemical production in a sender with sensory and behavioral consequences in a receiver, but the evidence supporting those links is rarely collected at the same biological scale. Pheromones have arisen through multiple evolutionary routes, including modification of pre-existing metabolites and recruitment of compounds already meaningful to sensory systems [1]. Work in *Drosophila* illustrates how production, sensory detection, neural processing, and behavioral output can be studied within one experimental lineage, while also revealing how unusual such integrative resolution remains across insect diversity [2]. Natural olfactory environments further complicate the chain because volatile information occurs in mixtures whose composition and temporal structure change between source and receiver [3]. Reviews of insect olfactory

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communication therefore emphasize that background odors, environmental chemistry, and changing ecological conditions can modify the effective information available to an insect [4].

A second problem is inferential rather than physical. Behavioral use of chemical information varies with internal state, external conditions, and phylogenetic history, so a measurable sensory response cannot be assumed to carry a fixed behavioral meaning [5]. Chemical information can also be modified or generated by organisms other than the nominal sender; floral microbes, for example, can alter volatile blends that insects detect and use [6]. This review consequently treats chemical communication as a set of linked but non-equivalent stages. The proposed synthesis separates signal production, environmental availability, peripheral detectability, neural interpretation, and context-dependent behavioral use. The separation is analytical, not a claim that every insect system implements the same mechanism. Its purpose is to identify where evidence is direct, where inference crosses biological levels, and where taxon, stage, environment, or method limits generalization.

Chemical signal production

Signal production begins with chemistry, but its biological provenance is diverse. In parasitoid *Nasonia* wasps, quantitative genetic and genomic analyses show that species-specific cuticular hydrocarbon profiles are associated with multiple genomic regions rather than a single universal determinant [7]. This supports treating the emitted chemical phenotype as a multicomponent trait whose genetic architecture may itself vary among lineages. In bark beetles, cytochrome P450 systems illustrate a different route: pheromone-related terpenoids can arise through metabolism of host-derived compounds as well as de novo biochemical processes [8]. Signal identity therefore does not reveal whether its precursors originated entirely within the insect.

Functional perturbation can strengthen inference when chemistry is linked to behavior within the same system. RNA interference against a pheromone-gland fatty acyl reductase in *Maruca vitrata* reduced pheromone biosynthesis and altered mating behavior, connecting a defined biosynthetic component with an organismal consequence under the conditions tested [9]. Heterologous expression provides another form of functional evidence. Expression of moth biosynthetic genes in *Nicotiana benthamiana* generated and released pheromone-related compounds, demonstrating biochemical capacity while remaining distinct from natural pheromone release by the insect itself [10]. Such engineered systems validate enzymatic function more directly than ecological deployment.

Signal provenance can also be mixed. In a moth courtship system, endogenous and plant-derived compounds jointly contributed to the male chemical display [11]. This finding resists a binary division between “produced” and “acquired” signals and suggests a more useful distinction among precursor origin, biochemical transformation, storage, release, and receiver function. The proposed synthesis therefore treats production as a layered state: a chemical phenotype may be genetically constrained, physiologically synthesized, environmentally sourced, or assembled from several routes. None of these production routes alone establishes what the receiver detects or how the signal will be interpreted after environmental transmission.

Release and environmental transmission

Release converts stored or synthesized chemistry into an environmental signal, but emission does not guarantee encounter. Free-flight odor tracking differs among closely related *Drosophila* species, showing that the behavioral consequences of a plume depend partly on species-specific sensory and locomotor organization [12]. At the physical level, windborne odor plumes are intermittent and spatially structured; insects navigate by integrating chemical encounters with airflow and movement information rather than following a static concentration gradient [13]. The relevant signal at the receiver is therefore a time series of encounters shaped by turbulence, source geometry, movement, and sampling behavior.

Experimental work further indicates that plume dynamics can carry information beyond average concentration. *Drosophila* can use directional features associated with odor motion to improve navigation in complex plume conditions [14]. Yet locomotor mode places an additional boundary on generalization. Comparisons of walking and flying insects in turbulent environments show different tracking responses, indicating that the same physical odor field need not pose the same information problem to animals moving through it differently [15]. Laboratory plume systems are valuable precisely because they isolate these variables, but their controlled geometry should not be equated with field transmission without validation.

Anthropogenic change can alter the environmental layer before any receptor is engaged. Changes in vegetation, atmospheric chemistry, and background odor composition can reshape insect odorscapes and potentially alter the

detectability or reliability of resource- and mate-associated chemicals [16]. These effects should be distinguished from changes in production by the sender and from changes in sensitivity of the receiver. The proposed architecture therefore defines environmental availability as a separate inferential stage: the biologically relevant input is not simply what the sender releases, but what persists, mixes, moves, and reaches the receiver in a form and temporal pattern that its sensory system can sample.

Peripheral detection

Peripheral detection is the first stage at which environmental chemistry becomes receptor-level biological activity, but it is not synonymous with recognition or behavioral meaning. In social insects, specialized odorant receptors can respond to cuticular hydrocarbons and candidate pheromonal cues, demonstrating that receptor repertoires can be tuned to ecologically important chemical classes [17]. Structural work on the conserved odorant receptor co-receptor Orco established a tetrameric ion-channel architecture, clarifying how insect odorant-receptor complexes are organized at the molecular level [18]. That structural knowledge constrains models of receptor function but does not specify the behavioral significance of any ligand.

Peripheral olfaction also includes soluble proteins and developmental regulation. Odorant-binding proteins and chemosensory proteins have reported functions extending beyond a simple carrier role, although the strength of evidence differs among proposed tasks [19]. Odorant-receptor repertoires and expression patterns vary through insect evolution and development, making receptor identity, life stage, and tissue context essential qualifiers when comparing systems [20]. Environmental chemicals can alter effective detection without changing receptor genotype: several commonly used repellents can reduce access of human odorants to *Anopheles* olfactory detection under experimental conditions [21]. Thus, apparent sensory “avoidance” need not always arise from direct activation of an aversive receptor pathway.

Ligand-recognition structures provide a complementary level of evidence. Structural analysis of an insect odorant receptor revealed molecular determinants of odorant recognition and tuning [22]. Yet receptor architecture is not uniform in its functional organization across insects. Locust odor detection shows unusually low redundancy relative to expectations from more familiar combinatorial coding models, providing a useful counterexample to assuming a single peripheral coding logic [23]. In the parasitoid *Campoletis chlorideae*, chemical identification, antennal physiology, receptor characterization, and behavior were linked within one sex-pheromone system, illustrating the stronger inference possible when multiple evidence levels converge [24]. Life stage remains another boundary: the compact larval sensory cone of *Anopheles coluzzii* produces complex neuronal odor responses despite its relatively simple anatomy [25].

These findings motivate a state-and-response distinction that prose alone can obscure. The same observed endpoint—such as attraction, non-response, or altered orientation—can arise from different peripheral states, and similar receptor responses can feed into different downstream interpretations. **Table 1** separates the major peripheral-detection states developed here without assigning unsupported scores or implying that they form a universal hierarchy.

Table 1. Peripheral-detection states that constrain what can be inferred from chemical exposure

Biological setting · Evidence	Interpretation permitted	Limits and uncertainty	Research or test · Synthesis standing
Specialized cue tuning			
Social insects and defined pheromonal systems **Receptor response to ecologically specific ligands**	Peripheral specialization can support selective detection	Receptor response alone does not establish behavioral valence	Link receptor perturbation to naturalistic behavior Evidence-supported
Core receptor architecture			
Insect odorant-receptor complexes **Structural organization of Orco or ligand-binding receptor components**	Molecular constraints on receptor operation and tuning	Structure does not identify ecological function by itself	Combine structure with ligand, neuron, and behavior assays Evidence-supported
Accessory-protein modulation			
Systems involving odorant-binding or chemosensory proteins	Soluble proteins may alter access, transport, or	Roles are heterogeneous and incompletely resolved across taxa	Test function in intact sensory environments

Binding, expression, localization, or functional perturbation	other chemosensory functions		Evidence-supported with unresolved breadth
Chemically masked access			
Mosquito host-odor detection **Reduced effective availability of host odorants under repellent exposure**	Detection can fail before receptor-level interpretation of the original odor	Mechanism depends on compound and assay context	Separate masking from direct receptor activation Evidence-supported
Low-redundancy peripheral coding			
Locust olfaction **Narrower-than-expected receptor/neuron redundancy**	Canonical combinatorial assumptions are not universal	Extent across Orthoptera and other orders remains uncertain	Comparative receptor-to-neuron mapping Evidence-supported
Life-stage-specific compact coding			
Mosquito larvae **Complex neuronal responses from a small sensory cone**	Small peripheral systems can still encode chemically rich inputs	Larval organization cannot be substituted for adult olfaction	Stage-matched functional and behavioral tests Evidence-supported
Convergent multilevel validation			
Defined parasitoid sex-pheromone system **Chemistry, antennal response, receptor function, and behavior aligned**	Stronger inference from chemical identity to peripheral relevance	Still system-specific; higher neural interpretation remains separate	Extend causal tests downstream of peripheral detection Evidence-supported
Detection-to-meaning gap			
Cross-system interpretive state **Peripheral activity without matched higher-order or behavioral evidence**	Detection should be reported as detection, not as fixed meaning	Downstream state, experience, and ecological setting may reverse or suppress output	Add neural and context-specific behavioral validation Proposed synthesis

Neural interpretation

Peripheral activity becomes behaviorally useful only after neural transformation, and the available evidence argues against treating this transformation as a passive relay. In *Drosophila*, functional and anatomical mapping of the lateral horn revealed structured higher-order olfactory organization associated with categories of innate response [26]. This supports a distinction between receptor-level detection and higher-order representation: even when a ligand activates a peripheral channel, its downstream significance depends on how activity is routed and combined in the brain.

Neural interpretation is also plastic. Experience-dependent tuning can modify olfactory processing at multiple levels, including changes that alter subsequent responses to familiar or conditioned odors [27]. Internal state adds another axis. In adult *Drosophila*, dopaminergic modulation in mushroom-body circuitry provides a mechanistic example of how hunger, motivational state, or related physiological conditions can change olfactory responsiveness without requiring a change in the external chemical itself [28]. The evidence is strongest within established model systems, so these mechanisms should not be generalized wholesale to all insect orders.

The resulting inferential problem is discordance: strong peripheral detection may coexist with weak higher-order engagement, robust neural representation may not produce the expected behavior, or the same sensory input may lead to different actions after learning or state change. **Figure 1** therefore uses a discordance-triage architecture rather than a linear sensory pipeline. Evidence-supported modules are separated from a proposed diagnostic logic that asks where correspondence between chemical exposure, peripheral activity, higher-order processing, and behavior breaks down.

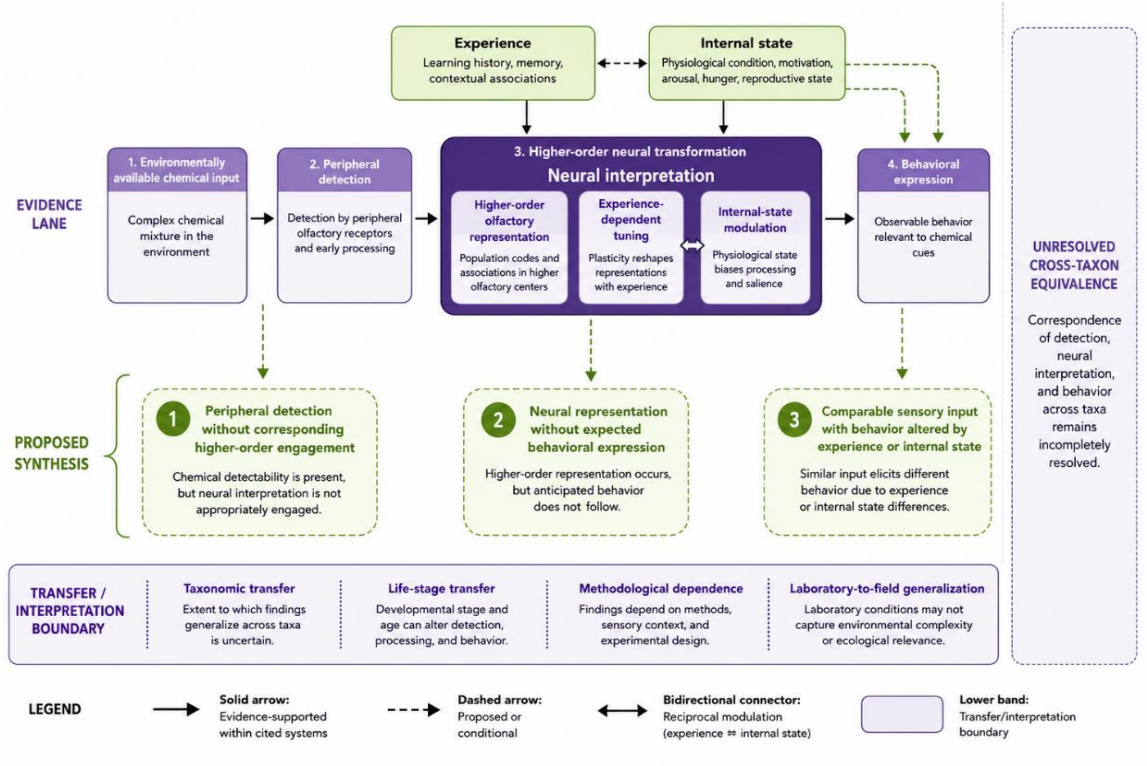


Figure 1. Locating where chemical detection ceases to predict behavioral interpretation

Context-dependent behavioral meaning

A chemical stimulus acquires behavioral significance only through the state of the receiving animal and the task in which the information is used. In *Drosophila*, innate and learned odor-guided behaviors can recruit overlapping dopaminergic circuitry while depending on distinct molecular signaling pathways [29]. This result is important because similar overt responses need not imply identical neural computations, and the same circuit can participate in behaviors with different histories of acquisition. Behavioral meaning should therefore be treated as an outcome of processing rather than a stable semantic property carried by the molecule itself.

Comparative evidence further weakens any one-to-one mapping between odor identity and action. Across *Drosophila* species, divergence in odor-guided behavior can reflect changes distributed across several processing levels rather than a single receptor or neural locus [30]. Experience-dependent tuning can alter olfactory processing [27], while internal-state modulation provides a separate route by which comparable sensory input can generate different behavioral weighting [28]. The proposed synthesis distinguishes four context states: relatively stable cue–response coupling, experience-modified use, internal-state modulation, and cross-species divergence in processing. These are analytical categories, not universal biological classes, and they should be validated separately in each taxon, life stage, and ecological setting.

A practical consequence is that attraction, avoidance, courtship, aggregation, or non-response should not be interpreted as intrinsic meanings of compounds without specifying the receiver, physiological state, prior experience, sensory background, and experimental context. **Table 2** separates mechanisms that change the relation between detected chemistry and observed behavior from the boundaries that limit inference.

Table 2. Context-dependent mechanisms that alter the relation between detected chemistry and behavioral meaning

Context-dependent state		
Relatively stable cue–response coupling		
Biological context · Evidence basis · Biological setting · Evidence	**Interpretation or consequence · Boundary or uncertainty · Interpretive consequence · Limits and uncertainty**	**Research or test · Synthesis status · Synthesis standing**

Defined laboratory or species-specific system **Repeatable behavior under a restricted stimulus and state range**	A chemical can predict behavior within the tested conditions Stability outside the tested state, stage, or environment is not established	Replicate across states and ecologically realistic backgrounds Evidence-supported only within tested conditions
Experience-modified use		
Biological context · Evidence basis · Biological setting · Evidence	**Interpretation or consequence · Boundary or uncertainty · Interpretive consequence · Limits and uncertainty**	**Research or test · Synthesis status · Synthesis standing**
Insects exposed to learning or prior odor experience **Behavioral or neural response changes after experience**	Prior experience can alter subsequent chemical-guided action Persistence and direction of plasticity vary by paradigm	Pair longitudinal behavior with neural measurements Evidence-supported
Internal-state modulation		
Biological context · Evidence basis · Biological setting · Evidence	**Interpretation or consequence · Boundary or uncertainty · Interpretive consequence · Limits and uncertainty**	**Research or test · Synthesis status · Synthesis standing**
Adult Drosophila and related model contexts **State-linked changes in dopaminergic or downstream olfactory processing**	The same input can be weighted differently as physiological state changes Mechanism is not established across all insect orders	Manipulate state independently of odor exposure Evidence-supported with taxonomic boundary
Shared circuitry, distinct molecular use		
Biological context · Evidence basis · Biological setting · Evidence	**Interpretation or consequence · Boundary or uncertainty · Interpretive consequence · Limits and uncertainty**	**Research or test · Synthesis status · Synthesis standing**
Drosophila innate versus learned odor behavior **Overlapping circuit participation with distinguishable signaling requirements**	Similar output does not imply identical molecular computation Circuit overlap does not prove equivalent ecological meaning	Combine pathway perturbation with matched behavioral assays Evidence-supported
Cross-species processing divergence		
Biological context · Evidence basis · Biological setting · Evidence	**Interpretation or consequence · Boundary or uncertainty · Interpretive consequence · Limits and uncertainty**	**Research or test · Synthesis status · Synthesis standing**
Comparative Drosophila **Behavioral differences associated with changes at multiple processing levels**	Species can assign different behavioral consequences to comparable odor information Evolutionary cause and adaptive value require separate evidence	Comparative functional tests across homologous levels Evidence-supported
Detection-to-meaning conditionality		
Biological context · Evidence basis · Biological setting · Evidence	**Interpretation or consequence · Boundary or uncertainty · Interpretive consequence · Limits and uncertainty**	**Research or test · Synthesis status · Synthesis standing**
Cross-system interpretive state **Chemical detection without complete state, experience, or ecological information**	Behavioral meaning should be inferred conditionally rather than assigned to a compound The relevant modifier may be unknown or unmeasured	Report receiver state and context as part of signal interpretation Proposed synthesis

Intraspecific versus interspecific communication

Chemical communication within species includes mating, aggregation, recognition, and social coordination, yet the evidential criteria differ among functions. Social Hymenoptera provide particularly rich evidence that cuticular hydrocarbons participate in kin and nestmate recognition, while comparative work also shows that the neural substrates and recognition architectures are not uniform across lineages [31]. Parasitoid sex-pheromone systems similarly demonstrate that chemical identity, antennal detection, receptor function, and behavioral attraction can be linked within a defined intraspecific interaction [24]. These cases support strong functional inference because sender, receiver, and behavioral context are specified.

The boundary becomes less secure when chemicals cross species or ecological partners. Floral microbes can alter volatile blends used by visiting insects [6], while plant-derived compounds can enter insect courtship displays

[11]. In such cases, chemical information may be biologically important without satisfying every criterion for an evolved signal from the organism that physically emits it. The distinction between signal and cue is therefore not merely terminological: it identifies whether evidence supports reciprocal communicative function, unilateral information use, or only correlated chemical exposure.

Cross-species comparison also shows why identical molecules cannot be assigned identical meanings. Closely related insects can differ at multiple olfactory-processing levels [30], whereas social recognition systems can emphasize lineage-specific relationships between chemical phenotype and receiver discrimination [31]. The proposed synthesis separates within-species communication, interspecific signaling, and interspecific cue use as evidence states that require different demonstrations of sender production, receiver detection, behavioral consequence, and evolutionary function.

Table 3 resolves this boundary by aligning chemical origin, receiver relationship, and the evidential step needed before a chemical interaction is described as communication rather than exposure or cue use.

Table 3. Evidence boundaries separating within-species communication, interspecific signaling, and chemical cue use

Interaction state	Intraspecific sex signaling	Social recognition	Environmentally supplemented display	Microbially modified information	Heterospecific cue use	Cross-species semantic divergence
Sender–receiver relationship · Evidence	Conspecific reproductive partners Identified chemical, sensory response, and mating-related behavior	Conspecific or colony members CHC profiles, sensory specialization, recognition behavior	Conspecific receiver; signal contains acquired material Plant-derived and endogenous compounds jointly associated with courtship	Insect receiver encountering chemically modified host/resource odor Microbial alteration of volatile blends with insect perception or response	Different species with no demonstrated reciprocal signaling function Receiver detects and uses another organism's chemical output	Closely related species Similar chemical inputs linked to different processing or behavior
Interpretation permitted	Chemical participates in a defined reproductive communication system	Chemical profiles can contribute to kin or nestmate discrimination	Signal phenotype can incorporate environmental chemistry	Third-party organisms can change information available to insects	Chemical can function as information for the receiver	Behavioral meaning is receiver-specific rather than molecule-fixed
Limits and uncertainty · Research or test	Components and mechanisms remain species-specific Test signal necessity and sufficiency under naturalistic conditions	Social-Hymenoptera evidence is not universally transferable Compare homologous recognition mechanisms across lineages	Acquired origin does not establish its evolutionary function Manipulate acquisition separately from biosynthesis	The microbe may not be an evolved sender to the insect Separate production, modification, and receiver benefit	“Communication” is not justified without sender-function evidence Test sender fitness consequences and receiver specificity	Cause may be receptor, neural, ecological, or combined Map homologous processing levels before inferring function
Synthesis standing	Evidence-supported	Evidence-supported	Evidence-supported	Evidence-supported with interaction boundary	Proposed classification built from evidence distinctions	Evidence-supported interpretation

The distinction is also easier to recover visually when sender–receiver relationships remain in parallel rather than being collapsed into one continuum. **Figure 2** therefore places conspecific communication, heterospecific information use, and third-party chemical modification in separate lanes and marks the evidence boundaries required before moving from chemical occurrence to receiver use and then to stronger claims of communication.

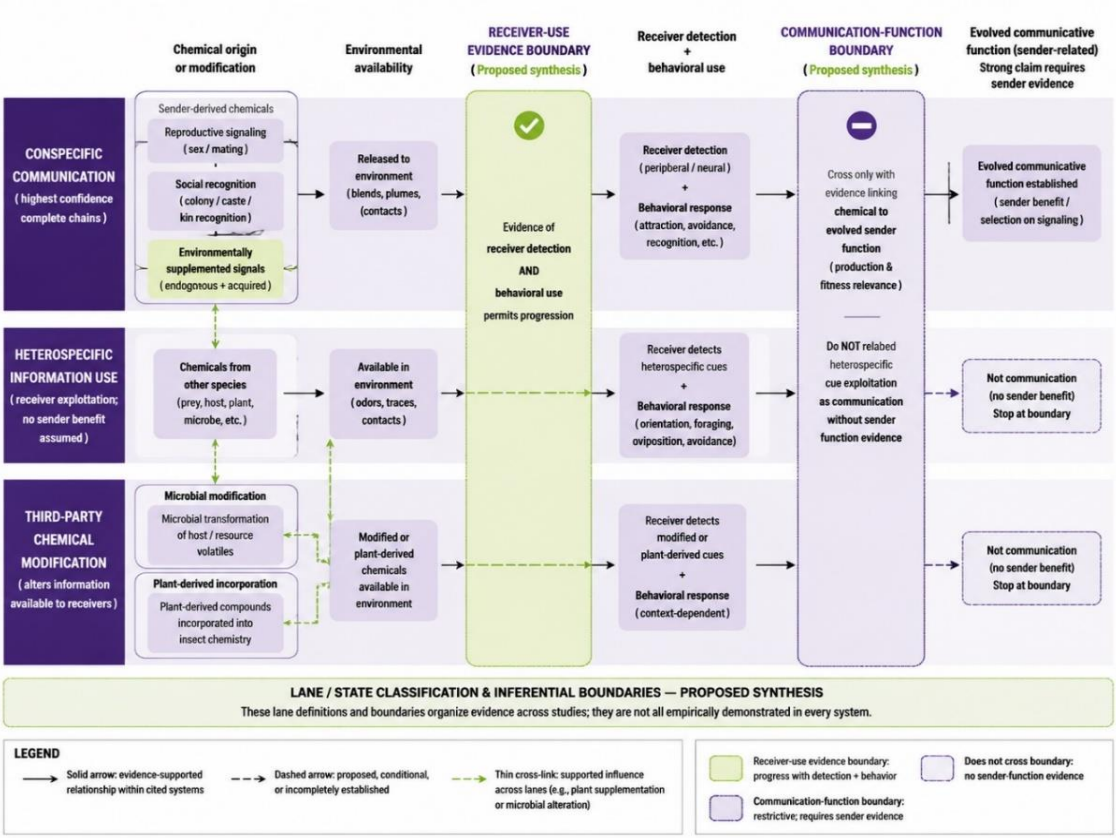


Figure 2. Where chemical exchange crosses the boundary between signal, cue, and context-dependent information

Environmental disruption of chemical signaling

Environmental disruption can act before, during, or after transmission, so ecological effects should not be assigned automatically to sensory failure. In a field pollution experiment, anthropogenic air pollutants reduced insect-mediated pollination measures, demonstrating an ecological consequence under realistic exposure while leaving several possible causal pathways open [32]. Direct chemical evidence is stronger in drosophilids exposed to ozone: oxidation degraded unsaturated pheromonal compounds and disrupted sexual communication [33]. The contrast is analytically useful. One study demonstrates ecosystem-level impairment under complex field conditions; the other connects atmospheric chemistry more directly to alteration of signal molecules and behavior.

The proposed synthesis therefore treats disruption as stage-specific: pollutants may transform a released compound, alter its signal-to-background ratio, interfere with effective access to receptors, or modify downstream behavior through stress and context. Experimental work showing that chemicals can mask access of host odorants to mosquito detection illustrates why reduced behavioral response need not arise from direct receptor antagonism [21]. These mechanisms should not be merged unless measured in the same system. Chemical susceptibility also depends on molecular structure, so ozone-sensitive pheromones cannot stand for all insect semiochemicals. Field generalization requires joint measurement of atmospheric chemistry, plume dynamics, sensory exposure, and behavior rather than inference from any one level.

A further boundary concerns mixtures. In natural settings, a receiver rarely encounters one focal compound against a chemically empty background. Pollutants may remove one component, create oxidation products, or shift relative blend composition while host, microbial, and vegetation volatiles continue to vary. Consequently, preserved detection of one component cannot demonstrate preservation of the original communication function. Conversely, behavioral disruption after pollution exposure does not identify which step failed unless chemical transformation, sensory availability, and downstream processing are measured together. Temporal scale also matters: acute atmospheric exposure and chronic ecological change can produce different signal environments, while insects may alter movement or sampling in ways that partially compensate for degraded information. Such compensation should be described as behavioral adjustment unless evidence demonstrates improved fitness or

evolutionary adaptation. This stage-resolved view provides testable alternatives to the broad claim that pollution simply "blocks olfaction."

New technologies and open questions

New methods make these inferential separations experimentally tractable. Advances in behavioral tracking and neural recording can connect naturalistic movement with temporally resolved sensory and neural events [34]. Mosquito neurogenetics now includes increasingly precise genetic manipulation, imaging, and cell-resolved approaches that permit stronger causal tests of olfactory circuits [35]. In parallel, insect odorant receptors are being incorporated into biosensor platforms, creating opportunities to examine receptor performance outside the intact animal while also exposing engineering limits in stability, specificity, and ecological equivalence [36].

The most important open problem is therefore not simply identifying additional compounds or receptors. It is validating transitions across levels. Studies should combine controlled manipulation of signal production, measurement of what reaches the receiver, receptor-level perturbation, neural recording, and behavior under state- and environment-matched conditions. Comparative designs are especially needed outside Diptera, Lepidoptera, Hymenoptera, and a small number of established models. Life-stage transitions, sex differences, fluctuating atmospheric chemistry, and multispecies chemical backgrounds remain major transfer boundaries. Technologies that improve resolution will be most informative when they preserve these ecological dimensions rather than replacing them with increasingly precise but isolated measurements.

Conclusion

Insect chemical communication cannot be reduced to the presence of a molecule, activation of a receptor, or observation of a behavioral response. Signal production has heterogeneous biochemical origins; environmental transmission changes what is available to detect; peripheral systems differ across taxa and life stages; neural processing is modified by experience and internal state; and behavioral meaning depends on the receiver and ecological context. The principal contribution of this review is a proposed inferential separation among production, environmental availability, peripheral detectability, neural interpretation, and behavioral use. This separation does not impose a universal mechanism. Instead, it identifies where evidence changes level and where additional validation is required. Treating those boundaries explicitly should make comparative chemical ecology more precise, particularly when extending laboratory mechanisms to field behavior, comparing species, or interpreting anthropogenic disruption.

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