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Multi-generational adaptation to *Solanum nigrum* increases reproduction and decreases microbial diversity of *Aphis gossypii*

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Aphis gossypii Glover (Hemiptera: Aphididae) causes considerable damage to crop
yields globally. *Solanum nigrum* (Solanales: Solanaceae), an annual malignant weed,
serves as a crucial weed host for *A. gossypii*. However, the potential mechanisms
by which *A. gossypii* adapts to different hosts during the transition between crops,
such as *Gossypium hirsutum* (Malvales: Malvaceae) and *S. nigrum* remain elusive.
We calculated the life table parameters of *A. gossypii* after rearing on *S. nigrum*
for ten generations. The fifth generation of *A. gossypii* (T5) exhibited the strongest
adaptability to *S. nigrum*, demonstrating notably higher values of r (intrinsic
rate of increase), λ (finite rate of increase), and fecundity compared to the first
generation of *A. gossypii* (T1). Upon retransferring T1, T5, and the tenth generation of
A. gossypii (T10) were retransferred to *G. hirsutum* (designated as T1-M, T5-M,
and T10-M, respectively), the T5-M showed superior r, λ, and fecundity compared
to both T1-M and T10-M. 16S rRNA sequencing and qPCR analyses indicated a
significant decrease in the diversity of the symbiotic bacterial community in both
T5 and T10. Notably, *Buchnera* and *Arsenophonus* were two dominant symbiotic
bacteria related to metabolism and host adaptability in *A. gossypii*. The relative
abundance of *Buchnera* in T5 and T10 significantly increased compared to M and T,
while the relative abundance of *Arsenophonus* decreased markedly. KEGG (Kyoto
Encyclopedia of Genes and Genomes) function prediction analysis suggested
that the roles of symbiotic bacteria in *A. gossypii* are primarily linked to metabolic
processes. Therefore, the adaptation of *A. gossypii* to *S. nigrum* enhances its
population expansion on *G. hirsutum*, potentially involving the metabolic functions
of *Buchnera* and *Arsenophonus*. These findings provide a theoretical foundation
for the scientific management of *A. gossypii* and *S. nigrum* in the fields.

KEYWORDS

cotton aphid, 16S rRNA, life table, host shift, symbiotic bacterium

1 Introduction

Aphis gossypii Glover (Hemiptera: Aphididae) is a polyphagous pest renowned for causing substantial losses to both crop yields and quality across the globe (Morando et al., 2021). Additionally, non-crop plants (such as weeds) might contribute to the host transfer process of *A. gossypii*. These weeds, located within or adjacent to agricultural fields, can serve as alternative hosts, supporting the growth and reproduction of aphid populations (Caballero-López et al., 2011). And the secondary metabolites of different plants are different, and aphids that feed on different host plants for a long time may have population differentiation (Razmjou et al., 2010; Vorburger et al., 2017), thus increasing the biodiversity of farmland pests. However, there are several aspects remain elusive: the specific selection of plant hosts during aphid's transfer from overwintering hosts to crops, the precise role of weeds in the aphid's adaptation to host crops, and the underlying adaptive mechanisms that facilitate aphid's transition between various hosts.

Microbial symbiosis is widely present in insects, with bacteria and insects co-evolving over hundreds of millions of years. This symbiotic relationship is vital for the survival and reproduction of insects. In the case of aphids, bacteria offer numerous benefits, including nutrition supply (Douglas et al., 2001; Rabatel et al., 2013) and protection from natural predators (Frago et al., 2017; Hrček et al., 2016). The symbiotic microorganisms harbored by aphids play a pivotal role in the process of host transfer. Typically, a shift in hosts alters the bacterial community structure within *A. gossypii* (Zhao et al., 2016). Furthermore, the bacterial symbionts present in aphids are influenced by the types of plants the aphids consume (Chandler et al., 2008). Notable differences exist in populations of *Acyrthosiphon pisum* on peach trees, *Medicago sativa*, and clover, and these variations are closely linked to their symbiotic microflora (Simon et al., 2003). Similarly, *Aphis craccivora* demonstrated distinct microbial communities when feeding on *M. sativa* and *Robinia pseudoacacia*, indicating a broad association between bacterial symbionts and host plants (Brady and White, 2013). Studies indicates that when the same aphid species feeds on different host plants, the prevalence of their symbionts often varies (Henry et al., 2015). Specifically, *Hamiltonella* was only detected in *A. craccivora* feeding on *M. sativa*, whereas *Arsenophonus* was exclusively present in *A. craccivora* feeding on *R. pseudoacacia* (Brady and White, 2013). However, there is a dearth of studies exploring the microbial changes of *A. gossypii* upon its transfer from cotton to alternative host plants. In consequence, it remains unclear how host adaptation alters the diversity of microbes within *A. gossypii*.

Solanum nigrum (Solanales: Solanaceae) is an annual broadleaf weed that grows rapidly in the field, distinguished by its vigorous growth, high fecundity, brief growth cycle, and persistent fruitfulness (Zhao et al., 2017). When fully mature, *S. nigrum* can occupy significant space, impeding light penetration and competing for nutrients with crops. These competitions lead to slower growth of crops, ultimately reducing both yield and quality. *S. nigrum* serves as an alternative host for aphids, especially in environments where cultivated crops are temporarily unavailable. Therefore, *A. gossypii* (Perng, 2002), *Myzus persicae* (Almohamad et al., 2006), *Aulacorthum solani* (Milbrath and Biazzo, 2012) and

Brevicoryne brassicae (Coutts et al., 2006) often utilize *S. nigrum* as a host for growth and reproduction. In addition, *S. nigrum* stands as a important weed in corn and soybean fields (Dalley et al., 2004), with the potential to be parasitized by aphids. This host adaptability can pose a threat to crops, yields and ultimately food security. Nevertheless, the mechanisms by which *A. gossypii* adapts to *S. nigrum*, as well as the subsequent effects on its population expansion capacity upon returning to the original host crop, remains undefined.

Numerous studies have investigated the adaptability of *A. gossypii* to various host plants and the alterations in their internal microorganisms. However, the shifts in the symbiotic bacterial community of *A. gossypii* following host transfer, as well as their adaptive mechanism to plant hosts during this transition is not clear. Therefore, this paper initially constructed a life table for multi-generational growth of *A. gossypii* on *S. nigrum*, thereby assessing its adaptability to this host. Subsequently, utilizing 16S rRNA sequencing technology, we analyzed the dynamics of symbiotic microbial communities during *A. gossypii* adaptation to *S. nigrum*.

The results of this study offer insights into the adaptive mechanism of *A. gossypii* to the weed host *S. nigrum*, which is instrumental in unveiling its broader adaptive strategies following host transfers. Ultimately, this research provides theoretical guidance for the scientific prevention and control of *A. gossypii*.

2 Materials and methods

2.1 Insects and plants

A. gossypii used in this study were collected from the cotton seedlings of the experimental farm of the Institute of Cotton Research of CAAS (Anyang City, Henan Province). These collected aphid were confirmed by examination of the mtDNA COI gene sequences as *A. gossypii* (Wang et al., 2016). *A. gossypii* were subsequently reared in laboratory for multiple generations without exposure to insecticides. Additionally, seeds of *Gossypium hirsutum* (Malvales: Malvaceae) (CCRI49) and *S. nigrum* sourced from the same experimental farm. *A. gossypii*, *G. hirsutum*, and *S. nigrum* were maintained under controlled environmental conditions (temperature 25 ± 1°C, relative humidity 65 ± 5%, and photoperiod 14 h: 10 h photoperiod).

2.2 Construction of life table for *A. gossypii*

Fresh leaf of *G. hirsutum* or *S. nigrum* were positioned in a plastic petri dish (9 cm diameter, with a 1 cm layer of 1.8% agar). A wingless adult aphid was placed onto the leaf. The nymph of *A. gossypii* was transferred on a new leaf of *G. hirsutum* (labeled M) and *S. nigrum* (labeled T1). Subsequently, the nymph borning from T1 adult was moved to fresh *S. nigrum* leaf (labeled T2), and this process continued until T10. Concurrently, nymph from T1, T5, and T10 was transferred to *G. hirsutum* leaves (designated as T1-M, T5-M, and T10-M, respectively). Aphid growth was monitored daily, noting their lifespan and fecundity until their demise. Each aphid served as an individual replicate, with 60 replicates per generation. The leaves are replaced every 2 to 3 days, and the feeding conditions of *A. gossypii* are the same as mentioned above.

2.3 16S rRNA sequencing

Thirty adults of M, T1, T5, and T10 were gathered within 48 h after the final molt. These samples underwent sterilization with 75% alcohol for 5 min (Chang et al., 2023), followed by quick-frozen with liquid nitrogen, and were then stored at −80°C. From each generation, four samples were collected. The total DNA of *A. gossypii* samples was extracted using the FastDNA Spin kit for soil (MP Biomedicals, United States). The concentration and purity of the extracted DNA were determined using NanoDrop 2000C (Thermo Scientific, United States), and the integrity of DNA was assessed by 1.2% agarose gel electrophoresis.

The genes in the V3 ~ V4 region of bacterial 16S rRNA were amplified with universal primers 338F (5′-ACTCCTACGGG AGGCAGCA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) (Xu et al., 2016), with the extracted DNA as template for 16S rRNA sequencing. PCR amplification, quantification, identification, and purification PCR product, and library preparation as described previously (Zhao et al., 2016). Sequencing was then performed on an Illunina Miseq PE 300 platform of Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). Details of the analysis process can be found in Supplementary Method S1. Sequencing data have been uploaded to NCBI (BioProject ID PRJNA1155176).

2.4 Absolute quantification of bacterial community

Based on the results of 16S rRNA sequencing, three symbiotic dominant bacteria (bacteria with relative abundance greater than 10% were defined as dominant bacteria) were chosen for absolute quantitative analysis. The copy numbers across various generations were calculated. The bacterial target sequence was cloned into a pUC19 cloning vector (Zhili Zhongte Wuhan Biotechnology Co., Ltd., China), which subsequently served as a standard vector (confirmed through sequencing). The copy numbers calculation process and method of the sample target bacteria refer to previous studies (Chang

et al., 2023). Primer sequences (Supplementary Method S2) and PCR amplification efficiency were shown in Supplementary Table S1. It was ensured that the amplification efficiency (E value) fell within the 0.9 and 1.1, with a correlation (R^2) is above 0.99. The quantitative polymerase chain reaction (qPCR) were set up according to the MonAmp™ SYBR® Green qPCR Mix manual (Wuhan Mona Biological Co., Ltd.) and executed using the quantitative fluorescence PCR instrument (CFX Opus 96, Bio-rad, Singapore).

2.5 Statistical analysis

Utilizing the theory of age-stage, sex life table theory, the raw life table data of all individuals were analyzed through TWOSEX-MSChart program (http://140.120.197.173/Ecology/, Ver. 24/01/2023) (Chi, 1988; Chi and Liu, 1985). Bootstrap technique was used to estimate the variance and standard deviation of population parameters. Paired bootstrap test in TWOSEX-MSChart program was used to test the difference significance of the data. Additionally, GraphPad Prism (9.0.0) (GraphPad Software Corporation) was used to plot. Student's *t*-test and Log-rank (Mantel-Cox) test were executed via IBM SPSS Statistics 20 (International Business Machines Corporation), with $p < 0.05$ indicating statistical difference.

3 Results

3.1 Effects of *S. nigrum* on multigenerational life table parameters of *A. gossypii*

The life table parameters of different generations of *A. gossypii* reared on *S. nigrum* are shown in Table 1. The results showed that, excluding T5 (0.382 d⁻¹) and T6 (0.371 d⁻¹), the *r* (intrinsic rate of increase) value of M (0.408 d⁻¹) was significantly greater than that of other generations. The λ (finite rate of increase) of each generation was

TABLE 1 Life table parameters of different generations of *A. gossypii* on *S. nigrum*.

Parameters	r (d⁻¹)	λ (d⁻¹)	APOP (d)	TPOP (d)	Longevity (d)	Fecundity (nymphs per female)
M	0.408 ± 0.009a	1.505 ± 0.013a	0.03 ± 0.02a	5.20 ± 0.09c	16.79 ± 0.52bc	32.43 ± 1.57ab
T1	0.341 ± 0.017c	1.406 ± 0.023c	0.10 ± 0.07a	5.70 ± 0.19ab	16.73 ± 0.94bcd	22.59 ± 2.86de
T2	0.340 ± 0.014c	1.406 ± 0.019c	0.03 ± 0.03a	5.27 ± 0.13bc	14.80 ± 1.01d	19.40 ± 2.53e
T3	0.370 ± 0.010bc	1.448 ± 0.014bc	0.00 ± 0.00a	5.37 ± 0.14bc	16.40 ± 0.68 cd	23.96 ± 1.78de
T4	0.358 ± 0.012bc	1.430 ± 0.017bc	0.03 ± 0.03a	5.43 ± 0.13abc	16.54 ± 1.02bcd	25.61 ± 2.83cde
T5	0.382 ± 0.010a	1.465 ± 0.015b	0.00 ± 0.00a	4.90 ± 0.09d	19.97 ± 0.60a	35.61 ± 2.09a
T6	0.371 ± 0.009a	1.449 ± 0.014bc	0.07 ± 0.05a	5.20 ± 0.13 cd	20.46 ± 0.82a	34.45 ± 2.40a
T7	0.353 ± 0.014bc	1.423 ± 0.020bc	0.00 ± 0.00a	5.17 ± 0.10 cd	15.59 ± 1.14 cd	25.56 ± 3.59cde
T8	0.358 ± 0.009bc	1.431 ± 0.012bc	0.03 ± 0.03a	5.37 ± 0.12bc	17.50 ± 0.87bc	27.20 ± 2.18bcd
T9	0.361 ± 0.014bc	1.435 ± 0.020bc	0.03 ± 0.03a	5.80 ± 0.17a	17.50 ± 0.68bc	26.57 ± 2.23cde
T10	0.357 ± 0.010bc	1.429 ± 0.014bc	0.03 ± 0.03a	5.63 ± 0.14ab	19.36 ± 1.04ab	31.60 ± 2.38abc

Values in the table represent mean ± SE. Different lower-case letters in each row indicate significant differences between treatments at the level of $p < 0.05$ (Student's *t*-test). *r*, intrinsic rate of increase (d⁻¹); λ, finite rate of increase (d⁻¹); APOP, adult pre-reproductive period (days); TPOP, total prereproductive period (days); Fecundity, offspring number per female.

significantly lower than that of M (1.505 d^{-1}), yet T5 (1.465 d^{-1}) exhibited the highest λ among all generations. In comparison to M (5.20 d), the TPOP (total prereproductive period) of T1 (5.70 d), T9 (5.80 d), and T10 (5.63 d) increased significantly, whereas the TPOP of T5 (4.90 d) decreased notably. The longevity of T5 (19.97 d) and T6 (20.46 d) was surpassed that of M (16.79 d) significantly, and their fecundity also proved higher across all generations. Moreover, the l_x (age-specific survival rate) of T5 was elevated compared to other generations between 15 to 20 days (Figure 1A), the m_x (age-specific fecundity) of M was superior to other generations (from 3 to 10 days), followed by an alternating leadership between T5 and T10 in m_x (Figure 1B).

The life table parameters of *A. gossypii* after transferred from *S. nigrum* to *G. hirsutum* are shown in Table 2. According to the population parameter listed in Table 1, the T1, T5, and T10 of *A. gossypii* were retransferred to their original host (*G. hirsutum*). The results revealed that the r and λ values of T5-M ($r = 0.528$ d^{-1}, $\lambda = 1.695$ d^{-1}) were significantly higher compared to those of T1-M ($r = 0.470$ d^{-1}, $\lambda = 1.599$ d^{-1}) and T10-M ($r = 0.430$ d^{-1}, $\lambda = 1.538$ d^{-1}). Furthermore, the fecundity of T5-M (53.43) and T10-M (52.20) proved to be significantly greater than that of T1-M (47.70). However, the longevity of T5-M (22.23 d) was considerably shorter than that of T10-M (25.77 d). No substantial disparities were detected in APOP (adult pre-reproductive period) and TPOP across the three generations. The value of l_x of T5-M was higher than that of T1-M and T10-M (from 16 to 23 days) (Figure 1C). Additionally, the m_x of T5-M prevailed over other two generations (from 5 to 10 days), while the m_x of T10-M emerged as the highest after 13 days (Figure 1D).

3.2 Summary of the 16S rRNA sequencing

To clarify the differences in microbial community diversity of *A. gossypii* on *S. nigrum* and *G. hirsutum*, the M, T1, T5, and T10 of *A. gossypii* were selected for sequencing, based on distinct biological data. A total of 799,239 high-quality, optimized sequences, representing 343,078,429 bases. The average sequencing coverage exceeded 99% across all groups, demonstrating adequate sequencing quantity and reasonable depth (Supplementary Table S2).

Rarefaction curves based on Sobs index (Supplementary Figure S1A) and Shannon index (Supplementary Figure S1B) showed that increasing the sample volume would not produce more OTUs (operational taxonomic units), suggesting that the data accurately reflects the composition of the majority of bacterial communities present in the samples. In comparison to M and T1, the Shannon index for T5 and T10 decreased, while the Simpson index increased (Supplementary Table S2). Furthermore, both Chao 1 (decreased 18.11%) and Ace (decreased 22.64%) indices decreased relative to M after continuously feed *A. gossypii* with *S. nigrum*.

3.3 Influence of bacterial community of *A. gossypii* feeding with *S. nigrum*

M, T1, T5, and T10 exhibited unique OTUs with counts of 33, 22, 16, and 76, respectively, while 119 OTUs were shared by the four groups (Figure 2A). Principal Co-ordinates Analysis (PCoA) revealed significant disparities in genus level composition of *A. gossypii* among M, T5, and T10 (Figure 2B).

FIGURE 1
Age specific survival rate (l_x) **(A)** and fecundity (m_x) **(B)** of *A. gossypii* from *S. nigrum* ten generation and on *G. hirsutum*. Age specific survival rate (l_x) **(C)** and fecundity (m_x) **(D)** of *A. gossypii* on *S. nigrum* retransferring to *G. hirsutum*.
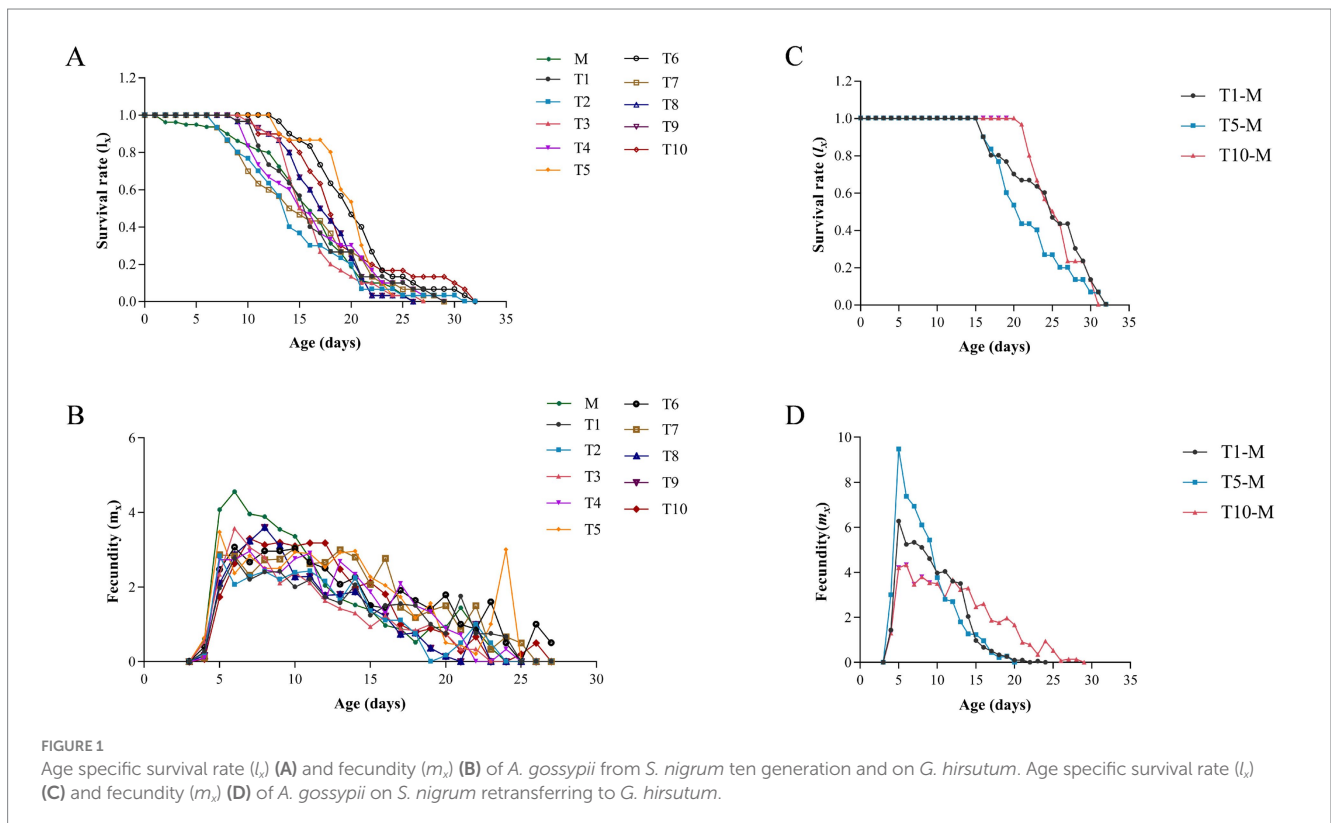
TABLE 2 Life table parameters of *A. gossypii* on *S. nigrum* retransferring to *G. hirsutum.*

Parameters	r (d^{-1})	λ (d^{-1})	APOP (d)	TPOP (d)	Longevity (d)	Fecundity (nymphs per female)
T1-M	0.470 ± 0.007b	1.599 ± 0.012b	0.00 ± 0.00a	4.67 ± 0.09a	24.60 ± 0.97ab	47.70 ± 1.32b
T5-M	0.528 ± 0.006a	1.695 ± 0.011a	0.00 ± 0.00a	4.60 ± 0.09a	22.23 ± 0.88b	53.43 ± 0.90a
T10-M	0.430 ± 0.008c	1.538 ± 0.013c	0.00 ± 0.00a	4.77 ± 0.08a	25.77 ± 0.58a	52.20 ± 1.47a

Values in the table represent mean ± SE. Different lower-case letters in each row indicate significant differences between treatments at the level of $p < 0.05$ (Student's t-test). r, intrinsic rate of increase (d^{-1}); λ, finite rate of increase (d^{-1}); APOP, adult pre-reproductive period (days); TPOP, total prereproductive period (days); Fecundity, offspring number per female.

FIGURE 2
Influence of continuous feeding of *S. nigrum* on bacterial community of *A. gossypii*. The Venn diagram **(A)** illustrates the number of shared and unique bacteria in the four treatments. **(B)** Difference of OTUs types in different treatments based on Principal co-ordinates analysis (PCoA). The relative abundance of dominant bacterial communities of *A. gossypii* at the phylums **(C)** and genus **(D)** levels after feeding on *S. nigrum*. **(E)** Heatmap shows the relative abundance of the dominant bacterial community at the genus level for each sample.
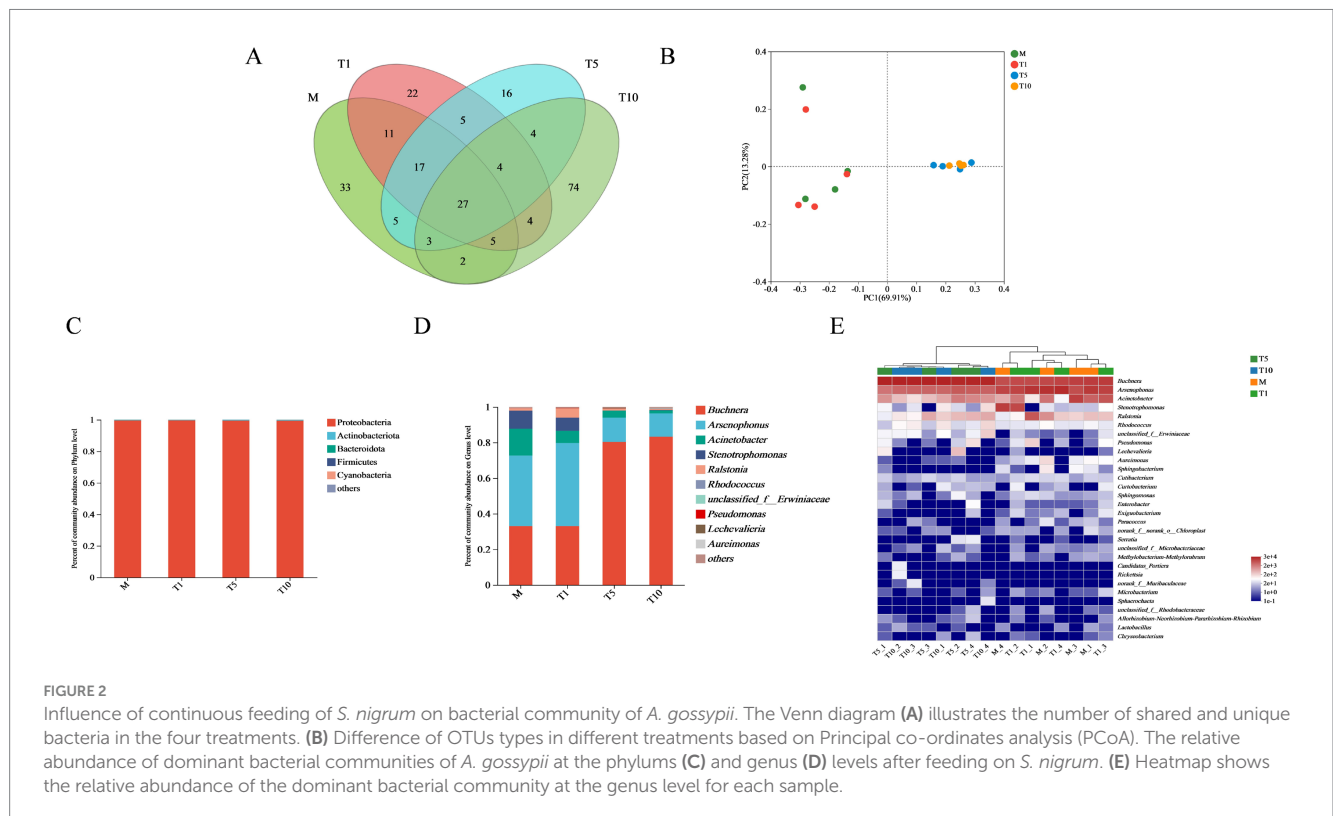
The histograms of bacterial phylums and genus in four groups of *A. gossypii* were mapped to visualize the composition and distribution of bacterial communities. Then, the difference of symbiotic bacteria abundance among each group was compared at each taxonomic level by averaging the samples within each group. At the phylum level, the five most abundant bacteria were identified as Proteobacteria, Actinobacteriota, Bacteroidota, Firmicutes, and Cyanobacteria (Figure 2C). Notably, Proteobacteria was the highest relative abundance, accounting for 99.58% in M, and similarly high percentages in T1 (99.62%), T5 (99.48%), and T10 (99.41%).

At the genus level, *Buchnera* and *Arsenophonus* were the dominant bacteria all four groups (Figure 2D). Specifically, the superiority bacteria in M were *Arsenophonus* (39.59%), *Buchnera* (33.02%), *Acinetobacter* (15.14%), and *Stenotrophomonas* (10.15%) (Supplementary Table S3). In T1, the relative abundance of *Buchnera*, *Acinetobacter*, and *Stenotrophomonas* decreased to 33.01, 6.89, and 7.37%, respectively. In compared to M, the relative abundance of *Buchnera* in T5 and T10 increased to 80.30 and 83.28%, respectively. Conversely, the relative abundance of *Arsenophonus* decreased to

13.68 and 13.11%, respectively, while those of *Acinetobacter* decreased to 3.95 and 1.66%, respectively.

The aggregation of bacterial community at the genus level in *A. gossypii* was visualized through a heat map (Figure 2E). In general, the relative abundance of *Arsenophonus*, *Buchnera*, *Acinetobacter*, and *Stenotrophomonas* in *A. gossypii* was higher in all groups. The relative abundance of *Buchnera* in T5 and T10 was higher than that in M and T1, whereas the relative abundance of *Arsenophonus*, *Acinetobacter*, and *Stenotrophomonas* was comparatively lower in T5 and T10 than in M and T1.

The significant changes in bacterial abundance were compared among the four groups (Figure 3). There were no significant alterations in the abundance of the four prevalent bacteria (*Arsenophonus*, *Buchnera*, *Acinetobacter*, and *Stenotrophomonas*) in T1 compared with M (Figure 3A). However, compared with M, the abundance of *Buchnera* in T5 increased significantly by 58.88%, while the abundance of *Arsenophonus* decreased significantly by 65.44% (Figure 3B). Similarly, the abundance of *Buchnera* in T10 rose significantly by 60.35%, and the abundance of *Arsenophonus* dropped significantly by 66.89%
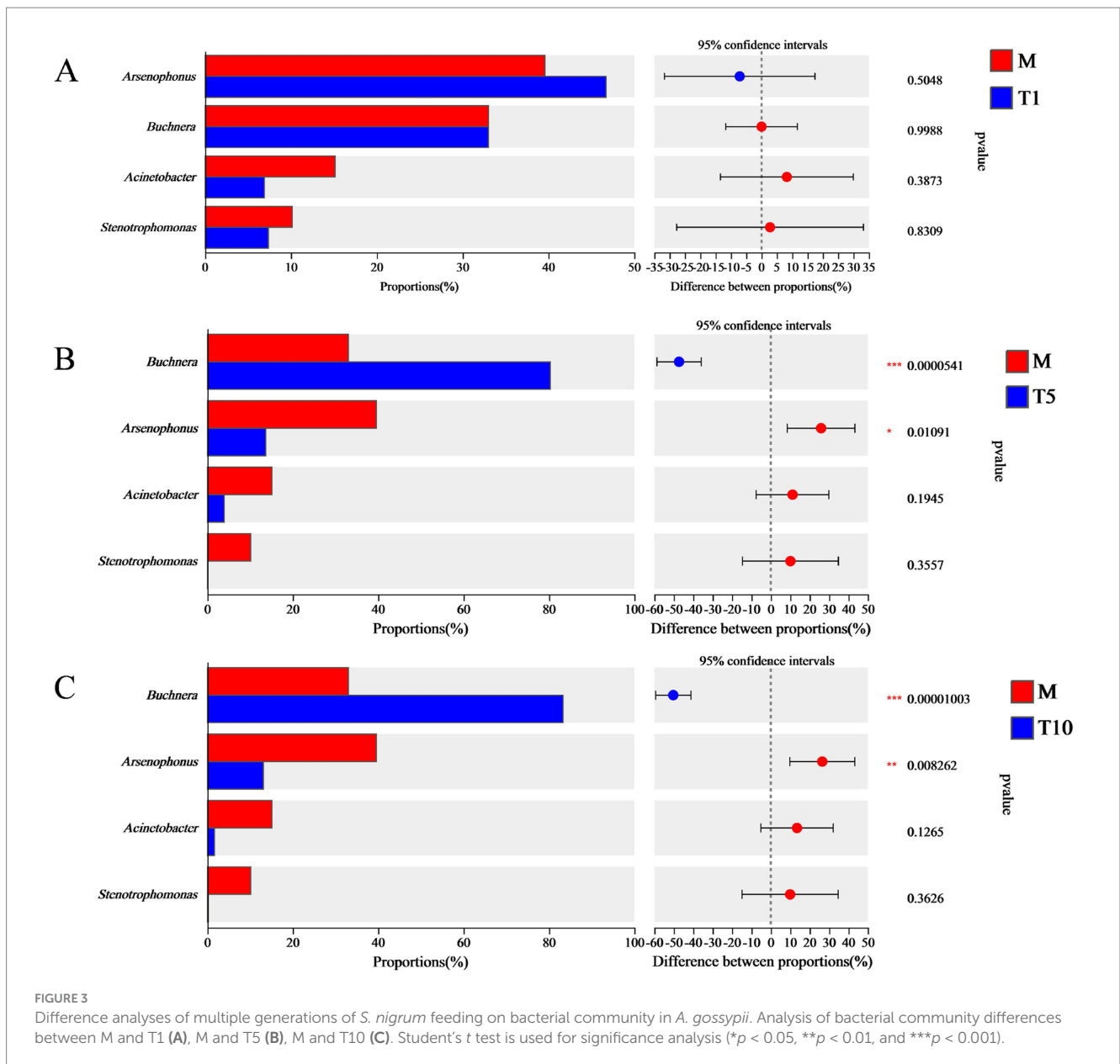
FIGURE 3
Difference analyses of multiple generations of *S. nigrum* feeding on bacterial community in *A. gossypii*. Analysis of bacterial community differences between M and T1 **(A)**, M and T5 **(B)**, M and T10 **(C)**. Student's *t* test is used for significance analysis (*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$).

(Figure 3C). Nevertheless, the abundance of *Acinetobacter* and *Stenotrophomonas* remained largely unchanged in both T5 and T10.

3.4 Absolute quantitative analysis of dominant bacteria

Analysis of dominant bacteria (*Buchnera*, *Arsenophonus*, and *Acinetobacter*) in M, T1, T5, and T10 of *A. gossypii* by qPCR found that, the abundance of *Buchnera* was higher in all groups, with a significant increase in copy number observed in T5 and T10 compared to T1 and M. Conversely, the copy number of *Arsenophonus* was significantly reduced in T5 and T10 compared to T1 and M. No notable difference was detected in the copy number of *Acinetobacter* among the four groups (Figure 4).

3.5 Functional prediction

To investigate the role of different microbial communities in *A. gossypii* after host shift, PICRUSt2, combined with KEGG database, was used to predict and analyze the function of these microbial community. The analysis revealed that 73.41% of the microorganisms in *A. gossypii* were involve in metabolism (Supplementary Figure S2). According to the KEGG secondary classification function prediction, the top five predicted functions fall under "global and overview maps," "carbohydrate metabolism," "amino acid metabolism," "metabolism of cofactors and vitamins," and "energy metabolism" (Figure 5). Furthermore, microorganisms in T5 and T10 displayed a notable concentration in "carbohydrate metabolism," "membrane transport," "cellular community-prokaryotes," "signal transduction," and other pathways, compared with those in T1 and M. While the symbiotic bacteria in T1 and
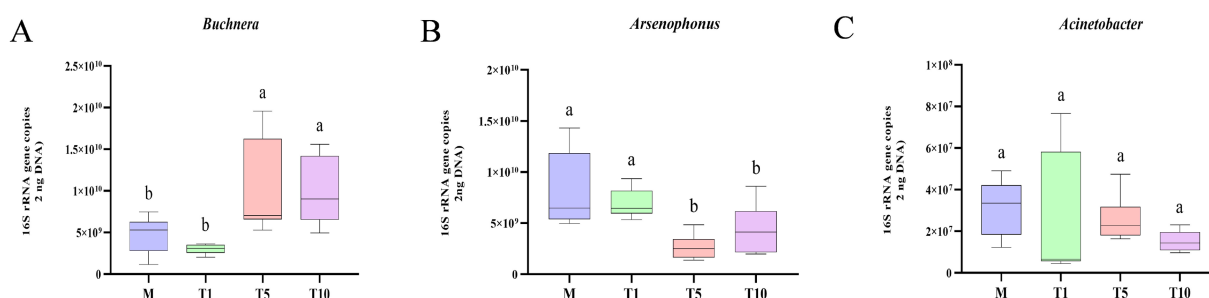
FIGURE 4
The 16S rRNA gene copy number of bacterial community in *A. gossypii* fed on *G. hirsutum* and different generations of *S. nigrum*. The lower-case letters in each figure indicated that there was a significant difference between the control group and the treatment group at the $p < 0.05$ level (Student's t-test).
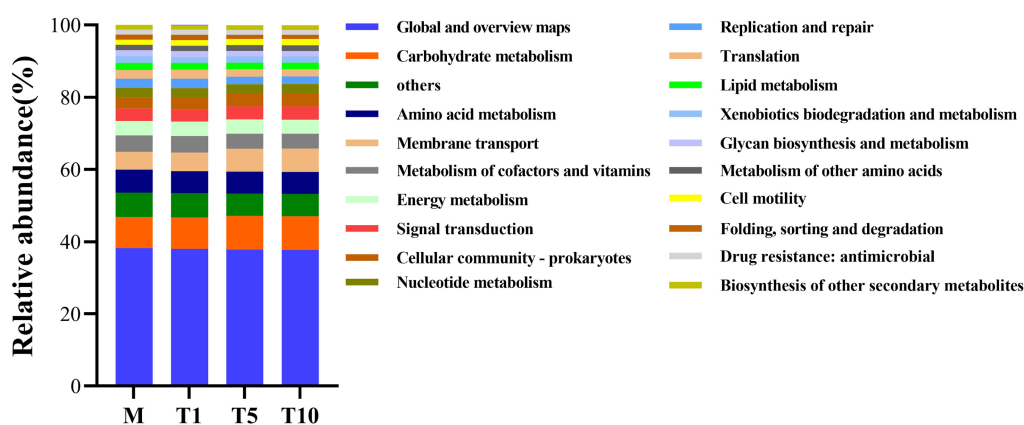

FIGURE 5
Functional prediction of KEGG secondary classification of microbes in *A. gossypii* under different groups.

M showed a significant focus on "metabolism of cofactors and vitamins," "energy metabolism," "nucleotide metabolism," and other functions (Supplementary Figure S3).

4 Discussion

Although *A. gossypii* is hosted by numerous plants, research on the role of weeds in its host shift remains limited. *S. nigrum* stands as a prominent weed in agricultural fields. Nevertheless, the adaptability mechanism of *A. gossypii* to *S. nigrum*, and the subsequent effects on its population expansion capacity upon returning to original host crop, are still not fully understood. *S. nigrum* serves as an alternative host for *A. gossypii*, particularly in environments where cultivated crops are temporarily unavailable. Our research emphasizes the multi-generational adaptation of *S. nigrum* and its role in enhancing the reproduction rates of *A. gossypii*. This adaptation of the weed may increase habitat suitability for the aphid, thereby facilitating its population growth. Elevated aphid populations can significantly impact crop yields through direct feeding damage (Ramalho et al., 2012) and the transmission of plant viruses (Smith and Chuang, 2014). In regions such as the North China Plain, where crops like cotton, corn, and vegetables are essential, the increased reproduction of *A. gossypii* could result in considerable economic losses (Zhang et al., 2018). *A. gossypii* can diminish plant vigor, stunt growth, and reduce both the quality and quantity of agricultural produce (Zhong et al., 2022), directly affecting farmers' livelihoods and regional food supplies.

Host adaptation is a long process. The research revealed that no significant difference in *r* between *A. gossypii* initially reared on *Hibiscus syriacus* and those on *Cucumis sativus* after three generations (Zheng et al., 2007). When *Tetranychus viennensis* transfers from apple trees to other fruit trees, the first generation experiences negative effects on life table parameters, but these effects dissipate in succeeding generation (Li et al., 2006). *A. gossypii* develops faster on the original host compared to non-original host, and its *r* is higher on the original host (Satar et al., 2013), indicating inhibited development on the non-original hosts. Transferring *A. gossypii* from cotton to *C. sativus* and *Abelmoschus manihot* for four consecutive generations did not enhance its development (Satar et al., 2013). The first-generation life table parameters of *Amphitetranychus viennensis* suffered when transferred from *Prunus serotine*, which is conducive to its growth, to *Malus domestica* (Kafil et al., 2007). Likewise, when *A. viennensis* was transferred to *Prunus avium*, its first-generation life table parameters fared better than the third generation, showing no gradual adaptation to *P. avium* (Kafil et al., 2007). However, the difference of life table of a pest on different host crops may be caused by the difference of secondary metabolites (Abdelsalam et al., 2016), more experiments are essential to uncover the exact mechanism.

Our results demonstrated that *A. gossypii* gradually adapted to *S. nigrum*, with T5 demonstrating significant progress. The shape of l_x and m_x curves illustrate the interplay of life history traits and

determine r, a common indicator for evaluating the adaptability of pest to plants (Bethke et al., 1998; Sandström and Pettersson, 1994). A later decline in the l_x curve and higher peak in the m_x indicate a the greater r and, consequently, higher aphid population growth potential. The r of *A. gossypii* on *S. nigrum* peaked at T5, signifying the highest population growth potential for this generation on *S. nigrum*. In the absence of alternative crops like *G. hirsutum*, *A. gossypii* can rapidly multiply on *S. nigrum*, maintaining a dense population.

Microbial symbionts play a pivotal role in enhancing the adaptability of pests to their hosts. In this study, significant changes were observed in the bacterial community of T5 and T10 of *A. gossypii* feeding on *S. nigrum*. At the phylum level, the abundance and species of bacterial communities remained stable across all groups, and the highest abundance of bacteria was Proteobacteria. Proteobacteria are recognized as a vital component of the intestinal flora in numerous herbivorous insects and fostering a beneficial symbiotic relationship with their hosts (Show et al., 2022). These insects provide a stable environment for Proteobacteria, which, in turn, endow their hosts with novel metabolic capabilities (Latorre et al., 2003).

Buchnera is a member of the Proteobacteria, which is the dominant bacterium in aphids growing on various host plants (Ma et al., 2021). Its roles extend to DNA replication, transcription, protein translation, secretion, energy metabolism, and amino acid biosynthesis for aphids (Baumann et al., 1995; Richards et al., 2010; Tian et al., 2023). In our study, a notable increase in the relative abundance of *Buchnera* was observed in T5 and T10, while no significant alteration was detected in the M and T1. Similarly, *Buchnera* content was significantly higher in *A. gossypii* reared on *C. sativus* for over 10 years compared to those on cotton (Zhang et al., 2016). The relative abundance of *Buchnera* in *A. gossypii* reared on *Cucurbita pepo* was also significantly higher than those on cotton (Xu et al., 2023). Collectively, the elevated abundance of *Buchnera* is related to the adaptation of *A. gossypii* to new host plants.

Arsenophonus (Proteobacteria) is an intracellular symbiotic bacteria of insects, generally belonging to the secondary symbiotic bacteria, which has a wide range of hosts and rich biodiversity (Chen et al., 2014). This bacterium plays a crucial part in enhancing the growth performance of aphids during amino acid deficiency (Tian et al., 2023; Wang et al., 2024). Furthermore, it mitigates the harmful effects of parasitic wasps to aphids (Heidari Latibari et al., 2023) and mediates host specialization of aphids (Tian et al., 2019). Notably, *Arsenophonus* is also the dominant bacteria in *A. gossypii* (Xu et al., 2020; Zhang et al., 2021). In our study, the relative abundance of *Arsenophonus* was significantly lower in T5 and T10 compared to M and T1. This finding suggests a decline in *Arsenophonus* as *A. gossypii* adapts to *S. nigrum*. Similar study has showed that a reduction in *Arsenophonus* abundance of *plutella xylostella* after treatment with the insecticide sulfoxaflor (Shang et al., 2021).

Based on the changes in the abundance of symbiotic bacteria and predictions from the KEGG function database, *Buchnera* and *Arsenophonus* may regulated metabolic processes, enabling *A. gossypii* to gradually adapt to the *S. nigrum*. Across various life stages of *Adelphocoris suturalis*, the function of symbiotic bacteria predominantly focuses on metabolic pathway (Xue et al., 2021). The signal transduction function of intestinal bacteria increased after 17 generations of *P. xylostella* shifted from *Raphanus sativus* to *Amygdalus persica* (Yang et al., 2020). In comparison to the findings of this study, KEGG function prediction analysis suggests that *Buchnera* and *Arsenophonus* contribute to the adaptation of *A. gossypii* to *S. nigrum* by engaging in metabolic functions, particularly in "carbohydrate metabolism," "membrane transport," "metabolism of cofactors and vitamins," "energy metabolism," and so on.

To gain a comprehensive understanding of these disparities, further investigation is necessary, possibly including metagenomic analyses to explore the functional significance of these symbiotic bacteria and to unravel the causal relationships.

In this study, the growth and reproduction parameters of *A. gossypii* demonstrated a gradual adaptation process as its generations progressed on *S. nigrum*. Notably, the T5 generation of *A. gossypii* exhibited the highest level of adaptation to *S. nigrum*. Upon transferring *A. gossypii*, which had been domesticated by *S. nigrum*, back to *G. hirsutum*, T5-M displayed the greatest values for r, λ, and fecundity. Furthermore, significant changes were observed in the symbiotic bacteria of *A. gossypii* after several generations on *S. nigrum* compared to those on *G. hirsutum*. The abundance of *Buchnera* in T5 and T10 of *A. gossypii* reared on *S. nigrum* increased significantly, whereas the abundance of *Arsenophonus* decreased significantly.

The adaptability of *A. gossypii* to transition between distinct host species, for instance, from *S. nigrum* to *G. hirsutum*, underscores the intricate interactions within agricultural ecosystems. These interactions can impact biodiversity and crop yields, as the presence of adaptable pests like *A. gossypii* has the potential to exacerbate pest infestation on economically crucial crops such as cotton, corn or soybean. By comprehending the mechanisms of host adaptation and the symbiotic relationships involved, more effective strategies could be devised to reduce the negative influence of *A. gossypii* on food production.

5 Conclusion

In conclusion, this article unveils the consequences of adaptation of *A. gossypii* to *S. nigrum* on their capacity for population growth and the abundance of dominant bacteria, while clarifying the function of *S. nigrum* in the host transition process of *A. gossypii*. The findings of this study offer valuable insights for the development of an innovative control technology system targeting *A. gossypii*, as well as advancing scientific and comprehensive methods for managing pests and weeds in fields.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: https://www.ncbi.nlm.nih.gov/, PRJNA1155176.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

PW: Formal analysis, Investigation, Writing – original draft. Y-XJ: Formal analysis, Investigation, Writing – original draft. Y-JM: Conceptualization, Supervision, Writing – original draft. DW: Investigation, Resources, Writing – original draft. Y-PS: Formal analysis, Writing – original draft. HH: Investigation, Software, Writing – original draft. CW: Data curation, Investigation,

Writing – original draft. X-PS: Methodology, Supervision, Writing – original draft. XR: Methodology, Validation, Writing – original draft. YM: Project administration, Writing – review & editing. XM: Funding acquisition, Writing – review & editing.

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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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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2024.1523123/full#supplementary-material

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