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Research Article

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A Sorghum-Rice-Barley diet reshapes maternal gut microbiota and metabolites in sows to improve lactation efficiency and neonatal piglet growth

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Abstract: Maternal nutrition during late gestation and lactation profoundly influences the development of porcine offspring. This study investigated the effects of replacing a conventional corn – soybean meal diet (CON) with a sorghum – rice – barley (SRB) diet on sow lactation performance, maternal gut microbiota, and fecal metabolites, as well as on metabolic profiles in neonatal piglets. A total of 56 second-parity PIC hybrid sows were randomly assigned into two dietary treatment groups from day 112 of gestation until day 21 of lactation, with 28 sows per group. The SRB diet was formulated to have the same net energy content as the CON diet but with more fiber and slightly less crude protein. Compared to the CON group, sows on the SRB diet had significantly greater litter weight ($P = 0.021$) and individual piglet weight ($P = 0.010$) at weaning, as well as higher piglet average daily gain ($P = 0.070$). Microbial 16S rDNA sequencing revealed that the SRB diet increased the abundance of fiber-fermenting bacteria, including *Subdoligranulum*, *Megasphaera*, and *Coprococcus* ($P < 0.05$). Metabolomic analysis showed that the SRB diet significantly altered fecal metabolites associated with the serotonergic-synapse, bile-secretion, and phenylpropanoid-biosynthesis pathways. Notably, maternal fecal levels of 2-N-propylthiazolidine-4-carboxylic acid, N-hydroxy-L-tyrosine, and carnosol were positively correlated with concentrations of these metabolites in piglet plasma, suggesting potential vertical metabolite transfer. In conclusion, dietary inclusion of SRB positively reshapes maternal gut microbiota and metabolite profiles, consequently improving lactation efficiency and neonatal piglet growth. These effects may be partially mediated by the maternal microbiota – metabolite axis and the potential transfer of bioactive compounds from sows to offspring.

Key words: Maternal nutrition; Lactation efficiency; Gut microbiota; Fiber-rich diet; Sow

1 Introduction

Nutritional management of sows during late gestation and lactation is crucial for optimizing reproductive performance, milk production, and the growth of neonatal piglets (Liu et al., 2021). During these periods, the maternal gut microbiome undergoes substantial remodeling, including shifts in microbial composition and in metabolic outputs such as short-chain fatty acids (SCFAs), bile acids, and aromatic metabolites (Koketsu et al.,

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2017, Costermans et al., 2020). Microbially derived metabolites have been reported to cross the maternal intestinal barrier, enter circulation, and in part be secreted into colostrum and milk, thereby potentially shaping neonatal physiology via the maternal microbiota-metabolite-milk axis (Wang et al., 2022, Chen et al., 2024, Le Bourgot et al., 2024, Tang et al., 2025). Thus, the maternal gut microbiome plays a key role in perinatal programming beyond its digestive function.

In hyperprolific sows, nutritional and microbial support is particularly important because large litter sizes increase metabolic demands during lactation and heighten the risk of energy deficits and health issues (Tokach et al., 2019, Ferreira et al., 2021). Dietary strategies such as fermentable fiber or probiotics have been shown to enrich beneficial bacteria, enhance gut integrity, and promote metabolites with anti-inflammatory and energy-supporting roles (Tian et al., 2020, Law et al., 2024). For example, inulin supplementation has been found to increase the Firmicutes-to-Bacteroidetes ratio in the maternal gut microbiota, reduce neonatal diarrhea incidence, and improve piglet growth (Paßlack et al., 2015, Li et al., 2021). Probiotic interventions have demonstrated dual benefits for both sows and their litters, increasing the abundance of *Lactobacillus* and *Bifidobacterium* while reducing colonization by potential pathogens (Zhu et al., 2022, Ma et al., 2023).

Most nutritional interventions for sows have focused on individual dietary additives. However, reformulating the basal diet by incorporating alternative cereal grains remains a relatively unexplored strategy. Conventional corn-soybean-meal diets are nutritionally balanced but are increasingly constrained by sustainability challenges and volatile ingredient costs. Alternative grains such as sorghum, rice, and barley offer complex polysaccharides and phytochemicals that serve as substrates for hindgut microbial fermentation, potentially enhancing microbial diversity and function (Moen et al., 2016, González-Ortiz et al., 2020, Pan and An, 2020). Such cereal-based diets may enhance microbial diversity, increase SCFA production, and generate metabolites beneficial to gut and systemic health. However, the ability of these alternative grain diets to modulate the maternal microbiota-metabolite axis and improve neonatal outcomes remains poorly characterized.

In this study, we employed an integrative multi-omics strategy to assess the effects of a sorghum-rice-barley (SRB) diet on maternal gut microbiome and fecal metabolite profiles, and their downstream impact on lactation performance and neonatal growth. Late-gestation PIC hybrid sows were fed a diet in which corn and soybean meal were replaced with sorghum, rice, and barley. We characterized the changes in the sow fecal microbiome and metabolome using 16S rDNA sequencing, untargeted metabolomics, and short-chain fatty-acid quantification. Additionally, we analyzed metabolites in piglet plasma to explore metabolic relationships between the sows and their offspring. We hypothesized that the SRB diet would improve lactation efficiency and neonatal piglet growth by modulating the maternal microbiota-metabolite axis.

2 Materials and methods

2.1. Animal ethics statement

This study was carried out in accordance with the guidelines for animal welfare, and all experimental procedures involving animals were approved by the Institutional Animal Care and Use Committee of Huazhong Agricultural University (approval number HZAUSW-2025-0020).

2.2 Animals and experimental treatments

The experimental diets were formulated based on NRC (2012) recommendations for lactating sows, assuming second-parity sows weighing 210 kg and nursing 12 piglets (average initial weight: 1.4 kg). The diets were balanced with crystalline amino acids (lysine, methionine, threonine, tryptophan, and valine) to maintain consistent standardized ileal digestible (SID) amino acid ratios (100:53:63:19:84). Ingredients and nutritional composition are detailed in Table 1 and Supplementary Table 1. The feed was fed as wet mash. Antibiotics were not administered during the study period.

2.3 Diets and feeding management

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2.4 Measurement of backfat, fecal consistency, and lactation performance of sows

Backfat thickness at position P2 (65 mm off the midline at the second-to-last rib) was measured on days 1 and 21 postpartum using ultrasound (Renco89372, USA). Fecal consistency was assessed at 7:00 AM on days 1, 7, and 21 postpartum using a standardized five-point scoring system (1 = hard, dry feces; 5 = watery diarrhea; see Supplementary Table 2 for details). Lactation performance was assessed by recording sow feed intake and piglet growth. Individual piglet weights were recorded on days 1 and 21 of lactation to calculate average daily gain (ADG). Sow total feed intake was also recorded to calculate average daily feed intake (ADFI).

2.5 Collection and analysis of sow fecal samples and piglet plasma samples

2.5.1 Fecal and plasma sample collection

On days 7 and 21 of lactation, we collected fresh fecal samples from eight randomly selected sows per group. To minimize environmental contamination, only the internal portion of the feces was collected and homogenized for bacterial DNA analysis. The samples were immediately snap-frozen in liquid nitrogen and stored at -80°C until further processing. Concurrently, venous blood samples were obtained from the anterior vena cava of eight piglets per group on days 7 and 21 of age (one piglet per litter, corresponding to the sows from which fecal samples were taken). Blood samples were allowed to clot at room temperature for 30 min, centrifuged at 3000 *g* for 15 min to separate plasma, and stored at -80°C for subsequent metabolomic analysis.

2.5.2 Analysis of sow gut microbiota

Microbial DNA was extracted from fecal samples using the QIAamp DNA Stool Mini Kit (Qiagen, Germany) according to the manufacturer's instructions. The bacterial 16S rRNA genes were amplified using primers targeting the V3-V4 regions. Universal primers 338F and 806R were used for PCR amplification of the V3-V4 hypervariable regions of 16S rRNA genes (338F, 5′-ACTCCTACGGGAGGCAGCA-3′; 806R, 5′-GGACTACHVGGGTWTCTAAT-3′). We then sequenced amplicons on an Illumina MiSeq platform to analyze the composition and diversity of the gut microbiota. Bioinformatics processing of sequencing data involved trimming of low-quality reads. Sequences were then clustered into amplicon sequence variants (ASVs) using DADA2. Next, we obtained the ASV unique representative sequences. Chimeras were filtered out by UCHIME (v4.2.40); ASV representative sequences were taxonomically classified using Ribosomal Database Project (RDP) Classifier v.2.2 trained on the database. Alpha and beta diversity analyses were conducted using QIIME2 and visualized using Principal Coordinates Analysis (PCoA). Differences between groups were assessed by permutational multivariate analysis of variance (PERMANOVA, 9,999 permutations, $P < 0.001$) based on Bray-Curtis distances. Differential bacterial features were identified using linear discriminant analysis (LDA) effect size (LEfSe) analysis (LDA threshold > 3, $P < 0.05$). Microbial functional profiles were predicted by PICRUSt2. We deposited the raw sequences of gut microbiota from sows at 7 and 21 days postpartum in the

National Center for Biotechnology Information (NCBI) under accession number PRJNA1232412.

2.5.3 Piglet plasma metabolomics

Plasma samples were analyzed for metabolomic profiling using liquid chromatography-mass spectrometry (LC-MS). Samples were prepared by mixing 100 μL of plasma with 400 μL of acetonitrile to precipitate proteins. The mixture was vortexed, rested at 4°C for 10 minutes, and centrifuged at 10000 *g* for 15 minutes. The supernatant was transferred to a new tube and evaporated to dryness under nitrogen. The residue was reconstituted in 100 μL of 50% methanol, and 10 μL was injected into the LC-MS system. Metabolites were annotated based on mass-to-charge ratio (m/z), retention time, and spectral similarity against a curated library. Where available, we confirmed identity using authentic standards. Data were processed using MetaboAnalyst software to perform multivariate statistical analyses (Pang et al., 2022).

2.5.4 Determination of short-chain fatty acids in fecal samples

Fecal SCFAs (acetic acid, propanoic acid, butanoic acid, valenic acid, hexanoic acid, isobutyric acid, isovaleric acid, and isohexanoic acid) were quantified by gas chromatography. In brief, 1 g of fecal samples was weighed into a 2-mL centrifuge tube, followed by the addition of 1 mL methanol. After being vortexed for 60 s, each sample was centrifuged at 12000 *g* at 4 °C for 10 min. The supernatant was transferred to a centrifuge tube (2 mL) and mixed with 20% solution of 25% metaphosphoric acid. After 30 min at 4 °C, the tubes were centrifuged at 12000 *g* at 4 °C for 10 min. 1 μl of the supernatant was injected into an Agilent 8890-7000D. Calibration curves (0 - 500 μg/mL) were used for quantification.

2.6 Statistical analysis

We performed statistical analysis and results visualization using GraphPad Prism software (v 8.0), R (v 4.2.3) and Excel 2021. Prior to statistical analysis, all data were tested for normality of distribution using the Shapiro-Wilk test. A nonparametric Kruskal-Wallis test was used to determine the alpha diversity indices of bacterial communities and the relative abundance of gut microbiota. We assessed data on short-chain fatty acids by one-way analysis of variance (ANOVA) with Tukey's post hoc test. Significance is presented as $^*P < 0.05$, and $^{**}P < 0.01$. All data are represented as mean ± SEM.

3 Results

3.1 Sorghum-rice-barley diet enhanced lactation performance and piglet growth

The SRB diet did not affect sow body condition or daily feed intake (Table 2). Backfat thickness at days 1 and 21 postpartum was comparable between the groups ($P > 0.80$), as was backfat loss during lactation ($P = 0.806$). Average daily feed intake during lactation was similar ($P = 0.490$). The post-weaning estrus return rate, however, was numerically higher in the SRB group. Fecal scores were improved with SRB: sows had firmer stools on day 7 ($P = 0.003$), with a trend toward improvement already observable on day 1 ($P = 0.061$). Litter birth weights were similar (~21.4 kg), but at weaning, SRB litters weighed significantly more ($P = 0.021$). SRB piglets also gained more weight daily ($P = 0.070$), resulting in heavier individual weaning weights ($P = 0.010$). These results indicated enhanced lactation efficiency in SRB-fed sows without negative impacts on sow condition.

3.2 Sorghum-rice-barley diet reshaped maternal gut microbiota

16S rDNA sequencing revealed increased microbial richness in SRB sows at day 7 (according to the Chao1 index, an estimator of species richness) (Fig. 2A), whereas overall diversity remained unchanged (according to the Shannon index, which reflects species richness and evenness) (Fig. 2B). Principal coordinate analysis

(PCoA) showed modest separation between the groups (PERMANOVA, $P < 0.05$; Fig. 2C). Taxonomic profiling identified significant diet-associated shifts in bacterial taxa (Fig. 2D). Ten genera with relative abundance > 0.1% exhibited significant differences, with eight enriched in the SRB group: *Megasphaera, Solobacterium, Lachnospiraceae AC2044 group, Subdoligranulum, Coprococcus, Olsenella, Muribaculaceae*, and *Marvinbryantia* (day 7 and/or day 21 postpartum). In contrast, no genera were significantly more abundant in CON sows at day 7 compared to SRB sows. By day 21, *Treponema* and *Anaeroplasma* were significantly decreased in SRB sows. LEfSe analysis at the species level showed that SRB sows were characterized by higher abundances of *Muribaculaceae, Lachnospiraceae*, and *Megasphaera* at day 7, and that *Subdoligranulum* and *Marvinbryantia* were prominent at both time points (Fig. 2E-F).

To further investigate the metabolic potential of the microbiota affected by the SRB diet, we conducted PICRUSt2-based functional prediction of MetaCyc pathways using 16S rRNA gene-sequencing data (Fig. 2G). Several microbial pathways were differentially enriched between the SRB and CON groups at days 7 and 21 postpartum. Among the most enriched pathways in SRB-fed sows were those involved in carbohydrate fermentation and lipid biosynthesis, including L-1,2-propanediol degradation, lactose and galactose degradation I, and mevalonate pathway I. These changes suggest greater microbial adaptation to fiber-rich substrates from sorghum, rice, and barley. In contrast, pathways associated with amino acid degradation, such as L-histidine degradation II and L-tryptophan degradation to 2-amino-3-carboxymuconate, were markedly downregulated in the SRB group, particularly at day 21 (fold change < 0.75). This indicates reduced proteolytic fermentation with the lower-protein SRB diet. Additionally, the ADP-L-glycero-β-D-manno-heptose biosynthesis pathway, involved in bacterial outer membrane structure, was consistently elevated in SRB sows at both time points, potentially reflecting a shift toward more robust and fermentative microbial populations. These functional predictions were consistent with the observed increases in fiber-fermenting bacteria in the SRB group.

3.3 Sorghum-rice-barley diet altered sow fecal metabolomic profiles

To investigate functional consequences of these microbiota changes, we performed untargeted metabolomic analysis of sow fecal samples. Multivariate analysis revealed a diet-associated divergence in the fecal metabolomic profile. Fecal samples from the SRB and CON groups formed clearly separated clusters in the PCA score plot at both day 7 and day 21 postpartum (Fig. 3A). Compared with the CON group, sows in the SRB group exhibited a significantly higher number of differentially expressed metabolites: 350 upregulated and 176 downregulated at day 7 (Fig. 3B, Supplementary Table 3), and 424 upregulated and 178 downregulated at day 21 (Fig. 3C, Supplementary Table4, VIP > 1, $P < 0.05$; FC > 1.2 or < 0.83). Notably, 318 metabolites were consistently upregulated at both time points in the SRB group, indicating sustained metabolic shifts associated with the dietary intervention (Fig. 3D). Pathway-enrichment analysis revealed that these upregulated metabolites were associated with several key metabolic processes, including diterpenoid biosynthesis (e.g., gibberellic acid, gibberellin A8 and A29, ginkgolide A), serotonergic synapse signaling (e.g., 5-hydroxy-L-tryptophan, prostaglandin E2, leukotriene C4), type II polyketide product synthesis (e.g., tetracycline, aclacinomycin S), phenylpropanoid biosynthesis (e.g., isoformononetin, sinapic acid, esculetin), toluene degradation, and bile secretion. In contrast, only 11 metabolites were consistently downregulated in SRB-fed sows (Fig. 3F), mainly those associated with bile secretion (e.g., morphine-6-glucuronide, pravastatin, methotrexate) and sphingolipid metabolism (e.g., dihydroceramide, SM(D18:0/18:0)).

Integration of microbiota and metabolome data using MetOrigin 2.0 (Yu et al., 2024) revealed that 13 out of 27 KEGG-annotated metabolites were of microbial origin (Supplementary Fig. 1). Further correlation analysis between altered microbial genera and fecal metabolites revealed distinct patterns. Upregulated metabolites in the SRB group exhibited significant positive correlations with fiber-fermenting genera enriched in SRB-fed sows, such as *Megasphaera*, *Subdoligranulum*, and *Lachnospiraceae AC2044*. Conversely, metabolites enriched in CON sows correlated with genera more abundant in that group (Fig. 4). *Treponema* abundance was positively correlated with 5-hydroxy-L-tryptophan levels, suggesting that the SRB diet promoted serotonin precursor synthesis via specific microbial pathways. Similarly, *Anaeroplasma* abundance correlated with tetracycline levels, indicating possible microbially mediated production of antibiotic-like compounds. Negative correlations between certain bacterial genera and sphingolipid-related metabolites in CON sows further suggested that the SRB diet reduced lipid-associated metabolic pathways in the gut.

3.4 Sorghum-rice-barley diet altered maternal fecal short-chain fatty acids

Short-chain fatty acids (SCFAs) are major end-products of fiber fermentation and can contribute to host energy and intestinal health. At day 7 postpartum, sows fed the SRB diet tended to have numerically higher concentrations of acetic (Fig. 5A), propionic (Fig. 5B), butyric (Fig. 5C), valeric (Fig. 5D), hexanoic (Fig. 5E), and isovaleric acid (Fig. 5G) compared to the CON group, although group differences were not statistically significant ($P > 0.05$). By day 21, no significant differences in SCFA concentrations were observed between the two groups. Within-group comparisons over time showed that isohexanoic acid levels significantly declined from day 7 to day 21 in both groups (Fig. 5H, $P < 0.05$), while isobutyric acid levels remained stable (Fig. 5F, $P > 0.05$). Other SCFAs did not exhibit significant time-dependent changes within groups. To explore potential microbial drivers of SCFA profiles, we performed Spearman correlation analysis between SCFA levels and the abundance of differential genera (Fig. 5I). Isohexanoic acid was negatively correlated with *Muribaculaceae, Lachnospiraceae AC2044, Coprococcus,* and *Subdoligranulum*. In contrast, isobutyric acid showed positive correlations with *Muribaculaceae, Lachnospiraceae AC2044, Olsenella, Coprococcus, Megasphaera, Subdoligranulum*, and *Marvinbryantia*. Hexanoic acid and *Olsenella, Megasphaera, Coprococcus,* and *Marvinbryantia*. Propionic acid and *Muribaculaceae, Lachnospiraceae AC2044*, and *Olsenella*. These results suggest that specific fiber-fermenting genera may influence SCFA synthesis and partially account for the modest SCFA elevation trends observed in SRB-fed sows.

3.5 Sorghum-rice-barley diet altered piglet plasma metabolome

To determine whether maternal dietary effects extended to the offspring, we analyzed the plasma metabolomic profiles of piglets nursing from CON or SRB-fed sows. Given that piglets consumed only sow milk by day 21, observed plasma metabolite differences were likely reflective of maternal dietary effects. Beta diversity analysis showed no clear separation between SRB and CON groups at either day 7 or day 21; however, a marked distinction was observed between 7- and 21-day-old piglets, indicating dynamic age-related metabolic shifts (Fig. 6A). At day 7, 43 metabolites were significantly upregulated and 8 downregulated in the SRB group versus CON (Fig. 6B, Supplementary Table 5). Significant upregulated metabolites included (S)-abscisic acid, 2-N-propylthiazolidine-4-carboxylic acid, sebacoyl-L-carnitine, 3,4-dimethylhippuric acid, carnosol, and N-hydroxy-L-tyrosine. At day 21, 12 metabolites were significantly upregulated and 80 downregulated in SRB versus CON piglets (Fig. 6C, Supplementary Table 6). Among these, 2-N-propylthiazolidine-4-carboxylic acid, (S)-abscisic acid, sebacoyl-L-carnitine, and N-propylthiazolidine-4-carboxylic acid remained significantly elevated in the SRB group. Seven metabolites were consistently altered at both time points, including solasodine, 3,4-dimethylhippuric acid, carnosol, N-hydroxy-L-tyrosine, 2-N-propylthiazolidine-4-carboxylic acid, sebacoyl-L-carnitine, and (S)-abscisic acid. Of these, three (2-N-propylthiazolidine-4-carboxylic acid, N-hydroxy-L-tyrosine, and carnosol) were also identified in sow feces (Fig. 6D), suggesting potential maternal-offspring metabolite transfer. To explore this further, we plotted the relative abundance of these three overlapping metabolites between sow feces and piglet plasma (Fig. 6E). Positive correlations were observed, particularly for 2-N-propylthiazolidine-4-carboxylic acid, indicating that increased maternal fecal levels were associated with increased plasma levels in piglets. These findings support the hypothesis that certain bioactive metabolites generated in the maternal gut were transferred to offspring, potentially via lactation, and influenced neonatal metabolism.

4. Discussion

This study shows that a sorghum﹣rice﹣barley (SRB) diet, which is higher in fiber and slightly lower in protein than the conventional corn﹣soybean diet, can alter the maternal gut microbiota and fecal metabolite profile over the course of the lactation period. Ultimately, these diet-induced changes appear to enhance lactation performance and neonatal piglet growth. Despite similar feed intake and body condition in both groups, sows on the SRB diet weaned heavier litters with faster-growing piglets, strongly suggesting improved milk production and/or quality. Although milk yield and composition were not directly measured, the ~9% increase in individual piglet weaning weight in the SRB group suggests more efficient nutrient transfer through lactation. These performance improvements are likely mediated by physiological and metabolic effects of the SRB diet, particularly its capacity to alter gut microbial composition and fermentation outcomes.

Sows fed the SRB diet exhibit higher fecal abundance of several SCFA-producing bacterial taxa, including *Subdoligranulum*, *Marvinbryantia*, *Megasphaera*, *Lachnospiraceae*, and *Olsenella*. These bacteria are known fiber fermenters capable of producing butyrate, propionate, and acetate (Zhang et al., 2019, Oh et al., 2021). Similar enrichment of butyrate-producing genera has been reported in sows supplemented with inulin (Li et al., 2021) and lactating sows fed fiber-rich diets (Tian et al., 2020), supporting the robustness of our findings. For example, *Megasphaera* elsdenii ferments lactate into a broad range of SCFAs (Mutuyemungu et al., 2024), while *Subdoligranulum* produces butyrate as a major metabolic end-product (Van Hul et al., 2020). Although total fecal SCFA concentrations did not differ significantly between the two groups, upward trends in butyrate, acetate, and propionate, together with increased abundance of known SCFA-producing bacteria, suggest that actual production may have been higher in SRB-fed sows but not fully captured in fecal measurements due to rapid absorption (Van de Wouw et al., 2018). The increased abundance of SCFA-producing taxa suggests improved fiber fermentation and greater availability of energy-yielding metabolites, which may contribute to higher milk output. Such potential increases in SCFA production are biologically meaningful, given their established roles in intestinal and systemic physiology.

Short-chain fatty acids, particularly butyrate, support gut-barrier function, modulate immune response, and provide energy to colonocytes (Van de Wouw et al., 2018). An increase in butyrate-producing Lachnospiraceae AC2044 and Marvinbryantia may reinforce intestinal integrity and reduce inflammation during the peripartum period, a time of heightened physiological stress. Improved gut health could enhance nutrient absorption, allowing nutrients to be partitioned more efficiently toward milk synthesis. Moreover, metabolites related to serotonergic synapses, such as 5-hydroxy-L-tryptophan, are enriched in SRB-fed sows. This pattern may reflect increased serotonin synthesis in the gut, since SCFAs are known to stimulate enterochromaffin cells to produce serotonin. Serotonin promotes gut motility and secretion, which could potentially reduce constipation in late gestation—a known risk factor for prolonged farrowing and stillbirths (Bellono et al., 2017). The combined elevation of SCFA- and serotonin-associated metabolites suggests that the SRB diet improves gastrointestinal comfort and function during the peripartum period, indirectly supporting lactation performance.

Additionally, untargeted fecal metabolomic analysis revealed that several metabolic pathways were enriched in the SRB-fed sows, notably pathways related to bile secretion, diterpenoid metabolism (plant secondary metabolites), and phenylpropanoid biosynthesis. These changes suggest interactions among the diet's constituents, the gut microbiome, and the host's digestive physiology. Enhanced fecal "bile-secretion" pathway activity suggests an increase in bile acids or related metabolites. High-fiber diets can increase bile-acid turnover by binding bile in the gut and promoting its excretion, which in turn stimulates new bile synthesis (Singh et al., 2019, Fuchs and Trauner, 2022). Indeed, pigs on high-fiber diets show greater bile flow and increased fecal bile loss (Wilfart et al., 2007, Hu et al., 2023). In our study, the upregulation of bile-related metabolites suggests that the SRB diet prompts sows to secrete more bile into the intestine. Ample bile flow improves fat emulsification and digestion, ensuring that sows extract energy from the diet more efficiently to support the high-energy demands of lactation. Beyond digestion, bile acids also act as signaling molecules via FXR and TGR5 receptors, influencing glucose and lipid metabolism as well as hormone releasing in the gut (Li and Chiang, 2014). Although we did not measure circulating bile acids, the SRB-driven shift in bile acid metabolism may contribute to improved metabolic health in the sows. This finding is consistent with reports that soluble fiber can modulate bile-acid metabolism and thereby lower circulating lipid levels, potentially reducing metabolic stress during lactation (Tian et al., 2020)

The SRB diet's impact on diterpenoid and phenylpropanoid metabolism likely reflects the rich array of phytochemicals in sorghum, rice bran, and barley. For example, sorghum contains phenolic compounds (such as tannins and flavonoids) and a cyanogenic glycoside (dhurrin) derived from L-tyrosine (Xiong et al., 2019). Similar observations have been reported in broilers, where rosemary-derived diterpenoids improved antioxidant status and gut health (Wang et al., 2024), highlighting the cross-species relevance of plant polyphenols. Pathway analysis identified N-hydroxy-L-tyrosine (an intermediate in sorghum’s dhurrin biosynthesis) among the differentiating metabolites. This finding indicates that unique plant-derived compounds from the SRB diet enter the hindgut and are metabolized there. The gut microbiota can transform dietary polyphenols and terpenoids into bioactive metabolites (phenylpropanoids, for instance, are a class of aromatic plant compounds). Many of these microbial metabolites have antioxidant, antimicrobial, or anti-inflammatory properties that could further shape the gut microbial community and benefit the host (Catalkaya et al., 2020, Gade and Kumar, 2023). A prime example is carnosol, a diterpenoid polyphenol that we detected at higher concentrations in the feces of SRB-fed sows. Carnosol is typically found in herbs like rosemary (Johnson, 2011). Its presence in our samples suggests that it could originate from dietary plant-derived components or be generated through microbial transformation of dietary precursors, although the experimental diets themselves were not directly analyzed for carnosol content.. Notably, carnosol is a potent antioxidant that activates the Nrf2 pathway, thereby reducing oxidative stress and improving intestinal barrier function (Yan et al., 2018, Islam et al., 2023). Previous studies in pigs and poultry have shown that carnosol and related rosemary compounds can protect intestinal epithelial cells and alleviate heat stress and oxidative stress (Wang et al., 2024). Thus, the SRB diet appears to either directly supply such protective metabolites or induce their production in the sow’s gut. These metabolites are known to possess antioxidant and anti-inflammatory properties. While oxidative stress parameters were not measured in this study, it is plausible that such compounds contribute to improved maternal physiological resilience during lactation. Furthermore, plant polyphenols and their microbial metabolites might suppress pathogenic bacteria while favoring beneficial ones, thereby reinforcing the positive shifts observed in the microbiota. In summary, the enrichment of phenolic and terpenoid metabolic pathways in SRB-fed sows suggests a functional link in which dietary phytochemicals are converted into compounds (such as N-hydroxy-L-tyrosine, carnosol, and others) that enhance antioxidant capacity, modulate the microbiome, and support a sow’s physiological resilience during lactation.

Importantly, several metabolites identified in sow feces were also detectable in the plasma of suckling piglets, with significant positive correlations between maternal fecal levels and piglet plasma levels. This finding aligns with earlier work showing vertical transfer of milk-derived metabolites (Hojgaard et al., 2020; Le Bourgot et al., 2024). Given that the neonatal piglets in this study depended entirely on sow’s milk, the most likely route of transfer is through the milk. Phenolic compounds consumed by lactating mothers have been found in their milk and can be delivered to nursing infants (Zhang et al., 2015). In livestock, sow milk is known to contain diverse metabolites (fatty acids, amino acids, vitamins, etc.), and its composition can be influenced by the sow’s diet (Smink et al., 2010). The presence of carnosol in milk is plausible, since some plant antioxidants are absorbed by the sow and can partition into milk fat (López-Yerena et al., 2022). Our data suggest that bioactive metabolites such as 2-N-propylthiazolidine-4-carboxylic acid, N-hydroxy-L-tyrosine, and carnosol are indeed transferred from sow to piglet via milk.

This transfer of metabolites to piglets could have functional implications for their development. For instance, 2-N-propylthiazolidine-4-carboxylic acid (a thiazolidine-carboxylate) acts as a cysteine prodrug with hepatoprotective antioxidant effects in mammals (Roberts et al., 1987, Ni et al., 2022). It has been shown to improve oxidative damage in the liver by releasing cysteine, which in turn boosts glutathione production(Srinivasan et al., 2001). If piglets receive this compound through the milk, it might improve their antioxidant status or support the development of their liver function in early life. Carnosol, as discussed, is a strong inducer of cellular antioxidant responses via Nrf2, in addition to its antimicrobial and anti-inflammatory properties. Its presence in piglet plasma could help fortify the piglets' gut epithelial defenses and immune system, potentially reducing neonatal morbidity or enhancing growth. These hypotheses are supported by analogous findings on other diets. For example, when sows are fed antioxidant-rich diets or supplements (such as herbs or oils), their piglets often show improved antioxidant capacity and lower markers of oxidative stress (Meng et al., 2018). While our study did not directly measure piglet health parameters beyond growth, the observed correlations between maternal fecal metabolites and piglet plasma levels suggest a potential maternal influence on offspring metabolism, possibly mediated via milk transfer. In essence, the SRB diet not only shapes the maternal gut microbiome and its metabolic outputs but also likely influences neonatal metabolism through transfer of specific microbially derived metabolites. This maternal–offspring metabolic connection represents a novel mechanism by which dietary interventions in sows may enhance the early development and performance of piglets.

Thus, we were able to confirm our hypothesis in a very promising way; however the study does have some limitations. Milk and colostrum composition were not directly measured, omics analyses were performed on subsets of animals, and the use of 16S rRNA sequencing limited functional resolution. Moreover, the trial was conducted in a single-farm setting, which may affect generalizability. Our future work will therefore focus on direct profiling of colostrum and milk, tracer studies to confirm maternal–milk–offspring metabolite transfer, and validation of the benefits of the SRB diet under different farm conditions. From a practical standpoint, sorghum, rice, and barley are promising alternatives to corn and soybean meal. Defining optimal inclusion levels and evaluating feed cost, sow performance, piglet growth, and environmental impact will provide the basis for evidence-based recommendations for commercial application.

5. Conclusions

In conclusion, the SRB diet for sows increased the abundance of *Subdoligranulum*, *Marvinbryantia*, *Megasphaera* and other fermentative bacteria. Coupled with increased production of SCFAs, neuroactive compounds, and antioxidants, this provides a plausible mechanistic basis for the improved lactation performance and piglet growth we observed. The diet appears to contribute to a more favorable gut environment characterized by enriched fermentative bacterial populations and increased production of bioactive metabolites. Although butyrate, bile acids, and oxidative stress were not directly quantified, the metabolomic and microbiota data suggest improvements in gut function and host-microbiome interactions. This dual influence on the mother's capacity to nourish and the quality of her milk highlights the critical role of maternal diets in animal production. These findings align with growing evidence that modulation of the maternal gut microbiome is a key strategy for improving piglet health and growth. Future research should aim to identify the specific components of the SRB diet (e.g., sorghum polyphenols, barley β-glucans, rice bran fiber) that drive microbial and metabolic changes, and clarify how these translate into alterations in milk composition. From an applied perspective, this study suggests that incorporating diverse, fiber-rich ingredients like sorghum, rice, and barley in sow diets represents a promising strategy to enhance both maternal productivity and offspring vitality via microbiome-mediated mechanisms. This mechanistic understanding reinforces the idea that sow nutrition should be formulated not just for basic nutritional needs, but also to favorably sculpt the maternal gut ecosystem and metabolic profile, thereby imparting lasting benefits to the next generation of pigs.

Data availability statement

The raw sequences of gut microbiota from sows at 7 and 21 days postpartum in the National Center for Biotechnology Information (NCBI) under accession number PRJNA1232412.

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Author contributions

Mei Shan and Qin Jiang performed the experimental research and data analysis, wrote and edited the manuscript. Qin Jiang and Xianghua Yan contributed to the study design, writing and editing of the manuscript. All authors read and approved the final manuscript and, therefore, had full access to all the data in the study and take responsibility for the integrity and security of the data.

Compliance with ethics guidelines

Mei Shan, Xianghua Yan, and Qin Jiang declare that they have no conflict of interest. All experimental procedures involving chickens were approved by the Institutional Animal Care and Use Committee of Huazhong Agricultural University (approval number: HZAUSW-2025-0020).

Table 1 Ingredient composition and calculated nutrient levels of lactation diets (as-fed basis)

Item	CON1) Group	SRB2) Group
Ingredient composition, as-fed basis, %		
Corn (8.0% protein)	67.62	-
Sorghum 3)	-	25.00
Barley	-	25.00
Extruded Full-fat Soybean	10.00	-
Broken Rice	-	25.00
Soybean Meal (43%)	19.16	16.60
Sunflower Meal	-	3.50
Calcium Hydro Phosphate	1.46	1.31
Calcium Carbonate	0.92	1.05
Soybean Oil	0.12	1.50
L-Lysine HCl (98.5%)	0.12	0.29
L-Threonine (98.5%)	-	0.08
Valine (98%)	0.05	0.12
Salt	0.35	0.35
Mineral and Vitamin Mix 4)	0.20	0.20
Total	100	100
Calculated net energy, kcal/kg	2520	2520
Analyzed nutrient contents, %		
Dry Matters	89.50	90.26
Crude Protein	17.50	16.00
Crude Fiber	2.95	3.45
Ether Extract	5.55	4.38
Calcium	0.80	0.80
Total Phosphorus	0.60	0.60
Soluble Dietary Fiber	0.73	1.37
Insoluble Dietary Fiber	11.92	8.29
Total Dietary Fiber	12.65	10.74
Starch	43.64	49.68
SID5)-Lysine	0.85	0.85
SID-Methionine + Cystine	0.53	0.53
SID-Threonine	0.63	0.63
SID-Tryptophan	0.19	0.19
SID-Valine	0.84	0.84

1) CON = control diet, corn﹣soybean meal-based.

2) SRB = sorghum﹣rice﹣barley-based diet.

3) Sorghum tannin: 0.02% (US origin).

4) Premix provided per kg diet: Minerals: Cu 30 mg; Fe 160 mg; Zn 160 mg; Mn 55 mg; I 0.5 mg; Se 0.5 mg; Co 0.8 mg; Cr 0.2 mg; Vitamins: Vitamin A 14000 IU; Vitamin D3 2900 IU; Vitamin E 120 mg; Vitamin K3 6mg; Vitamin B1 2.4 mg; Vitamin B2 8.5mg; Vitamin B6 4.5 mg; Vitamin B12 0.03 mg; Biotin 0.55mg; Pantothenic acid 30mg; Folic acid 5mg; Nicotinamide 50mg.

5) SID = standardized ileal digestible.

Table 2 Effects of dietary treatment on sow performance and piglet growth during lactation

	Treatments			
	CON1) Group	SRB2) Group	SEM6)	*P*-Value
Sow Performance				
Parity	2	2		
Backfat thickness [mm]				
d 13)	13.41	13.53	0.55	0.830
d 214)	12.38	12.4	0.44	0.963
Backfat loss [mm]	1.03	1.13	0.40	0.806
Average daily feed intake (d 1 to d 21) [kg/d]	5.52	5.39	0.18	0.490
Mating rate within 7 days post-weaning [%]	86.67	93.33		
Fecal score				
d 1	3.36	3.03	0.17	0.061
d 75)	3.78	3.32	0.15	0.003
d 21	3.39	3.36	0.16	0.823
Litter Performance				
Litter size [n]				
d 1	14.03	14.03	0.17	0.999
d 21	12.64	12.68	0.33	0.913
Litter weight [kg]				
d 1	21.41	21.38	0.62	0.956
d 21	62.98	69.35	2.67	0.021
Litter weight gain [g/d]				
d 1 to 21	2291	2590	113	0.011
Individual piglet weight [kg]				
d 1	1.52	1.54	0.04	0.726
d 21	4.99	5.44	0.17	0.010
Individual piglet weight gain [g/d]				
d 1 to 21	181.5	204.1	8.12	0.070

1) CON = control, conventional corn-soybean based diet

2) SRB = sorghum rice and barley -based diet.

3) Day 1 postpartum.

4) Day 7 postpartum.

5) Day 21 postpartum.

6) SEM = standard error of the mean.

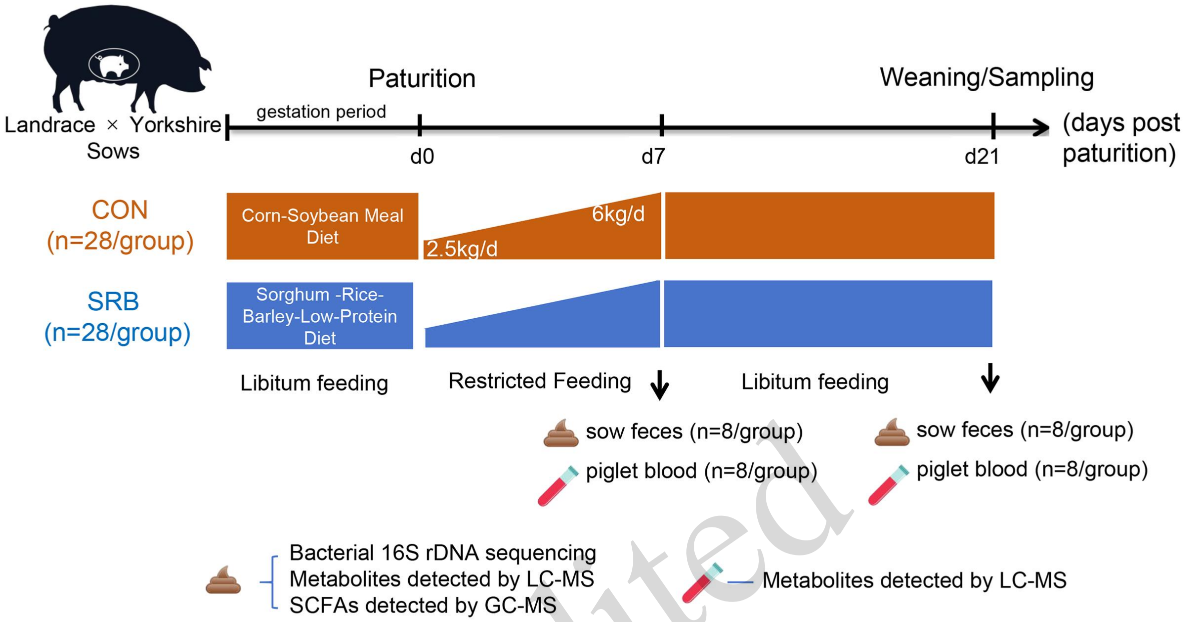

Fig. 1. Schematic overview of the experimental timeline and sample-collection strategy.
Twenty-eight sows per group were fed either a control corn-soybean meal diet or the sorghum-rice-barley (SRB) low-protein diet. Diets were provided at 2.5 kg/day during gestation (restricted feeding) and ad libitum (up to ~6 kg/day) during lactation (day 0 to 21 postpartum). Fecal samples (n = 8 sows/group) and blood samples from piglets (n = 8/group) were collected on days 7 and 21 of age (which corresponds to days 7 and 21 postpartum). Fecal microbiota were analyzed by 16S rDNA sequencing, fecal metabolites by LC–MS, and fecal short-chain fatty acids (SCFAs) by GC–MS. Piglet plasma metabolites were analyzed by LC–MS.

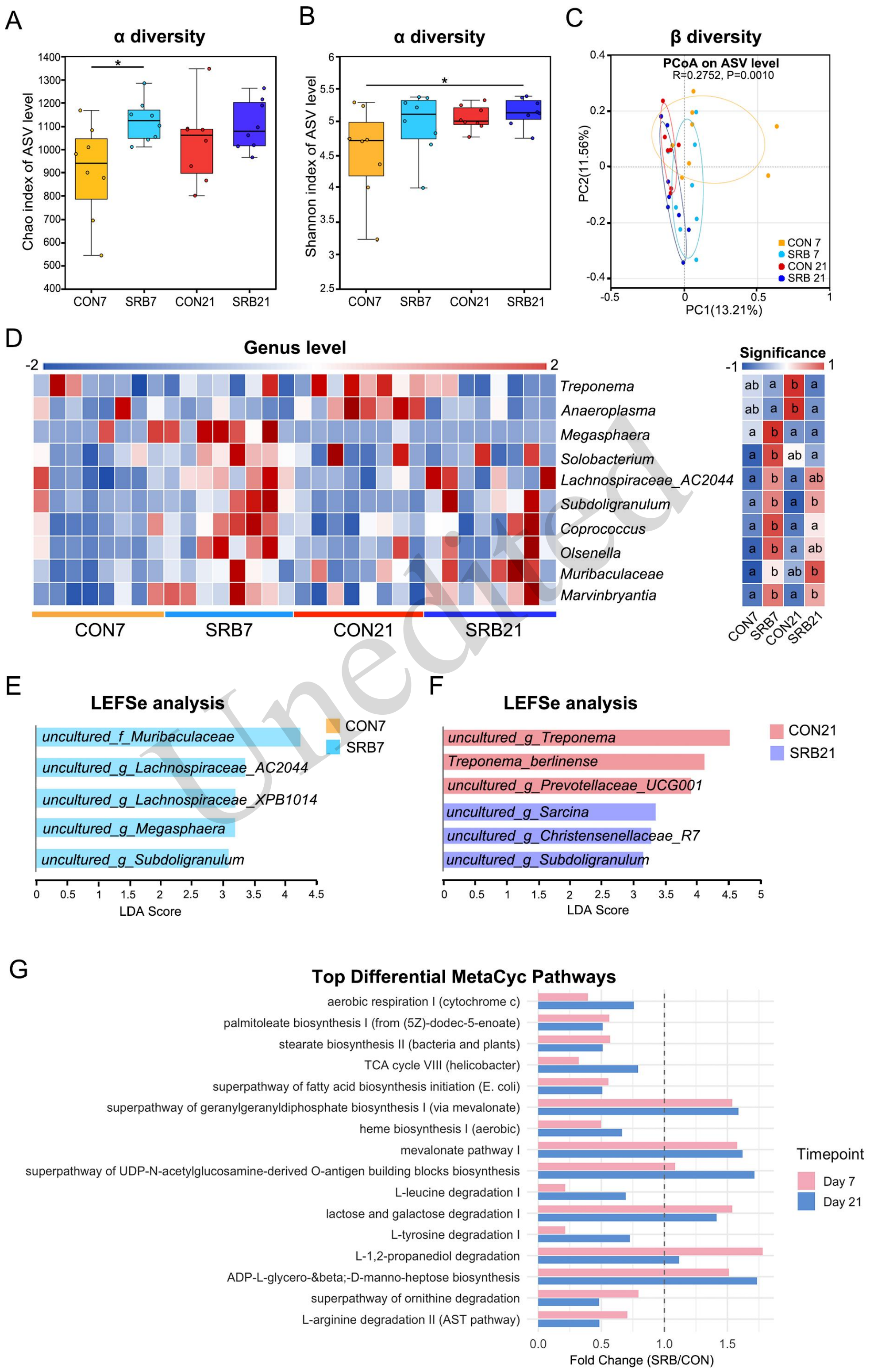

Fig. 2. Effects of the SRB diet on sow fecal microbiota diversity and composition.

(A) Bacterial alpha diversity determined by Chao index. (B) Bacterial alpha diversity determined by Shannon index. (C) Scatterplot from PCoA in bacterial communities based on weighted unifrac distance. (D) Relative abundance of significantly changed genera (relative abundance > 1%). Relative abundance at the genus level was scaled by row. Significance denotes the statistically significant differences among various groups, as determined by Kruskal-Wallis test. (E-F) Linear discriminant analysis (LDA) score plot of the featured microbial species in pig colonic microbiomes (LDA score > 3, P < 0.05) between CON with SRB at (E) day 7 and (F) day 21 postpartum. (G) Differentially predicted microbial MetaCyc pathways in sow fecal microbiota at days 7 and 21 postpartum. Bar plots show the fold changes (SRB/CON) of the top five most upregulated and downregulated MetaCyc functional pathways as predicted by PICRUSt2, based on 16S rRNA gene sequencing. n = 8 sows/group, * $P < 0.05$.

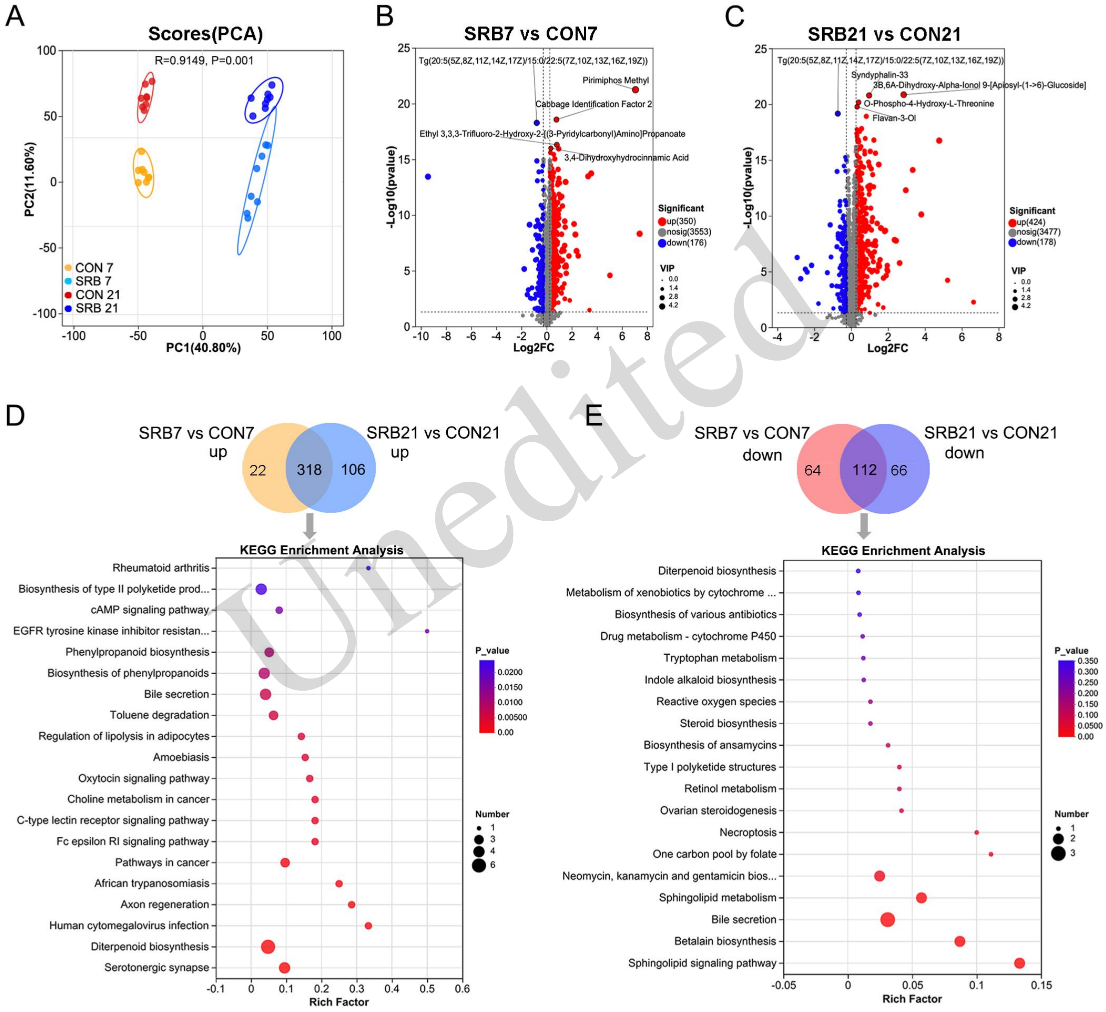

Fig. 3. Fecal metabolomic differences between CON and SRB sows.

(A) Principal component analysis (PCA) score plot of fecal metabolomes for CON and SRB groups at days 7 and 21 postpartum. (B-C) Volcano plot of differential metabolites in sow feces between the SRB and CON groups at (B) day 7 and (C) day 21 postpartum. Red represents up-regulated metabolites; Blue represents down-regulated metabolites; Gray represents metabolites with no significant change. (D-Up) Venn diagram of upregulated metabolites of SRB vs CON at days 7 and 21 postpartum. (D-Bottom) KEGG pathway enrichment analysis for 318 metabolites were consistently higher in SRB feces at both day 7 and day 21 postpartum. increased in SRB vs CON feces . (E-Top) Venn diagram of upregulated metabolites of SRB vs CON on days 7 and 21 postpartum. (E-Bottom) KEGG pathway-enrichment analysis for 318 metabolites had consistently higher results for SRB feces on days 7 and 21 postpartum. increased in SRB vs CON feces. n = 8 sows/group.

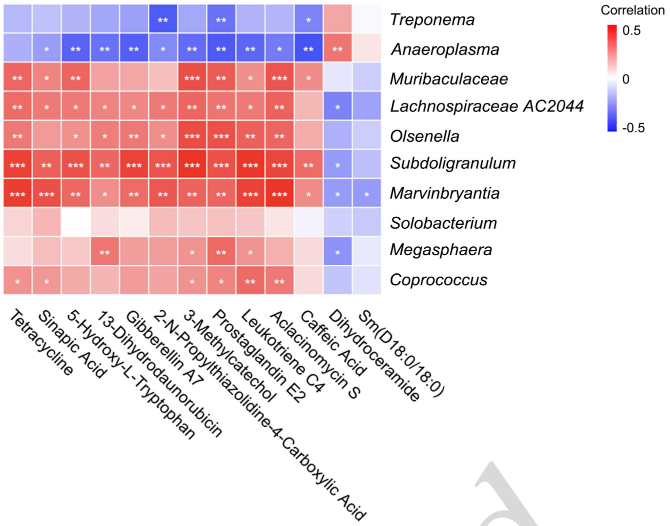

Fig. 4. Correlation analysis between differential fecal microbes and metabolites in sows.
Heatmap of the Spearman correlation between 10 bacterial genera and 13 fecal differential metabolites. Red squares indicate a positive relationship, while green squares indicate a negative relationship. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

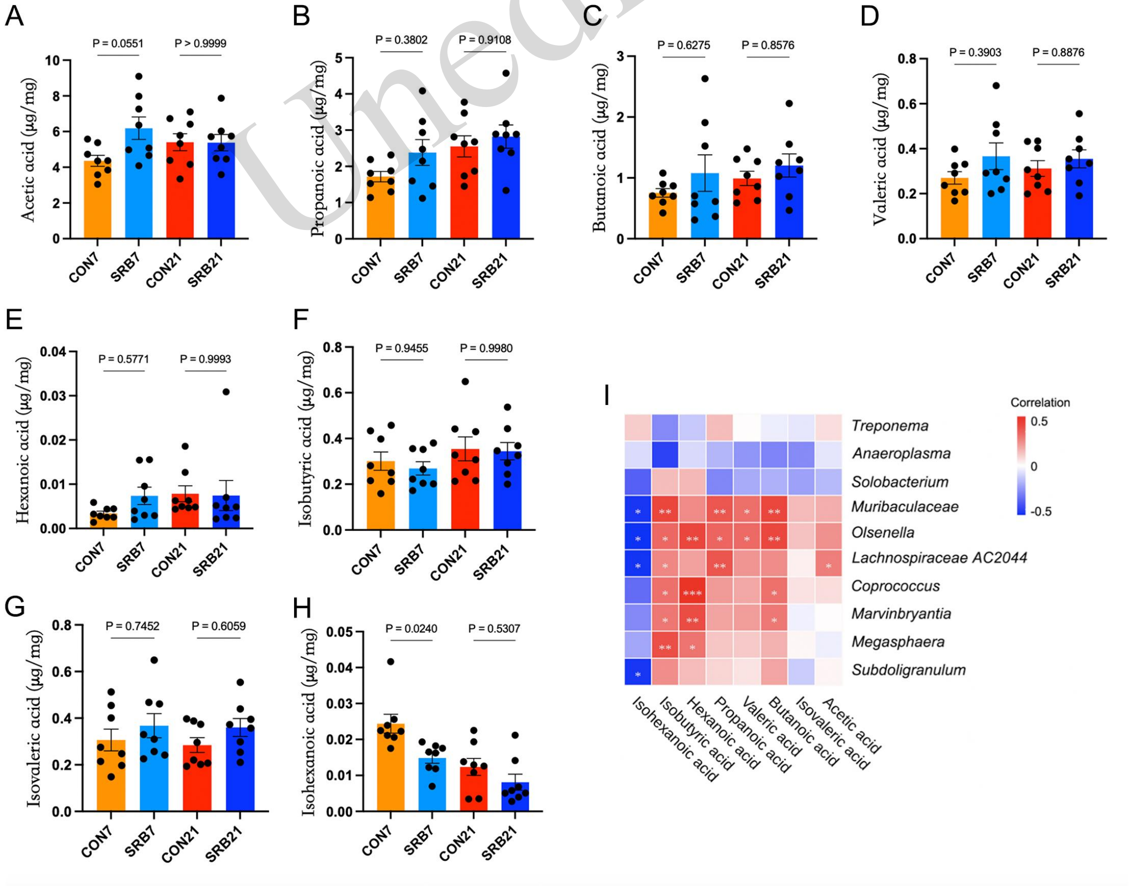

Fig. 5. Fecal short-chain fatty acids (SCFAs) and their association with differential gut microbes in sows.
Concentrations of Acetic acid (A), Propanoic acid (B), Butanoic acid (C), Valeric acid (D), Hexanoic acid (E), Isobutyric acid (F),

Isovaleric acid (G) and Isohexanoic acid (H) in sow feces from the CON and SRB groups at days 7 and 21 postpartum. (I) Heatmap of the Spearman correlation between 10 bacterial genera and 8 fecal SCFAs. Red squares indicate a positive relationship, while green squares indicate a negative relationship. n = 8 sows/group, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

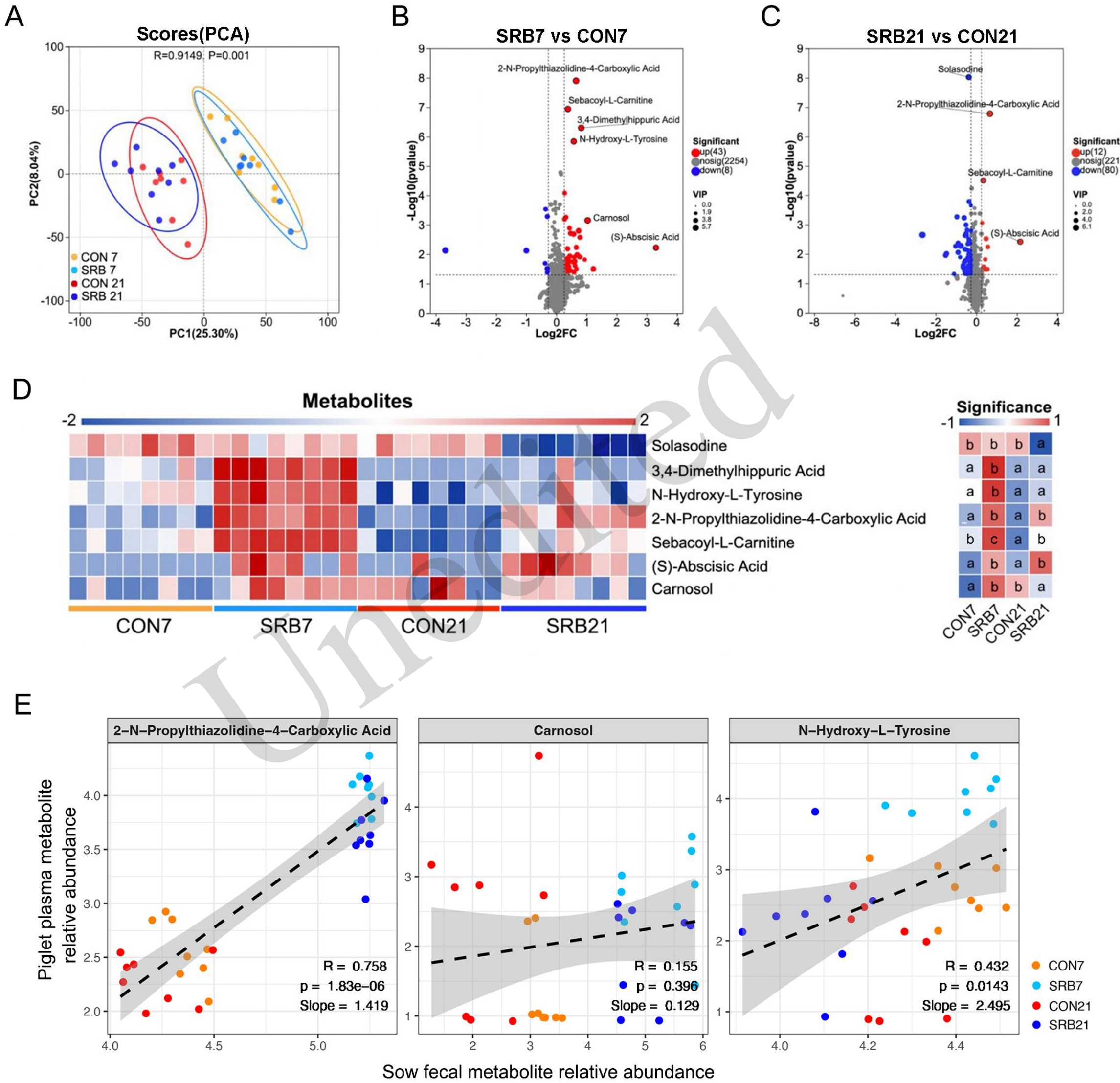

Fig. 6. Piglet plasma metabolome at weaning and overlap with maternal fecal metabolites.

(A) PCA score plot of plasma metabolites of piglets for CON vs SRB at days 7 and 21 postpartum. (B-C) Volcano plot of differential piglet plasma metabolites between the SRB and CON groups at (B) day 7 and (C) day 21 postpartum. (D) Relative abundance of significantly changed metabolites (n = 8). Relative abundance at the genus level was scaled by row. Significance denotes statistically significant differences among various groups, as determined by Student's t test. (E) Scatter plots of maternal fecal metabolite abundance vs. piglet plasma metabolite abundance for selected metabolites. Each plot represents a different metabolite, with points corresponding to individual samples, colored according to the experimental group (CON7, CON21, SRB7, SRB21). The Spearman correlation coefficient (R), *P*-value (adjusted), and slope of the linear fit are annotated on each plot. n = 8 piglets/group.

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Supplementary information

Supplementary Table1-6; Supplementary Fig.1