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Comparison of gut transcriptome and bacterial composition of the yellow peach moth, *Conogethes punctiferalis* larvae associated with host plants adaptation

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Abstract

The yellow peach moth, *Conogethes punctiferalis*, is one of the most destructive polyphagous pests to corn crops in the Huang-Huai-Hai summer corn region of China. However, little is known about the host plant adaptation mechanism of *C. punctiferalis*. In this study, we analyzed the performance of *C. punctiferalis* on two of its favorable host plants (corn and sorghum). Then, we used RNA-seq and 16S rRNA sequencing to explore the potential adaptation mechanism of *C. punctiferalis* on these two host plants. Results showed that *C. punctiferalis* gained more fresh weight on sorghum while its total lipid and triglyceride content was significantly lower than on corn. In total, 2155 genes weredifferentially expressed (DEGs) between corn and sorghum reared *C. punctiferalis*. Most of the DEGs were involved in nutritional biosynthesis and metabolism including amino acid biosynthesis, protein digestion and absorption, and glycolysis. Enzymatic analyses revealed that *C. punctiferalis* reared on corn had higher trypsin activity but lower P450 activity than that reared on sorghum. Meanwhile, *C. punctiferalis* reared on corn harbored more gut bacteria, while its diversity is lower than that reared on sorghum. The potential functional prediction of the gut bacteria revealed that nutritional metabolism functions were differently enriched between two host plants of *C. punctiferalis*. Taken together, these findings clarify the impact of host plants on the gene expression and gut bacteria in *C. punctiferalis*. They also suggest that the plasticity of gene expression and gut bacteria cooperatively contribute to insect host adaptation of insects.

Keywords *Conogethes punctiferalis*, Host plants adaptation, Transcriptional analyses, Gut bacteria

Introduction

The yellow peach moth, *Conogethes punctiferalis* (Guenée; Lepidoptera: Crambidae), is a severe agriculture pest in tropical and eastern Asia and Australia with a wide range of host plants (Lu et al. 2010; Li et al. 2015; Wang and Wang 2019). *Conogethers punctiferalis* has been reported to attack more than 120 plants including important crops like cotton, cocoa, orange, grapes, mango, apple, peach, pear, sunflower, guava, pomegranate, castor, mulberry, banana, sugarcane, corn, sorghum, zingibers, etc., belonging to diverse families

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and in India alone the insect attacks more than 35 plant species belonging to 19 families (Lu et al. 2010; Du et al. 2016; Wang and Wang 2019; Jing et al. 2020). However, the adaptation mechanism of this pest to different host plants is still unclear.

It has been a long-standing enigma of how phytophagous insects cope with various nutritive values and defensive allelochemicals from different host plants (Mathers et al. 2017; Scully et al. 2018; Amezian et al. 2021; Breeschoten et al. 2022). Genomic analyses of *Spodoptera frugiperda* indicated the expansion and widespread expression of the cytochrome P450 gene family might be involved in its polyphagia by degrading the plant's toxic defense chemicals (Xiao et al. 2020). Exposure to xenobiotic significantly induced the P450 gene expression (Amezian et al. 2021). Functional investigations about the CYP9A cytochrome P450 genes revealed that CYP9As could detoxify imperatorin and xanthotoxin, two plant defense compounds (Shi et al. 2023). Knockout of *CYP9As* by CRISPR-Cas9 made *S. frugiperda* more susceptible to these two plant phytochemicals (Shi et al. 2023). Besides P450 genes, other detoxification genes, such as glutathione S-transferases (GSTs) and UDP-glycosyltransferases (UGTs), are also involved in detoxifying plant defensive toxins (Amezian et al. 2021). In *Myzus persicae*, comparative genomic analyses and RNA interference-mediated functional investigations revealed that the rapid transcriptional plasticity contributed to its adaptation to diverged plant species (Mathers et al. 2017). A comprehensive analysis of the superfamilies of detoxification genes in the genus *Spodoptera* revealed the crucial role of detoxification genes in the adaptation to overcome plant defense mechanisms (Amezian et al. 2021). Thus, research is required on the contribution of detoxification genes to the plant adaption in *C. punctiferalis*.

The relationship between associated microbes and their host organisms has been of great research interest in recent years (Liu et al. 2020; Steele et al. 2021; Chen et al. 2022; Kang et al. 2022, 2024; Serrato-Salas and Gendrin 2022; Luo et al. 2023a, 2023b; Tian et al. 2023). Numerous studies have revealed that gut microbiota play important roles in insect-plant interactions (Engel and Moran 2013; Francoeur et al. 2020; Zhang et al. 2020). For example, the gut isolate *Enterobacter* sp. AZA_4_5 of *Trypoxylus dichotomus* showed highly efficient degradation ability on the bamboo lignocellulose (Huang et al. 2022). Gut symbiotic bacteria aid *Dendroctonus valens* to live on pine by degrading the pine phloem enriched deterrent carbohydrate D-pinitol (Liu et al. 2022). Similarly, gut microbiota can help the primary insect pest of coffee, *Hylobius abietis* degrade caffeine (Ceja-Navarro et al. 2015). Eliminating gut microbiota by antibiotic treatment significantly abolished the caffeine detoxification ability of *H. abietis*, thereby impairing its reproductive fitness (Ceja-Navarro et al. 2015). In Lepidoptera, the gut bacterial community is linked to host plants/diet. For example, Acetobacteraceae was the dominant bacteria in fruit-feeding *Grapholita molesta*, but its abundance in shoot-feeding *G. molesta* was lower than 1% (Liu et al. 2019). Yuan et al. (2021) also found that host diets influenced the gut bacteria composition of *G. molesta*. Antibiotic treatment significantly reduced the gut bacteria diversity, and affected the normal larval development and adult performance of *G. molesta* (Zhang et al. 2022b). Previous study had shown the bacteria composition of peach tree collected *C. punctiferalis* larvae, and the dominant gut bacteria of *C. punctiferalis* larvae were Enterobacteriaceae and Enterococcaceae (Liu et al. 2019). However, the impact of different host plants on the gut bacteria composition of *C. punctiferalis* is still unknown.

Corn and sorghum are two of the most frequently planted cereal crops in Shandong province and are heavily damaged by *C. punctiferalis*. This study originated from field monitoring conducted at the corn and sorghum experimental field station of Shandong Agricultural University in Tai'an, Shandong Province, China. Larvae from these two crops showed significant differences in fresh larval weight and lipid content. Comparative transcriptomic analysis revealed the potential roles of the differentially expressed genes related to nutritional and drug metabolism in the host adaption. Gut bacterial composition and functional classification analyses suggested that gut bacteria also contributed to the host adaption of *C. punctiferalis*. The findings of this study provides fundamental knowledge for analyzing the host adaption mechanism of *C. punctiferalis* to understand plant–insect interactions.

Materials and methods

Insects

All *C. punctiferalis* larvae were collected from the corn and sorghum experimental field of Shandong Agricultural University (Tai'an, Shandong Province, China). Two experimental fields are approximately 3 km apart and separated by cotton fields. The larvae were collected from two fields at first instars respectively, and were reared into 3rd instar using fresh corn or sorghum grains (25 °C, 60 ± 5% RH and 16L:8D).

Measurements of the weight and nutrients of *C. punctiferalis* larvae

Fresh weights of 3rd instar larvae of *C. punctiferalis* were weighted by electronic microbalance (Sartorius analystic, Germany; N = 18). Then, these *C. punctiferalis*

larvae were dried in an oven (Yiheng, Shanghai, China) at 60 °C for 72 h. After drying, dry weight was measured by electronic microbalance (Sartorius analystic, Germany; N = 18). Water content was calculated as: (fresh weight-dry weight)/fresh weight*100 (Chen et al. 2023).

The protein content of 3rd instar larvae of *C. punctiferalis* weas determined by the total protein assay kit (with standard: BCA method) (Cat No. A045-4–2; Nanjing Jiancheng Bioengineering Institute, Nanjing, Jiangsu, China) following the standard procedure. For the total lipid content measurement, fresh and dry weights of 3rd instar larvae of *C. punctiferalis* were measured as described above. After the fresh weighting, each larva was moved into a new Eppendorf tube with 500 µl of chloroform–methanol (2:1). All samples were homogenized and centrifuged at 2,600 g for 10 min. After the centrifugation, supernatants were discarded. The left pellets were re-homogenized with chloroform–methanol and centrifuged as described above. Finally, these pellets were dried and weighted. Total lipid content was calculated as (fresh weight-pellet weight)/dry weight (N = 18). The triacylglycerol content of the sorghum and corn reared *C. punctiferalis* larvae were analyzed using a triglyceride assay kit (Cat No. A110-2–1; Nanjing Jiancheng Bioengineering Institute, Nanjing, Jiangsu, China) following the manufacturer's protocol (Chen et al. 2023). Differences in weight and nutrients between the sorghum and corn-reared *C. punctiferalis* larvae were analyzed using Student's *t*-test at $P < 0.05$ (GraphPad Prism 8, GraphPad Software, Inc.; San Diego, CA, USA).

Transcriptome of *C. punctiferalis* larvae

Total RNA of the whole larval body (3rd instar) of the sorghum and corn-reared *C. punctiferalis* were extracted using RNAiso Plus (Cat No. 9109; Takara, Shiga, Japan) following the manufacturer's instructions (N = 3, 5 larvae per replicate). RNA integrity was assessed by 1% agarose gel. The quantity and quality of RNA were preliminarily determined by Nanodrop (Life Technologies, CA, USA). Three biological high-quality and quantity samples for each treatment were sent to Novogene Bioinformatics Technology Co., Ltd. (Beijing, China) for cDNA library construction and sequencing on the Illumina HiSeq 4000 sequencing platform (Illumina, Inc.; San Diego, CA, United States). All the bioinformatic analyses were conducted by Novogene Bioinformatics Technology Co., Ltd, as the previous paper described (Ye et al. 2024). The differentially expressed genes were determined based on the (fragments per kilobase per million reads (FPKM) values with *P*-value < 0.05 and $\log_2$foldchange > 1. Heatmaps in this study were constructed by pheatmap package in R 4.0.4 (http://www.r-project.org). RT-qPCR was used to verify the transcriptome results. Primers used in this study were provided as Table S1. RP49 was used as a reference gene (Jing et al. 2020). RT-qPCR was performed as our previous paper described (Chen et al. 2023). Four biological replicates were used, and cDNA from five *C. punctiferalis* larvae was set as a replicate for each treatment. Differences in the expression of selected genes were determined by Student's *t*-test at $P < 0.05$ (GraphPad Prism 8, GraphPad Software, Inc.; San Diego, CA, USA). The raw data of all transcriptome experiments has been deposited in the NCBI SRA database (BioProject ID: PRJNA1051371).

Measurements of the activities of trypsin, amylase, P450 and GSTs

Trypsin and amylase activities of corn and sorghum-reared *C. punctiferalis* larvae were measured with trypsin (Cat No. A080-2) and amylase (Cat No. C016-2–1) assay kit (Nanjing Jiancheng Bioengineering Institute, Nanjing, Jiangsu, China). P450 activities were determined by insect cytochrome P450 (CYP450) elisa kit (Shanghai Enzyme-linked Biotechnology Co., Ltd., Shanghai, China). GSTs activities were measured using glutathione S-transferase (GSH-ST) assay kit (Colorimetric method) (Cat No. A004-1; Nanjing Jiancheng Bioengineering Institute, Nanjing, Jiangsu, China). All the measurements of trypsin, P450 and GSTs activities were conducted according to the standard protocol of these kits. Student *t*-test was used to analyze the differences in trypsin, P450 and GSTs activities between corn and sorghum-reared *C. punctiferalis* larvae ($P < 0.05$).

Gut bacterial community analyses

Total DNA of gut bacteria from corn and sorghum reared *C. punctiferalis* larvae were extracted by sodium dodecyl sulfate (SDS) method as our previous paper described (Liu et al. 2022). All the reagents used in this experiment were filtered with sterile 0.22 µm filter to remove the environmental bacteria contamination. The total gut bacterial loads of corn and sorghum-reared *C. punctiferalis* larvae were determined by qPCR using universal 16S rRNA primers (F: TCCTACGGGAGG CAGCAGT; R: GGACTACCAGGGTATCTAATCCTG TT) and reference gene RP49 primers (Liu et al. 2022; Jing et al. 2019, 2020).

Besides measuring the total gut bacterial loads, we also conducted the 16S rRNA amplicon metagenomic sequencing in Novogene Bioinformatics Technology Co., Ltd. (Beijing, China). The sequencing libraries were constructed using NEBNext® Ultra™ IIDNA Library Prep Kit (Cat No. E7645; New England Biolabs, Inc., MA, USA), and then these libraries were sequenced on an Illumina NovaSeq platform (Illumina, Inc.; San Diego, CA, United States). FLASH (Version 1.2.11), the fastp

(Version 0.20.0) and Vsearch (Version 2.15.0) were used to emerge and qualify filter the paired-end reads. QIIME2 was used for the species annotation, phylogenetic relationship, alpha diversity, and beta diversity of the gut bacterial community of corn and sorghum-reared *C. punctiferalis* larvae. LEfSe analysis was performed using the LEfSe software (Version 1.0). Potential functions of the gut bacteria were predicted with the PICRUSt2 (Version 2.1.2-b). The raw 16S rRNA transcriptome data has been deposited in NCBI SRA database (BioProject ID: PRJNA1051534). The correlation and RDA/CCA analyses between transcriptomics data and 16S rRNA was performed using the OmicShare tools, a free online platform for data analysis (http://www.omicshare.com/tools).

Results

The biological performance of *C. punctiferalis* larvae on different host plants

The fresh weights of sorghum-fed *C. punctiferalis* larvae were significantly heavier than that of corn-fed *C. punctiferalis* larvae (Fig. 1a, t = 2.276, $P = 0.0293$), while there was no difference in the dry weight between them (Fig. 1b, t = 1.229, $P = 0.2274$). The total lipid (Fig. 1c, t = 2.139, $P = 0.0397$) and TAG (Fig. 1d, t = 4.386, $P = 0.0118$) contents in corn-reared *C. punctiferalis* larvae were significantly higher than that in sorghum reared *C. punctiferalis* larvae. No difference was observed in protein (Fig. 1e, t = 0.5647, $P = 0.6024$) and water (Fig. 1f, t = 0.9359, $P = 0.3559$) content between the sorghum and corn-reared *C. punctiferalis* larvae.

Identification and functional classification of DEGs for *C. punctiferalis* larvae reared on different host plants

To investigate the potential molecular mechanism in response to different host plants, we analyzed the differentially expressed genes (DEGs) using transcriptome. In total, 48,470 unigenes were obtained, and the mean length was 1045 (Table S2, Supporting Information). 1015 genes were predominately expressed in sorghum-fed *C. punctiferalis* larvae, while 1140 genes were significantly highly expressed in corn-fed *C. punctiferalis* larvae (Fig. 2a). The difference clustering result showed that there were nine clusters (Fig. 2b). Based on the KEGGs annotation of these DEGs, nutritional biosynthesis and metabolism pathways were enriched including biosynthesis of amino acids, protein digestion and absorption,

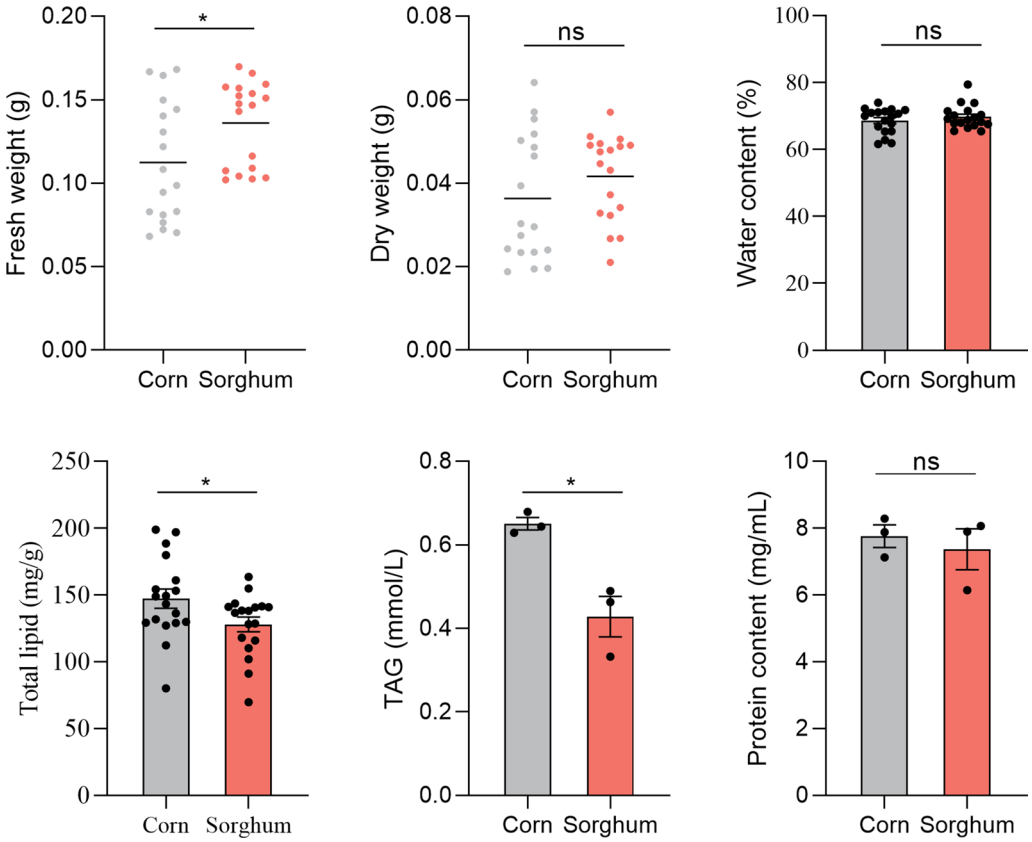

Fig. 1 Body weight and nutritional accumulation analyses of *C. punctiferalis* larvae reared on different host plants

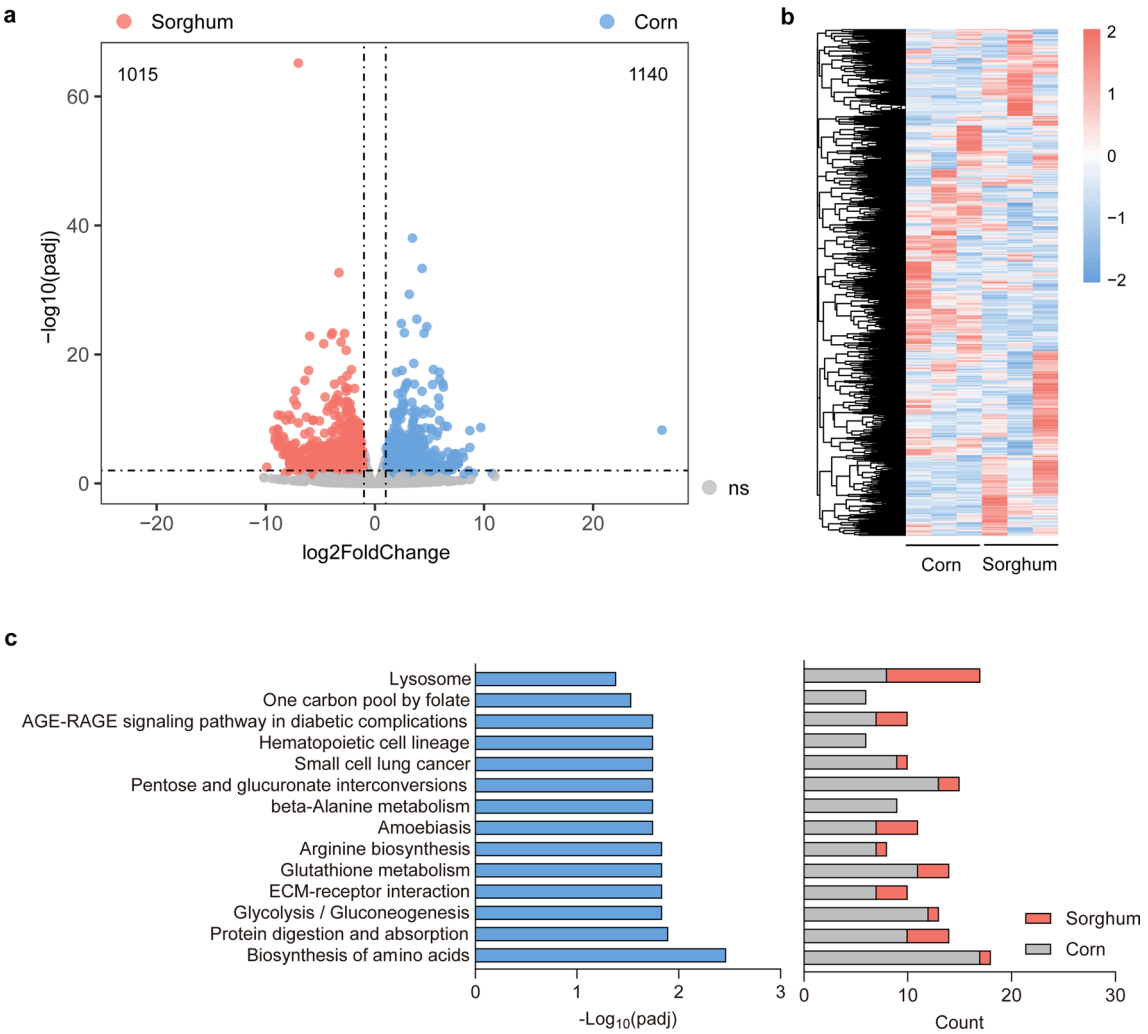

Fig. 2 Transcriptome analysis of corn and sorghum reared *C. punctiferalis* larvae. **a** Vocano plot of differentially expressed genes (DEGs). **b** Hierarchical clustering analysis of DEGs in corn and sorghum reared *C. punctiferalis* larvae. **c** The distribution of pathways of DEGs annotated in KEGG

glycolysis/gluconeogenesis and arginine biosynthesis (Fig. 2c).

As for genes involved in amino acid synthesis and glycolysis, almost all these DEGs were significantly higher expressed in corn reared *C. punctiferalis* except Cluster-8561.19676 (Fig. 3a) and Cluster-8561.19907 (Fig. 3b). Three unigenes were annotated as amylase genes and differentially expressed between corn and sorghum reared *C. punctiferalis* larvae (Fig. 3c). As our prior results showed that *C. punctiferalis* larvae reared on corn had higher lipid and TAG contents, our transcriptome results also indicated significantly higher expression of major lipid metabolism genes in corn-fed *C. punctiferalis* larvae compared to sorghum-fed *C. punctiferalis* larvae (Fig. 3d). Several genes involved in protein digestion and absorption were highly expressed in corn-fed *C. punctiferalis* larvae than sorghum-fed larvae (Fig. 3e). Consistent with that, trypsin activity also showed higher activity in corn-fed *C. punctiferalis* larvae (Fig. 3f). Furthermore, corn-fed *C. punctiferalis* larvae have significantly higher amylase activity than sorghum-fed *C. punctiferalis* larvae (Fig. 3g-i).

Twenty-four genes involved in the detoxification showed significantly higher expression levels in corn-fed *C. punctiferalis* larvae, while eighteen detoxification genes were predominately expressed in sorghum-fed *C. punctiferalis* larvae (Fig. 4). Furthermore, sorghum-fed *C. punctiferalis* larvae also presented higher P450 activity than corn reared *C. punctiferalis* larvae (Fig. 4i, $t=2.903$, $P=0.044$). There was no difference in GST activity between them (Fig. 4j, $t=2.18$, $P=0.0948$).

Only 21 chemosensory genes were differentially expressed between corn and sorghum-fed *C. punctiferalis* larvae including 3 odorant-binding proteins (OBPs,

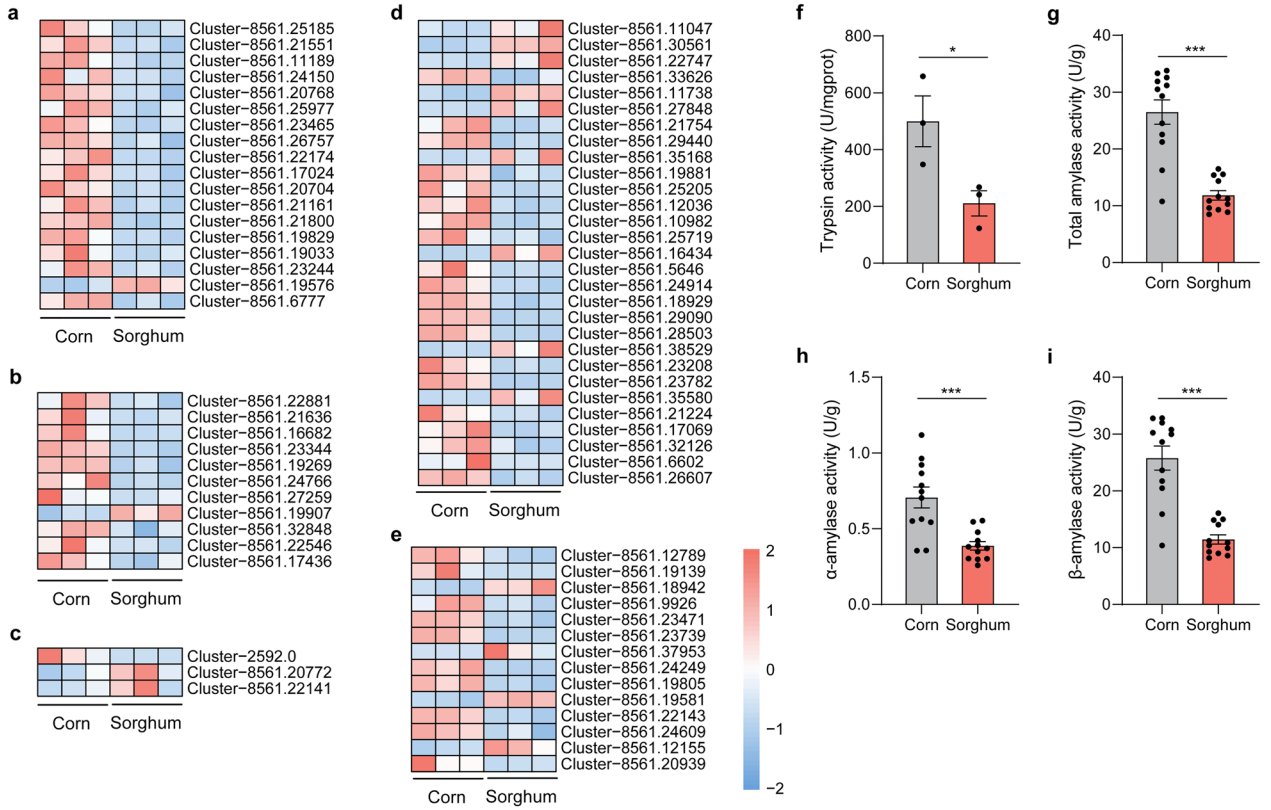

Fig. 3 Heatmap of the genes involved in nutritional metabolism of *C. punctiferalis* larvae response to different host plants. **a** Biosynthesis of amino acids. **b** Glycolysis/Gluconeogenesis. **c** Starch metabolism. **d** Lipid metabolism. **e** Protein digestion and absorption. **f** Trypsin activity. **g** Total amylase activity. **h** α-amylase activity. **i** β-amylase activity. *means $P < 0.05$, ***means $P < 0.001$ (Student's *t* test)

Fig. 5a), 5 chemosensory proteins (CSPs, Fig. 5b), 2 sensory neuron membrane proteins (SNMPs, Fig. 5c), 2 odorant receptors (ORs, Fig. 5d), 2 gustatory receptors (GRs, Fig. 5e) and 7 inotropic receptors (IRs, Fig. 5f). RNA-seq results were verified by qRT-PCR of several selected genes (Fig. S1, Supporting Information).

Effects of host plants on the gut bacterial community

Gut bacterial load in corn-fed *C. punctiferalis* larvae was significantly higher than that in sorghum-fed *C. punctiferalis* larvae (Fig. 6a). Gut bacterial diversity was measured by four alpha diversity indices including Chao1 (Fig. 6b), Simpson (Fig. 6c), Shannon (Fig. 6d) and observed OTUs (Fig. 6e). Chao1 (Fig. 6b), Shannon (Fig. 6d) and observed OTUs (Fig. 6e) showed no significant difference between corn and sorghum reared *C. punctiferalis* larvae. Sorghum-fed *C. punctiferalis* larvae showed higher bacterial diversity than corn reared *C. punctiferalis* larvae based on the Simpson indexes (Fig. 6c). Beta diversity analysis revealed that there was an obvious difference in gut bacterial community between corn and sorghum-fed *C. punctiferalis* larvae (Fig. 6f). The relative abundances of the top 10 bacteria showing bacterial community structure at genus level (Fig. 6g; Fig. S2, Supporting Information). Both corn and sorghum-fed *C. punctiferalis* larvae were dominated by Enterococcus (Fig. 6g). Abundance of bacteria from the genera of *Enterococcus* in corn-fed *C. punctiferalis* larvae was relatively higher than that in sorghum-fed *C. punctiferalis* larvae, while the relative abundance of the genera *Klebsiella*, *Enterobacter*, *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* and *Pantoea* showed significantly higher abundance in sorghum reared *C. punctiferalis* larvae (Fig. 6g). Consistent with the relative abundance of bacteria at the genus level, 12 bacteria taxa in Proteobacteria were enriched in sorghum-fed *C. punctiferalis* larvae (Fig. 6h; Fig. S2, Supporting Information). Five bacteria taxa in Firmicutes were enriched in corn reared *C. punctiferalis* larvae (Fig. 6h; Fig. S3, Supporting Information). Potential functional prediction of gut bacteria showed gut bacteria in corn-fed *C. punctiferalis* larvae preferred to participate in nutritional metabolism. In contrast, the gut bacteria in sorghum-fed *C. punctiferalis* larvae are predominately involved in toxic detoxification (Fig. S3, Supporting Information).

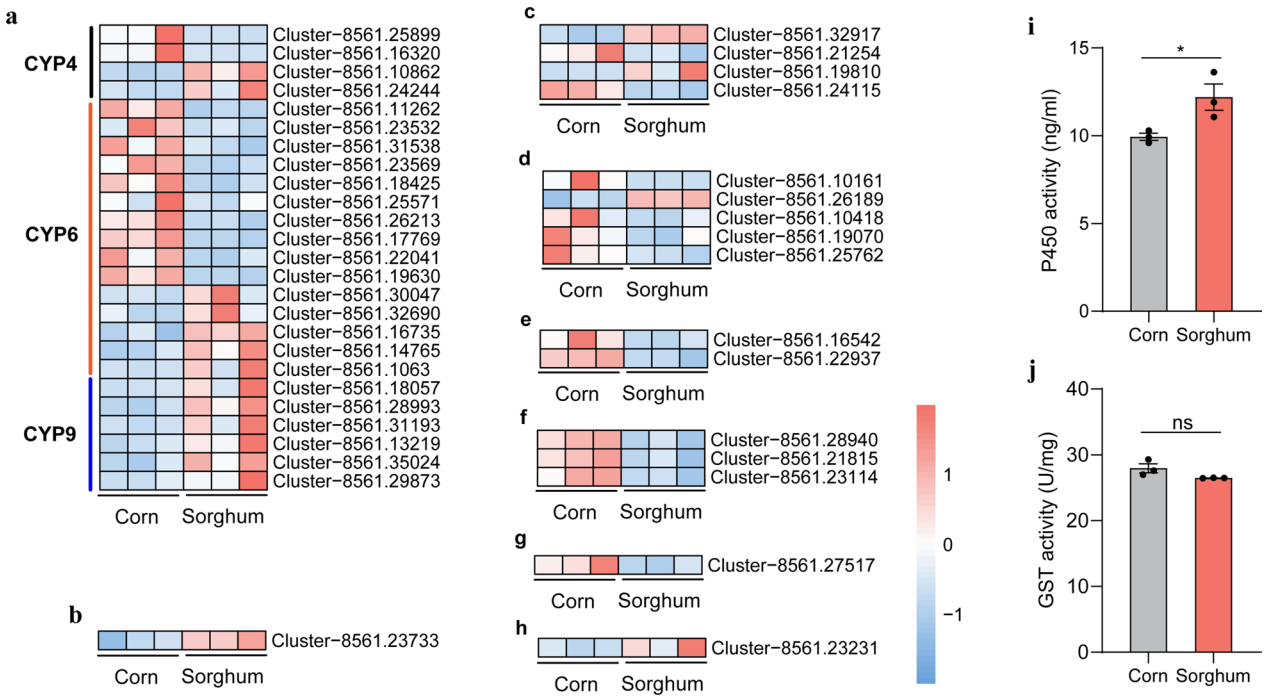

Fig. 4 Heatmap of normalized FPKM of DEGs related to detoxification **a**–**h** and enzymatic activities of P450 **i** and GST (j). **a** cytochrome P450. **b** indole-3-acetaldehyde oxidase. **c** glutathione S-transferase. **d** UDP-glucuronosyltransferase. **e** uridine phosphorylase. **f** dihydropyrimidine dehydrogenase (NADP +). **g** ATP-binding cassette. **h** xanthine dehydrogenase. *in **a**–**h** means $\log_2$foldchage > 1 and $P < 0.05$. *in **i** means $P < 0.05$, and ns in **j** means no significant deference

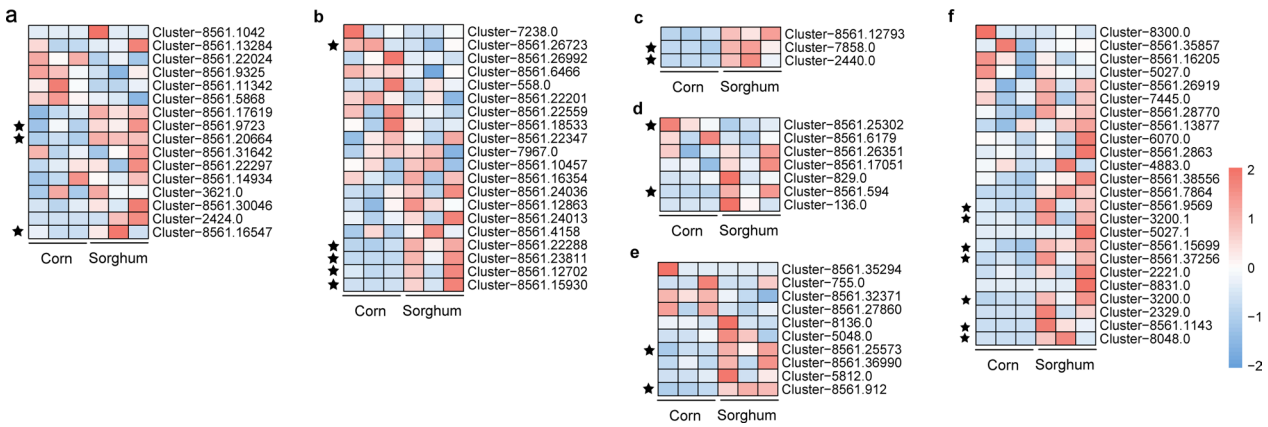

Fig. 5 Heatmap of the chemosensory genes in *C. punctiferalis* larvae associated with different host plants. **a** OBPs. **b** CSPs. **c** SNMPs. **d** odorant receptors. **e** gustatory receptors. **f** ionotropic receptors

Integrative analysis of transcriptome and 16S rRNA sequencing.

The correlation between the gene expression and gut bacteria abundance showed a positive correlation between Enterococcus and gene involved in nutritional metabolism (Fig. 7a). On the contrary, *Pantoea* was negatively correlated with the expression of nutritional related genes (Fig. 7a). *Enterobacter* exhibited higher positive correlation with genes related to lipid metabolism and detoxification especially CYP9 (Fig. 7a, b). *Tsukamurella* had no significant correlation with genes involved in nutritional metabolism but positive correlation with genes in the cluster of CYP9 (Fig. 7b). Acinetobacter are mainly negatively correlated with genes related to nutritional metabolism and detoxification (Fig. 7a, b). Redundancy (RDA) analysis was used to analyze the correlation

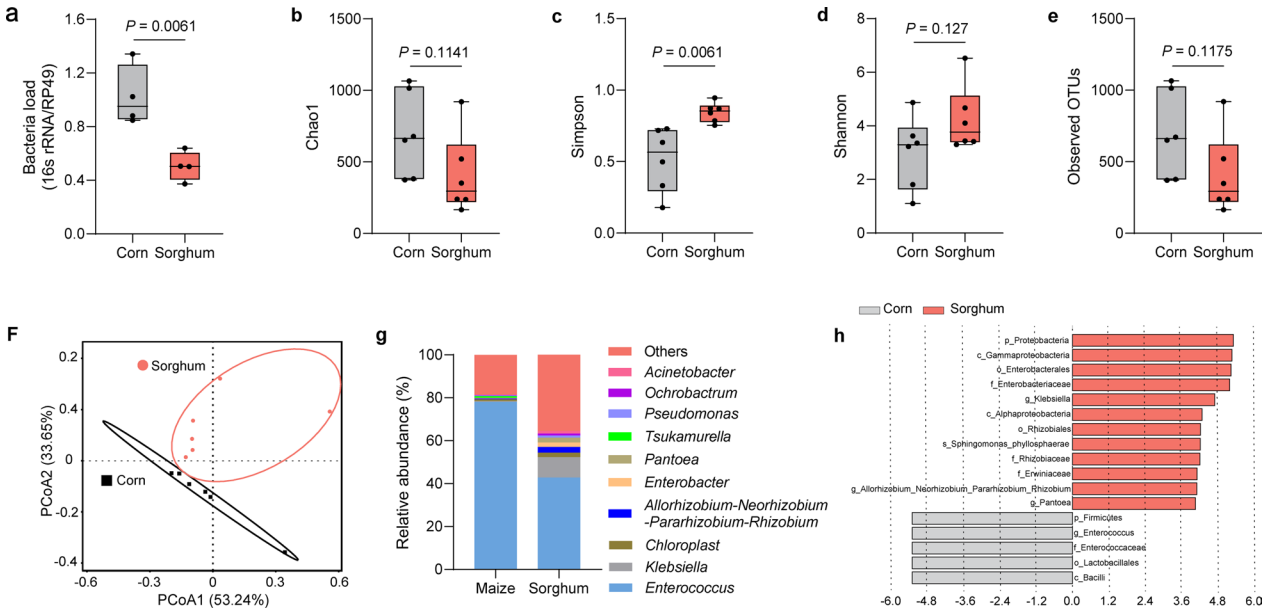

Fig. 6 Comparison of gut bacterial abundance and diversity between corn and sorghum reared *C. punctiferalis* larvae based on 16S rRNA sequencing data. **a** Microbiome load. **b**–**e** Scatterplots representing Chao1 (**b**), Simpson (**c**), Shannon **d** and Observed OTUs (**e**). **f** Principal coordinates analysis (PCoA) of beta diversity based on weighted UniFrac distances representing the differences between corn and sorghum reared *C. punctiferalis* larvae. **g** Relative abundance of top 10 bacteria showing bacterial community structure at genus level. **h** LEfSe Bar diagram for different host plant reared *C. punctiferalis* larvae with LDA scores higher than 2.0. A higher LDA score represents that this bacterial taxon has a greater contribution to the differences

with the gene expression and the abundance of gut bacteria (Fig. 7c). Genes expression of sorghum-fed *C. punctiferalis* larvae positively correlated with the abundance of *Chloroplast*, *Enterobacter*, *Pantoea*, *Pseudomonas*, *Ochrobacterium*, *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium*, *Acinetobacter* and *Klebsiella* but negative correlated with the abundance of *Enterococcus* and *Tsukamurella* (Fig. 7c). Similar to that, major genes involved in nutritional metabolism showed positive correlation with the abundance of *Enterococcus* and *Tsukamurella* based on the 20 features (Fig. 7c). Rest of the top 10 gut bacteria positively correlated with three genes related to detoxification and two genes involved in nutritional metabolism within the 20 features (Fig. 7c).

Discussion

C. punctiferalis is one of the most economically important polyphagous insect pests damaging over than 100 plants (Lu et al. 2010). Even it has broad range of hosts, due to the differences of nutritive values and plant allelochemicals, the performance of *C. punctiferalis* on different host plants varied widely (Lu et al. 2010; Li et al. 2015; Rodriguez-Saona et al. 2016; Wang and Wang 2019; Tang et al. 2020). Li et al. (2015) and Chen et al. (2018) found *C. punctiferalis* larvae reared on corn performed better than on plum, apple, pear, and peach. Consistent with that, Tang et al. (2020) found that corn had the highest fitness among the selected host plants, including corn, soybean, cotton and peach. In this study, we found *C. punctiferalis* larvae fed on sorghum growth heavier than that fed on corn. However, it reserved more energy resources as higher lipid and TAG contents were observed in corn-fed *C. punctiferalis* larvae. In insects, lipid is one of the major energy sources for growth and survival. In *Nilaparvata lugens*, fed on resistant rice significantly decreased the lipid and TAG content, and the lipid composition of *N. lugens* fed on resistant and susceptible rice plants was different (Zhang et al. 2018; Zheng et al. 2020). Transcriptome analyses suggested that feeding on resistant plants influenced the expression of genes involved in lipid metabolism, resulting in a lower content of lipids (Zheng et al. 2020; Li et al. 2022). Similarly, in this study, we also found different host plants altered the expression of genes related to lipid metabolism. Twenty of 29 differentially expressed lipid-related genes presented higher expression in corn-fed *C. punctiferalis* larvae. In addition, previous studies have shown that corn is more suitable for *C. punctiferalis* than other host plants, and corn grains had higher lipid content than sorghum grains (Li et al. 2015). Research about the field experiment of *Eoreuma loftini* demonstrated that corn could be used as a "trap" crop to divert the *E. loftini* away from sorghum.

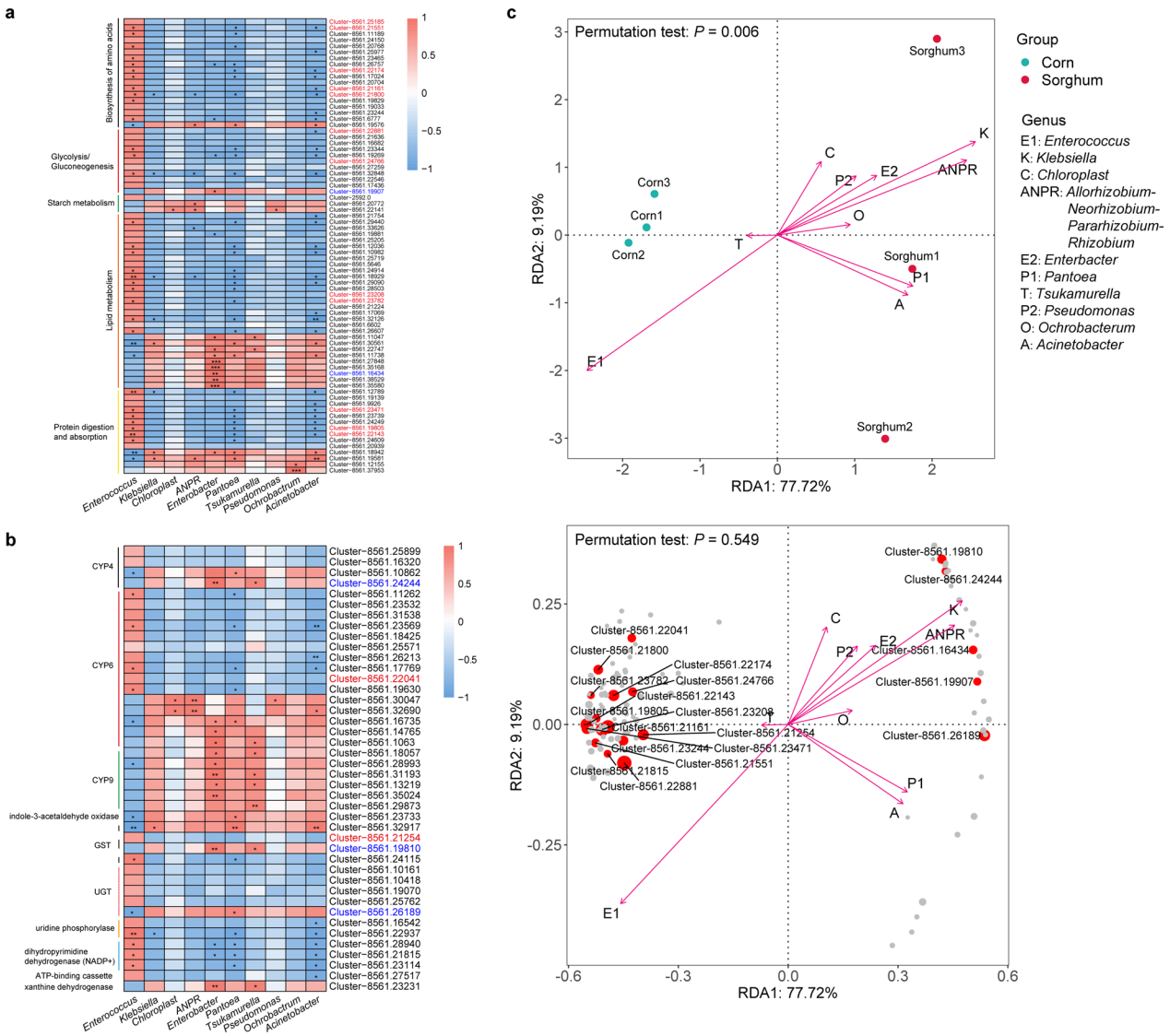

Fig. 7 Integrated analysis of transcriptomics and 16S rRNA gene sequencing. **a** Correlation analysis between the expression of genes related to nutritional metabolism and the relative abundance of gut bacteria (top 10 most abundance genus) using pearson method. ANPR: *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium*. **b** Correlation analysis between the expression of genes related to detoxification and the relative abundance of gut bacteria (top 10 most abundance genus) using pearson method. **c** RDA analysis of the expression of genes related to nutritional metabolism and detoxification, and the relative abundance of gut bacteria (top 10 most abundance genus) with 20 features. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$

Additionally, the functional prediction of 16 s rRNA results also showed that these microbial communities in maize fed *C. punctiferalis* enriched in Beta-ketoacyl reductase that is a component of the fatty acid elongase required for the biosynthesis of very long chain fatty acids, and acetyl-CoA carboxylase, which is the first committed step pf lipid biosynthesis (Fig. S4 b and c). Taken together, these results suggested that *C. punctiferalis* larvae fed on corn had better fitness and reserved more lipids by influencing the expressions of lipid-related genes and gut bacteria community.

Based on the KEGG enrichment analyses, different host plants significantly influenced genes linked with amino acid, carbohydrate and protein metabolism. Several DEGs related to amino acid (17 of 18), carbohydrate (10 of 11) and protein metabolism (11 of 14) were up-regulated by feeding on corn. Consistent with that, the trypsin protease activity of corn fed *C. punctiferalis* larvae was also significantly higher than

that of sorghum-fed pests. Trypsin protease is one of the major gut proteolytic enzymes (Li et al. 2017). In *Spodoptera litura* and *Anticarsia gematalis*, inhibition of trypsin activity significantly decreased the larval body weight and survival of early instar larvae (Bhattacharyya et al. 2007; de Almeida Barros et al. 2020). Similarly, knockdown of trypsin-like protease genes resulted in slower growth (shorter in body length and lower body weight) in *Bactrocera dorsalis* larvae (Li et al. 2017). Previous nutritionally analyses of corn and sorghum grains showed that sorghum has relatively higher carbohydrate content than corn, but lower crude protein content that corn (Dharmaputra et al. 2012; Langa et al. 2016). Correspondingly, corn-fed *C. punctiferalis* larvae had higher the amylase activity than sorghum-fed *C. punctiferalis* larvae. Thus, these results suggested *C. punctiferalis* larvae might be able to modulate their digestive enzyme activities and nutritional metabolism systems to get enough nitrogen and carbon resources from different host plants.

Sorghum is widely recognized for its high concentration of bioacitive compounds in both its leaves and seeds. It is important to note that certain bioactive compounds are toxic or act as deterrents to insect herbivores (Dicko et al. 2005; Kariyat et al. 2019). For example, triterpenoids with insecticidal activity are rich in sorghum leaf waxes but absent from corn (Busta et al. 2021). Dhurrin is another plant defensive compound in sorghum (Tattersall et al. 2021; Cheng et al. 2013; Yadav et al. 2023). Synthesis of dhurrin in *Arabidopsis thaliana* by transgenic biotechnology increased its resistance to *Phyllotreta nemorum* by reducing the leaf mining of its larvae and increasing larval mortality (Tattersall et al. 2021). In this study, the P450 activity of sorghum-fed *C. punctiferalis* larvae was significantly higher than corn-fed larvae. More interestingly, the potential function prediction of gut bacteria also showed a higher enrichment of GST in sorghum fed *C. punctiferalis* larvae than corn fed larvae. All these results suggested that *C. punctiferalis* may alter its detoxification gene expression and gut bacteria composition to cope with the plant's defensive secondary metabolites, thereby improving its performance.

As mentioned earlier, corn and sorghum contain varied nutritional conditions and defensive allelochemicals. Gut bacteria have been identified to be involved in insects' nutrition and toxins metabolism (Pelloquin et al. 2021; Liu et al. 2022; Šigutová et al. 2023). Our growth performances suggested corn is a better host than sorghum for *C. punctiferalis*. Consistent with that, the bacteria load of *C. punctiferalis* fed on corn was considerably higher than that of *C. punctiferalis* fed on sorghum. On the contrary, the diversity of the gut bacteria of *C. punctiferalis* fed on corn was significantly lower than that of *C. punctiferalis* fed on sorghum. *Enterococcus* was the dominant bacteria member in both corn and sorghum-fed *C. punctiferalis*, while it has a relatively higher abundance in corn-fed *C. punctiferalis*. RDA analysis also suggested that *Enterococcus* positively correlated with the expression of genes involved in nutritional metabolism. In animal breeding and apiculture, *Enterococcus* strains are often used as probiotics (Zheng et al. 2016; Costa Sousa et al. 2019; Du et al. 2021). Colonization of *Enterococcus faecium* in microbiota-free *Aphis mellifera* significantly increased its gut weight (Du et al. 2021). Similarly, the dominant bacterium *Enterococcus innesii* also modulated the metamorphosis of *Galleria mellonella* (Kong et al. 2023). The relative abundance of *Klebsiella* showed a tremendous increase in sorghum-fed *C. punctiferalis*. In previous studies, *Klebsiella* can degrade plant secondary compounds, various insecticides and environmental toxins, which suggested that *Klebsiella* might be involved in the detoxification of sorghum bioactive compounds in *C. punctiferalis* (Kwon et al. 2002; Elshikh et al. 2022; Zhang et al. 2022a). A recent study showed that plant pathogenic *Penicillium* infection in apples significantly enhanced the fitness of *C. punctiferalis* (Li et al. 2024). Based on the gut bacterial community and gene expression analyses, it was speculated that this beneficial contribution may be due to the alteration of gut bacteria and gene expression (Li et al. 2024). Taken together, our findings suggested that feeding on different host plants affects gene expression, bacterial structure, and diversity of *C. punctiferalis* larvae, which ultimately contribute to the host adaptation gut in *C. punctiferalis*.

In conclusion, our results showed that *C. punctiferalis* larvae obtained more energy resources but had lower fresh weights. The comparative transcriptome analyses revealed differentially expressed genes related to nutrition metabolism and detoxification systems. Gut bacterial composition and functional prediction also showed cooperation with host genes. Currently, it is unclear whether *C. puntiferalis* is capable of adapting to different plants or if different plants impact its physiology and alter its gut bacteria.

Supplementary Information

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Supplementary Material 1. Fig. S1 qRT-PCR verification of the transcriptome results. *means $P < 0.05$. Fig. S2 Relative abundance of top 10 bacteria showing bacterial community structure at genus level. Fig. S3 Cladogram indicates the phylogenetic distribution of microbial communities between corn and sorghum reared *C. punctiferalis* larvae. Yellow nodes represent microbial taxa with no significant difference between different host plant reared larvae, while red and green nodes represent microbial taxa that are significantly enriched in corn (red) and sorghum (blue) reared

C. punctiferalis larvae respectively. Fig. S4 Prediction of KEGG functions of gut bacteria involved detoxification (a), lipid metabolism (b and c), glycolysis (d-f) and biosynthesis of amino acid (g-j) within top 35. Table S1 Primers used in this study. Table S2 Summary of the transcriptome of corn and sorghum reared *C. punctiferalis* larvae.

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Author contributions
YG, MJ, SL, SW and YZ performed the experimental trial. YG, MJ and SL conceived of the study, analyzed data and interpreted results. YG, MJ, FL and ZK wrote the paper. YX, ZC, JS, FL and ZK reviewed the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials
The transcriptome sequence data has been deposited in NCBI SRA database (BioProject ID: PRJNA1051371 for RNA-seq and PRJNA1051534 for 16S rRNA sequencing).

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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