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Plant chemical mediation of ant behavior

Annika S Nelson[1,2], Nalleli Carvajal Acosta[1] and Kailen A Mooney[1,2]

Ants are ecologically dominant members of terrestrial communities. Ant foraging is often strongly associated with plants and depends upon associative learning of chemicals in the environment. As a result, plant chemicals can affect ant behaviors and, in so doing, have strong multi-trophic indirect effects. Plant chemicals mediate ant behaviors in the contexts of floral visitation, seed dispersal and predation, leaf cutting, interactions with ant-mutualist host plants, interactions with mutualist and prey insects in plant canopies, and plant predation of ants by carnivorous plants. Here, we review what is known about these differing contexts in which plant chemicals influence ant behavior, the mechanisms by which ants are affected by plant chemicals, and future directions within these topics.

Addresses
[1] Department of Ecology and Evolutionary Biology, University of California at Irvine, 321 Steinhaus Hall, Irvine, CA 92697, United States
[2] Rocky Mountain Biological Laboratory, PO Box 319, Crested Butte, CO 81224, United States

Corresponding author: Mooney, Kailen A (mooneyk@uci.edu)

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Introduction

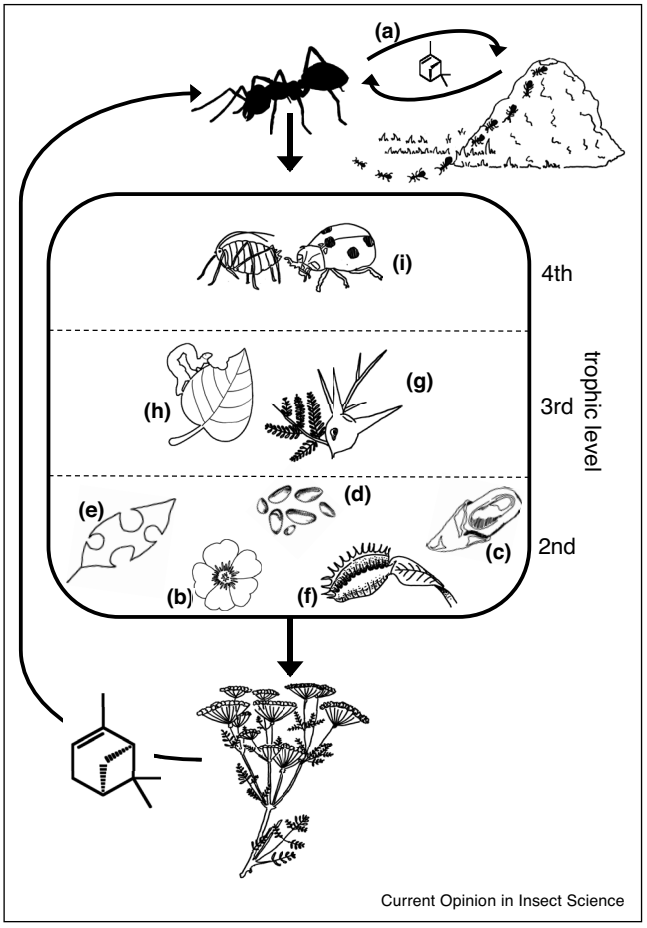
Because ants have large ecological effects in virtually every terrestrial ecosystem, it is important to understand the mechanisms by which ants forage [1]. Ants occupy many different trophic levels and roles within communities, with different species or individuals within species acting as secondary predators, primary predators, herbivores, herbivore mutualists, plant mutualists, and plant prey [2]. Ants rely heavily on chemical cues for foraging [3], and ant foraging is often strongly associated with plants [4]. Accordingly, unraveling the chemical basis of plant mediation of ant foraging is key for understanding interactions between ants, plants, herbivores, and predators from both an ecological and evolutionary perspective [5]. In this review, we assess what is known about associative learning of plant chemicals by ants, discuss how ant responses to plant chemicals may mediate ant–plant interactions in a variety of contexts (Figure 1), and point to a few particularly promising future research directions on this topic.

Mechanisms of ant response to plant chemicals (Figure 1a)

Ant foragers are well known to use pheromone trails for navigation [6,7], and there is also evidence that they use the non-pheromonal (hereafter 'ambient') chemicals in the environment to discover food resources and provide landmarks for complex navigation [3]. Ambient chemicals from plants are associated with all below-ground and above-ground plant tissues, including seeds (Figure 1). These chemicals consist of non-volatile compounds present on tissue surfaces and detected tactilely, as well as airborne volatile compounds (volatile organic compounds [VOCs], including herbivore-induced plant volatiles [HIPVs]). Although adaptive responses by ants to ambient chemicals from plants may be innate in highly specialized interactions [8,9], in most cases associative learning is involved [7]. A number of studies have demonstrated ant associative learning of ambient chemicals, where individual foragers or colonies form positive or negative associations with pure chemical compounds in a laboratory setting [10,11]. Less common are realistic field studies based on plant-derived compounds. Along these lines, Helmy and Jander [12] demonstrated that wild ant colonies exposed to chemical cues while visiting food rewards subsequently recruited to those same cues, demonstrating positive associative learning. At the same time, Saverschek *et al.* [13] demonstrated that leaf-cutting ants avoided the chemical cues associated with plant species that were unsuitable for their fungal gardens, demonstrating aversive associative learning. In our own work, we have demonstrated learning in two ant species (*Tapinoma sessile* and *Formica podzolica*) based upon artificial rewards provided in association with cues (leaf extracts) from two plant species, one hosting a mutualist aphid (*Aphis helianthi* feeding on *Ligusticum porteri*) [14] and the other attracting ants with extrafloral nectar (*Helianthella quinquenervis*) [15].

While associative learning of ambient chemicals by individual ant foragers is a neurological process [3], social learning (i.e. at the level of the ant colony) might occur through two non-mutually exclusive mechanisms. First, individual foragers may learn associatively and then

Figure 1



A schematic representation of the contexts and mechanisms by which plant chemicals influence ant behavior. **(a)** *Mechanisms of ant response to plant chemicals*. Ant responses to plant chemicals may be innate or through associative learning at the level of the individual and the colony. **(b)** *Flower visitation*. Ants may use chemicals to locate floral nectar but are mostly ineffective pollinators, and plants employ multiple chemical mechanisms to deter ants. **(c)** *Seed dispersal*. Ant collection of plant seed provisioned with food rewards (myrmecochory) is facilitated by chemical cues. **(d)** *Seed predation*. Ants prey upon seeds to the detriment of plant fitness, using seed-derived volatiles to locate food. **(e)** *Herbivory by leaf-cutting ants*. Leaf-cutting ants use plant chemicals to identify host plants that are suitable as the nutritional substrate for their fungal colonies. **(f)** *Carnivorous plants* use chemicals to attract ants as prey. **(g)** *Myrmecophytes.* Ants use plant chemical compounds to locate host plants providing nesting space and food rewards and, in return ants provide protection against herbivores, competing plants, and pathogens. **(h)** *Plant cry for help*. Plants emit volatiles in response to herbivore damage that attract predatory ants. (i) *Ants as herbivore mutualists.* Ants engage in protection mutualisms with herbivorous insects, where nutritional rewards are provided to ants in exchange for protection from the herbivore's natural enemies.

recruit additional foragers who may (or may not) also learn associatively. This mechanism almost certainly occurs, based upon what is known about associative learning in individuals and colony-level recruitment behaviors (see above). Second, individual foragers may learn associatively and then transmit this learning to naive nestmates. This later mechanism has been demonstrated to occur via mouth-to-mouth food exchange (trophallaxis) [16,17], where ants preferentially recruit to resources associated with the chemicals that were present in the food received from nestmates. There is also some evidence for associative learning from exposure to chemicals not shared via trophallaxis, with ants preferentially recruiting to compounds likely detected on their nestmates' bodies [18•]. This latter mechanism is especially important as it provides a means for social learning of plant chemical cues that are not ingested, such as the secretions of leaf or stem glandular trichomes. Ultimately, both individual-level and colony-level associative learning likely work synergistically to optimize colony foraging.

Interactions mediated by plant chemistry

Ant behavior is mediated by plant chemistry in a diversity of contexts, including both mutualistic and antagonistic interactions, and such interactions can be organized around the trophic position that the ants occupy (Figure 1). For example, where ants consume plant tissues, they occupy the second trophic level and have detrimental effects on plants. Alternatively, when ants consume herbivores, they occupy the third trophic level and have beneficial effects on plants. Finally, when ants consume predators to the benefit of mutualist herbivores, they occupy the fourth trophic level and again have detrimental effects on plants. Below, we discuss multiple contexts in which plant chemicals mediate ant behavior and the potential outcomes for the plants.

Ants as consumers of plants and plants as consumers of ants (2nd trophic level)

Flower visitation (Figure 1b)

Ants may use volatiles to locate floral nectar, but plants may deter such visits. Ants are by and large ineffective pollinators due to their small size, hairless bodies, and low mobility, and they may deter legitimate pollinators by removing nectar or harassment [19•]. As a result, plants employ multiple mechanisms to distract or deter ants from flowers, including morphological barriers, extrafloral nectar as a decoy, pollen-derived or nectar-derived secondary compounds and VOCs that chemically repel ants [reviewed by Refs. 19•,20], or chemical deterrents secreted by pollinators [21]. A recent study of 49 Costa Rican plant species found that one-third of those species deter ants from flowers, primarily through repellent pollen [22]. In locations such as Hawaii where ants have historically been absent, plants have convergently lost floral defenses against ants [23]. Terpenes such as linalool, as well as some volatiles that are components of ant alarm pheromones (e.g. *E*,*E*-α-farnesene), may be particularly effective chemical deterrents of ants from flowers

[24]. However, studies have failed to find ant repellent 'syndromes' in bouquets of floral scents [23].

In contrast, some plants are specialized for ant pollination, and in such cases, floral volatiles may attract ant species that provide pollination services [25,26]. In one interesting case, the attraction of ants by floral volatiles was shown to enhance plant reproductive output, not because the ants pollinated the plant, but because they deterred ineffective bee pollinator species [27]. As a result, larger, more effective bee pollinators that experienced a lower risk of ant predation were more attracted to ant-harboring plants where competition for resources was lower [27].

Seed dispersal (Figure 1c) and predation (Figure 1d)

A plant's provisioning of seed with food rewards (e.g. arils and elaiosomes) to encourage ant dispersal – so-called myrmecochory – is mediated not only by the nutritional rewards [e.g. 28] but also by seed chemicals. A large body of research suggests that chemical cues are more important for ant-assisted seed dispersal than nutritional rewards. For example, otherwise mutualistic ants can fail to collect seeds cleansed of their chemical cues [29], while ants continue to collect seeds whose elaiosomes had been removed [30•]. Furthermore, seed collection by ants has been shown to be more strongly associated with chemical cues than seed nutritional quality or benefits to colony fitness [31•]. Additionally, it has been proposed that some chemical cues in seeds evolved as a form of insect mimicry [32•]. For example, epiphyte seeds may attract ants by mimicking ant brood [33], and one compound (oleic acid) that induces ants to collect the bodies of deceased nestmates as a hygienic behavior occurs in seeds, where it induces collection [34]. Ants may also prey upon seeds to the detriment of plant fitness. Although there is evidence suggesting that harvester ants use olfactory or chemical cues to locate food sources [35,36], the chemical basis for seed foraging by ants in non-myrmecochorous systems is relatively unstudied.

Herbivory by ants (Figure 1e)

Leaf-cutting ants (belonging to the genera *Atta* and *Acromyrmex*) select plant species based upon their suitability as the nutritional substrate for fungal colonies. Accordingly, ant foragers discriminate among host plants [37•]. In a laboratory assay, Roces [11] showed that ants conditioned with artificial scents associated with their fungal colony in turn oriented toward those same compounds while foraging for plant leaves. Saverschek *et al.* [13] demonstrated that ants learned to avoid plants with naturally occurring fungicidal activity and those experimentally laced with fungicide, and that this conditioning lasted for up to 18 weeks. Similarly, Howard *et al.* [38] demonstrated associative learning, where foragers began cutting leaves and recruiting other foragers more quickly for previously encountered plant species. Recent work from Arenas and Roces [18•] shows that leaf-cutting ants learn to discriminate between scents from high and low quality plants using olfactory cues from the fungus and waste chambers, respectively.

In addition to leaf-cutting ants, ants in co-evolved associations with myrmecophytes may reduce competition between their mutualistic hosts and neighboring plants by pruning or injecting competing plants with formic acid [e.g. in Devil's gardens; 39,40].

Carnivorous plants (Figure 1f)

Carnivorous plants have been found to use volatiles to attract insects, including ants, as prey [41]. These cues can be emitted at high rates and are proposed to mimic other resources attractive to insects, such as fruits or flowers [42]. In a Y-tube olfactometer experiment, ants were attracted to volatiles produced by pitchers of a carnivorous plant [43•]. Specifically, ants were attracted to the nectar-secreting rims of the pitchers, which produced volatile blends mimicking floral scents, including terpenes and fatty acids that are often used in ant recruitment and trail pheromones [43•].

Ants as defenders of plants against herbivores (3rd trophic level)

Myrmecophytes (Figure 1g)

In co-evolved ant–plant associations, plants provide nesting space (i.e. specialized leaf pouches, swollen thorns, or hollow stems termed 'domatia') and food rewards (i.e. food bodies and extrafloral nectar [EFN]) for ants in return for protection against herbivores, competing plants, and pathogens [44,45]. Ant queens use plant-derived chemical compounds to locate the myrmecophytic host plants in which they and their colonies reside. Naive ant queens can distinguish the volatiles of their hosts from those of other sympatric non-host plants, including both other myrmecophytes and non-myrmecophytes, demonstrating this to be an innate behavior [8,9]. Queens may also recognize plants as suitable hosts through surface contact, likely via chemoreception [46]. In addition, ant queens can use plant compounds to distinguish between high and low quality host plants, both within and among species, and choose optimal hosts based upon host plant food rewards, nesting space, and previous damage by herbivores and pathogens [47•,48].

Moreover, chemicals in the food rewards produced by myrmecophytic plants attract and retain ants. For example, upon consuming sucrose-free EFN produced by their *Acacia* host plant, *Pseudomyrmex* ants lose the ability to consume sucrose-containing liquids because chitinase in the EFN inhibits the activity of invertase, which would otherwise break down sucrose in ant midguts. As a result, *Pseudomyrmex* ants depend exclusively on the rewards produced by their *Acacia* host plant [49]. In addition, protease inhibitors present in *Acacia* food bodies have

been found to inhibit the activity of digestive proteins in non-adapted, exploiter ant species [50].

Plant cry for help (Figure 1h)

In a so-called 'cry for help', plants emit volatiles (herbivore-induced plant volatiles; HIPVs) in response to herbivore damage to attract herbivore enemies or parasites [51]. The role of HIPVs in ant recruitment has been studied in various ant–plant systems, with most work focusing on obligate ant–plant systems, in which domatia and food rewards are provided by the plant [52–54]. The strength of ant responses to HIPVs can be correlated with the strength of the ant–plant relationship (e.g. obligate versus facultative); Mayer *et al.* [55] found that resident ants responded more strongly to damaged leaves from ant-obligate versus ant-facultative *Piper* species. Similarly, Schatz *et al.* [56] show that plant-obligate ants responded to damaged leaves of their host plant more strongly than other ant species, while Leal *et al.* [57•] found that only the most aggressive ant species responded to host HIPVs in epiphytic gardens occupied by multiple ant species.

The importance of HIPVs in mediating less specialized interactions among ants and plants has been less studied. In plants producing extrafloral nectar (EFN), these ant-attractive secretions and HIPVs may interact to fine-tune indirect defense from ants [58•], although EFN appears to be a more effective ant-attractant than HIPVs [59,60]. Recent work by Schettino *et al.* [61•] found that some crops (potato and cucumber) emitted different volatile profiles when under attack by caterpillars versus ant-tended aphids, and ants were capable of differentiating between these volatile blends, preferring volatiles emitted by caterpillar-infested plants over those emitted by undamaged or aphid-infested plants.

Ants as herbivore mutualists (4th trophic level) (Figure 1i)

Ants engage in protection mutualisms with herbivorous insects, including hemipterans in several families and lycaenid larvae (Lepidoptera), where nutritional rewards are provided to ants in exchange for protection from the herbivore's natural enemies [62]. These ant-mutualist herbivores are most often dietary specialists, feeding on one or a few closely related host plants [62]. As a result, ants may use host plant cues to locate these mutualists and their rewards, although to our knowledge, no study has documented this dynamic. Interestingly, herbivore protection mutualisms also often occur on myrmecophytic host plants [63]. In addition, other herbivores not engaging in coevolved protection mutualisms may benefit from ant consumption of arthropod predators, with potential cascading effects on plant fitness [64].

Future directions

Many topics outlined above have received substantial attention, although there is nevertheless opportunity for additional studies to explore the generality or context-dependence of these findings. Essentially unstudied are many questions regarding the community ecology of ant responses to plant chemicals, and how this community context affects the evolutionary ecology of focal plant–ant interactions. Questions surrounding plants include: Does ant learning depend on plant community diversity or composition? Are there evolutionary constraints (physiological or ecological costs and trade-offs) on the composition of plant chemicals mediating ant behavior, and how evolutionarily labile are such phenotypes? Questions surrounding ants include the following: In unspecialized systems, do ant species respond similarly to plant volatiles? Does variation in associative learning of plant chemistry represent an axis of variation mediating ant coexistence? Are there certain environments, in which ant behavior is more or less strongly mediated by plant chemistry? And finally, questions surrounding other community members include: How do ant-mutualist herbivores and ant prey evolve and respond ecologically to plant chemical mediation of ant behavior? Because of the ecological dominance of ants, addressing these questions may provide critical insight into the forces structuring higher levels of biological organization.

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Conflict of interest statement

Nothing declared.

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