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RECEIVED 28 February 2023

ACCEPTED 30 March 2023

PUBLISHED 02 May 2023


## CITATION

Smith EJ, Vizueta J, Younger MA, Mullen SP  
and Traniello JFA (2023) Dietary diversity,  
sociality, and the evolution of ant gustation.  
*Front. Ecol. Evol.* 11:1175719.  
doi: 10.3389/fevo.2023.1175719

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# Dietary diversity, sociality, and the evolution of ant gustation

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Ants have remarkably diverse diets and extraordinary species richness, making them an excellent model system to study the evolution of taste. In this entirely eusocial clade, food choice and the mechanisms that regulate feeding have both individual and social dimensions. How taste receptors and sensory processing drive food preferences to generate dietary breadth in ants is poorly understood. It is additionally unclear how elements of colony organization such as division of labor and social food flow impact the mechanistic basis and evolution of taste. Previous work on dipteran, lepidopteran, and hymenopteran gustatory systems, while foundational, provide limited insights into ant dietary specialization. Here we synthesize and analyze research on ant gustation to identify mechanisms, sociobiological correlates, and phylogenetic patterns. We discuss the current state of genomic analyses of taste and future research. We propose that strikingly polymorphic species of *Pheidole*, *Cephalotes*, *Camponotus*, and leafcutter ants (*Atta* and *Acromyrmex*) offer compelling social systems to explore adaptive variation in gustation because of their pronounced division of labor in which morphologically, behaviorally, and neurally differentiated workers vary in feeding behavior. Research on ant gustation within and among species will advance our understanding of sensory systems and provide insight into the impact of taste on the evolution of species diversity and how social organization influences gustation.

## KEYWORDS

diet, foraging ecology, Formicidae, genomics, gustatory receptors, sensory shift, taste perception, worker polymorphism

## Introduction

Sensory systems are interfaces between an animal and its environment, enabling adaptive response to variation in environmental stimuli. Because fitness depends on identifying and extracting nutrient and energy resources for metabolism, chemoreception is an important target of selection required for dietary optimization and fitness. Chemoreception includes olfaction (smell: detect volatile chemicals) and gustation (taste: detect soluble chemicals). Gustation coevolves with diet and nutritional ecology as the mechanistic basis of food preference and a driver of species diversification (Li and Zhang, 2013; Baldwin et al., 2014; Tu et al., 2018; Vizueta et al., 2019; Toda et al., 2021; Frank et al., 2022).

The exceptional dietary diversity of ants makes them excellent models to integrate foraging ecology, taste, nutrition, and sociobiology in phylogenetic context. An estimated 20 quadrillion ants inhabit the Earth (Schultheiss et al., 2022); there are 14,000 identified species in 16 extant subfamilies within the eusocial family Formicidae (Bolton, 2023). Feeding in ants has both individual and colony-level components that involve colony nutrition and growth, caste evolution, and division of labor. Ant foraging ecology has shaped community and ecosystem structure as well as biodiversity (Davidson et al., 2004; Parker and Kronauer, 2021). The evolutionary and ecological importance of ants can be attributed to their sociality and roles as scavengers, predators, herbivores, granivores, and plant mutualists. Gustation is a core determinant of ant feeding ecology.

Despite the importance of taste in ant foraging ecology, gustation is poorly understood. Indeed, in Hölldobler and Wilson's (1990) seminal tome *The Ants*, the terms *diet*, *feeding*, *food*, and *taste* are not indexed. Open questions include: How does gustation vary intra- and interspecifically? How did molecular mechanisms of gustation evolve with changes in diet? How has sociality impacted taste? How has taste influenced species diversity? Here we address these questions and present a prospectus for future research.

## Ant gustation

### Diet preferences

In the well-studied fruit fly *Drosophila melanogaster*, sugars, amino acids (AAs), and water are attractive, whereas deterrent ("bitter") compounds are aversive. Salts and acids are attractive at low concentrations but aversive at high concentrations (Ahn et al., 2017; Jaeger et al., 2018). *D. melanogaster* can also detect water, polyamines, lipopolysaccharides, ammonia, calcium, and H<sub>2</sub>O<sub>2</sub> (Chen and Dahanukar, 2020). Honey bees (*Apis mellifera*) notably lack a bitter receptor or typical behavioral and electrophysiological responses to bitter chemicals, which instead inhibit sugar receptors (de Brito Sanchez et al., 2005, 2014).

Among ants, there are generalist and specialist predators, omnivorous scavengers, and consumers of extrafloral nectar, fungi, fruits, seeds, and honeydew. Army ants are voracious mass-raiding predators that rely on chemical senses (Kronauer, 2020; McKenzie et al., 2021). Specialist predators hunt spider eggs, springtails, centipedes, or termites (Azorsa et al., 2022). Nectarivores tend gardens to obtain extrafloral nectar (Mayer et al., 2014) or consume honeydew excretions of hemipteran mutualists (Cicconardi et al., 2020). Fungus-growing ants mulch their fungal garden with freshly cut leaves (Hölldobler and Wilson, 2010). This remarkably wide dietary variation is likely reflected in gustatory profiles.

Behavioral studies are foundational to understanding gustation, but research that comprehensively compares sugar preferences is limited to 30 species from four subfamilies. Comparisons are constrained by methodological inconsistencies (Ricks and Vinson, 1970; Shetty, 1982; Vander Meer et al., 1995; Cornelius et al., 1996; Cannon, 1998; Völkl et al., 1999; Tinti and Nofre, 2001; Barbani, 2002; Boevé and Wäckers, 2003; Blüthgen and Fiedler, 2004b; Detrain et al., 2010; Horta-Vega et al., 2010; Detrain and Prieur, 2014; Zhou et al., 2015a,b; Madsen et al., 2017; Madsen and

Offenberg, 2020; Jaleel et al., 2021; Renyard et al., 2021). Studies suggest that ants discriminate among sugars and that preference for sucrose, a major component of nectar and honeydew (González-Teuber and Heil, 2009; Shaaban et al., 2020), is conserved. Sucrose attraction increases with concentration (Horta-Vega et al., 2010; Detrain and Prieur, 2014). Species, body size, and sucking pump activity affect sucrose uptake, which is regulated by serotonin (Davidson et al., 2004; Falibene et al., 2009; Josens et al., 2018, 2021). Melezitose (produced exclusively by hemipterans), glucose, fructose, raffinose, and maltose appear to be preferred to other sugars. In comparison, honey bees prefer sucrose, glucose, fructose, maltose, melezitose, and trehalose to other sugars (Von Frisch, 1934). While attractive sugars vary among ant species, preferences also sometimes differ with concentration or methodology (Horta-Vega et al., 2010).

There is limited research on taste in respect to other nutrients. Many ants prefer sugar to AAs and select a combination of sugar and AAs over sugar alone (Lanza, 1991; Blüthgen and Fiedler, 2004b). There is variability in AA preferences among species, as in lepidopterans (Lanza and Krauss, 1984; Blüthgen and Fiedler, 2004b; Agnihotri et al., 2016), but most studies have not comprehensively tested AA preference. Granivores prefer seeds with higher concentrations of AAs and fatty acids (Reifenrath et al., 2012). Leafcutter ants adjust plant substrates for their fungus based on protein-carbohydrate ratio, likely requiring sugar and AA detection (Shik et al., 2021). Electrolyte studies are limited, but *Solenopsis richteri* workers prefer zinc, magnesium, and ammonium, whereas sodium preference varies (Vinson, 1970). Ants exhibit a geographical gradient in sodium consumption correlating with distance from the ocean, and higher sodium consumption in non-predatory than predatory species (Kaspari et al., 2008, 2020). Bitter taste in ants has not been comprehensively evaluated, although quinine is aversive to *Lasius niger* (Wenig et al., 2021), high concentrations of caffeine in sucrose reduced feeding in *Oecophylla smaragdina* (Madsen and Offenberg, 2019), and alkaloids reduced feeding in *Ectatomma ruidum* (Bolton et al., 2017). Leafcutter ants avoid leaves with anti-fungal terpenoids (Howard et al., 1989), but anti-fungal tannins do not affect cutting (Crumièrè et al., 2022). Bitter chemical detection may be especially important for evaluating foods with high levels of toxins.

### Cellular mechanisms

The cellular mechanisms underlying ant taste are unstudied. In insects, soluble chemicals are detected through activation of taste receptors on the dendrites of sensory neurons within gustatory sensilla, small hairs with a single lymph-filled pore (Clyne et al., 2000; Dunipace et al., 2001; Chen and Dahanukar, 2020). Putative gustatory sensilla have been identified on the antennae, mouthparts, and foreleg tarsi (Barsagade et al., 2013, 2017; Jaleel et al., 2021; Masram and Barsagade, 2021), mirroring the distribution in honey bees (Bestea et al., 2021). Gustatory receptor neurons in insects project primarily to the subesophageal zone of the brain in a pattern categorized by taste modality and sensilla location (Wang et al., 2004). Gustatory receptors (GRs)—a large family containing most arthropod taste receptors—detect sugars, AAs, and deterrent compounds. Some ionotropic receptors

(IRs), a family that also functions in olfaction, detect organic acids, fatty acids, AAs, and salts (Benton et al., 2009; Croset et al., 2010; Ganguly et al., 2017; Rimal et al., 2019; Brown et al., 2021). Certain pickpocket channels (PPKs), insect orthologs of the degenerin/epithelial sodium channel (DEG/ENaC) superfamily, and transient receptor potential (TRP) channels are also taste receptors in invertebrates (Chen et al., 2010; Kang et al., 2010). More work is needed to determine broad preference patterns and cellular mechanisms and relate these to dietary variation in ants.

## Taste evolution

### Evolutionary history and genomics

Genomic analysis is needed to elucidate the mechanistic basis and evolution of taste in ants. GRs with gustatory functions likely evolved in the arthropod ancestor from a reduced number of GR-like genes which predated the ancestor of eukaryotes (Robertson, 2019; Benton et al., 2020; Vizueta et al., 2020). The GR family subsequently evolved across arthropods under a dynamic gene birth-and-death model influenced by episodic bursts of gene duplication yielding lineage-specific expansions (Robertson, 2019). Ionotropic receptors (IRs) and pickpocket channels (PPKs) also have ancient origins, but when they were historically co-opted for gustation remains unknown (Croset et al., 2010; Vizueta et al., 2020; Latorre-Estivalis et al., 2021). *Drosophila* have 60 GR, 66 IR, and 31 PPK genes (Croset et al., 2010; Joseph and Carlson, 2015; Latorre-Estivalis et al., 2021), but many have non-gustatory or unknown functions. The honey bee genome contains only 11 GRs, four of which have known functions, as well as yet-uncharacterized IRs and PPKs (Robertson and Wanner, 2006; Bestea et al., 2021).

Ancestral hymenopterans were once thought to have few chemosensory genes (Zhou et al., 2015c; McKenzie et al., 2016), but recent research suggests a parasitoid hymenopteran genome with many odorant receptor (OR) genes (Oeyen et al., 2020; Obiero et al., 2021). The early branching Symphyta (sawflies) similarly have more chemosensory genes than previously thought, including 30 GRs. Gene losses may explain lower numbers in some extant species like honey bees (Oeyen et al., 2020). Compared to ORs, hymenopterans other than ants have few GRs (10 to ~40), excepting lineage-specific expansions in two wasps (Oeyen et al., 2020).

Based on 24 sequenced genomes with annotated GRs, GR number appears variable, ranging from 17 to 219 (Table 1), although these estimations may be inaccurate due to difficulty producing high-quality gene annotations for GRs. There are minimally 13 GR subfamilies in ants, inferred from GR phylogenies of four species (Zhou et al., 2012); their functions are largely unknown. Phylogenetic comparisons with other insects reveal candidate sugar, fructose, and AA receptors in *Linepithema humile*, *Harpegnathos saltator*, and *Solenopsis invicta* (Bestea et al., 2021; Obiero et al., 2021). IR numbers are less variable (18–32 genes) and comparable to most other hymenopterans (Zhou et al., 2012; Obiero et al., 2021; Table 1). Phylogenetic analyzes have also revealed 13 ant subfamilies of “divergent IRs” (Zhou et al., 2012), as well as orthologs of taste implicated IR76b and IR23a from *Drosophila* (Obiero et al., 2021). PPKs (6–8) from four subfamilies have been identified in two ant species

(Latorre-Estivalis et al., 2021), and TRP channels (13–27) from six subfamilies have been identified in seven ant species (Peng et al., 2015), but their functions in gustation are unknown (Table 1). Recent research has elucidated the evolutionary origins of hymenopteran chemosensory receptors, but much remains unknown about their current identities and functions in ants.

### Phylogenetic patterns

Hummingbird umami receptors were co-opted to detect sugars (Baldwin et al., 2014; Toda et al., 2021), vertebrate bitter receptor numbers correlate with the degree of herbivory (Li and Zhang, 2013) and many carnivores lost sugar receptors through pseudogenization (Li et al., 2005; Zhao et al., 2010; Jiang et al., 2012). Dietary change in arthropods is also reflected in receptor evolution, with fewer GRs present in parasites than in generalists (Robertson, 2019). Within the Lepidoptera, divergent evolution resulted in GR expansion, including for lineage-specific receptors that detect bitter compounds (Wanner and Robertson, 2008; Engsontia et al., 2014). Lepidopterans with narrow diets are more sensitive to bitter compounds than species with broader diets (Zhang et al., 2013), suggesting that their dietary specialization is correlated with specific GR expansion (Agnihotri et al., 2016). In contrast, low GR numbers and lack of bitter taste in honey bees are also thought to result from diet specialization (Robertson and Wanner, 2006). Given the similarities and differences in gustatory coding and organization across phyla (Yarmolinsky et al., 2009), interspecific comparisons may reveal broad patterns in the evolution and mechanisms of gustation in ants.

Figure 1 illustrates subfamily variation in ant diets and their hypothesized origins, indicating a predator ancestor. The greatest dietary diversity is found in formicoid ants, which include the species-rich formicines and myrmicines. Correlations between diet diversity and speciation are yet unknown and may be confounded by other ecological factors and life history traits. Subfamily-specific patterns in mouthpart anatomy differ with diet (Paul and Roces, 2019) and receptors may similarly vary. Because ants can discriminate among sugars and have species-specific preferences, they may, like other insects, have multiple GRs tuned to different sugars (Chen and Dahanukar, 2020; Bestea et al., 2021). Receptors share a common insect ancestor, with evolution influenced by episodic bursts of gene duplication yielding lineage-specific expansions (Kent and Robertson, 2009). Variability in AA preferences suggests that AA receptors are similarly lineage-specific, as in other insects (Agnihotri et al., 2016).

Omnivorous generalists may require more receptors to evaluate diverse foods. Many invasive ant species are generalist scavengers that “overeat” imbalanced foods to acquire limiting nutrients (Csata et al., 2020; Shik and Dussutour, 2020). The ability to detect diverse foods by gene duplication or combinatorial pattern may partially underpin the success of these species as invasives. The high number of GRs in the invasive generalists *L. humile* (117), *Monomorium pharaonis* (159), and *S. invicta* (219) supports this hypothesis (Table 1). In contrast, primarily predatory ants may have comparatively few GRs and detect a narrower range of foods. These species do not appear to have the opportunity to sample their food before capture. Trap-jaw ants (e.g., *Odontomachus* sp.) use

TABLE 1 Reported GR number, IR number, TRP channel number, and diet information of species with annotated genomes.

Subfamily	Species	Diet	GRs	IRs	TRPs	References
Ponerinae	<i>Harpegnathos saltator</i>	☐☐☐☐☐☐	17	23	14	1, 4, 7
Dorylinae	<i>Eciton burchellii</i>	☐☐☐☐☐☐	20	23		9
	<i>Ooceraea biroi</i>	☐☐☐☐☐☐	27	26		6
Dolichoderinae	<i>Linepithema humile*</i>	☐☐☐☐☐☐	117	32	14	2, 4, 7
Formicinae	<i>Campanotus floridanus</i>	☐☐☐☐☐☐	63	31	22	1, 4, 7
Myrmicinae	<i>Acromyrmex charruanus</i>	SP	60			12
	<i>A. echinator</i>	☐☐☐☐☐☐	116 / 62		13	7, 8, 11
	<i>A. heyeri</i>	☐☐☐☐☐☐	61			12
	<i>A. insinator</i>	SP	61			12
	<i>Atta cephalotes</i>	☐☐☐☐☐☐	25/89/62	18	13	5, 7, 8, 11
	<i>A. colombica</i>	☐☐☐☐☐☐	62			12
	<i>Cardiocondyla obscurior</i>	☐☐☐☐☐☐?	34			8
	<i>Harpagoxenus sublaevis</i>	SP	52			10
	<i>Leptothorax acervorum</i>	☐☐☐☐☐☐	127			10
	<i>Monomorium pharaonis*</i>	☐☐☐☐☐☐	159			8
	<i>Pogonomyrmex barbatus</i>	☐☐☐☐☐☐	73	24	13	3, 4, 7
	<i>Pseudoatta argentina</i>	SP	27			12
	<i>Solenopsis invicta*</i>	☐☐☐☐☐☐	219		27	7, 8
	<i>Temnothorax americanus</i>	SP	41			10
	<i>T. longispinosus</i>	☐☐☐☐☐☐?	91			10
	<i>T. nylanderi</i>	☐☐☐☐☐☐	128			10
	<i>T. ravouxi</i>	SP	49			10
	<i>T. rugatulus</i>	☐☐☐☐☐☐?	106			10
<i>T. unifasciatus</i>	☐☐☐☐☐☐?	117			10	

Due to difficulties producing high quality gene annotations for GRs, these receptors are likely not comprehensively analyzed and inferences are limited. Diet is coded in accordance with Figure 1. SP Indicates social parasites. \* Indicates invasive species. ? Indicates uncertainty in diet information. / Indicates multiple GR numbers from different studies. Blank cells indicate a lack of published data for that species and receptor type. References: (1) Bonasio et al. (2010), (2) Smith C. D. et al. (2011), (3) Smith C. R. et al. (2011), (4) Zhou et al. (2012), (5) Koch et al. (2013), (6) Oxley et al. (2014), (7) Peng et al. (2015), (8) Zhou et al. (2015c), (9) McKenzie et al. (2016), (10) Jongepier et al. (2021), (11) Schrader et al. (2021).

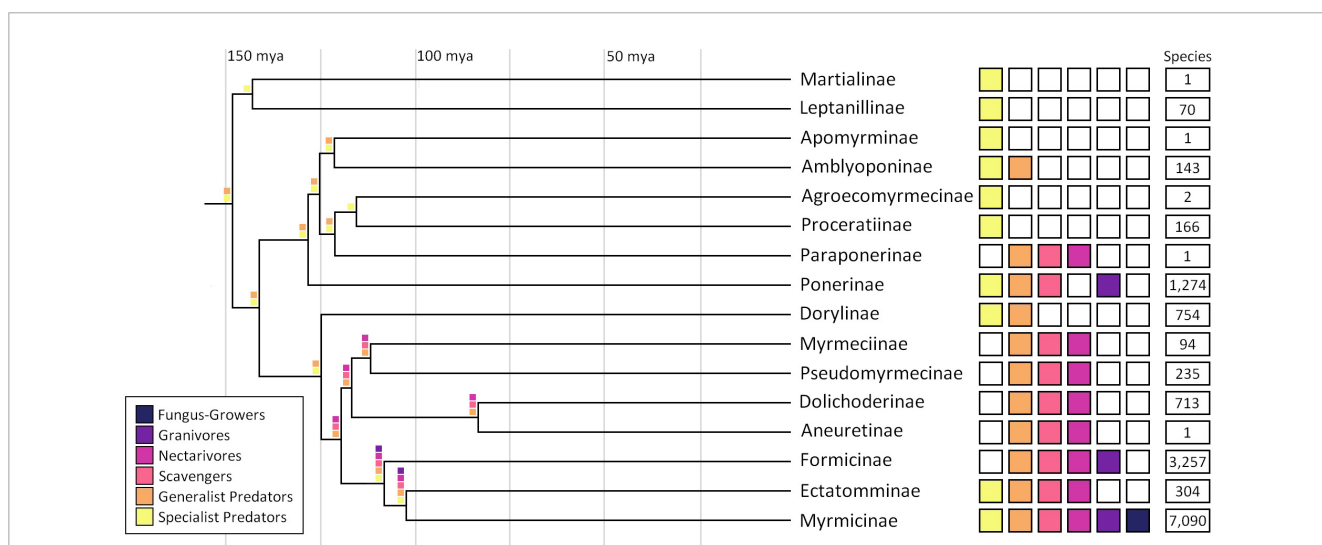


FIGURE 1

Ant phylogeny and dietary breadth. Phylogeny based on Romiguer et al. (2022). Diet descriptions from Jayasuriya and Traniello (1985), Lachaud (1990), Cook and Davidson (2006), Heterick (2009), Lenhart et al. (2013), and Ward (2014). Species richness from Bolton (2023).



“spring-loaded” mandibles that rapidly close on prey in response to activation of mechanosensory hairs (Gronenberg et al., 1993) and may instead rely on olfaction to detect prey repellency (Traniello, 1981; Manubay and Powell, 2020) or vision to identify prey (Azorsa et al., 2022). This hypothesis is supported by the fewer GRs in the generalist predators *Eciton burchellii* (20) and *H. saltator* (17) (Table 1).

Dietary specialists may vary in receptor profiles. Dulotic ants, which rely on workers of their host species obtained in raids to forage and tend brood, have half as many GRs as their hosts (Jongepier et al., 2021). Similar patterns are observed across other social parasites (Schradler et al., 2021). Other species have stronger attraction to macronutrients provided by their plant or hemipteran mutualists (Völkl et al., 1999; Blüthgen and Fiedler, 2004a; González-Teuber and Heil, 2009). Such patterns may be underpinned by positive adaptive selection in receptors that detect mutualist-provided chemicals, or relaxed selection on the remaining genes (Wang et al., 2019). In contrast, fungus-growing ants specialize on their fungal mutualist, but workers adjust foraging based on the nutritional needs of their cultivar (Shik et al., 2021), a complex adaptation likely requiring a wide range of receptors. Annotated genomes also support this hypothesis (Table 1). Further research is required to understand the relationship between diet and GR expression.

## Social dimensions of taste

Foraging ecology and dietary evolution in ants involves social behavior, and colony nutritional state regulates worker response to food (Traniello, 1977; Dussutour and Simpson, 2009; Greenwald et al., 2018). Hunger is communicated through solicitations between workers for regurgitated food, while satiation is regulated by speed of food offloading by returning foragers (Csata and Dussutour, 2019). Foragers deposit trail pheromone to share food quality and location (Czaczkies et al., 2015) and social and environmental cues regulate food acceptance or rejection during foraging (Arenas and Rocas, 2017, 2018; Csata and Dussutour, 2019). Trophallaxis, the sharing of stored liquids by regurgitation, is a social mechanism that informs foraging decisions (Farina et al., 2005; Csata and Dussutour, 2019) and may connect individual- and colony-level nutrition by influencing taste preferences. Gustation may thus transmit information that impacts foraging and nutrition and play a key role in ant social organization.

Because some GRs and PPKs detect pheromones (Montell, 2009; Liu et al., 2020), the number and combinatorial pattern of GRs and PPKs may also correlate with social complexity of colony organization, including queen number, colony size, worker polymorphism, foraging activity, and social communication (Anderson and McShea, 2001; Zhou et al., 2012). Colony size may also correlate with diet, as many large colonies are generalist omnivores or leafcutter ants, whereas many species that form small colonies are predatory (Dornhaus et al., 2012; Romiguier et al., 2022).

Worker size variation and colony demography may also affect the evolution of taste. The genera *Pheidole*, *Cephalotes*, *Camponotus*, *Atta* and *Acromyrmex* are characterized by morphologically distinct (polymorphic) worker subcastes with

task specialization. The diversification of tasks by polymorphic workers may have favored the evolution of gustatory phenotypes that vary between subcastes. Foragers, for example, may require expression of more taste receptors than non-foraging defense-specialized soldiers, which may rely on other sensory modalities (Arganda et al., 2020). This hypothesis is preliminarily supported by differences in sensilla size and number among polymorphic workers (Renthal et al., 2003; Masram and Barsagade, 2021), although there are only two GRs differentially expressed between major and minor workers of *Camponotus floridanus* (Zhou et al., 2012). Subcastes of *Camponotus mus* differ in sucrose feeding threshold, which may promote specialization on different nectar resources (Josens et al., 2018). *C. floridanus* major and minor workers also differ in olfactory sensitivity (Ferguson et al., 2023). Leafcutter ants have worker subcastes that perform leaf-cutting, fungus care, brood care, and defense (Muratore et al., 2022). Remarkable morphological, neural, and behavioral differentiation among subcastes (Arganda et al., 2020; Muratore et al., 2022) suggest that gustatory polyphenisms may support taste-based tasks in leaf selection and fungal condition assessment. Through roles in regulating colony nutrition and informing division of labor, taste likely plays an important role in ant social behavior.

## Discussion

### Future research

To understand the evolution and mechanisms of gustation in ants, we need to assess feeding behavior and preferences, annotate taste receptors to study phylogenetic patterns and their role in speciation, and investigate the role of taste in sociality. Quantifying taste preference is foundational, but research is methodologically inconsistent, phylogenetically narrow, and primarily investigates responsiveness to sugars. Behavioral assays should be complemented by dietary data for species in their natural habitats and encompass basal clades (Leptanillinae, Martialinae), predatory ants (poneroidea), and dietary specialists (granivores, fungus-growers, prey specialists) to reveal patterns of taste evolution.

Transcriptomic data from sensory tissues, whole genome sequencing, and high-quality gene annotations of chemoreceptors across dietary-diverse species are also needed to study gustatory gene evolution, receptor function, and the role of receptors in dietary change and species diversification. The Global Ant Genomics Alliance (GAGA) aims to sequence and compare diverse taxa (Boomsma et al., 2017). Such datasets will provide the basis for annotating ant GRs and studying their evolution and relationship with diet and sociality. GRs are often located in tandem duplication, which makes high-quality gene annotation difficult using common analysis pipelines. GRs thus require specific analyses or manual annotation to acquire high-quality datasets that capture the complete gene family (McKenzie et al., 2016; McKenzie and Kronauer, 2018) necessary to study the evolution of taste in ants.

Phylogenetic analysis of taste receptors could reveal conserved genes, pointing to potential functions of ant receptors through orthologs with known ligands in other species, although functional studies will be required to define their physiological role.

Gene subfamilies that originated in ants can also be identified, as well as patterns associated with evolutionary convergence (e.g., in honeydew specialization). Birth and death rate estimations for gustatory gene families may additionally reveal evolutionary patterns associated with dietary adaptation and speciation. The impact of colony size and worker size frequency distributions on diet in phylogenetic context require further research.

Polymorphic species provide models for elucidating the role of gustation in division of labor. Preference, sensitivity, and receptor expression differences between polymorphic workers may correlate with task specialization. Given their strongly differentiated subcastes and multiple taste-reliant tasks, polymorphic leafcutter ants (*Atta*) can be models to study the coevolution of gustation and division of labor. In *Pheidole pallidula*, differential expression of the *P. pallidula* foraging gene (*ppfor*) regulates behavioral differences between the defensive major and forager minor workers, with *ppfor* activation increasing defensive behaviors in majors and lowering foraging behaviors in majors and minors (Lucas and Sokolowski, 2009). Similarly, in *C. floridanus*, pharmacological reduction of histone deacetylation increased foraging behavior of majors and minors (Simola et al., 2016). Taste likely varies across subcastes and these manipulations could provide inroads to explore the pathways that regulate differences in taste.

Finally, ant gustation may adaptively evolve with dietary shifts in rapidly changing environments. Pavement ants (*Tetramorium sp. E*) colonizing urbanized landscapes have a dietary reliance on processed human foods (Penick et al., 2015). The role of taste receptors in such urban dietary adaptation is not known and may provide opportunities to examine the evolution of gustation over relatively short time scales.

## Conclusion

Gustation has evolved to meet nutritional needs as the mechanism underpinning food choice and dietary optimization. Nutritional decisions require taste perception; evolutionary changes in receptor alleles enable assessment of new food sources, driving selection for adaptive chemoreception. The remarkable dietary and species diversity of ants presents an outstanding opportunity to explore the evolution and mechanisms of gustation in eusocial species that make individual- and colony-level decisions based on taste.

Gustation influences species diversity through its role in dietary niche evolution. Dietary evolution in ants has broader significance

due to their striking ecological and evolutionary impact on the broad range of organisms they consume or with which they have dietary mutualisms, thus significantly affecting biodiversity. Gustation is therefore critical to understanding the impact of ants on ecosystem health.

## Author contributions

ES and JT conceived the review and prepared initial drafts of the manuscript. JV, MY, and SM developed and edited the manuscript. All authors read and approved the submitted version.

## Funding

JT was supported by National Science Foundation grant IOS 1953393. MY was supported by funding from the Searle Scholars Program, the Esther A. and Joseph Klingenstein Fund, and the Simons Foundation.

## Acknowledgments

We thank Zach Coto and Frank Azorsa for their insights on multiple drafts of the manuscript.

## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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