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RESEARCH ARTICLE

Harvester ant microbiome is associated with reproductive role

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Abstract
Host-associated microbes can impact host fitness, and it is therefore important to uncover the drivers of variation among hosts in their associated microbes. In social insects, microbiome composition differs based on both reproductive role and behavioral task. Here, we asked whether reproductive role or behavioral task is more important in determining the diversity and composition of host-associated microbes in the harvester ant *Veromessor andrei*. Specifically, we compared the bacterial communities between workers and reproductives by sequencing the 16 S rRNA gene region. We further compared the bacterial communities between workers that are foragers and those that perform nest maintenance, as well as between reproductives that are male alates and those that are female alates. We found that reproductive role was a better predictor of bacterial communities than behavioral task. Workers and reproductives differed in their bacterial communities. However, different types of workers (foragers and nest maintenance workers) and different types of reproductives (males and females) did not differ from one another in their bacterial communities. Our findings suggest that differences in reproductive roles are a better predictor for differences in microbial communities than behavioral tasks.

Keywords Microbiome · Harvester ants · Behavioral task · Reproductive role · Ant associates

Introduction

The relationship between insects and their associated microbial communities is vital to understand because of their ecological and evolutionary consequences. For example, bacteria found in various sites in a gut facilitate nutrient acquisition in fruit flies (*Bactrocera dorsalis)* (Akami et al. 2019), honey bees (*Apis mellifera)* (Engel et al. 2012; Motta and Moran 2024; Zheng et al. 2016), carpenter ants (*Camponotus floridanus)* (Feldhaar et al. 2007), and herbivorous turtle ants (*Cephalotes spp.)* (Hu et al. 2018). In addition, host-associated microbes assist with pathogen defense in bumble bees (*Bombus terrestris* and *B. impatiens*) (Koch and Schmid-Hempel 2011; Mockler et al. 2018), honey bees (*A. mellifera)* (Engel et al. 2016; B. Jones et al. 2018a, b), social wasps (family *Vespidae*) (Hoggard et al. 2011), and leaf-cutter ants (Genus: *Acromyrmex* and *Atta)* (de Souza et al. 2013; Heine et al. 2018). Thus, host-associated microbes may have important implications for host health and physiology.

In social insects, there is a relationship between social roles and associated microbes. Most social insect colonies are composed of morphologically distinct workers and reproductives, often referred to as 'reproductive castes' but here we choose to use the term 'reproductive roles', which is more culturally sensitive (Breed 2020). Reproductive role has been associated with microbial communities in many social insects. For example, in fungus-farming termites, the gut microbiome of the queen and king is less diverse and differs from that of soldiers and workers (Otani et al. 2019). In honey bees, the gut microbiome composition of queens and males is less diverse than that of workers (foragers and nurses) (Kapheim et al. 2015). In carpenter ants, males harbor distinct microbial communities compared to queens and workers (Koto et al. 2020). Finally, in the ant, *Diacamma. cf. indicum*, worker-specific bacteria are maintained and

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transmitted among workers but are not present in gamergates, which are functional queens (Shimoji et al. 2021). Uncovering differences in microbial composition based on reproductive roles may suggest important mechanistic processes that shape microbial diversity.

The behavioral tasks that workers perform have been linked to differences in host-associated microbial composition and diversity, primarily in honey bees and termites. Adult workers in a social insect colony perform a variety of tasks, including foraging, nest maintenance, and brood care. Workers who perform a certain task tend to interact more with one another due to spatial segregation between tasks (Mersch et al. 2013). Indeed, in honeybees, social interactions can lead to the homogenization of the microbiome (Liberti et al. 2022), and the social environment can determine microbial composition (Vernier et al. 2020). While Jones et al. (2018a, b) found differences in the gut microbiome across honey bee workers that performed different tasks (foragers, nurses, and food processors), Kapheim et al. (2015) did not find such differences between honey bee foragers and nurses. More recent work using shotgun metagenomics (Baud et al. 2023) identified strain-level, but not species-level, differences in the gut bacterial communities of honey bee nurses and foragers. Thus, task-based differences in microbial communities in honey bees may be quite nuanced. Furthermore, soldiers and workers differ in gut microbiota in fungus-farming termites (Otani et al. 2019). Because there are morphological differences between soldiers and workers, the observed microbial differences might be attributed to morphological and/or behavioral differences. Indeed, the morphological structure of an ant's gut can shape its microbiome composition (Flynn et al. 2021). Lab manipulations in which the microbiome is experimentally manipulated have shown a causal link between microbial communities and behaviors, such as mating preferences in fruit flies (*Drosophila melanogaster)* (Sharon et al. 2010; Venu et al. 2014), food preference in mosquitoes (Verhulst et al. 2011), kin recognition in hyenas (Rojas et al. 2020; Theis et al. 2012, 2013), and other microbe-mediated behavioral changes via the host's neuroendocrine system in mice (Bravo et al. 2011). In social insects, such experimental manipulations of the microbiome have shown impacts on nestmate recognition in honeybees (Vernier et al. 2020). In leaf-cutter ants (Teseo et al. 2019) and harvester ants (*Pogonomyrmex barbatus)* (Dosmann et al. 2016) manipulating the microbiome has been shown to impact both nestmate recognition and aggressive behavior. These experimental manipulations demonstrate a relationship between behavior and the microbiome in various systems, including ants. Thus, while much is known about how tasks and reproductive roles impact the microbiomes of honey bees (Nguyen et al. 2024) and termites (Sinotte et al. 2020), it is surprising that there is little work on the differences in microbial communities among behavioral tasks in ants (Liberti et al. 2024). This knowledge gap is especially surprising because there has been extensive behavioral work on the causes and consequences of task allocation in many ant species. Uncovering a relationship between host-associated microbes and behavioral tasks in ants could reveal new insights on how and why workers are allocated to various tasks.

Here, we investigate whether there is a relationship between social roles and host-associated microbes in the harvester ant *Veromessor andrei.* These ants are monogynous (one queen per colony), with monomorphic workers (similar sizes), and colonies can reach sizes of tens of thousands of individuals (Brown 1999). Specifically, we examined the bacterial communities of the microbiome across individuals that perform different behavioral tasks (foraging and nest maintenance) and individuals that belong to different morphologically determined reproductive roles (female and male alates vs. non-reproducing workers). Specifically, we tested two non-mutually exclusive hypotheses that: (1) behavioral task (foraging or nest maintenance for workers and males or females for alates) relate to the composition and diversity bacterial communities, because individuals that perform similar tasks interact more often with one another and potentially share more microbes with one another than with individuals that perform other tasks; and (2) reproductive roles relate to the composition and diversity of the bacterial communities, potentially due to physiological differences between reproductive (female and male alates) and non-reproducing workers (foragers and nest maintenance workers). If behavioral task relates to microbial communities, we predicted that bacterial communities extracted from workers of *V. andrei* would be more similar among workers that perform similar behavioral tasks (e.g., foragers) and reproductives that have similar behavioral roles (e.g., males), than among ants that perform different behaviors (i.e., foragers, nest maintenance workers, males, and females would each have distinct associated bacterial communities). If reproductive role (female and male alates vs. non-reproducing workers) relates to microbial communities, we predicted that *V. andrei* reproductives (female and male winged alates) would have different associated bacterial communities compared to those of non-reproducing workers (foragers and nest maintenance workers).

Materials and methods

Study site and sample collection

To investigate the relationship between bacterial community composition, behavioral tasks, and reproductive role,

we collected samples of foragers, nest maintenance workers, and reproductives (winged female and male alates) from eight *V. andrei* colonies in June 2023 (Fig. 1). Ants were collected from colonies in a serpentine grassland at the Sedgwick Natural Reserve in southern California. We used gloves and soft tweezers, sterilized with 90% ethanol, to collect all samples. Foragers were identified as individuals traveling on foraging trails with seeds in their mandibles (Fig. 1b). All foragers were collected from the foraging trail at least 1 m from the nest entrance. Nest maintenance workers were identified as individuals emerging from the nest entrance with dirt in their mandibles (Fig. 1c). Reproductives (female and male alates) were identified by their distinct winged morphology and collected as they emerged from the nest entrance (Fig. 1d). Female and male alates were distinguished by head size, with males having noticeably smaller heads than females. We collected at least 3–5 ants of each type from each colony. All collected ants were placed in a freezer at the field station and later transported in a cooler to the UCLA campus (approximately 2 h away). All samples were stored at -20°C until processing.

Sample processing

Sample preparation for DNA extraction: We washed all samples (ants) with 70% ethanol, 5% bleach, and sterile deionized water. Each washed sample was placed in a sterile 1.5 ml tube and crushed using a sterile pestle (Fisher Scientific). We followed the Qiagen DNEasy PowerSoil Pro kit protocol and added 800 µL of Solution CD1 (containing SDS for cell lysis) to the samples, then vortexed them. We incubated the samples overnight at 56°C in a shaking incubator to maximize cell lysis.

DNA extractions: After 24 h in the incubator, we extracted microbial DNA using the Qiagen DNeasy PowerSoil Pro kit, following the manufacturer's instructions. We sent 34 samples for 16 S rRNA gene amplification and library sequencing at the UCLA Microbiome Center. These samples included eight forager samples (each consisting of five foragers crushed together), eight nest maintenance worker samples (each consisting of three workers crushed together), seven male alates sample (each consisting of three males crushed together), eight female alate sample (each consisting of three female alates crushed together), and three control blank samples of 250 µl sterile distilled water, with no other material. Refer to the data in the GitHub repository: https://github.com/DAlejandraG/BT-microbes. Amplicon sequencing of the bacterial community targeted the V4 region of the 16 S rRNA gene using primers 515 F (59-GTGCCAGCMGCCGCGGTAA-39) and 806R (59-GGACTACHVGGGTWTCTAAT-39, following the Earth Microbiome Project (EMP) protocol (Caporaso et al. 2011; Jacobs et al. 2021).

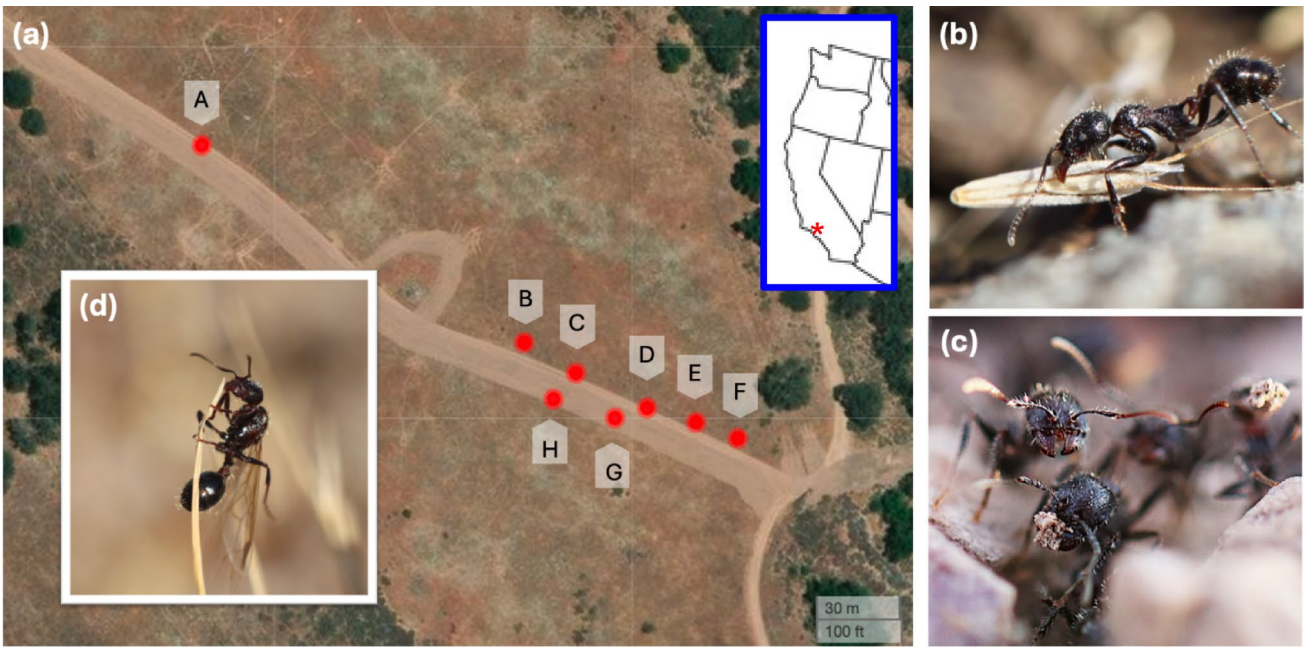

Fig. 1 Sample collection. **a** Map of the study site with the location of eight *V. andrei* colonies indicated with red dots and a corresponding letter ID for each colony. The inset shows the location of the field site on a map of the western United States, marked by a red asterisk. We collected at least **b** five foragers, **c** three nest maintenance workers, **d** three female, and three male alates (males not shown) from the nest mound and entrance each of the eight colonies. All photo credits: Noa Pinter-Wollman

Quantifying bacterial community diversity

To determine the bacterial community composition and diversity associated with each behavioral task (foraging and nest maintenance workers and male and female alates) and reproductive role (workers vs. winged alates), we processed the sequencing data using QIIME2 version 24.5 (Bolyen et al. 2019). We followed the demultiplexing and quality filtering steps described by Gamboa et al. (2025). The 16S rRNA gene amplicon sequencing raw reads are available from NCBI via BioProject record [PRJNA1311736]. The raw dataset contained a total of 1,692,186 reads. To visualize bacterial taxonomic composition with relative abundance plots at the phylum and order levels, we exported the feature table and analyzed the data using the 'phyloseq' package in R (McMurdie and Holmes 2013). Following quality control, we assessed alpha diversity using the 'iNEXT' (v3.0.2) package in R, based on ASVs (Hsieh et al. 2016). All three control blank samples were removed from further analysis of alpha and beta diversity due to low read numbers. We show the blank control samples in Fig. 3. The remainder of the analysis and figures include the 31 samples from the workers and reproductives, but exclude blank controls.

To determine how behavioral tasks and reproductive roles influence host-associated bacterial communities, we examined the beta (between samples) and alpha (within samples) diversity of ASVs. Beta diversity reflects differences in bacterial community composition across multiple samples, grouping them based on similarities in sequence abundances or the presence and absence of sequences (Borcard et al. 2018). Alpha diversity describes the distribution of microbes within a sample. To compare the microbial diversity of workers and reproductives, we quantified microbiome diversity with Hill numbers (q = 0, 1, 2) using the iNEXT framework. This method standardizes for differences in sequencing depth across samples through rarefaction (interpolation) and extrapolation and allows for statistical comparison (Chao et al. 2014). We calculated three distinct measures: *taxonomic richness* (q = 0): represents the total number of unique taxa defined as amplicon sequence variants (ASVs). *Shannon diversity* (q = 1): a measure that accounts for both species abundance and richness (Kim et al. 2011; Lemos et al. 2011). *Simpson diversity* (q = 2): assesses the dominance of abundant species in a sample, with higher values indicating lower diversity (Kim et al. 2017).

Statistical analysis

Beta diversity: To determine if beta diversity differed among behavioral tasks and reproductive roles, we applied a permutational multivariate analysis of variance (PERMANOVA) to a Bray-Curtis dissimilarity matrix, which assesses compositional dissimilarity among bacterial communities (Bray and Curtis 1957). The beta diversity analysis was conducted on rarefied data at a sampling depth of 4,853. Principal Coordinate Analysis (PCoA) ordination was generated from this matrix using the Adonis function in the Vegan package (Oksanen et al. 2001), with 999 permutations for the PERMANOVA. To assess differences in the amount of dispersion, we conducted a permutational analysis of multivariate dispersions (PERMDISP) by applying the betadisperser() and permutest() functions in the package 'Vegan' (Oksanen et al. 2001). PCoA plots were visualized with the 'ggplot2' R package (Wickham 2016).

Alpha diversity: To determine if alpha diversity differed among behavioral tasks and reproductive roles, we generated Rarefaction (interpolation) and extrapolation curves to compare taxonomic richness (q = 0), Shannon diversity (q = 1), and Simpson diversity (q = 2) across groups using the R package 'iNEXT' (v3.0.2) (Hsieh et al. 2016). Confidence intervals (95%) were calculated using 200 bootstrap replicates. Statistical comparisons were conducted on the 95% confidence intervals of the Hill numbers. Significant differences were inferred if the 95% confidence intervals did not overlap (Chao et al. 2014).

Data and analysis code are available on GitHub (https://github.com/DAlejandraG/BT-microbes).

Results

We found significant differences in microbial composition and diversity between reproductives (males and female alates) and workers (foragers and nest maintenance), but we did not detect statistically significant differences within each of these groups. Forager and nest maintenance workers did not differ in their microbial composition, and neither did male and female alates. Bray-Curtis distances, visualized by a principal coordinate analysis (PCoA), demonstrated that samples clustered by reproductive role (workers vs. reproductives) (Fig. 2). Whether samples came from foragers, nest maintenance workers, female alates, or male alates explained approximately 28% of the total variation (PERMANOVA: $F_{DF=3} = 3.50$, $R^2 = 0.280$, p-value = 0.001), this variation was not due to differences in dispersion (PERMDISP: $F_{DF=3} = 2.83$, mean sq = 0.092, p-value = 0.066). Beta diversity was significantly different between workers (foragers and nest maintenance) and reproductives (female and male alates) (PERMANOVA: $F_{DF=1} = 2.76$, $R^2 = 0.252$, p-value = 0.001) (Fig. 2; Table 1). However, within each reproductive role, we did not detect a statistically significant difference - foragers were not significantly different from

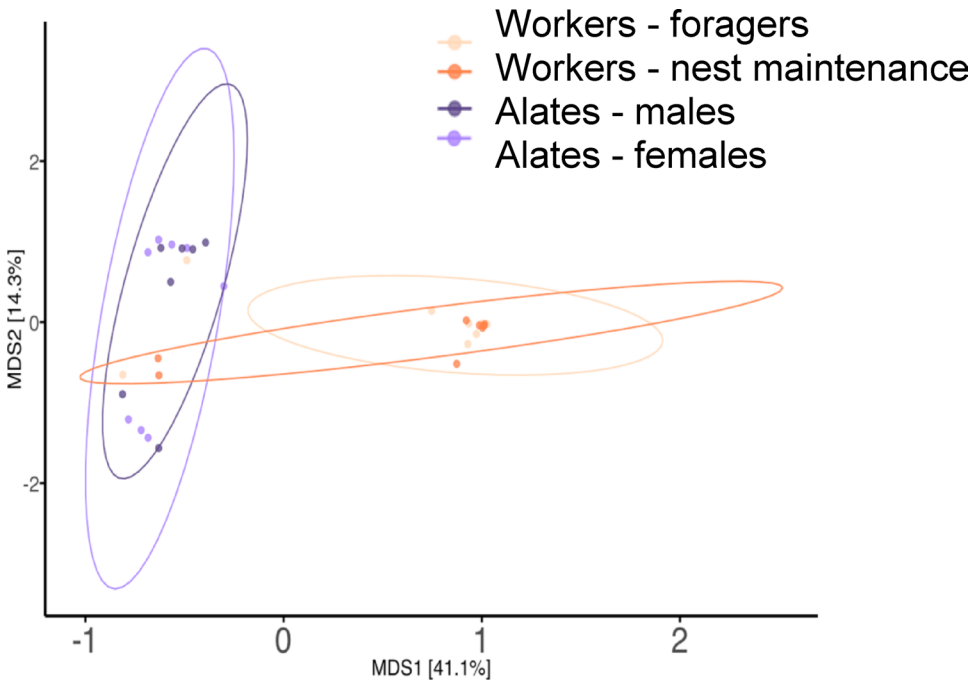

Fig. 2 Beta diversity principal coordinate analysis (PCoA) from a Bray-Curtis dissimilarity matrix. Each point represents a single sample, and the closeness of the points indicates high similarity between bacterial communities. Workers are represented in light orange for foragers and dark orange for nest maintenance. Alates are in purple - dark for males and light for females

Table 1 Pairwise PERMANOVA results comparing beta-diversity using Bray-Curtis distances between forager (FOR) and nest maintenance (NM) workers and female (FA) and male (MA) alates

Pairs	DF	Sum of Squares	F Model	R2	*P* value	*P* adjusted
FOR vs. NM	1	0.12	0.53	0.036	0.609	1
FOR vs. FA	**1**	**1.45**	**5.03**	**0.264**	**0.006**	**0.036**
FOR vs. MA	**1**	**1.33**	**4.44**	**0.255**	**0.008**	**0.048**
NM vs. FA	**1**	**1.60**	**5.57**	**0.285**	**0.007**	**0.042**
NM vs. MA	**1**	**1.45**	**4.90**	**0.274**	**0.005**	**0.030**
FA vs. MA	1	0.20	0.53	0.039	0.886	1

Significant differences are in bold

nest maintenance workers, and male alates were not significantly different from female alates (Table 1).

The relative abundance of bacterial ASVs differed between workers and alates, but not within each reproductive role, especially at the level of 'order' but less at the level of the 'phylum' (Fig. 3). When examining the alpha diversity of ASVs we found statistically significant differences between all four groups - none of the confidence intervals of the Hill number estimates overlapped (Fig. 4; Table 2). However, the effect size of the difference was very small within each reproductive category – the difference in alpha diversity between male and female alates and the difference between foragers and nest maintenance workers, were much smaller than the difference between reproductive and workers. Specifically, for Shannon diversity, the difference between foragers and nest maintenance workers was 0.191 (Hill numbers) and between male and female alates the difference was 0.55. The difference between female alates and forager workers was 8.78 and between male alates and nest maintenances workers we found the largest difference of 9.53 (Fig. 4; Table 2). Thus, the difference in Shannon diversity between worker tasks is approximately 2% of the difference in Shannon diversity between workers and reproductives. Similarly, for Simpson's diversity, the difference between foragers and nest maintenance workers was 0.0894 (Hill numbers) and between male and female alates the difference was 0.4978. The difference between female alates and forager workers was 3.088 and the difference between male alates and nest maintenance workers was the largest, at 3.6755 (Fig. 4; Table 2). Thus, the difference in Simpson's diversity between worker tasks is approximately 2.5-3% of the difference in Simpson's diversity between workers and reproductives. Finally, ASV richness showed a slightly more elaborate pattern. The largest difference was seen between foragers and female alates (which are repoductives and workers), however, the difference between male alates and nest maintenance workers was quite small (Fig. 4; Table 2), showing a slightly different pattern from the other two alpha diversity measures.

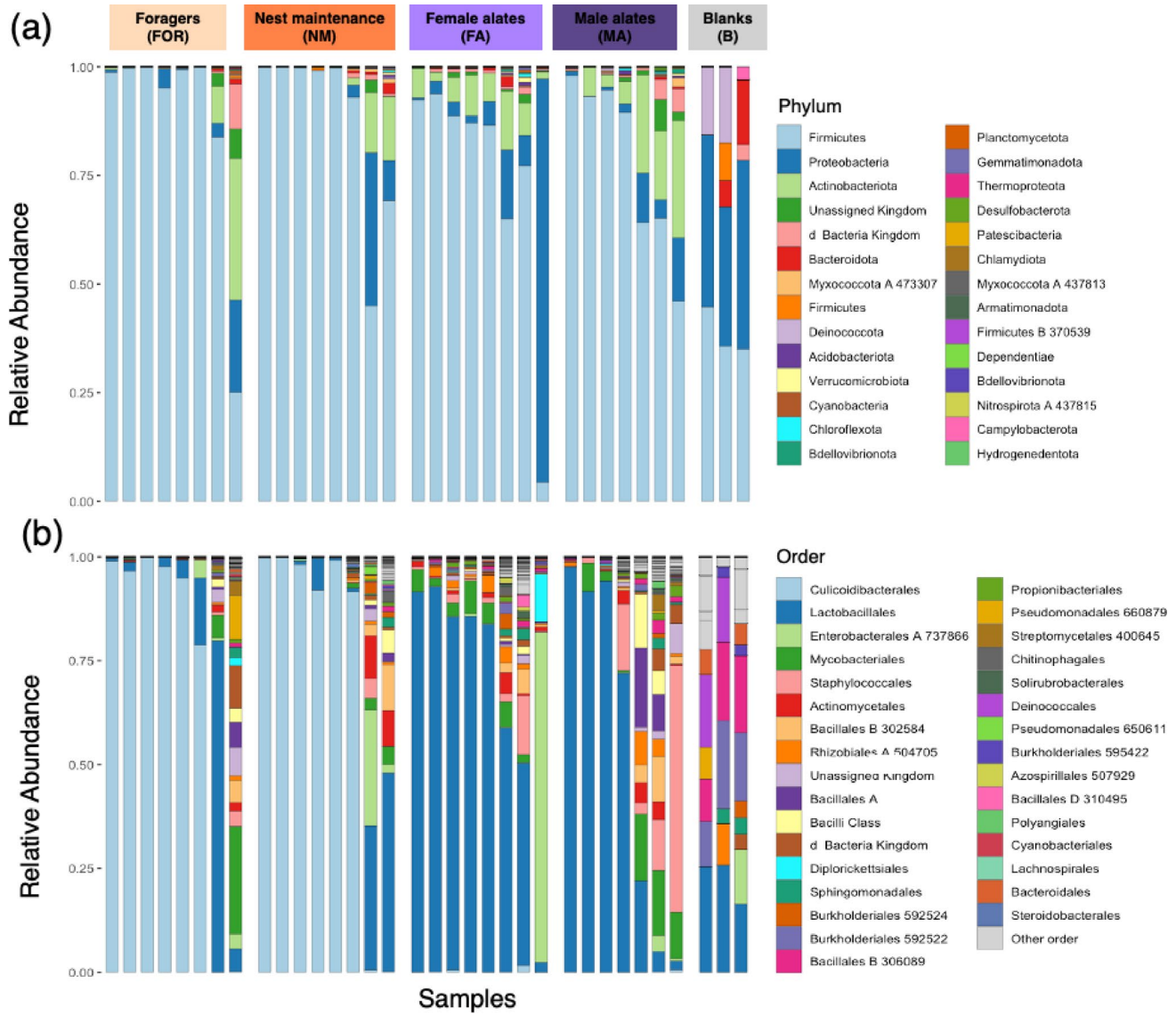

Fig. 3 Relative abundance of bacterial taxa at the phylum (**a**) and order (**b**) levels. Samples are grouped by social role: forager workers (FOR), nest maintenance workers (NM), female alates (FA), and male alates (MA). The blank control samples are shown in the last three bars, but are not included in the analysis of alpha and beta diversity. Each vertical bar represents one sample from a single colony, with color indicating the bacterial phylum or order based on ASV counts. The sampling depth was 4853 reads

Discussion

We found that reproductive role was a more important predictor of variation in host-associated microbes in *V. andrei* harvester ants than behavioral task (Fig. 2). Workers and reproductives differed in the composition and diversity of their host-associated bacterial communities (Figs. 3 and 4; Table 2). However, we did not find significant differences in beta diversity between forager and nest maintenance workers, nor did we detect a difference in beta diversity between male and female alates in their microbial communities (Table 1).

The bacterial phyla we found are similar to those identified in other ant species. Specifically, the *Firmicutes* bacterial phylum had the highest abundance in workers, while reproductives exhibited a more balanced distribution of *Firmicutes*, *Proteobacteria*, *and Actinobacteria* (Fig. 3). Similar bacterial phyla were found to differ between workers and reproductives in the ant *D. cf. indicum* (Shimoji et al. 2021) and in our previous research on *V. andrei* (Gamboa et al. 2025). *Firmicutes*, *Proteobacteria*, and *Actinobacteria* are typical bacterial phyla in herbivorous and omnivorous ant species (Russell et al. 2009; Anderson et al. 2012). Interestingly, the *Firmicutes* bacterial phylum is frequently observed in predatory ant species such as army ants (*Eciton*)

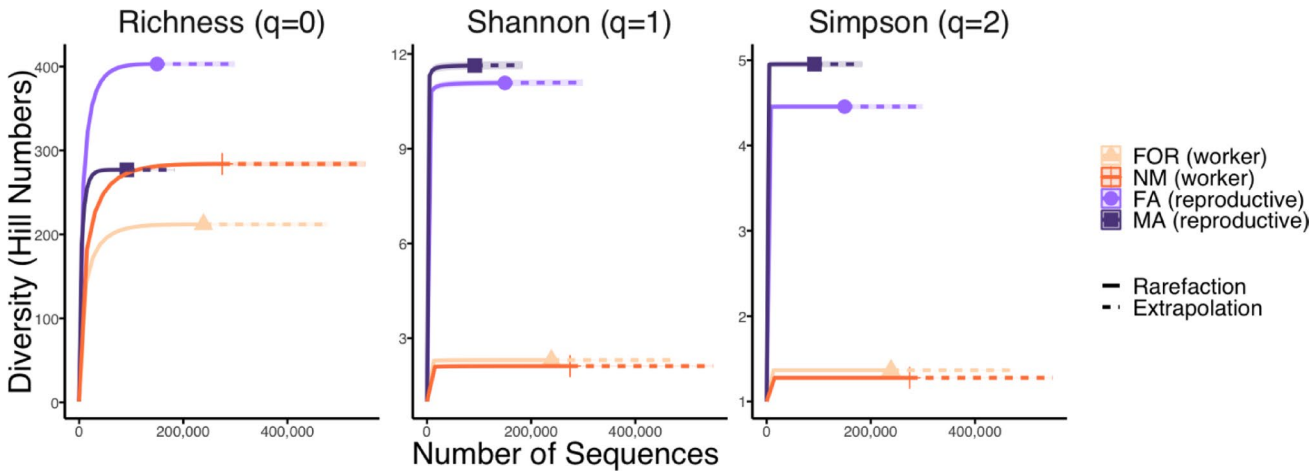

Fig. 4 Rarefaction and extrapolation curves of microbial alpha diversity across foragers (FOR), nest maintenance (NM) workers, female (FA), and male (MA) alates. Workers are represented in light orange for foragers and dark orange for nest maintenance. Reproductives are represented in light purple for female alates and dark purple for males alates. Diversity is represented by three Hill numbers: Richness (q = 0), Shannon diversity (q = 1), and Simpson diversity (q = 2), plotted against sequencing depth. Solid lines represent interpolated (observed) data and dashed lines represent extrapolated (predicted) diversity. The shaded regions denote 95% confidence intervals derived from 200 bootstrap replicates. Non-overlapping confidence intervals indicate significant differences in diversity between groups. Shapes represent the observed diversity for each sample type and marks the transition between interpolated (solid line) and extrapolated (dashed line) diversity estimates

Table 2 Asymptotic estimates of alpha diversity across forager (FOR), nest maintenance (NM) workers, female (FA) and male (MA) alate samples

Diversity	Assemblage	Observed	Estimator	SE	LCL	UCL
Taxonomic richness	FOR	212	212	1.821	212	215.57
	NM	284	284	2.432	284	288.77
	FA	403	403	2.615	403	408.13
	MA	277	277	0.554	277	278.09
Shannon diversity	FOR	2.31	2.31	0.009	2.30	2.33
	NM	2.12	2.12	0.008	2.11	2.14
	FA	11.08	11.10	0.065	10.97	11.22
	MA	11.63	11.65	0.084	11.49	11.82
Simpson diversity	FOR	1.37	1.37	0.002	1.36	1.37
	NM	1.28	1.28	0.002	1.27	1.28
	FA	4.46	4.46	0.015	4.43	4.49
	MA	4.95	4.95	0.022	4.91	5.00

Diversity values were calculated using Hill numbers: Taxonomic richness (q = 0), Shannon diversity (q = 1), and Simpson diversity (q = 2). The Observed column represents the raw number of detected features. The Estimator column represents the predicted "true" diversity at the asymptote. SE denotes the standard error. LCL and UCL represent the lower and upper 95% confidence limits, respectively, derived from 200 bootstrap replicates. Non-overlapping confidence intervals indicate significant differences in diversity between assemblages

and bullet ants (*Paraponera clavata*) (Anderson et al. 2012; Valdivia et al. 2023), and the prevalence of *Firmicutes* found here in *V. andrei* is consistent with previous studies of the microbiome of the same ant population (Gamboa et al. 2025). There are slight differences in the bacterial orders identified here and in Gamboa et al. (2025), most likely because assignment of ASVs to taxonomic classifiers is less reliable at more detailed taxonomic levels. Additionally, the software used to classify the ASVs taxonomically no longer supports the SILVA classifier (used Greengenes2 classifier), which was used to assign taxonomic groups in Gamboa et al. (2025). Still, it is interesting that, at the order level, worker microbiota appear largely dominated by bacteria from the *Culicoidibacterales* order, whereas reproductives show a high relative abundance of bacteria from the *Lactobacillales* order. Small amounts of microbes from both these orders were found in other ant species (Russel et al. 2009), and bees tend to have more *Lactobacillales* associated microbes than ants (McFederick et al. 2013). However, the function in ants of microbes from these orders has not been investigated. Future work on the functional significance of the microbes we identified will provide important insights about the mechanisms and function of differences in microbiota between workers and reproductives.

Our findings are consistent with those of many other studies on social insects, which have found differences in

microbial communities between reproductives and workers (Sinotte et al. 2020; Liberti et al. 2024). Reproductives of harvester ants (Gamboa et al. 2025) and *D. cf. indicum* (Shimoji et al. 2021) have higher alpha diversity of their bacterial communities compared to non-reproducing workers. In contrast, the microbiomes of reproductives were less diverse than those of non-reproducing workers in termites (Otani et al. 2019) and honeybees (Kapheim et al. 2015). Many factors that distinguish reproductive roles, including morphological differences, physiological pathways, diet, environmental differences, and developmental history, may mediate the observed differences between ants with different reproductive roles in host-associated microbes. For example, queens receive a different diet during development (royal jelly), which may explain why their gut microbiome differs from that of workers (Nguyen et al. 2024). Indeed, the microbiome of queens in bees changes throughout their development, initially being similar to the microbiome of larvae, and as they mature, their microbiome becomes more similar to that of workers (Tarpy et al. 2015). Similarly, larval developmental stages exhibit distinct microbial communities compared to those found in non-reproducing workers and reproductive adults of the same species in hornets (Cini et al. 2020) and in arboreal trapjaw ants (*Daceton armigerum*) (Ramalho et al. 2020). Perhaps in harvester ants, reproductives receive different diets during development compared to workers (Smith and Suarez 2010). Interestingly, a recent study on the microbiome of *V. andrei* (Gamboa et al. 2025) found that the bacterial communities of reproductives and brood are very similar to one another, but are distinct from those of workers. Perhaps if reproductives leave the nest soon after eclosion, their associated microbiota is more similar to that of their previous developmental stage (brood). Here we sampled alates, which are reproductives who recently left the nest and likely eclosed recently. It would be interesting to examine the microbiome of mature harvester ant queens with an established nest, and determine whether they harbor microbial communities that are more similar to workers' microbes. Outside workers have had more time elapse since their eclosion, exposing them to different microbes through their diet and/or environment. Furthermore, Gamboa et al. (2025) found that the associated bacterial communities of brood and reproductives in *V. andrei* were more similar to those of seeds than to the microbes of workers. Seeds are primarily fed to brood as a source of protein, whereas workers rely on other food items for primarily carbohydrates (Csata and Dussutour 2019). This difference in diet can further explain the differences we found here between workers and reproductives in their bacterial communities. Thus, the different nutritional needs of workers and reproductives might be an important driver of variation in host-associated microbial communities. Whether these differences in microbial communities are further determined by physiological mechanisms that drive morphological differences remains to be examined.

Our inability to detect differences in the beta diversity of host-associated bacterial communities of workers that perform different tasks is further consistent with prior work. Very few studies on ant microbiome have found differences in microbial communities based on behavioral tasks (but see (Sinotte et al. 2020; Liberti et al. 2024)). When applying the iNEXT analysis pipeline (Hsieh et al. 2016) to examine alpha diversity, we were able to detect significant differences in alpha diversity between tasks, but with extremely small effect sizes (Fig. 4; Table 2). The effect size of the difference in alpha diversity between workers and reproductives was substantially greater for the Shannon and Simpson indices. Interestingly, species richness differed more substantially between foragers and nest maintenance workers, as well as between male and female alates. In fact, male alates had similar species richness to nest maintenance workers. However, species richness is sensitive to rare species, whereas Shannon and Simpson's indices account for abundance. Thus, it is likely that the discrepancy between the results of these alpha diversity indices can be attributed to rare microbial species with very low abundance in our samples. Future work could expand the study of differences in microbial communities between workers that perform different tasks by including more task groups and by using methods other than 16 S to determine which microbial species are associated with each behavioral task. The very weak relationship we found between microbiome and task is surprising, given that work on other animals has found a relationship between microbiome and behavior. For example, in fruit flies (*Drosophila melanogaster)*, gut-specific microbes shape mating preferences (Sharon et al. 2010; Venu et al. 2014). The skin microbes of potential hosts influence food preference in mosquitoes (Verhulst et al. 2011). Furthermore, host microbiome mediates information transfer and social recognition, as seen in honeybees (Vernier et al. 2020), leaf-cutter ants (Teseo et al. 2019), and harvester ants (*Pogonomyrmex barbatus)* (Dosmann et al. 2016). In the case of leaf-cutter and harvester ants, the eradication of the microbiome affected nest-mate recognition and led to increased aggression against the treated ants. While differences in microbial communities among termite workers have been observed (Hongoh et al. 2006), these workers varied in age and morphotype, suggesting that morphology played an important role in determining their host-specific microbial communities. In honeybees, no differences were found in the microbiome of nurses and foragers (Kapheim et al. 2015); however, a shotgun metagenomics approach identified strain-level differences between nurses and foragers of honeybees (Baud et al. 2023). Thus, task-related

differences in host-associated microbial communities may be nuanced and require a fine-grained analysis to identify task-based differences in the microbiome. Finally, it is possible that because workers in harvester ants often switch among tasks (Gordon 1996), there is enough mixing within the worker population, and diet might not be sufficiently different across tasks to drive differences in microbiome. Foragers and nest maintenance workers both spend substantial amounts of time outside the nest. Perhaps, if outside workers are compared to inside workers (such as nurses), more differences in host-associated microbial communities would be found. Indeed, outside work alters the CHC composition of harvester ants (Sturgis and Gordon 2012). While Gamboa et al. (2025) sampled *V. andrei* workers from inside the nest, they did not distinguish between brood care workers and foragers that returned to the nest, or nest maintenance workers that are working inside, due to the destructive sampling of the nest itself. Thus, further work with more nuanced analysis of microbial communities and comparison of outside to inside workers might reveal substantial differences in host-associated microbes based on tasks in ants.

Finally, we found that colony ID explained 42–62% of the variation in the diversity of the microbial communities. Other studies of ant-associated microbial communities have found a significant effect of colony identity on the diversity of bacterial communities. Interestingly, colonies with more diverse bacterial communities produce more brood (Segers et al. 2019). The strong effect of colony ID that we observed could be driven by differences in the bacterial communities within the ant nests. The bacterial communities associated with the soil of *V. andrei* nests differ across nests and correspond to their geographical distribution. Nests that are more geographically distant harbor more distinct bacterial communities (Gamboa et al. 2025). Thus, the environment may play an important role in shaping the community of host-associated microbes in ants.

In conclusion, our work demonstrates that differences in reproductive role can be a reliable predictor of host-associated bacterial community differences in harvester ants. Our findings align with previous work on the relationship between social roles and host-associated microbial communities in social insects. We thus provide additional support for the potential role of diet, developmental trajectory, and environment in shaping the host-associated microbial communities of social insects.

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Author contributions DAG and NPW contributed to the conceptualization of the study questions and design. DAG collected samples from the field, processed and analyzed them, wrote code for data analysis, and produced data visualizations. DAG and NPW performed statistical analyses and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The datasets analyzed in the current study are available in this published article and the repository https://github.com/DAlejandraG/BT-microbes. All sequence data analyzed during this study are available on the NCBI BioProject record PRJNA1311736, http://www.ncbi.nlm.nih.gov/bioproject/1311736.

Declarations

Conflict of interest These authors declare that they have no competing interests.

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