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Interactions between insect species: their evolution and mechanistic architecture

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"Approximately one out of every two species on earth is a terrestrial arthropod. As such, it would seem statistically inevitable these organisms would interact.... It is quite likely, in fact, that each species of terrestrial arthropod interacts directly with at least one other arthropod species, as prey or predator, competitor, parasite, parasitoid, host, or commensal."
— David Grimaldi [1]

Ecosystems comprise networks of interacting species, but a missing piece of the evolutionary puzzle is how these interactions emerge and take on the forms that we observe. What we see as an intricate symbiosis, or a specialized predator-prey relationship, is in many cases the outcome of a long evolutionary process that left little trace of how the nascent interaction first arose. Similarly mysterious is the ensuing evolutionary path toward specialization: why did evolution follow the route ultimately taken? Interactions between different species are themselves abstractions of underlying molecular and cellular phenomena of which we still know very little. The mechanisms that control how species perceive, behaviorally engage with, and in many cases physiologically depend on each other routinely elude investigation. Ecological relationships are often challenging to reconstitute in the laboratory, and even harder to genetically deconstruct. Surely, though, a deeper understanding of them would help illuminate the evolved structure of our biosphere.

This Behavioral Ecology section of Current Opinion in Insect Science is a collection of articles spanning the scales of this problem, from the macroevolutionary and ecological down to the genomic, molecular, and neurobiological. The focus is specifically on interactions between insect species — a critical but understudied dimension of the living world that is rich in new biology. The contributions cover a diversity of taxa and types of interaction, the authors varying markedly in their approaches. Taking the broadest of views, David Grimaldi [1] offers a perspective on the emergence of insect–insect interactions over deep time using insights gained directly from the fossil record. Predatory interactions likely represent the earliest mode by which insect species interacted, with predation prevalent across many ancient insect lineages (dating to at least the early Carboniferous). Parasites and parasitoids appear later, with Jurassic origins of major parasitoid clades within Hymenoptera and Diptera. Radiations of chalcidoid and ichneumonoid wasps, two megadiverse clades of modern parasitoids, likely span the Late Cretaceous to Paleocene (105–55 Ma). In a window from the Jurassic to Upper Cretaceous, major evolutionary transitions occurred that yielded colony-forming eusocial insects within the Isoptera and repeatedly in the Hymenoptera. These fostered new, socially complex kinds of interspecies interaction in the form of trophobiotic mutualisms and social parasitism.

The various modes of specialized interaction each emerged from generalized precursors; in many clades of specialists, lineages have also transitioned from one type of interaction to another. Central to these profound changes in ecology is the insect nervous system. As Jessleen Kanwal and I [2] point out, knowledge of how the brains of insects — and indeed those of all animals — navigate the landscape of other living species is limited. So too is an understanding of how evolutionary changes within the nervous system have repeatedly fostered highly specialized relationships. Whether an interaction is between an obligate symbiont and its host, or between two species that exhibit reciprocal indifference toward each other, sensorimotor pathways must exist that process interspecies sensory information and select appropriate behaviors. We posit that insects with free-living ecologies may employ a 'heuristic classifier' to rapidly categorize the diversity of other species they encounter into broad classes — prey, predator, neutral, and so on — eliciting distinct behavioral responses. We discuss how, from this free-living neural ground plan, specialized interactions may emerge via increases in the perceived salience of certain heterospecific cues. Changes in the valence assigned to these cues may be important, leading to altered attraction or aversion to other species, with neuromodulation perhaps playing a causal role in modifying the underlying sensorimotor pathways.

Two papers provide case studies of how evolutionary changes in the nervous system contribute to lineages undergoing ecological specialization, and evolving trophic shifts that target other species. Paloma Gonzalez-Bellido, Jennifer Talley, and Elke Buschbeck [3] provide a discussion of the diversity of neural specializations observed in arthropod visual predators — both terrestrial and aquatic — that enable efficient prey-capture behavior. These include enhanced retinal resolution to identify prey objects, gaze-shifting to track prey as they move, and temporal precision to counter motion blur, with the authors highlighting the inherent trade-off between these axes of performance. The authors also discuss adaptive changes to neural circuits for prey information processing. Echoing Kanwal and Parker, they likewise emphasize the role played by heuristic rules in enabling rapid heterospecific classification. Some predatory flies, for example, use the ratio of prey size to velocity to decide whether to attack. Separately, Dan Peach and Ben Matthews [4] explore the origins of blood-feeding in culicomorphan Diptera. Remarkably, in this fly clade, which includes the mosquitoes, evidence points to an initial evolution of honeydew feeding, perhaps solicited from herbivorous insects such as aphids, as a steppingstone to feeding on animal blood, ultimately including that of humans and other mammals. The authors outline potential neural changes underlying these trophic shifts, and argue that the transition to blood-feeding may have had its origins in the similarity between chemical cues released by plants and mammalian hosts.

This question — why novel interactions arise and become established during evolution — is perhaps both the most fundamental and bewildering. Tom Naragon, Julian Wagner and I [5] approach it by focusing on rove beetles (Staphylinidae). In this hyperdiverse clade, a recurring evolutionary trend exists in which numerous lineages have evolved from free-living predators into social parasites of ant or termite colonies. What evolutionary contingencies send rove beetle lineages down these paths of symbiotic specialization? And what shapes the outcome? We discuss how the ancestral free-living ground plan of aleocharine rove beetles potentiates them forming facultative associations with ant and termite colonies, opening the door for obligate relationships to evolve. Specialization tends to follow a relatively small number of paths, involving adaptive changes in chemistry that include mimicry of host cuticular hydrocarbons, and the evolution of behavior-manipulating secretions from abdominal exocrine glands. Concerted changes in behavior also occur, such as the beetles switching valence from defensive to social interactions with ants. We discuss how these changes in ecology may alter the population genetic forces acting on these beetles, locking them into obligate dependencies where their fates hinge on those of their hosts, as well as their capacity to host switch.

A variety of other arthropod clades contain lineages that have forged close associations with ants. Wendy Moore, Giulia Scarparo, and Andrea Di Giulio examine adaptive features of paussine ground beetles that enable them to integrate deeply inside ant colonies [6]. Paussini comprises one of the largest radiations of obligate myrmecophiles, the beetles displaying dramatic anatomical and glandular novelties. As the authors describe, natural history observations and experimental studies point to these beetles mimicking host communication across multiple sensory modalities, including chemosensory and vibrational cues (the latter via remarkable stridulatory mimicry). These socially parasitic traits enable some paussines to execute sophisticated behavioral strategies, achieving nestmate or even queen-like status. Naomi Pierce and Even Dankowicz discuss recent findings on the evolution of ant-associated butterflies of the families Riodinidae and Lycaenidae [7]. The latter comprises a family of ~5000 species that has been the focus of extensive ecological and evolutionary studies over several decades due to their relationships with ants. These interactions range from mutualistic to parasitic and from facultative to obligate, or in some cases merely exploit the enemy-free space that ants create. The authors cover recent progress in deciphering the behavioral and chemical mechanisms used by caterpillars to integrate with their hosts, including studies of the larval exocrine glands that appear central to the symbiosis. They also discuss how the nature and stability of these butterfly–ant relationships are contingent on local environmental variables, including climate and soil-nutrient ratios, underscoring the vulnerability of intricate species interactions to anthropogenic change.

Integral to many interspecies partnerships is, of course, coevolution. The impacts exerted by predators, parasites, and parasitoids select for counter adaptations in prey and hosts, and have led to remarkable arms races. Bregje Wertheim outlines how multilevel coevolution shapes the genomes, immune systems, and behaviors of insect hosts and their parasitoids [8]. The author focuses on the genus *Drosophila* and its assemblage of hymenopteran parasitoids — a system that has proven tractable for dissecting coevolutionary processes at the molecular and cellular levels. Mechanisms of host finding and oviposition by parasitoids are summarized, along with recent work on the diverse neuronal mechanisms uncovered in *Drosophila* that enable hosts to create enemy-free space and evade parasitoids. Wertheim also describes recent studies on host physiological responses to counter parasitoid infection, their obstruction by parasitoid venoms, and the mechanisms parasitoids have evolved to manipulate superparasitism (infection of the same host by multiple parasitoids).

In a second article focused on coevolution, Marah Stoldt, Maide Nesibe Macit, Erwann Collin, and Susanne Foitzik [9] explore the coevolutionary processes that mediate social parasitic lifestyles in the Hymenoptera. Here, studies in ants, bees, and wasps have examined genomic and transcriptomic correlates of social parasitism in both the parasite and host colony. Genomic erosion appears to be a feature of ant social parasite genomes, including losses of chemoreceptors with probable ancestral roles in eusocial behaviors such as nestmate recognition. Specific loci underlying parasitic traits, or genes with unambiguous signatures of adaptive evolution in parasites, have proven harder to uncover; so too have the mechanisms underlying host-colony responses to social parasites, which include heightened aggression and changes in hydrocarbon pheromone diversity. Finally, Masaru Hojo gives an account of the coevolutionary dynamics of mutualisms, focusing on the trophobiotic partnerships that ants have forged with hemipterans and lycaenid caterpillars [10]. In these symbioses, the trophobionts provide nutritional rewards in exchange for protection from the ants — a reciprocal exploitation that appears prone to cheating. The author discusses how the formation and stability of these mutualisms hinge both on the efficacy of partners evaluating their respective payoffs, and the susceptibility of the interaction to selfish behavior. For example, some lycaenids produce honeydew that has been found to reduce dopamine levels in the brains of their attendant ants. These secretions effectively coerce worker ants to aggressively defend the caterpillar. Such manipulation may explain why mutualism breakdown, leading to parasitism, appears to have occurred repeatedly during lycaenid diversification.

Collectively, these articles provide an up-to-date set of perspectives on important systems and questions in the area of insect interactions. The hope is that gathering contemporary work on these systems in one place may help consolidate an embryonic field focused on the interspecific dimension of insect biology (analogous to how the study of interactions now pervades modern microbiology).

Conflict of interest statement

Nothing declared.

References

1. Grimaldi DA: **Evolutionary history of interactions among terrestrial arthropods**. *Curr Opin Insect Sci* 2022, **51**:100915.
2. Kanwal JK, Parker J: **The neural basis of interspecies interactions in insects**. *Curr Opin Insect Sci* 2022, **50**:100891, https://doi.org/10.1016/j.cois.2022.100891
3. Gonzalez-Bellido PT, Talley J, Buschbeck EK: **Evolution of visual system specialization in predatory arthropods**. *Curr Opin Insect Sci* 2022, **52**:100914.
4. Peach DAH, Matthews BJ: **Sensory mechanisms for the shift from phytophagy to haematophagy in mosquitoes**. *Curr Opin Insect Sci* 2022, **52**:100930, https://doi.org/10.1016/j.cois.2022.100930
5. Naragon TH, Wagner JM, Parker J: **Parallel evolutionary paths of rove beetle myrmecophiles: replaying a deep-time tape of life**. *Curr Opin Insect Sci* 2022, **51**:100903.
6. Moore W, Scarparo G, Giulio AD: **Foe to Frenemy: predacious Ant Nest Beetles use multiple strategies to fully integrate into ant nests**. *Curr Opin Insect Sci* 2022, **52**:100921.
7. Pierce NE, Dankowicz E: **Behavioral, ecological and evolutionary mechanisms underlying caterpillar-ant symbioses**. *Curr Opin Insect Sci* 2022, **52**:100898.
8. Wertheim B: **Adaptations and counter-adaptations in *Drosophila* host–parasitoid interactions: advances in the molecular mechanisms**. *Curr Opin Insect Sci* 2022, **51**:100896.
9. Stoldt M, Macit MN, Collin E, Foitzik S: **Molecular (co)evolution of hymenopteran social parasites and their hosts**. *Curr Opin Insect Sci* 2022, **50**:100889.
10. Hojo MK: **Evolution of chemical interactions between ants and their mutualist partners**. *Curr Opin Insect Sci* 2022, **52**:100943.