

*Annual Review of Entomology*The Hidden Secrets of
Psylloidea: Biology, Behavior,
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plant–insect interactions, microbiome, evolution, codivergence, adaptation, keystone species

Abstract

Psyllids constitute a diverse group of sap-feeding Sternorrhyncha that were relatively obscure until it was discovered that a handful of species transmit bacterial plant pathogens. Yet the superfamily Psylloidea is much richer than the sum of its crop-associated vectors, with over 4,000 described species exhibiting diverse life histories and host exploitation strategies. A growing body of research is uncovering fascinating insights into psyllid evolution, biology, behavior, and species interactions. This work has revealed commonalities and differences with better-studied Sternorrhyncha, as well as unique evolutionary patterns of lineage divergence and host use. We are also learning how psyllid evolution and foraging ecology underlie life history traits and the roles of psyllids in communities. At finer scales, we are untangling the web of symbionts across the psyllid family tree, linking symbiont and psyllid lineages, and revealing mechanisms underlying reciprocal exchange between symbiont and host. In this review, we synthesize and summarize key advances within these areas with a focus on free-living (nongalling) Psylloidea.

1. INTRODUCTION

The Psylloidea (psyllids) are an understudied and ecologically diverse superfamily in the suborder Sternorrhyncha, order Hemiptera. To date, more than 4,000 species have been described and classified into seven families (9) (**Figure 1**), although this is almost certainly an underestimate of the total diversity. Like related Sternorrhyncha groups, such as aphids, whiteflies, and coccoids (scales and mealybugs), psyllids feed on carbohydrate-rich plant sap, primarily by accessing the phloem sieve tube elements of plants. Within the past several decades, there has been a rapid increase in publications on psyllid biology, behavior, microbial associations, genomics, and ecology. Much of this research is focused on a handful of pest species, particularly those identified as vectors of unculturable, phloem-limited, bacterial plant pathogens in the *Candidatus Liberibacter* and *Ca. Phytoplasma* taxa (81). The research is primarily of an applied nature, but collectively,

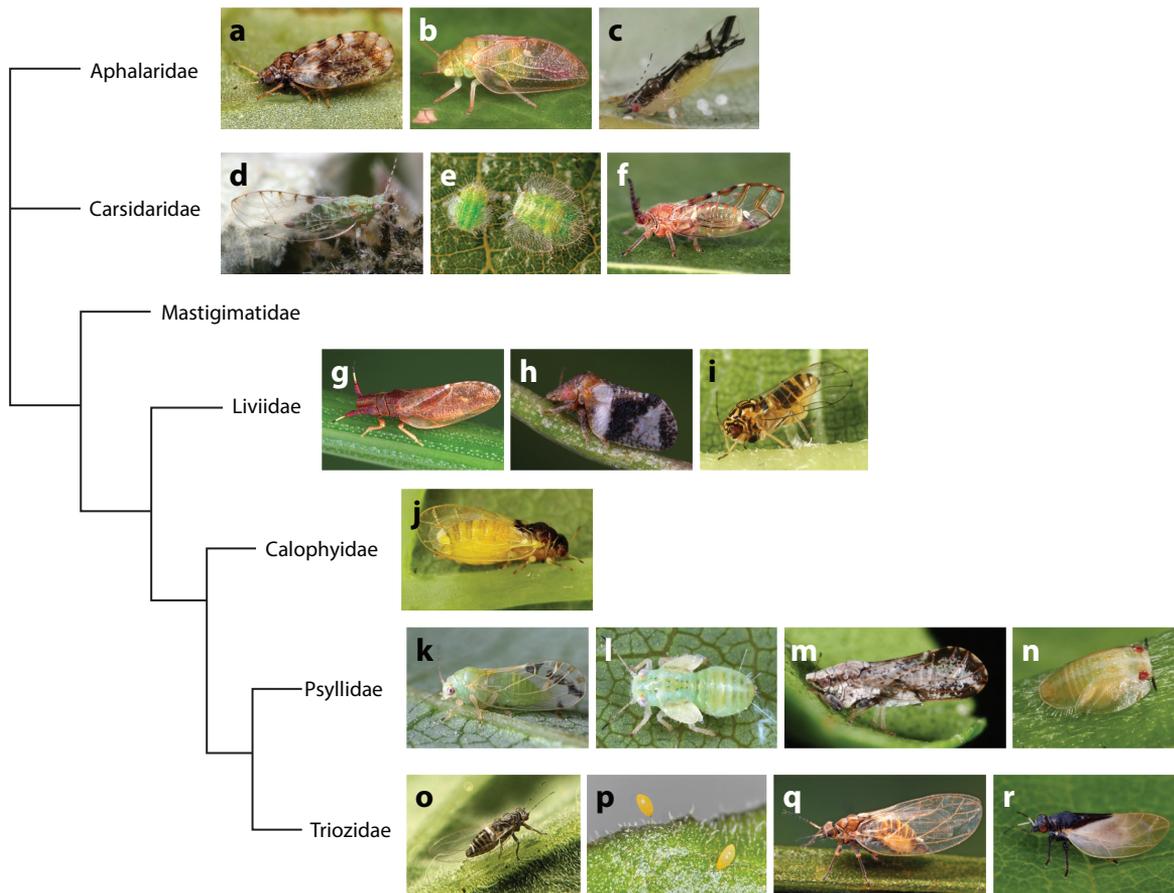


Figure 1

Cladogram representation of the classification of Psylloidea as reported in Reference 9, with images of representative species.

(a) *Aphalara sauteri*. (b) *Rhinocola aceris*. (c) *Cornegenapsylla sinica*. (d) *Mesobomtomota hibisci*. (e) *Homotoma ficus* (immatures). (f) *H. ficus* (adult). (g) *Livia junci*. (h) *Euphyllura phillyreae*. (i) *Paurocephala sauteri*. (j) *Calophya rbois*. (k) *Cacopsylla pulchella* (adult). (l) *C. pulchella* (immature). (m) *Diaphorina citri* (adult). (n) *D. citri* (immature). (o) *Bactericera cockerelli*. (p) Eggs of *B. cockerelli*. (q) *Trioza urticae*.

(r) *Eryngiofaga mesomela*. Photos in panels a, b, e–b, k, l, q, and r provided by Gernot Kunz. Photos in panels c, i, m, and n provided by Yi-Chang Liao. Photo in panel d provided by David Ouvrard. Photo in panel j provided by Gabrijel Seljak. Photo in panel o provided by Kerry Mauck. Photo in panel p provided by Jaimie Kenney.

this growing body of work is filling key gaps in our understanding of basic psyllid behavior, psyllid microbiomes, and mechanisms of host exploitation. Ecologically, psyllids occupy key positions in food webs, interact with diverse host assemblages, and play important but understudied roles in noncrop communities. Through production of carbohydrate-rich feces, psyllids form keystone interactions with other arthropods and avians that have cascading effects on whole ecosystems. Psyllids have also stoked research interest due to the diverse array of phenotypes that they induce on hosts through their salivary secretions. These range from leaf curling and unique senescence-like conditions to complex gall morphologies (11, 116). Genomic resources published within the past decade are helping to illuminate genes and proteins that underlie the induction of different host phenotypes. This review synthesizes and highlights key advances in our understanding of psyllid behavior, host feeding, microbial interactions, and ecological roles, with a focus on free-living psyllids that do not form galls on host plants (for reviews on gall-forming psyllids, see 116). We also point out best experimental practices and identify key priorities for future research.

Host plant: the host on which a psyllid can complete development; distinct from overwintering hosts (shelter plants) used only by adults

Microhabitat: the specific tissues of a host plant on which a psyllid can feed and develop

2. OVERVIEW OF PSYLLOIDEA DISTRIBUTION AND LIFESTYLES

2.1. Psylloidea Diversity and Global Distribution

The Psylloidea are characterized by specificity in host plant use for the purposes of feeding and reproduction (10). Fossil evidence suggests that radiations of their (largely) dicot hosts predate radiations of the monophyletic group of anatomically modern psyllids (98, 99). Thus, psyllid speciation may frequently involve sympatric host switching between related species or genera with similar characteristics or chemistries, rather than cospeciation with hosts (108). Some hotspots of psyllid biodiversity (**Figure 2**) are clearly the result of psyllid radiations on closely related, endemic host taxa. For example, Australia hosts approximately 15% of global psyllid diversity, with approximately 85% of these species having host plants in a single plant family (Myrtaceae). About 90% of these feed on a single plant genus within this family (*Eucalyptus*) (58, 148). The Myrtaceae is a relatively small plant family (approximately 4,700 species) but hosts >25 psyllid genera (99). Remarkably, this pattern appears to be quite common: Approximately 50% of psyllid genera are distributed among plant families with fewer than 4,000 species (with several having fewer than 1,000 species) (99). Fabaceae is the only large plant family (>19,000 species globally, and the third-largest plant family) that also hosts a correspondingly large proportion of psyllid diversity (approximately 14.4% of psyllid genera, the most of any single plant family).

We do not yet know how the unique host specificity and lineage-specific host associations of psyllids arose, or how we arrived at the current levels of biodiversity (**Figure 2**). An analysis of approximately 66% of known psyllid host plant associations documented on the Psyl'list website (<http://www.hemiptera-databases.com/psyllist>) is the most current attempt to document patterns and generate hypotheses (99). At the species level, radiation occurs primarily via shifts among related host plants, while at higher taxonomic levels, the analysis enabled detection of apparent host jumps to distant, novel host taxa, which are infrequent. Some psyllids have relatively indiscriminate egg placement (105), and these oviposition mistakes could play an important role in promoting divergence to related and unrelated taxa. Recent advances in gut content analysis of psyllids also reveal that adult feeding patterns include nonhost plant species (21), which could provide opportunities for off-target oviposition events. Close analysis of host association patterns across taxonomic levels in the Psyl'list data set also revealed evidence of niche partitioning. For instance, Triozidae and Psyllidae, two large families that include most recognized pest species, share several host families, but within some plant families, members of Triozidae and Psyllidae never co-occur on the same plant genus (99). It is notable that psyllids also exhibit rather extreme microhabitat preferences, which may indicate niche partitioning among related

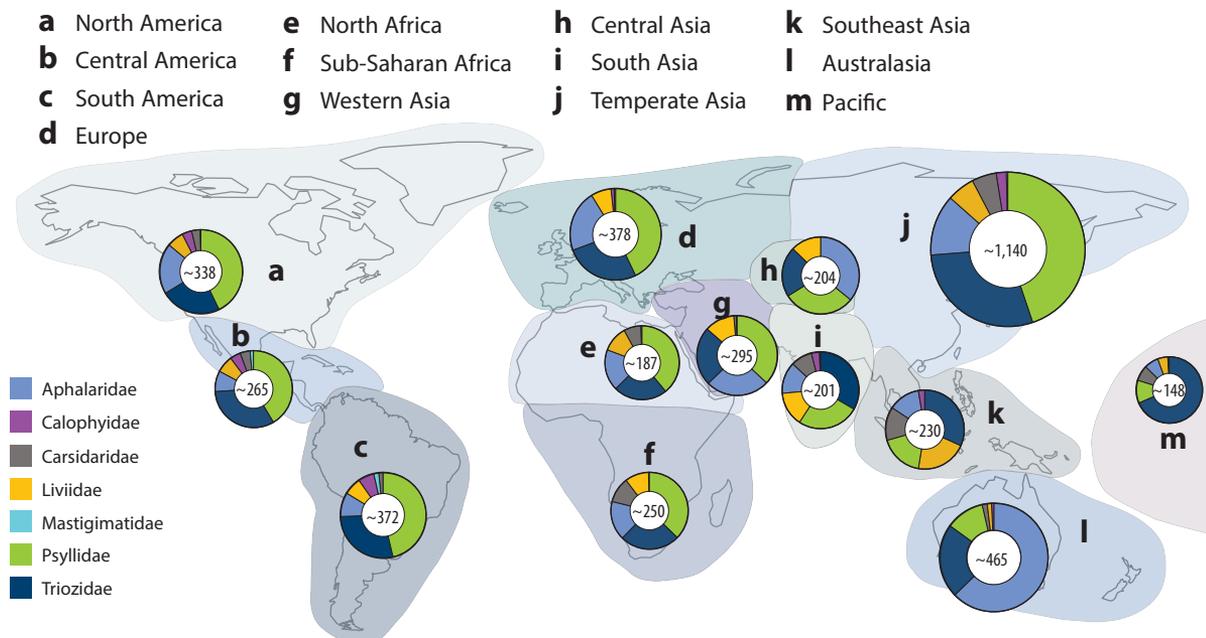


Figure 2

Overview of psyllid biodiversity by geographic area. Sunburst diagrams show the distribution of species diversity by family with the approximate number of described species per region. The geographic distribution summary is based on 4,468 geographic species records from the Psyl'list database (100) (146 records without geographic data were excluded). It is notable that these estimates have inherent biases due to uneven distribution of resources for discovering and characterizing insect biodiversity. For several decades, there have been calls to address this taxonomic impediment and to put even a fraction of the resources and funds put toward discovering other planets into increasing our understanding of taxonomy and knowledge of species diversity on this planet (112). However, this grand biological challenge has been addressed more successfully by some nations than others. Notably, over the past several decades, China has dedicated an impressive effort to the discovery and description of new species (78). These efforts are evident across all organism groups and can be seen for psyllid taxonomy in the comparatively large chart representing the Temperate Asia region. Although China includes regions of high species diversity, these are not considered more diverse than the regions of South America and Africa that have much smaller charts due to the relatively reduced taxonomic effort.

species on the same host (Section 4.1). There is also evidence of niche partitioning between psyllids and other Sternorrhyncha groups (e.g., aphids). Host-mediated competition between psyllids and other Sternorrhyncha lineages may have influenced the evolution and host specificity of these lineages (99). These hypotheses can now be tested more rigorously with the recent publication of robust Psylloidea phylogenies (9, 106), especially in the context of updated regional vascular plant phylogenies.

2.2. Psylloidea Biology and Lifestyles

Geographically, tropical regions host a greater diversity of psyllids than temperate regions (57). In a synthesis of psyllid life history traits, Hodkinson (57) suggested that the concentration of psyllid diversity in the tropics is linked to additional requirements for delayed or compressed life cycles associated with seasonality in higher latitudes. Voltinism and periodicity among psyllids is comparatively well studied and can be fluid depending on temperature and precipitation. Psyllids may or may not have periods of diapause, and the longest recorded life cycle, taking two years to complete, is found at high elevations. Most temperate species are univoltine, but some may have up to six generations a year depending on ambient temperature and humidity. In contrast,

tropical species can have more than 15 generations per year and no diapause period. Among psyllid lifestyles, gall-forming species are overrepresented in the tropics, with 50–60% of tropical psyllid species being gall formers versus 15% of psyllid species in temperate areas (11, 147). Gall formation may confer specific advantages in the face of the more diverse pathogen, predator, and parasitoid assemblages typical of tropical environments.

The timing of psyllid generations, regardless of location or life history, is strongly influenced by the phenology of host plants on which feeding and immature development takes place (see also Section 4.1). For example, the immatures of some *Cacopsylla* species consistently hatch within a few days of first bud break of their hosts, which gives them access to their preferred microhabitat of young shoot tissues (57). Remarkably, this synchrony is maintained even though the overall timing of these events varies according to ambient conditions from site to site and year to year. Similarly, there is close correspondence between new plant tissue growth and initiation of gall development that may maximize the efficiency of psyllid modifications to plant developmental pathways, as mediated by salivary effectors (116). Phenological synchronicity may also be important in promoting and maintaining speciation. This was evident for closely related psyllid species radiating in the Canary Islands; sympatric species that shared the same host tended to be separated from each other phenologically (104).

Psyllids are mainly obligate outbreeders with sexual ratios approximating 1:1. Unlike aphids, parthenogenesis in psyllids is rare, having been documented in only a few species with predominantly single-sex populations (96). Generations of new psyllids are, therefore, mostly produced through sexual mating. Recent reviews of vibratory communication in psyllids indicate systematically wide employment of biotremology in mate finding, guarding, and disruption, as well as in same-sex communication (5, 69). This may enable vibrational trapping for control of pest psyllids. Evidence of sex pheromone-mediated mate finding is available for only four species: two psyllid pests of pear (*Cacopsylla bidens* and *Cacopsylla pyricola*), the tomato psyllid (also known as the potato psyllid) (*Bactericera cockerelli*), and the Asian citrus psyllid (*Diaphorina citri*) (49, 122, 142, 151). The interplay between the environment, specifically plant substrate, and community behavior, such as levels of aggregation, influences tradeoffs in using vibration versus chemical signaling and single versus multimodal strategies (71).

Although we know that psyllids are selective in choosing hosts for reproduction, egg laying and host assessment during oviposition are poorly studied. Eggs are typically deposited on the plant surface with attachment via a pedicel (**Figure 1**), but a few species deposit eggs into plant tissue using shallow insertions (132). Egg structure may be mostly invariable or highly variable among closely related species (104, 105), but little is known about the adaptive or functional significance of these characters. Some species exhibit highly specific site selection on host organs, particularly on flower structures (104) or newly emerging shoot apex tissue (17). Species ovipositing on leaf laminae appear to be less discriminate but will often cluster eggs along leaf midribs, suggesting that they assess specific leaf traits to determine their oviposition sites (57, 105). For most species, host traits constraining oviposition and/or adult and immature feeding are not known. However, experiments with a limited number of pest species have started to unravel the intricacies of psyllid host assessment processes (see Section 4.1).

3. PSYLLID FORAGING AND HOST SELECTION BEHAVIOR

3.1. Overview of Psyllid Behavioral Processes Involved in Host Selection and Feeding

Host plant selection by any herbivorous flying insect, including psyllids, involves sequences of behaviors and multiple sensory modalities. Psyllids perceive distance-based cues (color, contrast,

Effector:
insect-secreted protein that modifies host plant physiology and/or disrupts defenses in ways that are advantageous to the insect

odors) that indicate the presence of a potentially suitable host plant (36, 101, 102). Orientation to these cues is limited by environmental variables, such as wind speed and temperature, which curtail movements of small flying insects beyond certain thresholds. Once contact with a potential host is established, psyllids will assess surface-level and internal host characteristics (6, 8). Surface-level cues may include odors and cuticular chemicals (8), which are perceived by chemoreceptors. Psyllids detect internal host cues through movements of the stylets on a largely intercellular pathway toward the phloem sieve tube elements (6, 43). These cues may include chemicals present in the apoplasmic space (e.g., sucrose gradients) and physical characteristics of the mesophyll that influence navigation toward the sieve tubes. Upon accessing the sieve tubes, psyllids uptake sap through a passive process that relies on phloem pressure (6). Feeding can then proceed for many hours and even days without much interruption (6). Additionally, there is evidence that psyllids can ingest moisture (xylem sap) from hosts that are not suitable for phloem sap feeding (6, 43), a behavior that may help psyllids to persist in challenging abiotic environments lacking sufficient resources. These feeding behaviors are likely typical of most, but certainly not all, psyllid species. For example, in a marked departure from the habits of other Sternorrhyncha, some species only ingest nutrients from mesophyll tissue during early instar development (30, 117).

3.2. Mechanisms of Host Location

Most information on psyllid host assessment comes from a limited number of species that damage crops or ornamental plants. Despite this limitation, the data to date strongly support vision as the primary sensory modality mediating host location during flight, with odor cues playing a minor role and only at close ranges. There is extensive evidence of well-developed color vision in psyllids (35, 36), as well as evidence that responsiveness to olfactory stimuli is weak in the absence of concurrent visual stimuli (102, 143). These behavioral responses to color and olfactory stimuli are similar to those documented for aphids and whiteflies, both of which show evidence of having color vision and strong olfactory-based preferences only in the presence of color stimuli (32, 128).

Aphids and whiteflies are attracted to targets with spectral reflectance in the green to yellow wavelength ranges (32, 128). However, recent studies suggest that psyllids have distinct color preferences, responding to specific wavelengths associated with preferred host plants and even preferred feeding locations within hosts (e.g., young versus old leaves). The best evidence of this comes from experiments with eucalypt-specialist psyllids endemic to Australia. Farnier et al. (35) quantified the color preferences of four psyllid species that specialize on different *Eucalyptus* hosts and feeding locations (*Ctenarytaina eucalypti*, *Ctenarytaina bipartita*, *Anoeconeossa bundoorensis*, and *Glycaspis brimblecombei*). For all four species, volatile cues did not play a role in host selection (34). While *C. eucalypti* and *C. bipartita* exhibited expected preferences for yellow and green targets (the colors of preferred feeding sites), *A. bundoorensis* and *G. brimblecombei* each preferred a red target more than yellow or green, with green being the least preferred option (35). This preference appears to be adaptive, as both *A. bundoorensis* and *G. brimblecombei* feed on newly emerged, reddish leaves (37). This perception of red wavelengths contrasts with the consensus concerning color vision capabilities for herbivorous insects; with the exception of select adult Lepidoptera, herbivorous insects lack red photoreceptors. However, follow-up experiments demonstrated that the two red-preferring psyllid species can discriminate a red object from a dark gray object of similar reflectance, and that preferences for red are much stronger than preferences for achromatic targets of varying contrasts against the background (37). This suggests that there is a red-sensitive photoreceptor in the eyes of *A. bundoorensis* and *G. brimblecombei*; this possibility can be investigated, with some difficulty, using electrophysiological techniques.

Psyllids in other families (e.g., Trioizidae and Liviidae) also use vision-based foraging (101, 138). Blocking or manipulating visual cues from host plants with white particulate films, such as kaolin

clay, can even significantly reduce attack by *D. citri* (109). There is preliminary evidence that *D. citri* can learn to respond to visual cues associated with suitable hosts, even cues that may be repellent on their own, through conditioning (127). Other visual stimuli, such as degree of UV reflectance, influence psyllid foraging activities and synergize with cues in the visible spectrum (44). A key priority for future research will be to explore the visual capabilities and ethology of a wider range of species across different families. Work should include behavioral experiments to quantify the roles of visual cues in foraging over different spatial scales and characterize morphological and physiological mechanisms underlying behavior.

3.3. Close-Range Host Assessment

Over the past two decades, there has been an intense research focus on plant volatiles as drivers of psyllid host preferences. Most of this work has focused on *D. citri* and, to a lesser extent, a few *Bactericera* and *Trioxa* pest species. However, there is little evidence of psyllids using volatile cues beyond a range of approximately one meter (24). For example, Davidson et al. (27) compared walking and flying responses of *B. cockerelli* to the attractant 2-undecanone. Despite evidence of a preference for 2-undecanone in Y-tube assays among walking insects, the compound was not attractive to insects in flight in either the wind tunnel or a potato field. Another field study on the carrot psyllid, *Dyspersa apicalis* (formerly *Trioxa apicalis*), demonstrated that terpene-emitting spruce sawdust protects carrots from psyllid damage but is only effective over a range of 10 cm (93). For pest insects, there is a temptation to extrapolate responses to volatile cues that operate over distances of a few centimeters, and only on the part of walking insects, to field-level processes occurring over several meters or more. However, few studies explicitly compare responses over multiple scales to establish relationships between distance and behavioral responses for different psyllid species, which severely limits our understanding of psyllid ethology.

A subset of factorial studies systematically evaluated contributions of different cues, alone and in combination, to the host selection process. In one of the first papers to examine the hierarchy of cue use by psyllids, Wenninger et al. (143) used factorial, multimodal assays to distinguish foraging behavior of *D. citri* at close range by insect sex and mating status. Critically, in all assays, insect motivation was assessed, allowing the researchers to draw conclusions about how stimulatory different cues are under fixed conditions. Host volatiles did not strongly stimulate foraging behavior and were not differentially attractive to psyllids in most assays unless they were combined with visual cues (yellow color stimulus). Females were more responsive to cues than males, and mated females responded more strongly to a wider array of volatile host plant blends in combination with visual stimuli relative to unmated females or males. A related study on *D. citri* by Volpe et al. (140) also reported improvements in odor assay participation when the arena included a yellow stimulus, as well as clearer preferences for host odors when associated with visual cues. These findings suggest that odor-based preference assays with psyllids must include a visual stimulus to yield biologically meaningful results.

Volatiles and color also interact to influence postcontact host assessment. Key evidence for this comes from a study on *D. citri* by Patt et al. (102). The researchers used a series of artificial feeding substrates (laboratory film and three-dimensional wax midribs mimicking leaf structure) to systematically quantify *D. citri* stylet probing responses to host odor blends and different saturation levels of chartreuse coloration. *Diaphorina citri* preferred more saturated substrates over paler ones and also preferred three-dimensional topographical features (raised wax droplets) over two-dimensional ones regardless of coloration. This suggests that leaf topography may be an overlooked element of host selection at close range. Once host volatiles were added, *D. citri* exhibited color-based preferences among scented wax droplets. In the presence of the visual wax droplet stimulus, walking psyllids could also discriminate among simple, artificially created volatile blends

Electrical penetration graphing technique: a system for studying feeding behavior; an insect becomes part of a circuit, which is completed when the insect probes a plant

and among three different blend concentrations. This work illustrates how attention to assay set up and factorial design yields basic knowledge with applied value.

Comprehensive, factorial studies of psyllid responses to multiple host cues are not available for most species. At the physiological level, electrical recordings from single olfactory sensilla demonstrate that psyllids in the genera *Trioza*, *Cacopsylla*, and *Ctenarytaina* can perceive volatiles of their host plants (2, 22, 42, 150) and shelter plants (62). Limited studies with Aphalaridae revealed that some species with strong visually mediated host preferences show no attraction to undamaged host plant volatiles in walking assays (34). This finding contrasts with the consistent attraction to host volatiles documented for *D. citri* and provides evidence that cue hierarchies may differ substantially among psyllid species.

4. MECHANISMS OF HOST EXPLOITATION

4.1. Microhabitat Selection

For psyllids, locating the correct microhabitat for feeding or reproduction is as critical as locating the right host plant in the landscape. In a survey of Psylloidea life histories, Hodkinson (57) summarized microhabitat preferences and found that over 47% of psyllids for which data were available feed exclusively on the shoot apex, while a separate, nonoverlapping 41% feed exclusively on expanded leaves (57). Only 7.4% of psyllid species with feeding site data available are known to attack multiple sites on a host plant. Psyllids are, therefore, not only specialized to host plant species, but also specialized to particular tissue types.

Why do psyllids exhibit such strict microhabitat preferences? Nutrition was hypothesized to be a primary driver. However, the role of nutrition is certainly not clear for psyllid shoot apex feeders. In a longitudinal study documenting the preference–performance relationships of two *Ctenarytaina* species on eucalyptus trees, Steinbauer (124) found that developing instars were strictly limited to the shoot apex and the first two to three leaf pairs from the apex region. However, amino acid concentrations in preferred versus nonpreferred leaves did not explain immature performance. A later study focusing on *C. bipartita* on five *Eucalyptus* hosts found no relationship between fecundity and free amino acids (total or essential) (126). There was also no relationship between essential amino acid concentrations in the insect bodies and essential amino acids in shoot apex versus expanded leaf microhabitats, indicating that nutritional symbionts (Section 5.1) are able to compensate for variation in amino acid availability.

The drivers of preference and performance on shoot apex sites must therefore encompass characteristics that provide advantages (e.g., higher humidity, protection from natural enemies) or that limit host exploitation of microhabitat sites (presence or absence of chemical or physical barriers). Evidence for this comes from studies on *D. citri*, which is limited to the shoot apex microhabitat (17, 57). Using microscopy, Ammar et al. (1) visualized stylet sheath termination points on susceptible and resistant hybrids of *Citrus* spp. and *Citrus trifoliata*. Adult *D. citri* exhibited a preference for feeding on the midrib of young (recently expanded) leaves of each hybrid. On the resistant hybrid, fewer stylet termini reached the vascular bundle, and this hybrid had a thicker layer of fibrous tissue (sclerenchyma) around the phloem, as do older leaves of susceptible hosts (1). A later study (43) used the electrical penetration graphing technique (6) to study probing, salivation, and ingestion behaviors of *D. citri* in relation to variation in fibrous ring thickness and lignin composition. Thicker, older fibrous rings significantly reduced phloem access and sap ingestion. *Diaphorina citri* behavioral preferences for color cues associated with the young leaves of the shoot apex (143) can now be clearly linked to performance within this microhabitat (17) and specific host traits (43). More studies are needed to determine if plant cellular architecture is a factor underlying feeding and oviposition microhabitat preferences of other shoot apex specialist psyllids. This can be

accomplished by combining electrical penetration graphing, stylet sheath quantification, and stylet path visualization approaches with host plant trait metrics.

These techniques are also useful for understanding preference–performance relationships for psyllids specializing in mature or expanded leaf microhabitats, as well as the remarkable array of feeding behaviors exhibited by Psylloidea. An early study using stylet track monitoring showed that the *G. brimblecombei* microhabitat preference for leaves over the shoot apex is reinforced by deterrent effects of epicuticular waxes only present on shoot apex tissue, as well as this species' inability to orient stylets toward the vascular bundle even when probing within a dewaxed shoot apex (8). A later study on this same species (30) used microscopy to characterize 18 anatomical foliar traits across four *Eucalyptus* species with and without infestation by *G. brimblecombei*. Stylet track imaging revealed that *G. brimblecombei* stylets can penetrate through parenchyma cells rather than between them (which is unusual, as most phloem-feeding Sternorrhyncha primarily navigate between cells). The stylets pass between the guard cells of the stomata and into the mesophyll tissue. Consequently, stomatal density was identified as a key trait underlying host use by *G. brimblecombei*. A similar feeding habit was also documented for *C. eucalypti*, which, during the first and second instars, only feeds from upper mesophyll parenchyma of juvenile *Eucalyptus globulus* leaves (not even reaching the phloem) (117). Access to this tissue is also via stomata, after which the stylet path is intercellular. Cells adjacent to the stylet path are altered to increase unloading of sugars (and potentially other nutrients) into the apoplast, where they are available for ingestion by early instars of *C. eucalypti*. These studies reveal that Psylloidea employ a fascinating array of adaptations for exploiting hosts in ways that are completely different from other, better-studied Sternorrhyncha.

4.2. Modification of Host Plant Phenotypes

Psyllid salivary components cause modifications to microhabitats to increase available nutrients, suppress defenses, and alter plant architecture. One host phenotype induced by groups of immatures of some species is a senescence-like appearance. This condition has been documented for numerous psyllids in the genus *Cardiaspina*, as well as some species in the genera *Creiis*, *Glycaspis*, *Lasiopsylla*, and *Boreioglycaspis* (57, 144). It is hypothesized that this phenotype is adaptive, and psyllids are manipulating mature host tissues to free up nutrients. In a microscopy study of mesophyll cell changes in response to feeding by sessile immatures of the eucalypt specialist *Cardiaspina retator*, Crawford & Wilkens (23) reported degeneration of chloroplast thylakoid membranes and breakdown of tonoplast membranes. This results in color changes that resemble natural senescence. However, the changes within cells are distinct for each process. During natural senescence, chloroplasts remain intact and apparently functional. In contrast, chloroplast breakdown due to *C. retator* feeding releases pigments, lipids, and proteins alongside hydrolytic enzymes from the tonoplast, resulting in a massive mobilization of nutrients. Therefore, the phenotype induced by *C. retator* only superficially resembles senescence and features changes that benefit sessile *C. retator* instars feeding on mesophyll for a portion of their development. A similar effect was observed for *Cardiaspina* nr. *densitexta* feeding on *Eucalyptus moluccana* (125): Feeding by groups of immatures induced an increase in free amino acids concurrent with leaf chlorosis resembling senescence. However, unlike in naturally senescent leaves, necrosis and abscission were inhibited by psyllid feeding, supporting the hypothesis that the *Cardiaspina*-induced phenotype is also a product of psyllid host manipulation, rather than a defense response by the plant.

Psyllids that feed on herbaceous crop hosts can induce feeding symptoms that are systemic, appearing at infestation sites and distal, noninfested tissues. Because symptoms such as stunting and yellowing appear throughout the plant, many of these phenotypes were previously thought to be

RNA interference

(RNAi): small, complementary RNAs disrupt translation of mitochondrial RNA by forming double-stranded RNA molecules in the cytosol and triggering innate double-stranded RNA defenses

Honeydew: a sugary fecal liquid produced in large quantities by sap-feeding organisms and used as a carbon source by many interacting species

the result of a psyllid-transmitted pathogen. While there are certainly pathogens involved in some etiologies (see Section 5.3), improved diagnostics to screen for pathogen presence have revealed that psyllid salivary components alone can produce these systemic effects. On crop hosts in the genus *Solanum*, infestation by the tomato (potato) psyllid, *B. cockerelli*, induces a systemic condition called psyllid yellows characterized by leaf stunting, chlorosis, and phloem necrosis. Working with potato hosts, Sengoda et al. (115) demonstrated that this condition is distinct from etiology induced by *Ca. Liberibacter solanacearum* (CLso), a phloem-limited plant pathogen and symbiont transmitted by *B. cockerelli* and other psyllid species (Section 5.3). The phenotype induced by *B. cockerelli* is detrimental for potato and tomato growth and crop yields (54, 115), but unlike senescence effects induced by *Cardiaspina* spp., *B. cockerelli*-induced changes may not benefit their survival or reproduction. For example, Harrison et al. (54) demonstrated that exposure to feeding by *B. cockerelli* for one week strongly induced plant defenses in tomato, and that such feeding was detrimental for the survival of later colonizing psyllids. Persistent feeding also inhibits plant growth and impedes phloem function (115), which are likely to increase *B. cockerelli* nymph competition. The physiological changes induced by *B. cockerelli* feeding on tomato and potato (which are not endemic to the native range of *B. cockerelli*) may actually be by-products of a mismatch in psyllid salivary effectors and host components, resulting in an extreme response by the plant host. It would be interesting to compare the effects of psyllid feeding on annual *Solanum* crop hosts to the effects of feeding on hosts endemic to the psyllids' range, such as perennial *Solanum umbelliferum* (74) and *Capsicum* spp.

Other than *B. cockerelli*, the best-studied triozid species from a plant manipulation perspective is *D. apicalis* (formerly *T. apicalis*) (13a), which is a specialist on Apiaceae and a pest on carrot crops in its native range (Northern and Central Europe). *Dyspersa apicalis* induces a systemic leaf curling and discoloration phenotype in carrots. Feeding by just a few individuals can induce this distortion phenotype in newly emerging, undamaged leaves (95). Valterová et al. (139) profiled oviposition preferences and induction of the leaf curling phenotype in 16 hosts of *D. apicalis*, including noncrop hosts such as the endemic wild carrot (*Daucus carota* subsp. *carota*). Wild carrot was preferred to the same degree as cultivated carrot for oviposition, and the leaf curling phenotype was also induced on this noncrop host. In fact, leaf curling occurred on multiple endemic host species that also had high oviposition rates. This suggests that the leaf curling phenotype is inducible in hosts to which *D. apicalis* is adapted and, therefore, may confer some advantages to developing immatures. Such was the case for another triozid species (*Trioza adverticia*), which induces leaf curling on juvenile *Syzygium paniculatum* leaves and, in doing so, creates a humid microclimate that improves instar survival (72). Unfortunately, we have little knowledge of the *D. apicalis* salivary components responsible for inducing unique and possibly adaptive phenotypes in apiaceous hosts. Leaf curling and similar phenotypes may also play a role in intraspecific and interspecific interactions among psyllids (e.g., competition), but this has not yet been explored.

Genomic resources required to illuminate host manipulation by free-living psyllids are only available for two species: *B. cockerelli* (NCBI GenBank BioProject PRJNA822651; see 65) and *D. citri* (BioProject PRJNA800468; see 12, <https://citrusgreening.org/>). These resources enable proteomic and transcriptome studies on specific tissues and the use of prediction pipelines to identify putative psyllid effectors secreted by salivary gland cells. De Souza Pacheco et al. (31) used this approach to identify candidate effectors in transcriptomes from *D. citri* heads. They profiled 12 candidates using RT-PCR, and those highly expressed in head tissues were pursued for functional analysis through RNA interference (RNAi). Using RNAi, they refined the list of candidates through analysis of stylet tracks, honeydew production, and mortality on plants and through electrical penetration graphing analysis of feeding behavior. Two candidate effectors (genes *DCEF28* and *DCEF32*) played a significant role in facilitating access to the phloem. Other *D. citri* candidate

effectors have been identified through comparative bioinformatic approaches (145), and these can now be evaluated with functional genomics tools like RNAi. New genomic resources for *B. cockerelli* will hopefully enable similar studies on this species and other *Bactericera* (65). Future research on mechanisms of host exploitation should prioritize sequencing additional genomes, especially of species in the Triozidae and Aphalaridae.

5. OBLIGATE AND FACULTATIVE ENDOSYMBIONT RELATIONSHIPS

5.1. Obligate Nutritional Symbionts

Phloem sap is deficient in essential amino acids and vitamins. To compensate for this, Sternorrhyncha contain nutritional symbionts in a specialized bacteriome organ located in the abdomen. In all psyllids investigated to date, the bacteriome contains uninucleate bacteriocyte cells housing a primary, obligate symbiont, *Ca. Carsonella ruddii* (Gammaproteobacteria: Oceanospirillales), referred to below as *Carsonella* (92). Molecular evidence supports a common origin for the symbionts of both psyllids and whiteflies (Aleyrodidae), which may derive from the common ancestor of Sternorrhyncha (123). In contrast, symbionts of other modern Sternorrhyncha lineages (e.g., aphids and coccids) are hypothesized to be the result of replacement of the symbiont associated with the most recent common ancestor of all Sternorrhyncha.

Carsonella exhibits extreme genomic reduction and degradation that places it at an intermediate step between living organisms and organelles, such as mitochondria and plastids (131). It has one of the smallest genomes of any cellular organism (160 kb) and the highest recorded adenine-thymine (AT) bias among symbionts; the guanine-cytosine (GC) content of the genome is only 16.5% (92). The mutational bias leading to accumulation of A and T nucleotides is due to an acceleration in DNA substitution rate and leads to a lower stability of the 16S ribosomal RNA (rRNA) secondary structure (67). *Carsonella* genomes also have extremely high gene density, with nearly all genes overlapping. Its genes are notably shorter than those in other bacteria (even other long-term symbionts). Remarkably, *Carsonella* also lacks functional genes for approximately half of the metabolic pathways involved in the biosynthesis of essential amino acids (92), which contrasts with the genetic complement of the better-studied *Buchnera* symbiont in aphids.

The unique properties of the *Carsonella* genome have stimulated efforts to understand how this organism accomplishes basic biological processes associated with bacterial life. By using a psyllid (*Pachypsylla venusta*) that does not harbor any additional symbionts, Sloan et al. (120) showed that the psyllid host is able to integrate the metabolic pathways absent in *Carsonella* by activating both native genes (16 genes) and horizontally transferred bacterial genes (10 genes), including one encoding argininosuccinate lyase that was likely acquired directly from *Carsonella*. The horizontal gene transfer events parallel what happens in other sap-feeding insects, such as the citrus mealybug, which hosts another obligate symbiont with a small genome, *Tremblaya princeps* (139 kb). Both insects have acquired genes that belong to the same functional categories, including amino acid biosynthesis and metabolism, riboflavin biosynthesis, and rRNA methylation (60).

5.2. Secondary Long-Term and Facultative Symbionts

Most psyllid lineages harbor at least one additional secondary, long-term symbiont (presumably in bacteriome syncytial cells) and, occasionally, one or more secondary facultative symbionts, which may be localized within cells of other tissues (59, 63, 129) (Figure 3). The ubiquity of long-term secondary symbionts across psyllid lineages could be due to the extreme genome reduction of *Carsonella*; secondary symbionts may compensate for the inability of *Carsonella* to provision some nutrients. The status of a symbiont as long term or facultative depends on the

Bacteriome:

a specialized organ that houses bacteriocyte cells containing symbiotic, intracellular bacteria

Long-term

symbiont: a symbiont that has been associated with a host lineage for a prolonged period, resulting in genome degradation and host dependence

Facultative symbiont:

a symbiont that invades diverse tissues and is not lineage specific, not required for reproduction, and capable of both horizontal and vertical transmission

combination of characters that it exhibits, which are summarized for the most frequently detected psyllid symbionts in **Figure 3**.

Long-term symbionts tend to have greater genome reduction and AT bias plus evidence of tightly coevolved associations with host insects, such as vertical transmission and bacteriome localization (**Figure 3**). In contrast, facultative symbionts tend to have characters that enable

Putative symbiont taxon	Evidence of long-term symbiont status										Key references	
	Reduced genome	Accelerated evolution	Gene loss	Gene degradation	Shortened gene length	Gene overlap	Evidence of AT bias	Codivergence with host	Localized to bacteriome	Vertical transmission		Horizontal transmission*
<i>Ca. Carsonella ruddii</i> [GammaProteobacteria Oceanospirillales]	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Red	Nakabachi et al. (2006), Sloan & Moran (2012), Thao et al. (2000)
<i>Ca. Profftella armatura</i> [GammaProteobacteria Burkholderiales]	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Nakabachi et al. (2013, 2020)
<i>Arsenophonus</i> and <i>Arsenophonus</i> -like [GammaProteobacteria Enterobacterales]	Orange						Blue		Orange	Blue	Orange	Hall et al. (2016) , Morrow et al. (2017), Nakabachi et al. (2022), Nováková et al. (2009)
<i>Sodalis</i> and <i>Sodalis</i> -like [GammaProteobacteria Enterobacterales]	Blue	Blue	Blue						Blue	Blue		Arp et al. (2014), Ghosh et al. (2020) , Kwak et al. (2021), Nakabachi et al. (2022), Sloan & Moran (2012)
<i>Carnimonas</i> [GammaProteobacteria Oceanospirillales]	Orange									Orange		Nakabachi et al. (2022)
<i>Enterobacteriaceae</i> OTUs [GammaProteobacteria Enterobacterales]							Blue		Blue	Orange		Fukatsu & Nikoh (1998) , Kwak et al. (2022), Morrow et al. (2017), Morrow et al. (2020), Nakabachi et al. (2022)
<i>Serratia symbiotica</i> [GammaProteobacteria Enterobacterales]										Orange	Orange	Nakabachi et al. (2022)
<i>Fukatsua symbiotica</i> [GammaProteobacteria Enterobacterales]										Orange	Orange	Nakabachi et al. (2022)
<i>Rickettsiella</i> -like [GammaProteobacteria Legionellales]							Orange	Orange				Morrow et al. (2017, 2020)
<i>Diplorickettsia</i> [GammaProteobacteria Legionellales]												Nakabachi et al. (2022a, 2022b)
<i>Rickettsia</i> [AlphaProteobacteria Rickettsiales]										Orange	Orange	Morrow et al. (2016, 2020), Nakabachi et al. (2022)
<i>Wolbachia</i> supergroups B & O [AlphaProteobacteria Rickettsiales]	Orange						Blue	Blue	Blue	Blue	Blue	Chu et al. (2019), Fromont et al. (2017) , Nakabachi et al. (2022a,b), Ren et al. (2018)
<i>Lariskella</i> [AlphaProteobacteria Rickettsiales]									Orange	Orange		Morrow et al. (2017)
<i>Spiroplasma</i> [Mollicutes, Mycoplasmatales]	Orange						Orange			Blue	Orange	Ghosh et al. (2020) , Kwak et al. (2021)

(Caption appears on following page)

Figure 3 (Figure appears on preceding page)

Summary of putative symbionts commonly detected in psyllids. Symbionts are listed in the left column (primary in *gray*, secondary long-term in *yellow*, and secondary facultative in *light blue*). In the center character matrix, red indicates evidence of the specified character in the symbiont from all psyllid taxa examined to date. Blue indicates evidence that a characteristic has been documented in that taxon for select psyllid hosts. Peach indicates probable characteristics of psyllid-associated symbionts based on relatedness to symbionts present in other insect taxa, particularly other Sternorrhyncha. White indicates lack of verifiable evidence for the presence of a character in the indicated psyllid-associated symbiont (opportunities for future research). Asterisks signify that the character is atypical of long-term symbionts. References in bold provide additional information beyond amplicon sequences (e.g., localization, vertical transmission test, genome sequences). Abbreviation: OTU, operational taxonomic unit.

symbiosis with less canalization to one host lineage or extreme genome degradation. Horizontal transmission has been documented for many facultative symbionts of related Sternorrhyncha (e.g., through shared host plant or parasitoid vectors) (14) and, occasionally, for secondary symbiont genera that include taxa ranging from facultative to long term (e.g., *Arsenophonus*) (97). Most secondary psyllid symbionts do not have full genome sequences, localization studies, or other biological data to help us understand whether they are obligate, long-term associates. However, we do have sequences of conserved genome regions, such as portions of the 16S rRNA gene, for symbionts from a wide variety of psyllid taxa (e.g., 51, 66, 83, 84, 87, 88). With these data, we can evaluate a subset of metrics in **Figure 3**. For example, Hall et al. (51) tested 35 psyllid species from seven families for evidence of symbiont–host codivergence. As expected, *Carsonella* phylogeny was highly predictive of host phylogeny. The dominant secondary symbiont across 34 of 35 taxa was *Arsenophonus*, which was present at 100% prevalence in samples of the 34 *Arsenophonus*-positive species. *Arsenophonus* was also vertically transmitted in a subset of these species for which this trait was examined. However, phylogenetic incongruence indicated that *Arsenophonus* distributions were the result of host switching and/or endosymbiont replacement. A similar finding was evident in a study by Kwak et al. (66), which examined symbionts of 44 psyllid species across 35 genera from five families. Two clades of operational taxonomic units (OTUs) within the *Enterobacteriaceae* exhibited genomic hallmarks of obligate symbiont status based on GC content analysis of a 429-nucleotide 16S rRNA gene sequence, and each clade was congruent with one psyllid family. However, OTUs fitting into each clade were not detected in all species screened within each family. These species may have lost these symbionts during a replacement event, but methods beyond amplicon sequencing are needed to verify this. Across codivergence studies, evidence suggests that psyllids typically harbor at least one long-term secondary symbiont that is at or approaching obligate status (with rare exceptions; see 120) but that the identity of this symbiont varies widely, even within lower taxonomic levels (39).

Selected secondary symbionts of psyllids have been studied in economically important species. *Diaphorina citri* and several other *Diaphorina* species (89) are unique in harboring the only other known organelle-like secondary symbiont: *Ca. Proffttella armatura*, referred to as *Proffttella* below (**Figure 3**). *Proffttella* is located in syncytial cytoplasm in the center of the bacteriome (26) and has a reduced genome (465 kb) (91). It contributes to the synthesis of a hemolysin (cell-rupturing) protein, the B vitamins riboflavin and biotin, and carotenoid pigments in a complementary fashion with *Carsonella* but does not synthesize essential amino acids (90). A large fraction (approximately 15%) of the genome is devoted to synthesis of diaphorin, a polyketide toxin with cytotoxicity to insects (including *D. citri* predators), as has been demonstrated by experimental injections (146). Diaphorin may, therefore, have a defensive or deterrent function. *Proffttella* has only been detected in members of the *Diaphorina* genus. It is likely that similar taxon-specific relationships between obligate secondary symbionts and psyllid hosts exist, waiting to be explored.

The genus *Wolbachia* is another psyllid symbiont group commonly detected in psyllids (**Figure 3**). *Wolbachia* sequences are recovered in nearly every psyllid microbiome effort, and

Cytoplasmic incompatibility: when intracellular bacteria in the cytoplasm of gametes cause incompatibility of egg and sperm, leading to no viable offspring

Wolbachia is often the only other symbiont recovered besides obligate and co-obligate symbionts. As in other insect groups, there is evidence of frequent horizontal transmission of *Wolbachia* among psyllid lineages (e.g., 39, 66, 87–89). The widespread prevalence of *Wolbachia* strains (typically of supergroup B) across psyllid lineages is probably a result of typical *Wolbachia* traits (vertical transmission) combined with horizontal transmission events and reproductive manipulation through expression of cytoplasmic incompatibility (increasing fixture within a lineage). These features enable reconstruction of psyllid population dynamics and introduction histories through understanding *Wolbachia* strain diversity (15). Despite *Wolbachia* being prevalent, their roles as psyllid symbionts are not well known, and our information comes almost exclusively from *D. citri*. In this host, *Wolbachia* titers vary with developmental stage and sex (33) and can have positive correlations with titers of primary symbionts and *Ca. Liberibacter* plant pathogens (59) but also show clear niche partitioning with other intracellular symbionts in localization studies (63). In *D. citri*, *Wolbachia* has been detected in many tissues, including salivary glands, where it may influence saliva components (149). In *B. cockerelli*, *Wolbachia* is associated with acquisition and transmission of CLso. Psyllids of a particular mitochondrial haplotype that lack *Wolbachia* are less efficient at acquiring and transmitting the pathogen (19).

Much work is needed to resolve the biological roles of psyllid secondary symbionts. A number of putative symbionts have been detected, repeatedly, in microbiome studies (e.g., *Rickettsia*) but only explored to the level of phylogenetic barcoding genes. Notably, up to half of all reads in typical microbiome studies can only be classified to OTUs at the family level within the *Enterobacteriaceae* (66, 83, 84, 88). Clades of OTUs in the *Enterobacteriaceae* exhibit key hallmarks of long-term symbiosis with hosts (66), but without additional genomic information, taxonomic placement and biological relevance remain unknown. It may be useful to organize a collaborative effort to tackle the black box of long-term, psyllid-associated *Enterobacteriaceae* symbionts. Another key issue is the method or combination of methods on which we base our inferences. When amplicon sequencing alone is used for detection, it is more likely that true symbionts present in low titer will be missed. This can have significant consequences for phylogenetic congruence studies. Likewise, amplification bias can create artificial differences in symbiont abundance within a single sample, obscuring patterns in symbiont titers. Future efforts should focus on revisiting data from past microbiome studies and identifying psyllid–symbiont associations for more detailed and accurate follow-up work ranging from the molecular to the population level. As sequencing costs decrease and bioinformatic tools improve, metagenomic deep sequencing will enable reconstruction of partial or whole genomes of nonculturable psyllid symbionts, providing new insight into their functional roles and evolutionary histories.

5.3. Facultative Symbionts as Plant Pathogens

Psyllids serve as both hosts and vectors for unculturable bacteria in the *Ca. Liberibacter* and *Ca. Phytoplasma* genera (Figure 4). These symbionts are acquired through vertical transmission (at variable rates), from systemically infected hosts (usually as immatures), or from pools of bacteria inoculated locally by females at oviposition sites on hosts. Evidence from studies with *Ca. Liberibacter asiaticus* (CLAs) and CLso suggests that ingested *Ca. Liberibacter* symbionts enter psyllid gut cells via endocytosis, where they undergo replication and formation of vesicles, likely in association with the endoplasmic reticulum (16, 70). Vesicles traffic to the cell membrane during egress into the hemolymph, which permits access to other psyllid tissues for colonization and replication, including salivary glands. After a latent period (usually several days to several weeks), symbionts can be transmitted to plant hosts when the psyllid host salivates into phloem sieve elements (for recent reviews, see 79 for *Ca. Liberibacter* spp. and 61 for *Ca. Phytoplasma* spp.). *Ca. Liberibacter* vectors include species in Triozidae and Psyllidae (*Diaphorina* genus, formerly in Liviidae) with

	Sec-secretion system	Type I secretion system	Effectors for plant infection	Effectors for psyllid infection	Vertical transmission possible	Fitness/performance possible	> 1 confirmed vector species	Vectors in multiple genera	
<i>Ca. Liberibacter africanus</i>	Blue	Blue	Blue						da Graca et al. (2022), Thapa et al. (2020)
<i>Ca. Liberibacter americanus</i>	Blue	Yellow	Blue						de Godoy Gasparoto et al. (2022), Thapa et al. (2020)
<i>Ca. Liberibacter asiaticus</i>	Blue	Blue	Blue	Blue	Blue	Blue	Yellow	Yellow	Clark et al. (2020), Mishra & Ghanim (2022), Thapa et al. (2020)
<i>Ca. Liberibacter brunswickensis</i>									Morris et al. (2017)
<i>Ca. Liberibacter capsica</i>	Blue	Blue							Hansen et al. (2022)
<i>Ca. Liberibacter caribbeanus</i>									Morrow et al. (2020)
<i>Ca. Liberibacter ctenarytainae</i>									Morrow et al. (2020)
<i>Ca. Liberibacter europaeus</i>									Frampton et al. (2018), Raddadi et al. (2011)
<i>Ca. Liberibacter solanacearum</i>	Blue	Blue	Blue		Blue	Blue	Blue	Blue	Nachappa et al. (2012), Reyes Caldas et al. (2022), Thapa et al. (2020)
<i>Ca. Liberibacter "uncharacterized"</i>									Chambers et al. (2020)
<i>Ca. Phytoplasma mali</i>	Blue		Blue		Yellow	Blue	Blue	Yellow	Jarausch et al. (2019), Kube et al. (2008), Mayer et al. (2009), Mittelberger et al. (2017), Siewert et al. (2014), Tedeschi et al. (2006)
<i>Ca. Phytoplasma prunorum</i>					Blue		Blue	Yellow	Jarausch et al. (2019), Tedeschi et al. (2006)
<i>Ca. Phytoplasma pyri</i>						Blue		Yellow	Jarausch et al. (2019), Tedeschi & Bertaccini (2019)
<i>Ca. Phytoplasma pyri</i> PD-TW strain						Blue		Yellow	Jarausch et al. (2019), Tedeschi & Bertaccini (2019)

Figure 4

Summary of facultative intracellular symbionts of psyllids that also exhibit plant pathogenic lifestyles. In the matrix, blue indicates evidence of the indicated characteristic being present for that bacterial taxon. Yellow indicates that at least one study found this character lacking for that bacterial taxon. White (*blank box*) indicates that no studies have explicitly evaluated the presence or absence of the indicated character for that bacterial taxon and highlight opportunities for future research.

probable vectors recently identified in the Aphalaridae (**Figure 5**). *Candidatus* *Phytoplasma* spp. are transmitted by psyllids in the genus *Cacopsylla* (family Psyllidae), as well as phloem-feeding species in the Auchenorrhyncha (61).

Plant-infecting psyllid symbionts have an obligate intracellular lifestyle and reduced genomes. For example, CLas and CLso lack genes for many metabolic activities; lack mechanisms for adapting to environmental perturbations; and have reduced secretory activities, presumably to

		North America						UK			Europe					Reference	
		A	B	G	F	Aph1	Aph2	Aph3	Cras1	Cras2	TW	C	D	E	H		U
Triozidae	<i>Bactericera cockerelli</i>	V	V	V*													Hansen et al. (2008), Mauck et al. (2019)
	<i>Bactericera dorsalis</i>		V														Cooper et al. (2022)
	<i>Bactericera maculipennis</i>		D														Borges et al. (2017)
	<i>Bactericera nigricornis</i>													V			Moreno et al. (2021)
	<i>Bactericera tremblayi</i>													D			Teresani et al. (2015)
	<i>Bactericera trigonica</i>													V	V		Moreno et al. (2021)
	<i>Heterotrioza chenopodii</i>							D									Grimm et al. (2022)
	<i>Trichohermes walkeri</i>										D						Kwak et al. (2021)
	<i>Dyspersa pallida</i> (= <i>Trioza anthrisci</i>)													V*			Sumner-Kalkun et al. (2020)
	<i>Dyspersa apicalis</i> (= <i>Trioza apicalis</i>)													V			Nissinen et al. (2014)
<i>Trioza urticae</i>																V*	Haapalainen et al. (2018)
Aphalaridae	<i>Aphalara curta</i>					D	D	D									Grimm et al. (2022)
	<i>Aphalara loca</i>					D											Grimm et al. (2022)
	<i>Aphalara persicaria</i>						D										Grimm et al. (2022)
	<i>Craspedolepta nebulosa</i>								D	D							Sumner-Kalkun et al. (2020)
	<i>Craspedolepta subpunctata</i>								D	D							Sumner-Kalkun et al. (2020)

Figure 5

Haplotype diversity of *Candidatus Liberibacter solanacearum* and associations with psyllids. In the matrix, V indicates confirmed vector status; V* indicates probable vector status; and D indicates that the haplotype was detected in the specified psyllid species, but that vector status has not been evaluated. Haplotype TW is a putative novel haplotype detected from *Trichohermes walkeri* in the study by Kwak et al. (66). Other haplotypes are described in the indicated references.

avoid detection in plant or insect hosts (for a recent review, see 79). Plant pathogenic symbionts (**Figure 4**) also encode canonical elements involved in plant infection, such as functional Sec and Type I secretion systems and putative effectors for facilitating invasion and proliferation in plant tissues (summarized with relevant literature in **Figure 4**). On the psyllid side, we know that infection with symbionts is usually for life, that infected cells are located throughout the insect body, and that symbiont titers can vary wildly among psyllid tissue types (79). The degree of infection also strongly depends on when a symbiont is acquired; successful infection establishment and replication are both generally higher in immature stages. Omics studies and microscopy work document immunity activation and apoptosis-like responses during the process of symbiont invasion of psyllid host tissues (e.g., 45), as well as changes in psyllid metabolism (e.g., 141). While some organismal-level studies report negative effects of symbiont infections on fecundity (85) or stage-specific survival (103), these effects are variable (**Figure 4**). Additional work suggests that the outcomes of *Ca. Liberibacter* or *Ca. Phytoplasma* symbiont infections in psyllids are influenced by host plant quality and identity (111), for instance, whether the host plant is infected with the symbiont as well (28, 73). Outcomes may also be influenced by coinfection with other

symbionts, such as *Wolbachia* (19, 59). A full accounting of the myriad interactions among psyllids, *Ca. Liberibacter*, and *Ca. Phytoplasma* is beyond the scope of this review. We highlight that future work should explore how these interactions relate to psyllid and symbiont evolution and whether the outcomes of molecular interplay have biological or epidemiological relevance at the population and community levels.

A key part of this effort will include discovering and characterizing a greater diversity of *Ca. Liberibacter* and *Ca. Phytoplasma* taxa outside of crop hosts and pest psyllid species. The CLso pathosystem serves as an excellent case study of the benefits of such efforts. CLso is a complex of host- and vector-specific haplotypes, with crop-pathogenic haplotypes mainly affecting solanaceous crops in North America (A and B) or apiaceous crops in Europe (C, D, and E) (**Figure 5**). Efforts to document patterns of host and psyllid associations for CLso outside of agriculture over the past decade revealed at least nine previously undetected CLso haplotypes and strong associations with potential vectors in an additional family: Aphalaridae (**Figure 5**). Most of the new haplotypes have no record of occurrence in crops and appear to be circulating entirely in noncrop habitats, even if they are also associated with pest psyllid species and sympatric with agricultural sites (e.g., haplotype G transmitted by *B. cockerelli* in California, United States) (**Figure 5**). Survey efforts of this type can now be combined with techniques for enriching extracts from psyllids for microbial cells to cost-effectively extract cleaner, more extensive genomic information from these unculturable symbionts (56). By applying these new genomic resources toward comparative studies, we can identify traits that enabled *Ca. Liberibacter* and *Ca. Phytoplasma* species to emerge as crop pathogens or to infect specific psyllid hosts (e.g., 52). We can also begin to track the distribution and abundance of these variants in noncrop habitats to understand their ecological roles in interactions among psyllids, host plants, and other microbial associates.

6. PSYLLIDS IN ECOLOGICAL COMMUNITIES: ROLES AND IMPORTANCE

Psyllids participate in a multitude of trophic interactions. Like other Sternorrhyncha, psyllids provide access to a usually inaccessible carbon resource (the phloem contents) through sap ingestion and excretion of sugar-rich feces (honeydew). This elevates the roles of psyllids in food webs beyond the relatively replaceable function of soft-bodied, minimally mobile prey items. In some food webs, psyllids and other honeydew-producing hemipterans are even considered to be keystone species because the honeydew resources that they produce have disproportionate impacts on the abundance of many other interacting species in the community (3). Honeydew consists mostly of simple sugars and trace amounts of amino acids but can also contain inorganic ions, proteins, and secondary metabolites from host plants (94). It is consumed by bacterial, fungal, arthropod, and vertebrate species. Removal of honeydew producers through predation will eliminate this resource. Because of this, various putatively mutualistic interactions have arisen between honeydew-producing insects and honeydew consumers (particularly ants) to prevent predation and preserve honeydew production (94).

These keystone interactions can have cascading effects on the entire community structure and also support arthropod biodiversity by supplementing floral resources. In boreal and arctic ecozones, where floral resources are often limited, multiple species of bumble bee (*Bombus* spp.) have been observed foraging on honeydew produced by *Cacopsylla macleani* on *Salix alaxensis* (107). This same honeydew resource also supplemented the diets of vespid wasps, which are key arthropod predators. This study and others on Sternorrhyncha–bee relationships (77) suggest that psyllid honeydew may promote hymenopteran species diversity. In agricultural environments, honeydew-mediated ant–psyllid mutualisms can have the opposite effect by reducing psyllid interactions with

predators and parasitoids. For example, tending of *D. citri* by non-native, invasive Argentine ants (*Linepithema humile*) in the western United States reduces control by syrphid flies and introduced hymenopteran parasitoids (76).

Compared to most of their Sternorrhynchan relatives, psyllids have taken the act of honeydew excretion to the next level. Psyllid honeydew can be packaged in wax tubes or shaped into different functional structures. Nymphs of some psyllid species form their rapidly drying honeydew secretions into small protective coverings known as lerps (57). These dwellings, made primarily of starch, are yet another psyllid-produced fecal product mediating keystone interactions (47). In Australian *Eucalyptus* forests, the lerps of various *Glycaspis* psyllid species serve as a primary food resource for honeyeater bell miner birds (*Manorina* spp.), which often consume lerps while leaving the psyllid nymph beneath it unharmed (and able to produce more lerp material) (55). These so-called despotic avians are highly aggressive and drive out other birds from their territory, thus removing most of the avian insectivores that keep psyllid populations on *Eucalyptus* in check.

Forests colonized by lerp-consuming bell miners frequently experience co-occurring psyllid outbreaks not only of *Glycaspis*, but also of more damaging leaf-feeding psyllids that do not form lerps, such as senescence-inducing *Cardiaspina* spp. (121). These outbreaks, when severe, cause dieback of multiple *Eucalyptus* species (for a review, see 68). Experimental removal of bell miners is followed by the return of diverse avian insectivores and reductions of psyllid outbreaks (68). This is more indirect evidence that psyllids are an important food source for avians in *Eucalyptus* forests, which may not have been evident without experimental work targeting the bell miner–psyllid interaction. Whether the bell miners or the psyllids arrive to the area first is not clear, but this research clearly demonstrates that psyllids can have far-reaching consequences for community- and landscape-level processes.

SUMMARY POINTS

1. Significant progress has been made in resolving psyllid taxonomy, characterizing psyllid diversity, and determining psyllid distributions. However, biases worldwide remain due to unequal resources and sampling efforts.
2. Psyllids exhibit extreme host specificity and microhabitat preferences. Evolutionary processes underlying this specificity are not well explored but could be resolved through efforts to document the natural histories of more psyllid taxa outside of crop pests.
3. Psyllids perceive visual and odor cues from host plants prior to contact, but hierarchies of cue use are only documented for a few species under very limited conditions.
4. Feeding by psyllids on preferred host plants is strongly constrained to specific tissue types. Establishing the drivers of microhabitat preferences is possible by combining approaches such as the electrical penetration graphing technique, stylet sheath visualization, and measurements of plant functional traits.
5. Psyllids secrete effector molecules to induce changes in host phenotypes. Often, these changes appear to be adaptive. Preference–performance studies across host species will reveal the circumstances in which psyllid-induced phenotypes are advantageous or detrimental.
6. Psyllids host a diverse complement of symbiotic bacterial associates, as revealed by microbiome studies. However, the functional significance, lineage specificity, and distributions of psyllid symbionts are not known for most psyllid taxa.

7. Psyllids are vectors of fastidious, phloem-limited bacterial plant pathogens, but we know almost nothing about psyllids as vectors, or the impacts of the bacteria they transmit, outside of crop systems.
8. Many organisms rely on psyllids as provisioners of carbon (e.g., lerps, honeydew) and as a food resource. Psyllids may function as keystone species, especially in resource-poor environments where floral resources for pollinators are limited.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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