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REVIEW

Aphid honeydew in ecosystems and the environment

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Abstract

Honeydew is a sugar-rich sticky liquid excreted by aphids and other hemipterous insects, such as scale insects, whiteflies, and psyllids, that feed on plant phloem sap. Compared to flower nectar, aphid honeydew contains the same primary sugars (sucrose, glucose, and fructose) as nectar, but also additional oligosaccharides, such as melezitose and erlose, which are synthesised by aphids. Honeydew deposited on leaf surfaces, other surfaces, and in soil plays various roles in the ecosystem, serving as an essential food source for ants, bees, and bumblebees, as well as a supplementary food source for many other animal groups. Bees and ants are important predators and pollinators, particularly in forest ecosystems. Consequently, honeydew produced by aphids and other sap-feeding insects plays a crucial role in maintaining ecosystem functioning. A direct ecosystem service provided by aphid honeydew is a particular honeydew honey, but a substantial part of uni- and multiflower honey may also contain honeydew. Other ecosystem services include enhanced soil microbial activity and reduced nitrogen leaching from forest soil. In urban environments, the honeydew of arboreal aphids can be a significant nuisance, as it coats walls, cars and playgrounds with a sticky layer that collects dust and pollen and supports the growth of sooty mould. Sooty mould growing on honeydew on the leaf surfaces of understory plants can reduce photosynthesis and plant growth. We conclude that extensive multi-trophic network mappings are needed to better quantify how honeydew links above-ground and below-ground food webs, particularly nutrient transfer pathways and cascading effects.

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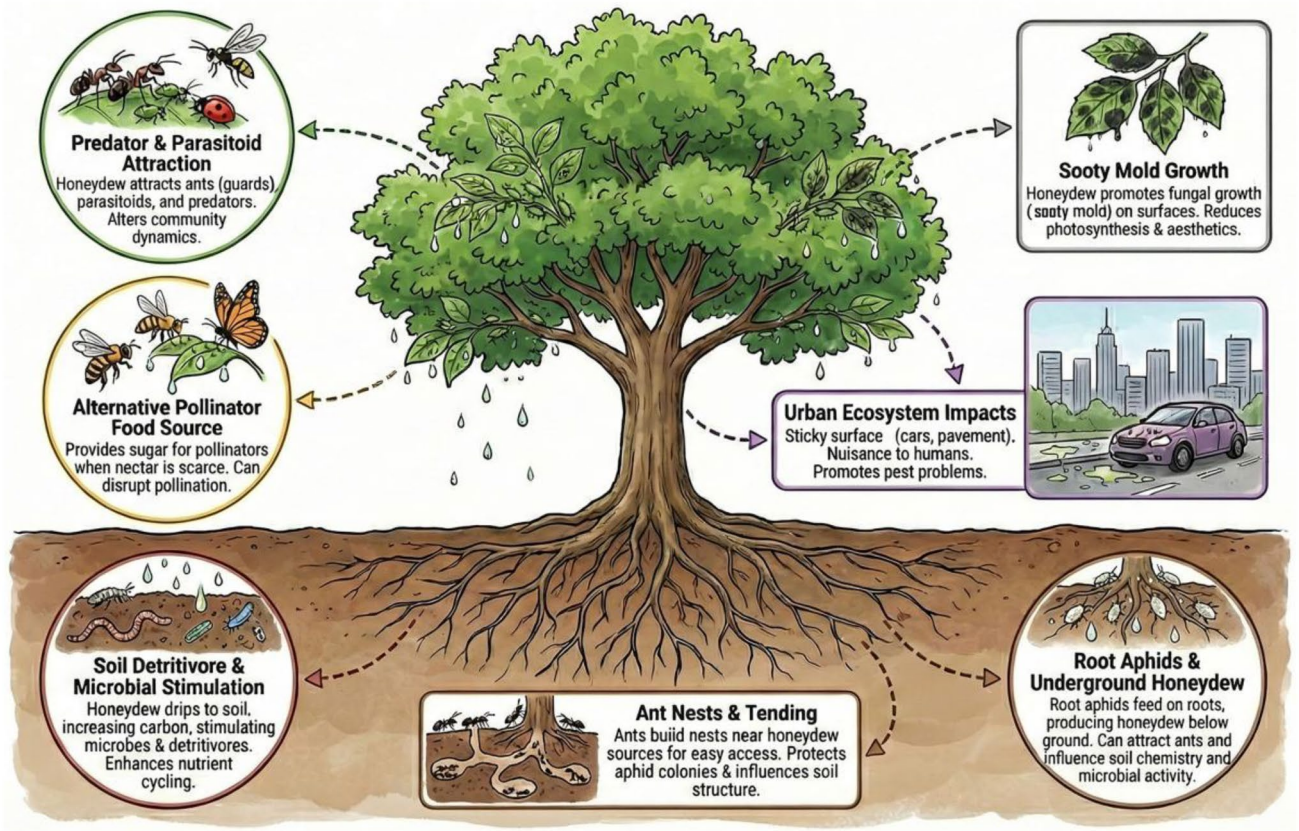
Graphical abstract



Keywords Aphidoidea · Ants · Phloem sap · Phloem-feeders · Carbohydrates · Honeydew honey

Introduction

Honeydew, the sugary excretion of phloem-feeding insects, is among the most abundant and widely available carbohydrate resources in terrestrial ecosystems, yet it is easily overlooked. In forests and many agroecosystems, honeydew is deposited onto foliage, bark, understorey vegetation and soil, where it sustains an extended community of microbes, ants, pollinators, predators, parasitoids and even vertebrates. The chemical basis for this resource lies in the composition of phloem sap, which transports the products of photosynthesis and is consequently rich in carbohydrates but poor in the amino acids insects require, resulting in a high carbon-to-nitrogen (C/N) ratio (Douglas 1993; Jensen et al. 2013). To obtain sufficient nitrogen, phloem feeders must process large volumes of sap and void the surplus carbohydrate; honeydew is therefore characteristically sugar-rich (Douglas 1993). Consequently, honeydew provides a carbohydrate-rich energy source for arthropods and other animals (Heinrich et al. 1992).

Honeydew production is concentrated in the Hemiptera, and within it in the suborder Sternorrhyncha, including aphids (Aphidomorpha: Aphidoidea), adelgids (Aphidomorpha: Adelgoidea), scale insects, mealybugs, whiteflies and psyllids—all of which feed on phloem sap. Some thrips (Thysanoptera) also feed on phloem and produce honeydew (Aravintharaj et al. 2020), although most thrips puncture individual leaf cells. By contrast, the xylem-feeding Auchenorrhyncha—cicadas, spittlebugs and many treehoppers and leafhoppers—exploit a dilute, low-C/N fluid and excrete watery, sugar-poor products such as “cicada rain” rather than true honeydew (Raven 1983; Chuche et al. 2017; Hoch et al. 2024). Further exceptions are moss-feeding aphids; the moss thallus lacks true phloem and vascular bundles; therefore, aphids feed on water-filled parenchyma cells (Albrecht 2015). Across all these taxa, the published record of honeydew production is dominated by aphids(Moir et al. 2018) (Table 1).

This review synthesises current knowledge of aphid honeydew as a multifaceted ecological resource and biogeochemical agent, integrating chemical ecology, trophic

Table 1 Numbers of known species in phloem-feeding hemipteran taxons and absolute and relative number of honeydew publications in Web of Science database

Phloem-feeding Hemipteran taxons	Common name	Number of known species	Publications in Web of Science (1975–2025)	Publications mentioning honeydew	Percentage mentioning honeydew ()
Suborder: **Sternorrhyncha**		~18 000[1]			
Aphididae	Aphids	~5 100[2]	8 926	233	2.61
Phylloxeroidea (Adelgidae + Phylloxeridae)	Adelgids and Phylloxerids	~140[2]	544	5	0.92
Coccoidea*	Scale insects and Mealybugs	~8 500[3]	1162**	46	3.95
Aleyrodidae	Whiteflies	~1 700[4]	4 417	118	2,67
Psylloidea	Psyllids	>4 000[5]	736	15	2,04
Suborder: **Auchenorrhyncha**		48 000[6]			
Fulgoroidea	Planthoppers	>14 000[7]	901	4	0.44
Cicadellidae	Leafhoppers	23 495[6]	4 499	51	1.13
Membracidae	Treehoppers	3 494[6]	596	28	4,68

Search field topics: 1) Liu et al. 2024a; 2) Favre, C. 2026; 3) Deng et al. 2025; 4) Selvaraj et al. 2025; 5) Mauck et al. 2024; 6)Dmitriev et al. 2026; 7) Bourgoin 2024; *The largest (~ 2,400 spp.) Coccoidea family, Diaspididae (armoured scale insects) feeds primarily on parenchymacells rather than phloem sap (Douglas 2006). **Diaspididae not included

interactions and ecosystem functioning. We focus on aphids because their honeydew sustains keystone consumers such as the wood ants of boreal forests, while drawing on examples from other phloem-feeding hemipterans where relevant. We hypothesise that honeydew is not merely a metabolic by-product of phloem feeding but (i) a key mediator of multitrophic interactions, (ii) an important energy source shaping microbial communities, plant physiology, and the behaviour and fitness of organisms ranging from mutualistic ants to pathogens, and (iii) a vector for systemic contaminants acquired from host-plant phloem, with wide-ranging ecosystem effects.

We further propose that pesticide residues translocated into the phloem and excreted in honeydew pose underappreciated risks to pollinators and natural enemies—including through indirect routes such as honeydew foraging and the incorporation of contaminated honeydew into honey—with potential consequences for pollinator decline and food safety. Variation in honeydew composition with aphid species, host-plant chemistry and environmental conditions is likely to modulate these ecological and toxicological outcomes, as well as effects on nutrient cycling, carbon fluxes and community structure. The need for such a synthesis arises from the fragmented state of the literature, which spans disciplines that rarely intersect and has so far precluded a holistic view of honeydew's ecological and societal significance—including its growing nuisance value in a warming climate, where honeydew accumulation promotes sooty mould and surface fouling in urban areas. By consolidating these strands, we aim to identify conceptual gaps and stimulate integrative research on this ubiquitous but overlooked component of terrestrial ecosystems.

Aphid biology

Aphids (Hemiptera: Aphidoidea) represent a group of widely distributed insects, but unlike many other major insect taxa, they possess the highest species richness in the temperate regions of the Northern Hemisphere rather than in the tropics (Dixon et al.1987; Heie 1994; Pautasso and Powell 2009). This phenomenon is partly explained by their complete adaptation to cold winters and by the flow of phloem sap in trees (Nilsson 2022), which shifts from foliage to storage during autumn and back to new foliage in early spring (Heie 1980; Babst and Coleman 2018). Aphid species that feed on deeper phloem tissues, including those that penetrate the phloem through the bark (Fig. 1), possess unusually elongated mouthparts. This inhibits their ability to withdraw their mouthparts and escape predators, thereby increasing their need for protection by mutualist ants (Shingleton et al. 2005). Particularly in boreal forests, the spatial distribution and success of aphids are directly tied to the proximity of *Formica* ant mounds (Domisch et al. 2011). Furthermore, high vegetational diversity in the tropics is considered a risk for aphids, which are inefficient at locating host plants and cannot remain away from them for long (Dixon et al. 1987). In boreal and temperate forest ecosystems, where vegetational diversity is relatively low, a single tree species can form large forest areas (Hordijk et al. 2024), and therefore, the access of aphids to a suitable new host plant is easier. In contrast, other phloem-feeding insect species, such as scale insects, mealybugs, and psyllids, are more typical honeydew producers in subtropical and tropical forests than in temperate and boreal environments (Martins-Mansani 2021).

Fig. 1 The black garden ant *Lasius niger* L. tending apterous female and nymphs of the Shiny birch aphid (*Symydobius oblongus* von Heyden) on birch bark. Ants induce aphids to excrete a drop of honeydew by touching the aphid's abdomen with their antennae and labial palps

Many aphid species shift between host plants over their life cycle, using different winter (primary) and summer (secondary) hosts, whereas others are restricted to a single host plant species. Approximately 10% of the ~ 5000 described aphid species show seasonal host alternation (heteroecy) (Blackman and Eastop 2008; Vericel et al. 2025). The nutritional basis for this strategy likely reflects seasonal variation in host quality: free amino acid concentrations in deciduous-tree phloem sap peak in spring during leaf flush and again in autumn during chlorophyll protein breakdown, reaching roughly twice the summer concentrations (Douglas 1993). Switching to herbaceous summer hosts can therefore allow aphids to exploit higher-quality nitrogen resources during summer (Yamamoto et al. 2020). This may be particularly advantageous in the boreal zone, where the growing season is short and fast-growing herbaceous plants typically have higher foliar and phloem nitrogen concentrations than deciduous trees in summer (Matson 1980). In contrast, non-alternating tree-living species may cope with low summer host quality via alternative strategies, such as producing a largely dormant summer generation (aestivation) or actively tracking nitrogen-rich tissues within the same host (e.g., colonising the youngest leaves or fast-growing saplings where growth and amino-acid translocation remain high) (Dixon 2005).

Three example aphid species, *Euceraphis betulae* Koch (Fig. 2a), *Rhopalosiphon padi* L. (Fig. 2b), and *Eriosoma ulmi* L. (Fig. 2c), all overwinter as eggs on tree bark in temperate and boreal environments but have different life-history strategies. The birch aphid, *E. betulae,* lives on leaves of *Betula pendula* Roth, and can breed on the same tree species several aphid generations during a growing season. However, all individuals in the parthenogenetic generations of the *E. betulae* population have wings and may migrate to other birch trees during the summer. Typically, *E. betulae* can undergo mass migrations, and the distance, depending on wind speed, can be up to 1000 km (Nieminen et al. 2000). Therefore, in Finland, it is possible to see in early summer on birch foliage both, small nymphs of local population emerged from overwintered eggs, and winged adults that have migrated e.g. from Poland (Nieminen et al. 2000). Outbreaks of this species on the common boreal tree species silver birch results in a massive honeydew load in birch forests and on ornamental trees in urban areas.

Host-alternating aphids alternate between two host plants, with the primary host usually the one in which the sexual generation develops. In temperate and boreal environments, the primary host plant of many aphid species is typically a woody plant, while the secondary host is usually a wild or cultivated herbaceous plant (Dixon and Dewar 1974; Dixon and Kundu 1994). The bird cherry-oat aphid (*R. padi*) eggs overwinter on the primary host, the bird cherry tree (*Prunus padus*), on the branch bark close to buds (Fig. 3). In early spring, nymphs of fundatrices (stem mothers) hatch from the eggs when the leaf buds start to open, and they feed

Fig. 2 Photos of different lifecycle stages of three aphid species: **a** alate of *Euceraphis betulae* on silver birch leaf, **b** alate *Rhopalosiphon padi* with nymphs on bird-cherry ready for spring migration, and **c***Eriosoma ulmi* fundatrix aphids and 2nd generation nymphs inside the leaf gall on wych elm

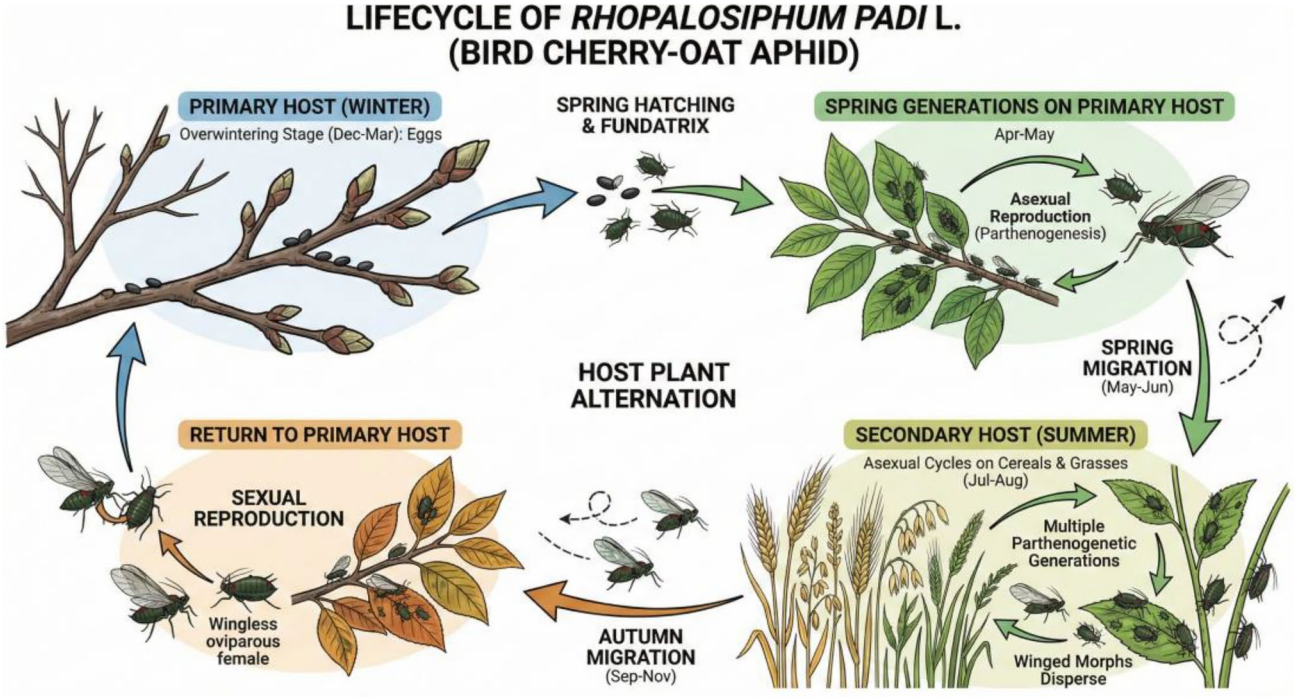


Fig. 3 A visual presentation of the annual lifecycle of a host-alternating aphid species *Rhopalosiphon padi* L

on developing bird-cherry leaves. Unwinged (apterous) fundatrix aphids give birth to nymphs that develop into winged (alatae) parthenogenetic females that will disperse to their secondary host plants, cereals, or other grasses, in late May–early June (Wiktelius 1984; Glinwood and Pettersson 2000a). These alate virginoparae are female aphids that reproduce parthenogenetically, and multiple generations will develop during the summer. In August, when the grains of cereals and grasses have ripened, the virginoparae aphids start to fly again to bird cherry leaves. First leaves are preparing for overwintering, and there are again high concentrations of amino acids in phloem sap as leaf chlorophyll gradually disintegrates (Glinwood and Pettersson 2000b; Holopainen and Peltonen 2002; Holopainen 2008). These aphids are gynoparae, which give birth to both females and males (Leather 1986). After mating, females lay overwintering eggs on the branch bark in the base of buds. Outbreaks are infrequent but can be massive with high honeydew production on cereals and grasses in warm summers.

The elm-currant aphid, *E. ulmi*, is an aphid species with two woody hosts; the secondary host is a *Ribes* spp. shrub, while the primary host is a tall tree, *Ulmus* spp. The first (fundatrix) and second (alate migrants) spring generations of *E. ulmi* are examples of aphid species that live inside leaf galls and are not attended by ants. Furthermore, a summer generation of *E. ulmi* lives as root aphids feeding on currant roots but is not attended by ants (Urban 2003). This contrasts with many other root aphids. This is not an outbreaking species, but galls are common on less resistant *Ulmus* individuals. Honeydew is produced both within the galls and in the soil.

How aphids transform phloem sap to honeydew

Photosynthesis takes place in chloroplasts, mostly in leaf mesophyll cells, from where the photosynthetic products, mainly sucrose, are transported into the sieve tube elements of phloem in leaf veins. This process is known as "phloem loading" (Braun 2022). From the site of production (source), typically mesophyll cells in mature leaves, photosynthates are transported to sinks (importing tissues such as roots, stems, fruits, and seeds) through the phloem in veins (Turgeon and Ayre 2005; Braun 2022). Several physiological mechanisms regulate this process, involving the movement of specific compounds. It is generally believed that an osmotically generated pressure gradient, particularly driven by sugars, facilitates the phloem mass flow from source to sink (De Schepper et al. 2013). Recently, it has been demonstrated that plant sugar transporter proteins play a crucial role in regulating and facilitating long-distance sugar transport from source to sink organs (Braun 2022; Liu et al. 2025). Sucrose and hexose transporters are active in phloem loading, especially in minor leaf veins (Lalonde et al. 2003). Sugar loading increases the osmotic pressure

inside the sieve tube elements, causing water to move into the adjacent xylem vessels by osmosis. The influx of water generates high hydrostatic pressure (turgor pressure) within the sieve tubes, which is counteracted by the rigid cell walls of sieve elements, creating a pressurised system. The turgor pressure is essential for phloem sap to flow through the inserted aphid stylet, and aphids do not need energy-consuming sucking activity. Aphids even have a specialised valve system to regulate the flow of phloem sap (McLean and Kinsey 1984). Stylectomy, in which the aphid stylet bundle is cut after feeding has started (e.g., with a laser), the aphid is removed, and phloem sap is collected from the stylet in microcapillary tubes, is considered the most authentic method for collecting plant phloem sap for chemical analyses (Lohaus 2022).

Phloem sap is relatively nutrient-rich and has a very low concentration of toxins and feeding deterrents compared to many other plant products (Douglas 2006). Phloem sap-feeding insects typically require more amino acids than the nitrogen-rich compounds in their phloem sap diet can provide. As a result, amino acids are selectively retained in the gut, and the surplus carbohydrate-rich fluid is excreted as honeydew (Douglas 2006; Schillewaert et al. 2017). Environmental factors can change the sugar composition in honeydew. For example, plant exposure to elevated temperature (+3 C) and doubling carbon dioxide levels (400 ppm 800 ppm CO_2) significantly increased fructose concentration, a main honeydew sugar in the honeydew of the black bean aphid (*Aphis fabae* Scopoli) when reared on *Vicia faba* L. (Blanchard et al. 2022).

It should be noted that aphid honeydew also contains free amino acids, which could originate from aphid symbionts or incomplete absorption of ingested amino acids from plants rich in amino acids in their phloem sap. Recent reports on broad bean (*Vicia faba*) (Leroy et al. 2011) and wheat (*Triticum aestivum*) (Bühler and Schweiger 2024) have shown that host plants can respond to aphid feeding by producing aphid-induced amino acids. Specialist aphids can be more efficient inducers of free amino acids in the host plant than generalist aphid species (Leroy et al. 2011).

Transformation phases of the phloem sap in the aphid digestive tract

Aphids transform plant phloem sap into honeydew through a sequence of physicochemical and enzymatic processes adapted to a diet that is extremely rich in sucrose but poor in essential amino acids. The pathway spans extra-intestinal modification of sap in the stylet, luminal hydrolysis and selective absorption in the midgut, powerful osmoregulatory mechanisms that remove excess water and sugars, microbial provisioning of essential amino acids, and rapid egestion of unassimilated solutes as honeydew. A summary of the main biochemical transformation processes is shown in Fig. 4. Below is a more specific 5-phased description of the feeding and digestion processes taking place in the aphid digestive tract before the release of honeydew droplets from the gut.

Phase 1) *Ingestion and extra-intestinal processing* start when an aphid has punctured phloem sieve elements, and sap flows passively into the food canal under positive

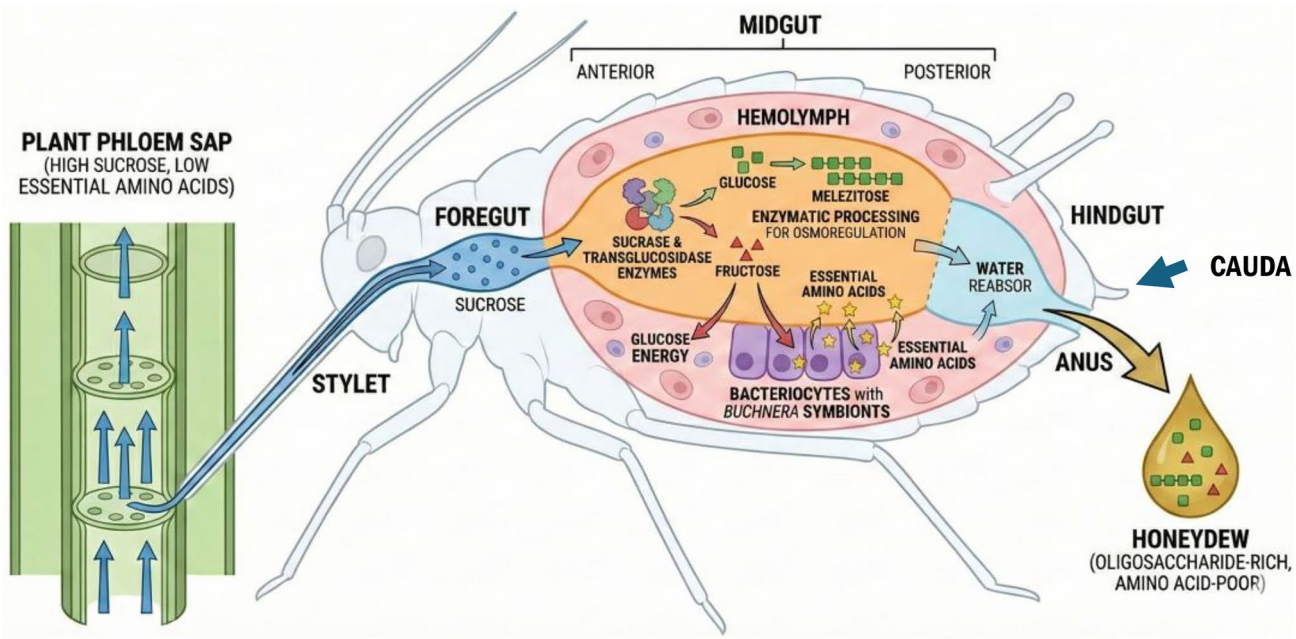


Fig. 4 Summary of the biochemical transformation processes of plant phloem sap to aphid honeydew transformation in the digestive tract of aphids

hydrostatic pressure (Douglas 2006). Before and during ingestion, aphids secrete a mixture of gelling and watery saliva. Salivary enzymes, including α-glucosidases, hydrolyse sucrose in the apoplast/sieve element lumen, lowering sap osmolality before it reaches the midgut, thereby facilitating ingestion and mitigating osmotic stress (Bos et al. 2010). Aphids also counter sieve-element occlusion by salivary effectors that reverse or prevent plugging, maintaining sap flow (Walker 2022).

Phase 2) *Midgut digestion and absorption*: In the gut lumen, sucrose is hydrolyzed to glucose and fructose (Price and Gatehouse 2014). Aphid midguts possess proteases and other enzymes that digest the small amount of phloem proteins and peptides (Cristofoletti et al. 2003). Amino acid uptake is selective; aphids preferentially assimilate essential amino acids while differentially handling non-essential ones, shaping the amino acid composition of honeydew (Douglas 2006; Karley et al. 2002).

Phase 3) *Symbiont-mediated nitrogen complementation*: The obligate endosymbiont *Buchnera aphidicola*, is essential for aphid survival, synthesises essential amino acids (EAA) that are scarce in phloem sap, enabling aphids to meet nitrogen demands despite a carbohydrate-biased diet (Douglas 1996; Douglas 2006; Wilkinson et al. 1997). *B. aphidicola* has coevolved with aphids for 100–250 Myr and occurs in 99% of species within specialised bacteriocytes, making it unculturable outside its host (Moran 2021). Some aphid lineages have lost *B. aphidicola. Geopemphigus* spp. harbour a maternally transmitted Bacteroidetes symbiont (Chong and Moran 2018) and Cerataphidini carry yeast-like symbionts (Manzano-Marin et al. 2023), each genetically able to assume nutrient provision. Repeated degradation of the *Buchnera* genome during coevolution has likewise driven aphids to acquire compensatory secondary partners (Manzano-Marin et al. 2023). Bacteriocytes form paired bacteriomes (mycetomes) in the abdominal and thoracic hemocoel, separate from the gut epithelium and lumen; *Buchnera* thus lies outside the digestive tract, with transporters moving amino acids between bacteriomes and gut lumen (Feng et al. 2019). Aphids depend on *Buchnera* for EAA biosynthesis and embryonic development (Moran 2021; Feng et al. 2019).

Facultative secondary symbionts—*Serratia symbiotica*, *Hamiltonella defensa*, *Regiella insecticola*—occupy more varied sites: some *S. symbiotica* strains share bacteriocytes with *Buchnera*, while others colonise the hemolymph and entire digestive tract, with densities rising along the gut (Zytynska and Weisser 2016; Renoz et al. 2022). They can indirectly stabilise and enhance the system's EAA output under abiotic stress but cannot match obligate-symbiont production rates (Burke et al. 2010; Oliver et al. 2010).

Phase 4) *Osmoregulation and fluid processing*: To reduce the extreme osmotic load of high sugar concentration of phloem sap, aphids use: (a) A filter chamber–like gut architecture that shunts excess water and solutes rapidly from anterior midgut to hindgut (Pompon et al. 2011; Douglas 2006). (b) Conversion of hexoses into higher oligosaccharides (e.g., melezitose, trehalulose) in the gut (Douglas 2006). (c) Strategic xylem ingestion to dilute gut contents and haemolymph when osmotic load is excessive, independent of dehydration status (Pompon et al. 2011).

Phase 5) *Honeydew formation and excretion*: After selective absorption of amino acids and a fraction of sugars from phloem sap by aphids, honeydew osmotic pressure reflects aphid regulation: it is typically lower than ingested sap due to sucrose hydrolysis and oligosaccharide synthesis but can vary with host plant chemistry and aphid physiology (Douglas 2006; Pringle et al. 2014). The honeydew is rapidly voided via the anus. Honeydew excretion rate correlates with phloem ingestion and is often copious; droplet frequency is often used as a proxy for ingestion in electrophysiological studies (Tjallingii 1995).

Phase 6) *Post-excretion stage: 'life with liquid marbles' is a special case faced by gall-forming aphids*: Aphids are at constant risk of being entrapped in their sticky honeydew droplets. In the absence of attendant ants, aphids kick the droplets off with a hind leg or by flicking them away with the cauda (Way 1963). Plant galls, deformed host growth induced by the female aphid, provide protected compartments for offspring. In adelgids (conifer specialists), the cytokinin analogue 6-benzylaminopurine is thought to be synthesised by the adelgid to control gall-tissue development, possibly phytohormone-regulated as in cone growth (Jia et al. 2020). But for sap-sucking gall-makers, excreting copious sticky honeydew and keeping the gall cavity clean are major challenges. However, adelgids and aphids solved this problem over 200 Myr ago by spreading powdery abdominal wax with their hind legs on honeydew droplets for storage inside a gall (Pike et al. 2002). In physics, aqueous droplets coated by hydrophobic powder are called "liquid marbles" (Aussillous and Quéré 2001). Honeydew marbles and an emerging new generation of aphids are released when the gall opens. Examples of gall-forming adelgids and aphids are the pineapple gall adelgid *Adelges laricis* (Fig. 5a) on Norway spruce, and *Eriosoma ulmi* (Fig. 5b) on wych elm.

Secondary compounds in aphid honeydew

Beyond its bulk sugars and amino acids, honeydew carries a trace chemical signature inherited from the host plant's phloem, which shapes how many consumers respond to it.

Fig. 5 Spherical aphid honeydew droplets (liquid marbles) (red arrows): **a** in the opening gall of the pineapple gall adelgid *Adelges laricis* (Hemiptera: Sternorrhyncha: Aphidomorpha). The last (3rd) instar nymphs crawl out from the gall and shed their last nymphal skin. **B** Large liquid droplets on the inner surface of the opening leaf gall of *Eriosoma ulmi* on wych elm leaf

The phytochemicals transported in plant phloem sap can be classified as (a) primary metabolites, associated with growth and development; (b) hormones, associated with regulation; and (c) secondary (specialised) metabolites/compounds, associated with interactions of abiotic and biotic environment (Erb and Kleibstein 2020; Ramawat and Merillon 2025). Many secondary metabolites play essential roles in plant physiology, including terpenoids such as isoprene and carotenoids, which act as membrane-stabilising agents (Velikova et al. 2011; Pollastri et al. 2023) and as light-harvesting pigments in photosynthesis (Stra et al. 2023). Current knowledge of their functional roles across several phases of plant life supports classifying these compounds as specialised metabolites or specialised compounds (Erb and Kleibstein 2020; Ramawat and Merillon 2025).

In honeydew, the term 'secondary compounds' (SCs)—for which the plant literature increasingly prefers 'specialised compounds' (Xu and Gaquerel 2025)—is probably the most appropriate label for compounds that are not major carbohydrates or nitrogen-containing compounds. Besides plants themselves, the metabolic origin of honeydew SCs can be a mould fungi growing on honeydew on plant leaves (Haituk et al. 2022). However, there is no evidence that SCs produced by plant symbionts are detectable in aphid honeydew, even though the fungal endophyte-derived alkaloids peramine and lolitrem B have been detected in the aphid *Rhopalosiphum padi* and its predators (Fuchs et al. 2013).

Most plant SCs serve functions that support ecological interactions, such as defence against pests, pathogens, and other environmental stresses (Ramawat and Merillon 2025). In honeydew, SCs originate mainly from plant phloem sap but can occasionally be modified by aphid or endosymbiont metabolism (Molyneux et al. 1990). There are also several reports of SCs in honeydew honey, which complicates the evaluation of their source, as bees and their symbionts may also contribute. Compared with sugars and amino acids, SC concentrations are much lower and are always host plant- and aphid species-specific (Pringle et al. 2014). The major groups of SCs are phenolics, terpenoids, and nitrogen-containing alkaloids, which are classified according to their biosynthetic pathways. Some minor SC groups, e.g., benzoxazinoids (Molyneux et al 1990) and glucosinolates (Kazana et al. 2007), can be detected in aphid honeydew. Derivative molecules may contain structural units (moiety) from multiple specialised SC pathways (Ji et al. 2024). In addition, some volatile higher alcohols, such as 2-methyl-1-butanol, can serve as plant aroma compounds and are found in aphid honeydew (Boullis et al. 2018). SC concentrations in aphid honeydew can affect higher honeydew consumers such as ants and many nectar feeders (Pringle et al. 2014).

Terpenoids

With more than 170,000 known terpenoid molecules/skeletons and their derivatives found from biological sources (Zeng et al. 2022), terpenoids are the largest group of SCs in nature. All terpenoids have the 5-carbon isoprene unit as a building block. Isoprene (C_5) is a highly volatile compound emitted by many plant and animal species (Holopainen et al. 2025). A volatile plant aroma compound, 3-methyl-2-buten-1-ol (prenol), is emitted from the honeydew of pea aphids (*Acyrthosiphon pisum* Harris) (Leroy et al. 2011; Boullis et al. 2018). The five-carbon backbone of prenol is derived from an isoprene unit, and therefore, this volatile alcohol can also be classified as a hemiterpenoid.

Highly volatile monoterpenes (C10) have two isoprene units. Nearly every green plant emits monoterpenes because part of the light-dependent monoterpene emissions is released from plant chloroplasts (Loreto and Schnitzler 2010). Many plant species also store monoterpenes, and their emissions are temperature-dependent (Holopainen et al. 2018). In studies of aphid honeydew on plant foliage, emission of volatile monoterpenes and other highly volatile compounds cannot be separated between honeydew and plant emissions (Hung et al 2020; Kivimäenpää et al. 2020). Leroy et al. (2012) collected honeydew of the aphid, *Megoura viciae* Buckton, on aluminium foil under leaves of heavily infested broad bean (*Vicia faba* L.) plants. Limonene was the only monoterpene detected in honeydew emissions.

In a study of pea aphid *A. pisum* honeydew on broad bean, limonene was again detected. It was the only monoterpene identified in the emission analysis, which also recorded non-terpenoid volatile compounds (alcohols, aldehydes, ketones, and acids). However, limonene was suggested to be produced by the honeydew-associated bacterium *Mammaliicoccus sciuri, (*previously *Staphylococcus sciuri)* (Leroy et al. 2011). In Linden honeydew honey, α-terpinolene was a dominating and characteristic monoterpene (Barbaric et al. 2025). Kus et al. (2017) analysed the headspace of fir honeydew honey and reported the monoterpenes borneol, α-terpineol, linalool, and linalool derivates and oxidation products. However, the major monoterpene of European silver fir, *Abies alba* emissions, α-pinene, was not detected, suggesting that the phloem sap of fir does not contain significant fir resin monoterpenes.

The sesquiterpenes (C15) are mostly semi-volatile compounds, i.e., they are not volatile at lower temperatures. The structure is based on the union of three C5 isoprene units. Some flower volatiles, such as the sesquiterpene (*E*)-β-farnesene, accumulate in the flower vascular system, where the phloem sap can be taken up by aphids (Dötterl and Gershenzon 2023). Aphids also synthesise (*E*)-β-farnesene as an aphid alarm pheromone. Aphids release their alarm and sex pheromones from a pair of distinctive, tube-like structures called siphunculi or cornicles, on the back side of their abdomen (Fig. 6a). The short cone-type cornicles are

Fig. 6 Two types of aphid siphunculi on aphid abdomen: **a** the tube-like siphunculi with sticky secretion containing alarm pheromone β-farnesene. The arctic raspberry aphid, *Macrosiphum rubiarctici*, on the Arctic raspberry leaf, **b** the short, cone-type siphunculi (*Cinara pinea* tended by *Formica rufa* -group ants on current-year Scots pine shoot)

associated with reliance on alternative defences, such as the secretion of protective waxes or myrmecophily (Michaud 2022), as seen e.g. in *Cinara* spp. (Fig. 6b). Secreted droplets also contain unsaturated triglycerides, fast-drying adhesives that can be lethal when smeared on natural enemies (Michaud 2022). The father of modern taxonomy, Carl von Linne, originally described the siphunculi as the source of aphid honeydew because a weak microscope did not detect the less visible anus (Hottes 1928). Sesquiterpene aldehydes, gossypol and hemigossypolone (classified also as terpenoid phenolics) have been detected in aphid honeydew from *Aphis gossypii* feeding on cotton plants (Hagenbucher et al. 2014).

Terpenoids with a higher number of C_5 isoprene units, diterpenoids (C_{20}), triterpenoids (C_{30}) and tetraterpenoids (C_{40}) are mostly non-volatile compounds. Diterpenoids and tetraterpenoids or their derivatives are not reported directly from aphid honeydew (e.g. Leroy et al. 2011). However, Molyneux et al. (1990) found that cardenolides (derivatives of triterpene terpenoids) were detected in the honeydew of oleander aphids (*Aphis nerii*) feeding on oleander (*Nerium oleander*), indicating that these compounds are translocated in the phloem of the host plant. Some plant terpenoids can attenuate the activities of essential detoxification enzymes in aphids and reduce aphid performance, indicating their potential as biopesticides (Zhao et al. 2021).

Phenolic compounds

These compounds are a broad class of plant chemicals with an aromatic ring and one or more hydroxyl groups, with over 8000 identified structures (de Oliveira et al. 2025). Polyphenols are a subgroup of phenolic compounds that feature more than one phenolic unit, or more than one hydroxyl group on a single ring. Polyphenols include ecologically important categories flavonoids, phenolic acids, lignans, and stilbenes, among others (Williamson 2025). Polyphenols play multifunctional roles in plant–herbivore interactions, including deterrent or antifeedant properties (Singh et al. 2021).

Hussain et al. (1974) documented 18 phenolic acids in the honeydew of the green peach aphid *(Myzus persicae*) feeding on radish (*Raphanus sativus*) seedlings. Five of these phenolic acids were also present in uninfested radish seedlings, indicating direct transmission from plant phloem to honeydew. Feeding of the pea aphid (*A. pisum*) on broad bean plants produced honeydew that contained salicylic acid (Schwartzberg and Tumlinson 2014). Salicylic acid is a phenolic acid that acts as an essential phytohormone that suppresses the production of another phytohormone (jasmonic acid) in a host plant (Schwartzberg and Tumlinson 2014).

Flavonoids in plant phloem sap have been observed in various studies (Stevenson et al. 1996; Hijaz et al. 2016; Teixeira et al.2023). Hesperidin (463 µ mole/kg fwt) was the most predominant flavonoid in young Pineapple sweet orange (*Citrus sinensis* (L.) Osbeck) plants (Hijaz et al. 2016). In experimental conditions, flavonoids act as antifeedants for aphids (Goławska et al. 2024; Zhang et al. 2025). Exposure of the cotton aphid (*A. gossypii*) to flavonoids such as naringenin, apigenin, and kaempferol resulted in deterred aphid settling, reduced the duration of phloem feeding, and reduced the level of honeydew production. Furthermore, they also negatively affect aphid growth and adult fecundity (Zhang et al. 2025). Based on the observations by Zhang et al. (2025), it can be supposed that the plants rich in flavonoids in their phloem sap are avoided by aphids. Reduced feeding activity means that flavonoid concentration in excreted honeydew might stay at extremely low levels. As a consequence, there are currently no published, peer-reviewed studies reporting exact quantitative concentrations of flavonoids in aphid honeydew. However, several studies, as summarised by Barbaric et al. (2025), have documented phenolic acids and flavonoids in honeydew honey and found the concentrations relevant to the antioxidant potential of honeydew honey. This suggests that bees that collect honeydew honey from flavonoid-rich plants use less freshly excreted honeydew directly from aphids. They probably prefer more honeydew that has accumulated and partially dried on various plant surfaces, such as leaves, needles, or bark, where evaporation has enriched flavonoid concentrations.

Alkaloids

Nitrogen-containing alkaloids form a diverse group of secondary compounds and can be divided into ten subgroups based on amino acid precursors, from which their nitrogen-containing heterocyclic ring is derived (Li et al. 2026). Most of the over 130,000 known biogenic alkaloid compounds are recognised for their toxicity to many herbivorous animals and have antibacterial, antifungal, and antiviral activities, among others (Li et al. 2026). Alkaloids are detectable in plant phloem sap, as many are translocated through the phloem for distribution throughout the plant. Phloem sap is alkaline, and not all alkaloid compounds are transported via phloem (Nowak and Selmar 2016). As shown by Molyneux et al. (1990), honeydew from green peach aphids (*M. persicae*), feeding on groundsel (*Senecio vulgaris*) flower buds, contained the pyrrolizidine alkaloid senecionine, its *N*-oxide, and hydrolytic products including retronecine. Furthermore, in contrast, honeydew from the wheat aphids (*Schizaphis graminum*), feeding on barley or wheat, lacked indole alkaloid gramine or alkane metabolites, such as, MBOA (6-Methoxy-2-benzoxazolinone), the breakdown product of a benzoxazinoid alkaloid DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) (Molyneux et al 1990). Broom aphids (*Aphis cytisorum*) feeding on broom plants (*Cytisus scoparius*) accumulated the quinolizidine alkaloids up to 500 µg g^{-1} fr. wt. whereas broom cultivars producing more bitter alkaloids were not infested by aphids (Wink et al. 1982). Later, it was observed that aphids feeding on legumes excreted more polar alkaloids in their honeydew and sequestered non-polar alkaloids in their bodies (Wink et al. 1991). These accumulated alkaloids in aphid bodies provide a significant defensive benefit against parasitoids and predators (Kumaraswamy and Huang 2024).

Nicotine and related nicotinoid alkaloids are important defence compounds that affect chewing insects in foliage (Baldwin 1988) and are traditionally used as insecticides (Gudeta et al. 2021). However, nicotine and plant-derived nicotinoids are synthesised in plant roots and transported almost exclusively in the xylem to the accumulation sites, the vacuoles of leaf cells (Morita et al. 2009). Therefore, nicotine does not accumulate in phloem sap and is not reported from aphid honeydew. In contrast, neonicotinoids are chemically engineered insecticides transported in both xylem and phloem, making them systemic insecticides, and are found in aphid honeydew (Calvo-Agudo et al. 2019). Both act as agonists of insect nicotinic acetylcholine receptors (nAChRs), but neonicotinoids were engineered to be far more selective for insect receptors and far less toxic to mammals (Tomizawa and Casida 2003).

Other secondary compounds

Glucosinolates are important defence compounds in many cultivated Brassicaceae species. They consist of a sulphur group, a glucose molecule, and a variable side chain. When tissue damage from chewing insects occurs, compartmentalisation is disrupted, allowing myrosinase to interact with glucosinolates. It breaks down glucosinolates into a range of active compounds, including isothiocyanates, nitriles, and indole products, which are responsible for biological activity (Manivannan et al. 2021). Glucosinolates are also found in plant phloem sap, where myrosinase is compartmentalised and thus physically separated from glucosinolates, and are taken up intact by aphids. Aliphatic glucosinolates, derived from simple aliphatic amino acids such as methionine or alanine, are excreted in generalist aphid (*M. persicae*) honeydew as intact glucosinolates (Kim et al. 2008). In contrast to aliphatic glucosinolates, indole glucosinolates undergo internal breakdown within the aphid *M. persicae*, and their breakdown products are the primary forms detected in honeydew (Kim et al. 2008). The indole side group is derived from tryptophan. It is a benzene ring fused to a pyrrole ring,

making it an aromatic, nonpolar compound. The resulting metabolites of indole glucosinolates accumulate in honeydew as conjugates with amino acids, particularly cysteine, as well as with glutathione and ascorbate. (Kim et al. 2008).

Specialist aphids of Brassicaceae plants, such as the cabbage aphid (*Brevicoryne brassicae*), sequester glucosinolates selectively for their own defence, as a "mustard oil bomb", against predators, and less is excreted in honeydew (Kos et al. 2012). As generalist *M. percicae* feeding also induces glucosinolate production in the host plant (Kim and Jander 2007), these results suggest that the honeydew of generalist aphids might contain more glucosinolates than specialist honeydew. However, direct evidence is not available. In contrast, winged (alate) *B. brassicae* aphids excreted significantly higher amounts of glucosinolate in the honeydew when compared with wingless aphids, which efficiently sequestered glucosinolates, and the larvae of the two-spot ladybird, *Adalia bipunctata*, were unable to survive when fed adult wingless aphids (Kazana et al. 2007). When *Osmia bicornis* solitary bees were confined to a single honeydew type, consumption of *M. persicae* honeydew was confirmed in 47% of the bees, and of *B. brassicae* honeydew in only 3%. Increased mortality in the latter treatment provided further evidence that specialist *B. brassicae* honeydew is an unsuitable food source for *O. bicornis* (Konrad et al. 2009). Furthermore, Blande et al. (2008) reported a significantly greater parasitoid *Diaeretiella rapae* (McIntosh) attack rate on the specialist aphid *Lipaphis erysimi* (Kaltenbach) than the generalist *Myzus persicae* (Sulzer) and suggested that the specialist aphid honeydew provides an important contact cue that may influence the residence time and attack rate of *D. rapae.*

Honeydew compared to floral and extrafloral nectar

Floral nectar, produced by flower nectaries (specialised glandular structures in plants that secrete nectar), is a major source of carbohydrates for many insects. Additionally, several plant species produce extrafloral nectar in nectaries found on flower buds, sepals, leaves, and stems (Holopainen et al. 2020). The main compositional differences between aphid honeydew and plant nectar are summarised in Table 2.

The main difference between flower nectars and aphid honeydew is in the sugar composition. Floral nectar typically contains sucrose, glucose, and fructose in variable ratios (often sucrose-dominant) (Corbet 2003), while aphid honeydew is characterized by high concentrations of oligosaccharides, particularly melezitose and other trisaccharides, alongside monosaccharides and disaccharides (Wilkinson et al. 1997; Wäckers 2001). Honeydew sugar profiles reflect both phloem composition and aphid digestive processing. Ants, some wasps, and certain bees are often well adapted to metabolize melezitose-rich honeydew and may preferentially exploit honeydew over nectar where available (Völkl et al. 1999; Makkonen 2005).

Specialised nectar-feeding pollinators (e.g. many bees) are generally adapted to sucrose/hexose mixtures at concentrations compatible with efficient ingestion and digestion and prefer nectar over honeydew (Seeburger et al. 2022). However, even highly oligosaccharide-rich nectar of seed-oil camelia (*Camelina oleifera* C. Abel) can reduce palatability and digestibility for honeybee (*Apis mellifera* L.), resulting in colonies exhibiting the decay of small larvae and pupae and bloating of adults. (Li et al. 2022). Furthermore, for bees that rely on flower nectar and pollen for the maintenance of the larval population, a small proportion of essential amino acids in nectar (Gardener and Gillman 2001) can be beneficial. In beekeeping the protein-rich supplemental food is often needed depending on the type of the natural nectar and pollen sources available (Ansaloni et al. 2025). In contrast, ants use the aphid-synthesized trisaccharides, specifically melezitose, as powerful phagostimulants. With lactic acid bacteria in their mouth cavity and enzymes in the gut, ants readily and rapidly cleave complex trisaccharides into simple, readily metabolised glucose and fructose for energy (Zheng et al. 2022). As a protein source for their larvae, ants prey on various insects and from their tended “aphid farms”, ants frequently cull aphids (Ivens et al. 2012; Matsuura et al. 2025).

Food webs supported by honeydew availability

Numerous microbe-animal interactions are closely related to honeydew. Following the formation and dispersal of honeydew from aphids, the sites of its effects include tree surfaces, undergrowth vegetation, soil surface litter and deep soil, as summarised in Fig. 7. The movement of aphids from overwintering in trees to reproducing in lower vegetation during summer will facilitate the honeydew of a single aphid species affecting more than one ecosystem.

Microbiome on honeydew deposited on the phyllosphere

Microbial activity plays a vital role in the aphid digestive tract, transforming plant phloem sap into honeydew. Microbial diversity continues to increase after honeydew is deposited on plant leaves and bark, and eventually in the soil. In both above- and below-ground environments, honeydew will be exposed to several new microorganisms.

Table 2 Comparison of nutritional content of flower nectar and aphid honeydew. Sources: Corbet 2003; Fischer and Shingleton 2001; Fischer et al 2005; Gardener and Gillman 2001; Göttlinger and Lohaus 2022; Pattrick et al.2025; Pleasants 1983; Stevenson et al. 2017; Wäckers 2001; Wilkinson and Douglas 2003

Compound/Property	Flower nectar	Aphid honeydew
Water content	20–80% (highly variable by species, time of day, humidity)	50–90% (generally more dilute)
Total sugars (dry mass basis)	20–80%	50–75%
Sucrose	Dominant in many species; sucrose:hexose ratio varies widely	Present but often in a lower proportion than in source phloem
Glucose & fructose	Abundant; ratio depends on invertase activity	Abundant; elevated relative to sucrose due to gut invertase activity
Oligosaccharides	Minor (e.g., raffinose, maltose)	Significant; melezitose and trehalulose are characteristic products of aphid metabolism
Sugar alcohols	Rare/trace	Present (e.g., sorbitol, mannitol); produced by aphid gut enzymes
Amino acids (free)	0.02–0.5% fresh weight; ~20 + amino acids, often proline-dominated	0.5–2.0% fresh weight; broader amino acid profile, often essential amino acids present
Proteins	Trace to ~ 1% (mainly enzymes, e.g., invertase, oxidase)	Trace to ~ 0.5% (gut-derived enzymes)
Lipids	Trace (< 0.1%)	Trace (< 0.1%)
Organic acids	Citric, malic, succinic acids; minor	More prominent; malic, citric, oxalic; partly from plant phloem and partly from aphid metabolism
Vitamins	Trace amounts (ascorbic acid, B vitamins)	Trace amounts; ascorbic acid documented
Secondary metabolites	Often abundant—alkaloids, phenolics, flavonoids, terpenes, glucosinolates, iridoids (concentration varies ~ 0.01–2% depending on plant species; can be deterrent or attractive to pollinators)	Lower and more variable; predominantly phloem-derived phenolics and glucosides, partly detoxified or modified by aphid metabolism, generally less chemically diverse than nectar
Antimicrobial compounds	Hydrogen peroxide (via glucose oxidase), lysozyme, nectarins (specific nectar proteins with antimicrobial roles)	Lower antimicrobial activity; some plant phenolics retained
Energy value (approx.)	~ 1–4 kcal/mL (~ 3–4 kcal/g dry mass); highly variable with sugar concentration	~ 0.5–2.5 kcal/mL (~ 2.5–3.5 kcal/g dry mass); slightly lower energy density per unit volume due to higher water and lower sugar concentration

For example, in an extensive analysis of the conifer phyllosphere microbiome, communities were predominantly bacterial rather than fungal (Bowers et al. 2025). The microbiome of aphid honeydew on the plant phyllosphere can be divided into three major categories: (1) bacteria, (2) yeasts (single-celled fungi), and (3) filamentous fungi (forming hyphae), each occupying a specific ecological role.

The protein diversity of fresh aphid honeydew reveals that a substantial portion of the microbiota originates from the host aphid, including the endosymbiotic bacterium *Buchnera aphidicola* and the facultative secondary symbiont *Serratia symbiotica*, as well as the gut flora (Sabri et al. 2013). One example is *M. sciuri,* a bacterium found on the pea aphid *A. pisum* honeydew (Leroy et al. 2011). This bacterium degrades the amino acid derivatives of honeydew and releases volatile compounds, such as 3-methyl-2-butenal. This volatile compound attracts predatory Syrphid flies (Diptera: Syrphidae) to oviposit near aphid colonies (Leroy et al. 2011; Glacet et al. 2025).

External sources of bacteria on honeydew can include airborne bacteria and bacteria maintained by the normal plant phyllosphere microbiome. A potential source of various *Lactobacillus* spp. is the aphid-attending ants. Zheng et al. (2022) showed that *Lactobacillus* and *Weissella* spp. are prevalent in the infrabuccal pockets of the oral cavity and in the crops of aphid-tending ants (e.g., *Formica* spp. and *Lasius niger*). These bacteria can metabolize sugars typical of honeydew (sucrose, trehalose, melezitose, raffinose), suggesting they are adapted to honeydew feeding.

Aphid honeydew consumption in the wheat phyllosphere by the naturally occurring saprophytic populations of pink and white yeasts (*Sporobolomyces* spp. and *Cryptococcus* spp., respectively) was observed by Dik et al. (1991). Honeydew production of bark-feeding *Cinara* spp. aphids on branches of Norway spruce (*Picea abies*) and the

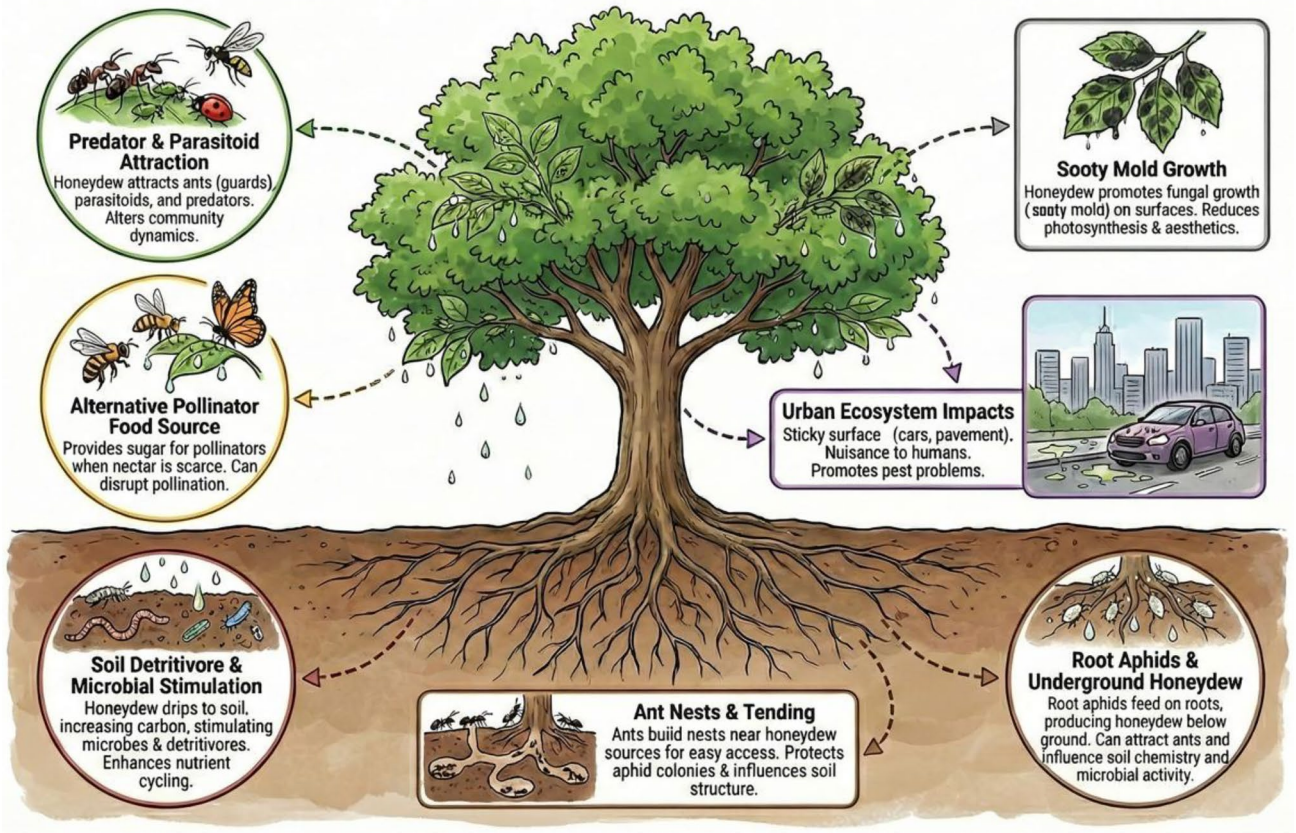


Fig. 7 Summary of biotic interactions and environmental effects related to honeydew of arboreal aphids

development of microbial communities has been monitored in Germany (Stadler and Muller 1996; Stadler et al. 1998). The presence of honeydew significantly increased the growth of bacteria, yeasts, and filamentous fungi on the surface of needles, and there was a pronounced seasonal trend, with the highest abundance in midsummer correlating with the period of peak aphid abundance. In needle samples, bacterial colonies were dominant, but yeasts formed more colonies than filamentous fungi during the peak of honeydew production in early July (Stadler et al. 1998).

Sooty mould is the black mycobiome growing on honeydew on various surfaces and is the most distinctive indicator of aphid infestation and honeydew production. In studies of foliar mycobiomes of deciduous trees in Central Europe (Flessa 2022), dark filamentous fungi genera such as *Cladosporium, Alternaria, Ascochyta,* and *Aureobasidium* were common on trees that were not infected with aphids. However, these dark fungal species were also found to grow on sooty mould of honeydew (Magyar et al. 2023). In addition to this, eight sooty mould-specific fungal species were detected: *Chaetocapnodium placitae*, *Capnodiaceae* sp., *Capnodiales* sp., *Capnodium* sp., C. *rhododendri*, and *Phaeoxyphiella phylicae* (Flessa 2022).

Sooty mould, when growing on the honeydew on green plant leaves, reduces light availability to photosynthetic machinery and can reduce photosynthetic photon flux density (PPFD) by up to 74% in *Citrus sinensis* plants (Insausti et al. 2015). Extra dense sooty mould cover on aphid honeydew on pecan (*Carya illinoinensis* (Wangenh.) K. Koch) leaves was observed to block light penetration to the leaf surface by up to 98%, leading to a 70% suppression of photosynthesis due to a blockage of PAR (Wood et al. 1998). In *C. sinensis,* the measured PPFD was sufficient to saturate the maximum net photosynthesis rate for much of the day. The reason for this was a clear acclimation response by increases in leaf chlorophyll content (Insausti et al. 2015).

Microbe communities associated with honeydew in soil

Soil biological communities, particularly in the plant rhizosphere zone, can be affected mainly by effects of herbivores on plant shoot and root growth, root exudates, and formation of mycorrhizae (Wardle et al. 2004). However, the direct effects of herbivore frass and honeydew on soil biology have been considered. The seminal paper by Owen and Wiegert (1976) presented a provocative hypothesis challenging the

traditional view of herbivory as purely antagonistic. The authors argued that consumers (herbivores) may enhance plant fitness through mutualistic interactions, analogous to flowers for pollinators or fruits for frugivores, by optimising nutrient cycling, removing senescent tissues, and stimulating compensatory growth. They suggested that herbivory could increase plant reproductive success by accelerating microbial activity, leading to nutrient turnover in ecosystems, particularly in nitrogen-limited environments. Their empirical support was drawn from observations in grasslands and aquatic systems, where grazing prevents resource stagnation (nitrogen immobilisation in bacterial and mycoflora) and promotes productivity (Owen and Wiegert 1976). In subsequent testing of the hypothesis, supporting experimental evidence has been gathered only from pot and mesocosm experiments involving chewing insect herbivores and their nitrogen-rich frass (Belovsky and Slade 2000). In forest floor nitrogen mobilisation experiments using ^{15}N-labelled gypsy moth frass, it was found that ^{15}N from frass was mobilised faster than from leaf litter. Still, most of the ^{15}N was incorporated into soil microbes and fauna, with less than 1% found in oak seedlings (Christenson et al. 2002).

Honeydew is a nitrogen-poor excrement, and up to 98% of its dry mass is carbohydrates (Ali et al. 2025). It can be expected that a carbon-rich deposition source exerts selective pressure, favouring copiotrophic microbial species that prefer environments with high concentrations of organic matter over oligotrophic species, thereby shifting the overall community composition of both bacteria and fungi. Indeed, Katayama et al. (2014) found that aphid honeydew deposition decreased inorganic soil nitrogen by 86% and reduced Leguminous plant nitrogen uptake via both direct root absorption and rhizobia-mediated pathways. The honeydew deposition of the Giant willow aphid (*Tuberolachnus salignus*) increased soil microbial biomass, soil respiration, and the total soil carbon (C), but not the total soil nitrogen content in the soil under the aphid-infested willow trees (Tun et al. 2020). Similarly, honeydew deposition significantly increased microbial biomass and respiration in willow (*Salix dasyclados* Wimm.) field plots, and no effects on leaf nitrogen content and tree shoot or root biomass were found (Milcu et al. 2015). Stadler et al. (2001) reported that leachates from needles and leaves of aphid- and moth-larva-infested conifer and deciduous trees contained higher concentrations of dissolved organic C and lower concentrations of NH_4–N and NO_3–N than those from uninfested trees. However, there was little difference between the chemistry of soil solutions collected from the forest floor beneath infested and uninfested trees, suggesting that the effects of above-ground herbivory can be obscured in the soil through buffering biological processes (Stadler et al. 2001).

Decay of organic material in soil has a dynamic effect on bacterial (Fierer et al. 2007) and fungal (Vivelo and Bhatnagar 2019) communities. A pulse of fresh aphid honeydew deposition on soil during an aphid outbreak induces a boost in specific bacterial taxa adapted to exploit readily degradable sugars. Bacillota bacteria (e.g., *Staphylococcus* spp.) and Gammaproteobacteria (e.g., *Erwinia* spp. and *Pseudomonas* spp.) respond rapidly, within 24 h (Glacet et al. 2025) to glucose and fructose inputs, exhibiting enhanced growth and metabolic activity. Additionally, *M. sciuri,* isolated from aphid honeydew (Leroy et al. 2011), is naturally enriched in honeydew and can proliferate upon reaching soil. γ-proteobacteria, such as strains of *Pseudomonas syringae*, rapidly mineralise polysaccharides and labile carbon and nitrogen, thereby increasing microbial activity and biomass in soil (Tun et al. 2020). After the initial bacterial dynamics on the surface layer deposited honeydew (Glacet et al. 2025), fungal growth (including yeasts and sooty moulds) becomes more prominent as honeydew ages beyond 48–72 h In the intermediate stages (5–30 days), fungal involvement increases, with Zygomycota and Ascomycota dominating as bacteria exhaust labile sugars, leading to shifts in community structure (Katayama et al. 2014). Late succession (> 20 days) involves Basidiomycota and specialised bacteria (e.g., Acidobacteria), which stabilise the community, facilitate lignocellulose degradation, and integrate carbon into soil organic matter (Malik et al. 2016).

Soil animals associated with honeydew soil depositions

The shift in the microbial community structure (specifically, the rapid increase in yeast and bacterial populations) provides a new, highly concentrated food source that influences the abundance of microbivorous consumers in soil, including protozoa (flagellates, amoebae), microbivorous nematodes, and invertebrates (mesofauna), such as mites and springtails. This is an alteration in the base of the soil food web, which then cascades up to their predators.

Protozoa play an essential role in releasing plant nutrients from bacteria (Bonkowski 2004). The principal food sources for small arthropod soil fauna are the microbes and protozoa that break down both living and dead plant and animal matter deposited in the soil. Both natural and simulated honeydew increased the activity density of an epigeic Collembola taxon, Bourletiellidae, but not that of the dominant *Hemisotoma thermophila* under *Populus canescens* saplings at a sandy soil site (Seeger and Filser 2008). The honeydew effect varied over time and across sites and was more pronounced at the nutrient-poor site for Collembola but not for microbial biomass. Ant consumption reduced the amount of honeydew reaching the soil surface by 50%.

The activity density of *H. thermophila* was negatively correlated with ants and spiders, suggesting top-down control. Seeger and Filser (2008) concluded that aphid honeydew clearly acts as a bottom-up force for soil organisms, but that this is only part of the complex network connecting the food webs of primary producers and decomposers. Tun et al. (2020) observed that honeydew deposition increased the soil microbial population, which in turn increased the abundance of Collembola and Astigmata mites. The abundance of predatory Gamasida mites was positively correlated with the abundance of their prey, namely Collembola, Astigmata, and Oribatida mites. A plot experiment with simulated honeydew in a field-grown *Salix* spp. plantation (Milcu et al. 2015) gave the opposite result. Although microbial and protozoan populations were increased, populations of Collembola and the mite taxa Prostigmata, Oribatidae, and Gamasida were decreased. However, in typical field soil, earthworms were abundant, and their numbers were significantly increased in the honeydew treatment (Milcu et al. 2015).

Wardle et al. (2010) demonstrated in the New Zealand southern beech (*Nothofagus* spp.) forest that invasive social wasps (*Vespula* spp.) that remove honeydew of native scale insects and prevent it from reaching the ground influence soil animal communities. Simulated normal honeydew deposition with synthetic, high C:N ratio honeydew promoted fungi and fungal feeding fauna (mites and fungivorous nematodes) at the expense of bacteria and bacterial feeders (bacterial-feeding nematodes and some protozoa/microarthropods). Reduced deposition reversed some of these effects (Wardle et al. 2010).

Fig. 8 An example of honeydew depositions on young conifer shoots: **a** the spruce shoot aphid (*Cinara pilicornis*) that is not attended by ants will provide honeydew for other pollinators, **b** the large pine aphid *Cinara pinea* is actively attended by ants, and less honeydew is accumulating on the aphid host plant

Aphid-ant mutualism

The diet of ants consists of proteins and carbohydrates. Proteins are mostly used for reproduction and growth of offspring, whereas carbohydrates are a source of energy for adult ants (e.g., Wilder et al. 2011; Domisch et al. 2016). Ants search for carbohydrates from floral and extrafloral nectars and honeydew. They are not only collecting honeydew; 41% of ant genera include trophobiotic species that exhibit special mutualistic behaviour with aphids and other honeydew-producing insects (Oliver et al. 2008). Likewise, among aphids, 40% of species are tended by ants (Stadler 1997). In this relationship, aphids provide honeydew for ants and ants protect aphids from parasites and other predators (e.g., Stadler and Dixon 2005). Interestingly, ants actively try to keep the aphid population productive through their predation behaviours. They predate a proportion of their tended aphids (Pontin 1958; Sakata 1994; Fischer and Shingleton 2001), most frequently targeting those aphids that fail to deliver honeydew (Matsuura et al. 2025).

The chemical composition of honeydew may have significant effects on the ant species that consume aphid honeydew. For example, the black garden ant (*Lasius niger* L.) does not collect honeydew from aphid species that produce honeydew, which do not contain trisaccharides (Völkl et al. 1999). Even the ratio of monosaccharide sugars may affect the honeydew preference of ants (Renyard et al. 2021). The spruce shoot aphid *Cinara pilicornis* (Hartig) is often mentioned as an aphid species not tended by ants, whereas other *Cinara* species are tended on the same spruce (*Picea abies* Karst.) tree (Völkl et al. 1999). This was also observed in an open-field conifer nursery, where *C. pilicornis* honeydew on spruce seedlings is not consumed by ants (Fig. 8a), unlike the honeydew of *Cinara pinea* (Mordvilko) on *Pinus sylvestris* (Fig. 8b**;** J.K. Holopainen, personal observation). In the forest environment, *C. pilicornis* honeydew accumulations are vital for bees in the collection of forest honey. However, the sugar or amino acid content in *C. pilicornis* honeydew did not differ significantly when compared to other spruce living aphids (Shaaban et al. 2020). Furthermore, in the first report of *C. pilicornis* on *P. abies* in South Korea, *Lasius* sp. were observed visiting aphid colonies of this aphid species (Lee et al. 2025), implying that host plant provenance and ant species community may affect this mutualistic interaction.

It has been hypothesised that, while aphids are harmful to plants, plants may benefit from ant-aphid mutualism through increased predation on other herbivores by aphid-attending ants (Way 1963). The effect of ant–aphid mutualism on tree growth has been shown to be positive in some deciduous tree species but negative in others (Whittaker and Warrington 1985; Sipura 2002). In conifers, aphid tending

by wood ants of the *Formica rufa* group showed some reduction in growth in heavily ant-visited trees (Wellenstein 1980; Rosengren and Sundström 1991; Kilpeläinen et al. 2009); however, the effect on the growth of Norway spruce (*Picea abies*) was suggested to be negligible at the stand and ecosystem level (Kilpeläinen et al. 2009). Trees may be able to partially offset this reduction in growth by accessing a larger supply of soil nutrients near ant nests (Frouz et al. 2008).

Ants can also use aphid honeydew as nest-building material. Ants of subgenera *Dendrolasius* and *Chthonolasius* of genus *Lasius* nourish fungi that reinforce nest walls built from fine wood and soil particles (Seifert 2018). It is suggested that ants protect the cultured fungi from fungal competitors (Schlick-Steiner et al. 2008). Ant attendance is clearly beneficial to aphids of forest trees, and the exclusion of forest ants may lead to a significant increase in the extinction rate of aphid colonies (Yao et al. 2000). Increased predation of more damaging herbivores by aphid-attending ants results in decreased plant damage and improved plant growth and reproduction (Styrsky and Eubanks 2010). However, a meta-analysis of ant-hemipteran mutualism by Zhang et al. (2012), including all honeydew-producing species, concluded that the mutualism had significant protective effects on host plants against other herbivores, although these effects did not lead to enhanced plant growth or reproductive performance.

Pollinators as honeydew consumers

Small egg- and aphid-parasitoid wasps, e.g., from the hymenopteran families Braconidae and Eulophidae, are significant pollinators of small flowers, such as those in the Apiaceae family (Jervis et al. 1993; Patt et al. 1997). They utilise aphid honeydew not only as a critical fuel source for survival and egg production but also as a chemical cue (kairomone) to locate their aphid hosts (Calvo-Agudo et al. 2019; Peñalver-Cruz et al. 2023). Honeybees are well-known collectors of honeydew, particularly in coniferous forests where the number of flowering plants is limited (e.g. Kunkel and Kloft 1977; Crane and Walker 1985; Rybak-Chmielewska et al. 2013). In addition, non-Apiaceae bees such as the solitary bee *Osmia bicornis* have been observed to consume aphid honeydew (Konrad et al. 2009). The honeydew collection of bumblebees has been described as rare (Brian 1957; Wagner and Cameron 1985; Bishop 1994; Cameron et al. 2019). The rarity of this behaviour is thought to be due to the lower sugar concentration of honeydew compared to floral nectar (Cameron et al. 2019). Within their invasive range, wasps of the genus *Vespula* (*V. vulgaris* and *V. germanica*) are known to rely strongly on honeydew produced by scale insects (Thomas et al. 1990; Beggs 2001), but, despite common knowledge, scientific records on aphid honeydew consumption by this genus are lacking.

Aphid honeydew is a critical carbohydrate source for many insects in the orders Diptera (flies) and Lepidoptera (butterflies and moths) (Winkler et al. 2005). While nectar is often the "preferred" food due to its higher quality, honeydew is frequently more abundant in agroecosystems and forests, serving as an essential energy reserve for survival and reproduction. The hoverflies (Diptera: Syrphidae) constitute one of the largest insect families of pollinators. Among hoverflies, species like *Episyrphus balteatus* and *Syrphus ribesii* are well-known honeydew feeders, and honeydew consumption significantly increases the longevity and egg-laying capacity, especially when floral nectar is scarce (Wäckers et al. 2008). Other reported dipterans feeding on aphid honeydew are gall midges (Diptera: Cecidomiydae) (Fratoni et al. 2020), and soldierflies (Diptera: Stratiomyidae) (Beuk 1990). Corke (1999) listed several butterfly species, including *Vanessa atalanta*, *Inachis io*, *Argynnis paphia*, and *Nymphalis polychloros*, that were observed feeding on aphid honeydew.

Aphid predators as honeydew consumers

The majority of nectar and honeydew-feeding insects in their juvenile stages are herbivores or carnivores. Among plant-pollinating social insects, ants, bees, and bumblebees of the family Apidae feed their larvae on sugar-rich nectar (Meurville and LeBoeuf 2021). In ants, additional protein sources include insect parts, and in bees, royal jelly, which contains pollen and microbes (Meurville and LeBoeuf 2021). By contrast, other social wasps, such as those in the genus *Vespula*, prey on aphids as a metabarcoding study of the larval guts showed (Drinkwater et al. 2025). *Vespula* or *Dolichovespula* wasps have been observed collecting aphids from bushes and forming an aphid ball to carry to the nest (J. Sorvari, personal observation). Observations of social wasps collecting honeydew on tree-top aphid colonies in late summer–early autumn likely mean that the wasps are collecting both carbohydrate-rich honeydew and aphids as a protein source. As this is the season when both aphid and social wasp colonies are peaking, this could mean that social wasps may be important predators, reducing tree-infesting aphids. However, scientific studies on this seem to be completely lacking.

Solitary wasps are effective predators of aphids. They are often specialised to predate on specific prey. Among the solitary wasp genera, *Psenulus*, *Pemphredon*, *Diodontus*, *Passaloecus*, *Stigmus* and *Nitela* are known to feed aphids to their larvae (Lomholdt 1984). In addition, some species, such as *Carinostigmus costatus* Krombein, are considered biological control agents for aphids in agroecosystems

(Udayakumar et al. 2024). The aphid midge, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae), is an aphid predator in the gall midge family, in which other members are aphid parasitoids. The adult midges use aphid honeydew as an energy source, but it is also known that honeydew-derived volatiles as kairomones to locate aphid colonies (Choi et al. 2004). Midges lay eggs among aphid colonies, and each emerged larva can kill up to 50 aphids.

One of the largest insect families that pollinate plants is the hoverflies (Diptera: Syrphidae). Hoverflies also consume honeydew as adults (Calvo-Agudo et al. 2019). However, larvae of several hoverfly species are specialised predators of aphids, but they do not directly consume honeydew or survive on a honeydew-only diet (Calvo-Agudo et al. 2019; Urena and Hanson 2010). Hoverfly larvae occur across different ecosystems and exhibit various feeding adaptations. There is a fascinating exception in the genus *Ocyptamus*. Some species in this genus have evolved a unique strategy involving honeydew: larvae have been observed coating their own bodies with honeydew or staying near honeydew deposits to attract adult flies (such as *Drosophila* sp.). Instead of eating the aphids or whiteflies, these larvae "fish" for larger, more mobile insects. When a fly probes the anterior portion of the larva's body, the larva moves its head extremely rapidly to capture the fly (Urena and Hanson 2010).

Table 3 Examples of major aphid parasitoid hymenoptera taxa recorded as honeydew users and their associated hosts

Parasitoid species	Family (subfamily)	Aphid host(s)	References
Aphidius ervi	Braconidae (Aphidiinae)	*Acyrthosiphon pisum*	Du et al. (1997)
Aphidius nigripes	Braconidae (Aphidiinae)	*Macrosiphum euphorbiae*	Bouchard and Cloutier (1984)
Aphelinus mali	Aphelinidae	*Eriosoma lanigerum*	Peñalver-Cruz et al. (2023)
Bathyplectes curculionis	Ichneumonidae	(benefits from *Acyrthosiphon pisum* honeydew Parasitoid of alfalfa weevils	Rand and Lundgren (2019)
Bracon cephi	Braconidae (Braconinae)	*Rhopalosiphum padi*	Rand and Lundgren (2019)
Edovum puttleri	Eulophidae	various potato-infesting aphids	Idoine and Ferro (1988)
Lipolexis scutellaris	Braconidae (Aphidiinae)	*Aphis craccivora*	Singh et al. (2000)
Trichogramma ostriniae	Trichogrammatidae	(*Rhopalosiphum maidis* honeydew used for adult feeding) Egg parasitoid of *Ostrinia* spp. moths	Fuchsberg et al. (2007)

Aphid parasitoids as honeydew consumers

Many parasitoid wasps of aphids are pollinators in the adult stage and normally use flower nectar as their primary energy source, but they may also consume aphid honeydew as a carbohydrate source that may increase their longevity (Rand and Waters 2020). Predominantly, the honeydew volatiles act as kairomones to aphid parasitoids to locate their preferred host aphid species (Peñalver-Cruz et al. 2023). Major representative Hymenoptera wasp species and their aphid hosts, as documented in the peer-reviewed literature, are listed in Table 3.

The family Braconidae (Hymenoptera), and particularly the subfamily Aphidiinae, are the most economically and ecologically significant parasitoids of aphids globally. Members of this subfamily are highly specialised and demonstrate profound behavioural, morphological, and physiological adaptations for honeydew exploitation (Liu et al. 2024b). Luquet et al. (2021) used sugar profile analyses to show that *Aphidius* parasitoids in cereal fields fed predominantly on honeydew, even when nectar-providing intercrops were available. Some large parasitoid wasps in the family Ichneumonidae are known to use aphid honeydew as an energy source, although they parasitise larger insects such as moth and beetle larvae (Rand and Lundgren 2019).

Among dipterans within the gall midge genus *Endaphis* (Diptera: Cecidomyiidae) are six aphid endoparasitoid species (Muratori et al. 2009). Females lay eggs on the plant near an aphid colony. Then, small larvae search for an aphid host, burrow inside, and feed and grow within a living aphid host before eventually killing it. Females use induced plant volatiles as orientation cues, but there is no report on honeydew use, although in laboratory conditions, flower honey availability extends the lifetime of females (Muratori et al. 2009).

Other honeydew-consuming arthropods

Various insect and other arthropod species from different families can opportunistically use aphid honeydew as an energy source. Lady beetles (Coccinellidae) are active predators of aphids. For example, a 4th instar larva of *Coccinella septempunctata* L. can eat nearly 260, and a female beetle nearly 160 *Lipaphis erysimi* Kaltenbach aphids per day (Gurung et al. 2025). Larvae of this species were attracted to aphid honeydew; they were shown to lick the honeydew and preferred the honeydew of one aphid species more than another one (Ide et al. 2007). The presence of

aphid honeydew also enhanced the mobility and foraging behaviour of the Coccinellid *Adalia bipunctata* L. and hoverfly *E. balteatus* (Glacet et al. 2024). The number of aphids consumed was significantly higher in the presence of honeydew of the black bean aphid (*Aphis* fabae Scopoli) and the pea aphid (*A. pisum*). The predators were more attracted to *A. fabae* in the presence of *A. pisum* honeydew, suggesting that *A. fabae* is recognised as a less desirable prey compared to *A. pisum* (Glacet et al. 2024).

The larval stages of soldier beetles (Coleoptera: Cantharidae) are predatory in soil litter, while adult beetles can be found on vegetation and feed on floral nectar and pollen. Adult Cantharid beetles in the genus *Malthodes* often prefer shaded habitats and can be found on the foliage of deciduous trees (Fender 1951). One *Malthodes* sp. individual was found collecting honeydew from a colony of the aphid *Aphis sambuci L.* on the leaf of red-berried elderberry, *Sambucus racemosa* (Fig. 9, personal observation, J.K. Holopainen).

Vertebrates as honeydew consumers

Honeydew is not a primary food source for vertebrates, but many species consume aphid honeydew, and, more often, birds, lizards, and mammals are predators of honeydew-consuming insects. In the island of northern New Zealand, carnivorous Gecko lizards were found to lick honeydew produced by the scale insect (*Coelostomidia zealandica*) from the bark of the native tree species and use it as a source of energy (Towns 2002). Similarly, nectar-feeding bird species were observed to accumulate on trees that were infested with honeydew-producing scale insects (Towns 2002). The author concluded that honeydew may significantly affect the carrying capacity of invertebrates and birds in mainland forests of New Zealand. Furthermore, hummingbirds and other nectar-feeding birds are frequent scale-insect honeydew feeders in southern Brazilian rainforests (de Mattos et al. 2025) and the temperate forests of Mexico (Lara et al. 2011). In Europe, the great spotted woodpecker (*Dendrocopos major* L.) has been reported to exploit galls of the Elm balloon-gall aphid (*Eriosoma lanuginosum* Hart.) by eating both aphids and their honeydew (Londei 2022).

Among mammals, nectar-feeding bats have been suggested to also eat honeydew. Little red flying-foxes (*Pteropus scapulatus*) have been observed to feed on psyllid lerps in New South Wales, Australia (Law and Lean 1992). Lerps are dried honeydew that protect psyllid nymphs. Nymphal instars use anal exudates (honeydew, waxes, amylose) to build a scalloped shelter, under which the psyllid individual completes its development (Makunde et al. 2023). In an analysis of the diet of the marsupial squirrel glider (*Petaurus norfolcensis*), in north-eastern New South Wales, Australia, feeding on arthropods was relatively unimportant in May and June when pollen ingestion was presumed to be high. Honeydew was also used in summer but was absent from the diet during winter (Sharpe and Goldingay 1998). Squirrels use honeydew as an energy source, but they prefer higher sugar content and therefore let extra water evaporate (Heinrich 1992). The European red squirrel (*Sciurus vulgaris* L.) feeds on honeydew from galls of European elm leaf curl aphids (*Eriosoma ulmi* L.) by opening the leaf roll galls and licking (Fig. 10) the spherical dried honeydew droplets together with the fundatrix aphid and the nymphal stages of the alate viviparous females that will soon migrate to the secondary host *Ribes* sp.

Fig. 9 Honeydew collecting pollinators. **a** A soldier beetle (*Malthodes* sp.) (Coleoptera: Cantharidae) collects honeydew from a colony of *Aphis sambuci L.* on the leaf of Red-berried elderberry, *Sambucus racemosa.* L. The insert shows how a beetle handles liquid food with labial palps, **b** A hoverfly (*Syrphus* sp.) collects honeydew from a colony of the woolly beech aphid, *Phyllaphis fagi* L., on the European beech *Fagus sylvatica* L., **c** bumble bees (*Bombus* sp.) collect *Cinara* sp. Aphid honeydew from fir *Abies* sp. branches?

Fig. 10 A European red squirrel (*Sciurus vulgaris*) on Wych elm (*Ulmus glabra*) foliage searches for aphid honeydew from the *Eriosoma ulmi* leaf curl galls. The insert shows the squirrel licking the contents of the open gall

Ecosystem services and disservices related to honeydew

Ecosystem services

All the benefits humans receive from functional ecosystems are called ecosystem services (ES), which can be divided into provisioning, regulating, and cultural services (Locatelli et al. 2017). Originally, the idea of ES was to assign monetary value to biological diversity and to show the real costs of biodiversity loss and the loss of natural functional ecosystems for human societies (Pimentel et al. 1997). This has led to improved ecosystem management aimed at maintaining biological diversity (Prešern et al. 2019; Lyytimäki et al. 2008).

Provisioning services. Honeydew produced by forest tree aphids and collected by bees as honeydew honey (Salonen et al. 2017) is an example of a direct-provisioning ES based on insect honeydew. Honeydew honey, or forest honey, is distinctively dark coloured, which is partly explained by high mineral content (Gonzalez-Miret et al. 2005), spores and hyphae of dark fungi and pollen of nectarless plants (Rybak-Chmielewska et al. 2013; Terrab et al. 2019). Carbohydrate content of honeydew honey has a generally higher content of oligosaccharides, melezitose or erlose, than floral honey (Rybak-Chmielewska et al. 2013; Salonen et al. 2017), and coniferous honeydew honey contains 6.0–10.0% less monosaccharides than floral honey (Rybak-Chmielewska et al. 2013). Furthermore, honeydew honey from conifer forests is significantly separated from blossom honey samples by its high content of phenolics and aldehydes with high antioxidant and antibacterial activity (Salonen et al. 2017; Stanek and Jasicka-Misiak 2018).

In northern Europe, the honeydew honey proportion of sold honey is much lower than in central and southern Europe (Table 4). This is primarily an ecological consequence of climate—cool temperatures suppress the thermophilic hemipteran insects that produce honeydew, shorten the foraging window, and favour rich floral nectar flows instead. This also leads to floral nectar competition in the north, clover in fields and heather in forests are abundant. Summer drought limits the nectar availability from flowers in Mediterranean host-plant/insect systems, and beekeeping traditions are built around more stable honeydew-producing systems, such as giant scale *Marchalina hellenica* on *Pinus halepensis* (Bacandritsos et al. 2006). Also, the type of honey preferred by honey consumers affects beekeeping specialisation: floral honey is preferred in the North, while at higher latitudes production is more honeydew-adapted (Bogdanov et al. 2008).

Table 4 Forest honeydew honey production in major European vegetational zones

Zone	Key hemiptera	Host trees	Honeydew honey share
Boreal	*Cinara* spp., *C. pilicornis, C.pini*, (Aphididae), *Physokermes hemicryphus* (Coccidae)[1]	Norway spruce, Scots pine	<5%, rarely tracked separately[2]
Temperate/Central	*Cinara pectinatae*, *C. piceae*, *C. pilicornis* (Aphidae); *Physokermes hemicryphus* (Coccidae); *Metcalfa pruinosa* (Flatidae)[1, 3]	Silver fir, spruce, oak, lime	~20–60% (varies by country and year; highest in Slovenia)[4]
Mediterranean	*Marchalina hellenica* (Margarodidae)[5]; *Physokermes hellenicus* (Coccidae); *Lachnus*[6], *Cinara* spp. (Aphididae)[7]	Aleppo pine, Calabrian pine, Greek fir, oak	~65–70% in Greece[5]; ~50% Turkey[6]; ~5–15% in Iberia

Key honeydew producers, host trees and the estimated proportion of honeydew honey in the commercially produced honey.

[1)]Shaaban et al. 2020; [2)]Salonen et al. 2017; [3)]Utzeri et al. 2018; [4)]Prezern et al. 2019; [5)]Bacandritsos et al. 2006; [6)]Ünal et al. 2017; [7)]Scheurer 1979

Regulating services. Regulating ES refers to the benefits derived from the regulation of basic ecosystem processes, such as climate regulation and water purification, by functional ecosystems (Locatelli 2017). Regulating ecosystem services of aphid honeydew include enhanced soil microbial activity, increased soil microbial biomass, soil respiration, and the total soil carbon (Tun et al. 2020; Stadler et al. 2001). This will reduce the potential of inorganic nitrogen leaching from forest soil. Regulating ES also includes valuable biological control, e.g., predatory ants that consume honeydew from non-pest insects and prey on several serious forest and

agricultural pest insect species (Thurman et al. 2019), and the maintenance of pollinators in the ecosystem (Bistline-East et al. 2018). In the urban environment, tree leaves and needles help remove harmful dust and aerosols from the air, depositing them onto vegetation and thereby improving air quality (Räsänen et al. 2013). If sticky honeydew deposition on tree leaves improves this capacity, it remains to be studied. Corke (1999) reported that in the protected forest area close to London, the number of honeydew-feeding butterfly species declined more steeply than that of flower nectar feeding species, in the late 1800's when soot deposition peaked. The author suggested that honeydew-feeding butterflies are adversely affected by particulate air pollution.

Ecosystem disservices

Ecosystem disservices (EDS) have been noted in urban areas, where biodiversity is maintained by various parks and forests under high human pressure (Lyytimäki et al. 2008; von Döhren and Haase 2015). EDS may be a direct nuisance to humans, such as sticky honeydew smearing human property (Dreistadt and Dahlsten 1988), reduction of plant growth by aphid feeding, or reduction of photosynthesis in vegetation, e.g., by sooty mould growth on aphid honeydew coating crop plants and understorey vegetation (Lemos Filho and Paiva 2006).

Crop plants or trees treated with systemic insecticides may result in insecticide-contaminated honeydew produced by the phloem-feeding insects. If contaminated honeydew is transported by attending ants or pollinators in their nests, there is a serious risk that key interactions can be disrupted, altering trophic chain function and ultimately contributing to population declines of insects in the food web (Calvo-Agudo et al. 2019, 2022). Consumption of honeydew by aphid predator hoverflies from trees treated with thiamethoxam resulted in 70–100% mortality within three days. More than half of the parasitic wasps died after feeding on honeydew from plants treated with systemic insecticides, either applied to the soil or sprayed on leaves (Calvo-Agudo et al. 2019).

Ants are frequent visitors to flowers, mostly searching for nectar, but also repelling other pollinators. By manipulating aphid densities and honeydew production on cotton plants, LeVan and Holway (2015) demonstrated that increasing cotton aphid (*A. gossypii*) abundance increased ant abundance on cotton plant leaves and floral visitation by ants. This resulted in shorter honeybee visits to flowers and incomplete pollination reduced seed yield (LeVan and Holway 2015).

Aphids feeding on photosynthetic products in the phloem and the aphid honeydew covering leaves may provide disservices that limit plant growth, which means that honeydew is always an indicator of certain types of disservices. Sooty moulds are fungi with dark hyphae that use honeydew carbohydrates for growth (Terrab et al. 2019). Coating on leaf surfaces with dark sooty mould fungi substantially reduces the photosynthetic photon flux density (PPFD) reaching the mesophyll, thereby depressing leaf photosynthesis (Wood et al. 1988; Ali et al. 2025). In sun-acclimated leaves on the outer portions of *Citrus* canopies, the saturation point is already reached at about one-third of full sunlight (Ort et al. 2011). Therefore, photosynthesis is not substantially decreased, and there is no effect on productivity (Insausti et al. 2015). Adaptations to cope with reduced light availability include: (i) the increase in chlorophyll synthesis and content, (ii) improved light-use efficiency at lower light intensities, (iii) shifting their photosynthetic apparatus toward shade-tolerance mechanisms, and (iv) leaf anatomy changes, shade leaves showed a narrow mesophyll to adapt to prolonged light limitation. In cloudy, humid conditions that promote fungal growth, the light-suppression effects of sooty mould on aphid honeydew and on net photosynthesis can be observed (Wood et al. 1988). More details of sooty mould effects are described in the section "Microbial communities on honeydew deposited on the phyllosphere".

Some invasive *Vespula* species use the volatiles emitted by endophytic sooty mould growing on honeydew to find carbohydrate sources (Brown et al. 2015). It is expected that this behaviour, which utilises generic signals, will contribute to the invasive capacity of this species, which is extremely damaging ecologically as a generalist forager (Brown et al. 2015). Ant-protected, bark-feeding large aphid colonies reduced Norway spruce tree growth only in 30-year-old trees and at the stand level, the effect was not detected (Kilpeläinen et al. 2009).

Aphid honeydew in forest management

Honeydew as an ecological resource

Honeydew produced by sap-feeding insects on trees constitutes an important carbohydrate resource that can contribute to energy flows in forest ecosystems. In Germany, the silver fir bark aphid (*Cinara pectinatae*) and the silver fir needle aphid *C. confinis* on Silver fir (*Abies alba*), the spruce shoot aphid (*C. pilicornis*), the mealy spruce aphid (*Cinara costata*) and the large spruce bark aphid (*C. picae*) on Norway spruce, are major aphid honeydew producers that contribute to honeydew flows to the ecosystem (Kloft and Kunkel 1985). Honeydew of *C. piliconis* is collected only by pollinators, and all others also by red wood ants (*Formica rufa* group) (Kloft and Kunkel 1985).

Relevance to forest management and ecosystem services

In forest management, optimising timber production while producing joint products such as berries, mushrooms, and honeydew is a challenging task (Miina et al. 2010; de Miguel et al. 2014; Kurttila et al. 2018; Strengbom et al. 2018). Traditional forest products are variable, and honeydew-based forest honey may have an important role in certain geographical areas for honey producers, such as in Greece, where over 70% of the produced honey is from honeydew honey from scale insects (Coccoidea) on conifer trees (Gounari et al. 2023). Honeydew also links canopy processes to belowground functioning; honeydew flows to ant nests can stimulate soil microbial activity (Jílková and Frouz 2014), and the amount of carbon brought annually into nests from honeydew, prey, and nest-building materials may range widely from 2.7 to 49.3 kg C ha^{-1} across stand ages (Finér et al. 2013).

Historical versus current practices in ant-mediated pest control

During the mid-twentieth century, the transplantation of red wood ant nests (nest mounds or anthills) became a widespread forest management practice in Germany, aimed at biological pest control. This utilitarian approach was championed by myrmecologists and foresters who viewed ants primarily as silvicultural tools. Nest mound transplantation as a forest management strategy is based on Gösswald's (1939) observations that pine and oak stands harbouring dense populations of wood ants that collect aphid honeydew showed markedly lower levels of pest defoliation during outbreak years. Gradually, several studies in the 1940s and 1950s showed that ants preferred aphid honeydew over defoliating insects and were not very efficient predators (Adlung 1966). The traditional technique of mound translocation involved digging up the nest in layers. It is critical to secure the lower layers, which contain the queens and larvae. The material is deposited at the new site in its original order (bottom layers first), maintaining the original north–south orientation (King and Balfour 2020). Traditionally, nests were moved using buckets and shovels. Modern methods often involve specialised machinery, such as tree spades or excavators, which can move the entire nest structure and surrounding soil as a single unit to minimise architectural damage. Nowadays, ant nest mound transplantation is primarily used to protect ant species or to improve restoration efforts (Sorvari et al. 2007, 2014; King and Balfour 2020). The surrounding soil is important for maintaining the microbiome associated with the mound.

Honeydew management in agriculture and horticulture

In agriculture and horticulture, plant growth is maximised by selecting fast-growing cultivars and by efficient fertilisation that also provides aphids with amino acid-rich phloem sap. This leads to rapid growth of harmful aphid populations and honeydew production on the host plant. Bacterial volatiles produced by aphid endosymbionts in the honeydew, e.g. in the honeydew of the pea aphid *Acyrthosiphon pisum*, are significant attractants and ovipositional stimulants for aphid-feeding hoverflies (Leroy et al. 2011). Thus, the honeydew produced by aphids supports natural biocontrol of these pests on crop plants. However, depending on the crop plant species, there are other, more harmful herbivores than aphids. The preference of parasitoid wasps for aphid honeydew as an energy source, even though the aphids are not their hosts (Fuchsberg et al. 2007; Rand and Lundgren 2019), suggests that aphids of weed and companion plants could be valuable for reducing pest insect attacks on the crop plant. The review article by Wade et al. (2008) about the spraying of carbohydrate-rich nectar or honeydew simulating food on crop plants showed that the density of natural enemies increased in 108 of the 124 trials (or 87% of cases) and pest populations declined in 28 of the 59 trials (or 47%), suggesting that an additional carbohydrate source can support natural enemies in the field ecosystem. There is also a risk that herbivorous insects may exploit the provided sugar and exhibit a prolonged lifespan (Winkler et al. 2005).

Banker plant systems in biological control aim to support natural biocontrol by maintaining non-pest aphid species on a reservoir host plant as an early host for aphid parasitoids. These aphids provide honeydew to parasitoids to maintain their egg-laying capacity and energy to fly to oviposit on pest aphids on crop plants early in the season, before pest aphid outbreaks occur. Also, flowering banker plants provide nectar carbohydrates that parasitoids use (Frank 2010). For instance, Fuchsberg et al. (2007) reported that *Trichogramma ostriniae* females provided with maize leaf aphid honeydew lived up to seven times longer and parasitised significantly more European corn borer (*Ostrinia nubilalis* Hbn.) egg masses than wasps given only water. In greenhouse applications, populations of the bird cherry-oat aphid *R. padi*, can be maintained on cereals as banker hosts for the aphid parasitoid *Aphidius colemani,* which is an essential component of biological control programs in several greenhouse crops (Prado et al. 2015).

Conservation biological control (CBC) seeks to enhance the efficacy of naturally occurring (or sometimes released) natural enemies, primarily parasitoids and predators, by supplying resources they require but that are deficient or unevenly distributed in managed agricultural landscapes

(Shields et al 2019). For several decades, research on CBC focused almost exclusively on floral nectar as the primary carbohydrate source for adult parasitoids, whose longevity and fecundity are acutely sensitive to sugar availability. More recently, however, a growing body of evidence has suggested that hemipteran honeydew is arguably the dominant and preferred sugar source for parasitoids in many agroecosystems (Tena et al. 2016; de Bobadilla et al. 2024). In the perspective paper by de Bobadilla et al. (2024), "honeydew management" was formally proposed as an explicit, integrated strategy within CBC, and banker-plant systems harbouring non-pest aphids are identified as one of the most practical implementations of honeydew management. It is clear that more research should be conducted on wild plants to assess which non-pest aphid species provide the most suitable aphid honeydew for the maintenance of each biocontrol organism.

Honeydew in urban and industrial environments

Urban climate and aphid population dynamics

Urban green spaces with trees in parks, yards, streetside, and roadside areas play a crucial role in improving air quality by absorbing carbon, producing oxygen, capturing dust and aerosols (Räsänen et al. 2013), and cooling the urban heat island (UHI) in industrial areas, towns and cities (Li et al. 2024). In large-scale modelling, the average surface temperature in forested and other dense vegetation areas surrounding urban areas was 3.7 °C cooler than the UHI (Kara and Yavuz 2025). The optimal temperature range is typical for all chemical and physiological processes in living organisms. Under optimal conditions, the reproductive rate is highest, but it can vary between early- and late-season aphid species on the same host plant (Dixon and Hopkins 2010). The thermal tolerance range for insect reproduction is approximately 20 °C in most insect orders (Dixon and Hopkins 2010), and thus they tend to respond positively to climate warming (Niu et al 2025; Lehmann et al. 2020). The reproductive capacity of the waxy pine needle aphid, *Schizolachnus pineti* (Fabricius) (Homoptera: Lachnidae), was studied in climate chambers at elevated temperatures under June conditions in central Finland (Holopainen and Kainulainen 2004). With a 2 °C increase within the 20–28 °C daytime local mean temperature range, aphids can increase their reproductive rate by up to 6 °C (at 26 °C) in mean temperature before a rapid decline begins at 28 °C (Holopainen and Kainulainen 2004). These observations suggest that aphids can take advantage of urban heat-island areas, increase their reproductive rates, and produce more honeydew. The main effect of climate warming in temperate regions might be on insect winter survival rather than on aphid reproduction rates during the growing season (Bale et al. 2002).

Aphids are among the most sensitive indicators of plant stress and physiological disturbances (Bale et al. 2002; Leybourne et al. 2021). Air pollutants such as sulphur dioxide (SO_2), nitrogen depositions, and fluorides (Bolsinger and Fluckiger 1987; Warrington 1987; Holopainen et al. 1991) have increased aphid growth and population size, whereas the effects of ozone are more mixed (Bede and Blande 2025). Arboreal aphids and other phloem-feeding and honeydew-producing herbivorous insects reduce the amount of photosynthesis products available for tree growth and defence, which may weaken tree growth, particularly in young trees and saplings (Collins et al. 2001). Furthermore, the shaded understory vegetation beneath the larger trees may suffer from direct honeydew deposition by aphids and the wash-off of honeydew sugars that have earlier accumulated on tree foliage. Stadler et al. (1998) estimated that a significant portion (often over 50% in heavy aphid infestations) of the sugar measured in throughfall of deciduous trees after a dry spell was remobilised from dry honeydew on tree leaves and bark. This delayed deposition can form an additional sugar crust on understory vegetation and other surfaces, further promoting sooty mould growth.

Ecological and aesthetic impacts of honeydew in urban vegetation

Accumulating honeydew under urban trees with a strong aphid population is a nuisance to human activities, leaving sticky, sooty, and ultimately mould-covered honeydew on various urban surfaces, such as buildings, cars, benches, traffic signs, pavements and understory vegetation (Fig. 11). Sugar composition affects the chemical and physical properties of sugary products e.g. when deposited on car windscreen or painted surfaces (Levine and Slade 1988). Fresh aphid honeydew can be washed away by rain as easily as phloem sap or tree flower nectar. Aphid honeydew has higher fructose and glucose content than, e.g. flower nectar, which is mostly sucrose. A significant difference between nectar and honeydew is the presence of the trisaccharide melezitose, which has very low water solubility (hydrophilicity) and very low moisture absorption (hygroscopicity). The high melezitose content in honeydew disrupts honey production, leading to low digestibility by honeybees and rapid crystallisation of honeydew honey (Seeburger et al. 2022).

In drier, sunny weather, when aphids are more active and producing honeydew, the honeydew's high fructose and glucose content can help absorb moisture and maintain

Fig. 11 Honeydew in an urban environment is often produced by **a** Alate viviparous females of the lime aphid (*Eucallipterus tiliae* L.) on the common lime tree (*Tilia x vulgaris*), **b** Alate viviparous females of the silver birch aphid (*Euceraphis betulae* Koch)on silver birch (*Betula pendula* Roth) leaves. *E. tiliae* honeydew with sooty mould on the surface of the parking lot sign (**c** and **d**), and **e** on the building wall, g) dense honeydew cover with sooty mould on the leaf of Norway maple (*Acer platanoides* L.) seedling leaf in the understory of a lime tree, and **f** 24 h accumulation of fresh honeydew droplets on the windscreen of a car parked under a birch tree during *E. betulae* outbreak

stickiness (Robinson and Stokes 2002). A sticky surface easily collects various dust particles, including pollen. As honeydew residue ages under solar UV and heat on car painting, additional components (pollen lipids and cuticular waxes) can reduce wettability, making it more challenging to wash away, as normal detergents are not efficient against oligosaccharides. Fresh honeydew has a pH of around 7.0 and does not harm acrylic melamine-based automotive clearcoat, which is the upper layer of car painting (Schmitz et al. 2000; Yari et al. 2011). Ageing honeydew, particularly when sooty mould is present, causes a pH drop to 4.0–5.0 via fermentation, which increases the risk of acrylic melamine etching on the same level as fresh bird droppings (Schmitz et al. 2000; Yari et al. 2011). Sooty mould growing on honeydew can increase aesthetic nuisance, and incur cleaning costs, and, in the worst case, require repainting or rebuilding structures covered by sooty mould.

To minimise the harmful effects of aphid honeydew in future urban greening, one option is to avoid tree species known to support dense aphid populations, such as large lime trees (*Tilia* sp.), which can host over one million *Eucallipterus tiliae* aphids at one time (Dixon 1971). In the boreal zone, lime and birch trees are used as street trees because of their resistance to air pollutants and their high capacity to collect particulate matter, such as tyre rubber dust (Lukowski et al. 2020). When electric vehicles become more common, air pollution will not limit the selection and planting of suitable street and park tree species.

Impacts of honeydew on food, material and energy production

Aphid species, mostly *Cinara* spp., feeding on *Picea abies*, produce honeydew that causes rapid crystallisation, "cement honey" in beekeeping and processing honey containing honeydew (Seeburger et al. 2022). The main reason for the problem is the high melezitose content of the honeydew in trees suffering drought. As phloem sap osmolality increases, melezitose production by aphids and other hemipteran species is indirectly enhanced (Seeburger et al. 2022).

In wine production and grape processing, the hemipteran honeydew with growth of sooty mould on grapes can increase solids, turbidity, influence must composition and sensory attributes, and in some cases force growers/winemakers to reject or downgrade fruit or adjust processing (extra cleaning, filtration, altered fermentations). Reviews and trials document the negative effects of honeydew/sooty-mould on grape/wine quality. (Yin et al. 2019).

A serious problem in industrial processes caused by honeydew of aphids (Cotton aphid, *A. gossypii*) and whiteflies (Silverleaf whitefly, *Bemisia tabaci*) is the stickiness of oligosaccharides melezitose and trehalose deposited on the surface of cotton fibres (Peralta et al. 2017; Behera et al. 2024). Cotton stickiness disrupts the growing, ginning, and spinning sectors, causing significant problems during carding and throughout spinning and often resulting in financial losses in the industry (Behera et al. 2024). Insect

sugars pose more problems as they accumulate on rollers and saws in rotors, and they quickly accumulate in spinning plants and cotton gins. The term "stickiness" has a technical definition, "the inclination of cotton fibres to stick to textile working surfaces" (Behera et al. 2024).

In solar energy science and technology, the accumulation of any foreign material on a panel's surface is called soiling. It prevents sunlight from reaching the photovoltaic cells, resulting in energy loss. It has been found that the subaerial (SAB) biofilm on solar panels is dominated by melanised microcolonial fungi. Microalgae and cyanobacteria are among the main SAB-forming microorganisms (Martin-Sanchez et al. 2018). The direct involvement of honeydew in the soiling of solar panels has not been studied. Fungal colonisation by dark fungi suggests that in urban areas, where solar panels are installed on house roofs, contamination by aphid honeydew from surrounding trees is possible. Current–voltage curve measurements showed losses of up to 30.7% in microbial-colonised biofilm samples (Olivares et al. 2026), suggesting that all factors that support fungal growth on solar panels should be studied and managed.

Conclusions

Our main hypotheses for this review were that honeydew is (i) a key mediator of multitrophic interactions, (ii) an important energy source influencing microbial communities, plant physiology, and the behaviour and fitness of a wide range of organisms, from mutualistic ants to pathogens, while also acting as (iii) a chemical vector for systemic contaminants such as pesticides acquired from host plants with wide-ranging effects in ecosystems. The scientific literature collected largely supports these hypotheses, but there are still knowledge gaps that should be considered in future research.

The main observations are that the carbohydrate-rich honeydew of aphids and other hemipterans has biological properties across multiple levels of ecosystem function. In urban environments, the same properties may also harm human activities. Aphid honeydew, particularly in conifer forests, plays an important role in maintaining species interactions and stabilising ecosystem function. There is growing evidence that, in sustainable food plant production, improved honeydew management can enhance biological control of crops and substantially reduce the use of certain systemic pesticides. Both neonicotinoid insecticides and climate change are major drivers of global insect declines (Potts et al. 2016). In both cases, hemipteran honeydew is involved when ecosystem function is disturbed. On a local scale, reduced use of the most harmful insecticides is a rapid remedy when alternative biological control methods are available. On a global scale, active climate change mitigation requires controlling the drivers of global climate change.

For a better understanding of the mechanisms by which honeydew mediates direct and indirect interactions in natural, agricultural and urban ecosystems, future research priorities may include:

- Improved chemical and toxicological profiling of honeydew composition. It gives valuable information for ecosystem food web research and honeydew management in order to reduce the harmful effects of pesticides.
- Conduct multi-trophic network mapping to quantify how honeydew links above-ground (ants, wasps, flies, birds) and below-ground (soil microbes, root-feeders, nematodes) food webs, particularly nutrient transfer pathways and cascading effects.
- Research on improved knowledge of honey-producing hemipteran fauna for plants used for honeydew management in agricultural systems, and screening of plants for future urban greening.
- Assessment of the role of honeydew in the formation of subaerial dark biofilms such as sooty mould. Essential information for urban screening when the transition from traditional, rooftop-mounted solar panels to vertical solar coverage (Building-Integrated Photovoltaics or BIPV) on urban building walls is a rapidly advancing strategy for achieving net-zero energy goals in cities

We hope that the current review will help plan and conduct further chemo-ecological studies of this natural sticky ecosystem glue and mitigate its harmful effects, particularly in urban ecosystems.

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Declarations

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