Animal Nutrition 20 (2025) 387–403

Contents lists available at ScienceDirect

Animal Nutrition

journal homepage: http://www.keaipublishing.com/en/journals/aninu/

Original Research Article

Maternal consumption of glycerol monolaurate optimizes milk fatty acid profile and enhances piglet gut health in association with G protein-coupled receptor 84 (GPR84) activation

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ARTICLE INFO

Article history:
Received 12 July 2024
Received in revised form
11 November 2024
Accepted 20 November 2024
Available online 31 December 2024

Keywords:
Fatty acid
Glycerol monolaurate
G protein-coupled receptor 84
Immunity transmit
Sow

ABSTRACT

This study evaluated the effect of maternal glycerol monolaurate (GML) supplementation during late gestation and lactation on sow reproductive performance, transfer of immunity and redox status, milk fat and fatty acid profile, and fecal microbiota. Eighty multiparous sows (Landrace × Large white) were randomly allocated to two treatment groups (with or without 1000 mg/kg GML) with 40 replicates per treatment. The feeding experiment lasted from d 85 of gestation (G85) to d 23 of lactation (L23). The samples were collected on d 1 (L1) and 21 (L21) of lactation. Our results showed that maternal GML supplementation significantly increased litter weight ($P = 0.002$), average daily gain of piglets ($P = 0.048$), and sow average daily feed intake ($P = 0.032$). Compared with CON group, the concentrations of lauric acid (C12:0; $P = 0.022$), C16:0 ($P = 0.001$), and total saturated fatty acids ($P = 0.006$) in colostrum as well as C12:0 in L21 milk ($P = 0.001$) were higher in GML group. Besides, the concentrations of immunoglobulin A (IgA) and IgG in colostrum as well as sow and piglet plasma, the total antioxidant capacity and superoxide dismutase activity in sow colostrum were also significantly higher in the GML group ($P < 0.05$). Microbiome results showed that GML addition increased fecal microbial alpha diversity as well as the relative abundances of short chain fatty acids producing bacteria Ruminococcaceae and *Parabacteroides*; and decreased the harmful Proteobacteria of sows ($P < 0.05$). The Spearman analysis showed that the microbial biomarkers Prevotellaceae, Ruminococcaceae, and *Parabacteroides* were positively correlated with IgA and IgG of sow plasma and milk ($P < 0.05$). Besides, maternal GML addition up-regulated the relative protein expressions of proliferating cell nuclear antigen, cyclin D1, G protein-coupled receptor 84 (GPR84) and phosphatidylinositol 3-kinase (PI3K)/protein kinase B (Akt) pathway in the duodenum and jejunum of piglets. Collectively, current findings suggested that maternal GML supplementation enhanced piglet growth during lactation, which might be associated with improving milk fat and lauric acid contents, microbiota derived immunoglobulins transfer, and gut health through potential involvement of GPR84 and PI3K/Akt signaling pathway.

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Peer review under the responsibility of Chinese Association of Animal Science and Veterinary Medicine.

Production and Hosting by Elsevier on behalf of KeAi

1. Introduction

Under the background of intensive agricultural production, improved genetic selection for modern high yielding sows demands sufficient nutrients to maintain abundant milk yield and litters during late pregnancy and lactation stages (Theil et al., 2022). High milk production and increased litters demand high energy in

https://doi.org/10.1016/j.aninu.2024.11.017

feed and if not supplied adequately, it may lead to increased fat mobilization and less body fat storage in sows to meet the nutrient deficiency (Gessner et al., 2015). Research has shown that sows have increased anabolism in late gestation and rapidly accelerated catabolism in the last 7 d of pregnancy and the initial 5 d of lactation (Costermans et al., 2020). However, excessive mobilization of body tissue reserves during lactation will damage the subsequent reproductive performance (Campos et al., 2012). Many studies have reported that dietary lipid supplementation increases the average daily energy intake of sows, which is used for more milk fat synthesis during lactation and promotes growth of the offspring (Llauradó-Calero et al., 2022; Rosero et al., 2016). Previous studies have found that dietary medium-chain fatty acids (MCFA; C8 to C12) and its glyceride derivatives consumption improved the sow lactation performance and gut health of suckling offspring during late gestation and lactation (Azain, 1993; You et al., 2023). Thus, it is critical to formulate nutritional intervention strategies for the improvement of sow reproductive performance and offspring growth during late gestation and lactation.

Glycerol monolaurate (GML) is a monoglyceride of lauric acid (LA) and is naturally found in milk fat and coconut oil (Li et al., 2009; Schlievert et al., 2019). As a food additive, GML is officially recognized by the Food and Drug Administration and its dose ranges from 10 to 2000 mg/kg (Jiang et al., 2018). Besides, GML as a lipid has been used as an effective dietary supplement in animal production due to its distinguished growth-promoting, antiviral, and antibacterial functions (Lan et al., 2021). Glycerol monolaurate is broad-spectrum bactericidal to most gram-positive pathogens and gram-negative bacteria and inhibits exotoxin production (Mueller and Schlievert, 2015; Schlievert and Peterson, 2012). Additionally, GML in liquid conditions destroyed the infectivity of the African swine fever virus in feed and simian immunodeficiency virus in vitro (Jackman et al., 2020; Li et al., 2009). It is worth noting that GML as a typical glycerol derivative of lauric acid (C12:0), can be directly absorbed by the portal system of the intestine due to the short carbon chain length. Similar to the metabolic process of MCFA, GML is transported via the hepatic portal to the liver. Moreover, MCFA can enter mitochondria independently to undergo β-oxidation and eventually be metabolized into ketones body with the absence of fatty acid-binding proteins (Schönfeld and Wojtczak, 2016; Zhao et al., 2019). Besides, MCFAs and their glycerol derivatives, medium chain triacylglycerols, can also be rapidly oxidized to provide energy (Mo et al., 2021). Previous studies have shown that dietary GML supplementation could reduce diarrhea rate, while improving intestinal morphology and immune level in weaned piglets (Dahmer et al., 2022; Li et al., 2022a). The above studies have shown that GML as an effective energy-supplying substrate and antibiotic substitute, positively affected the growth performance of piglets.

Recently, maternal supplementation of 1000 or 2000 mg/kg GML through feed was shown to alter milk fatty acids of sows and increase the growth performance of piglets at weaning (Li et al., 2023). However, the effect of maternal dietary supplementation of GML during late gestation and lactation on sow reproductive performance, transfer of immunity and redox status, and intestinal health of offspring are still unclear. Therefore, we hypothesized that a diet supplemented with GML would increase the sow reproductive performance, fat and lauric acid contents in colostrum, and antioxidant capacity and immunoglobulins transfer. We further hypothesized that these changes might improve the intestinal health and growth performance of suckling piglets. To test the hypothesis, the present study aimed to determine the effect of maternal GML supplementation on sow reproductive performance, the transfer of redox status and immunity, milk fatty acids profile, and gut health of piglets.

2. Materials and methods

2.1. Animal ethics statement

All animal experimental protocols performed in the present study were according to the guidelines of the South China Agricultural University Animal Care and Animal Use Committee (no. SYXK2019-0136), Guangzhou, China.

2.2. Experimental animals and diets

This trial was conducted in a commercial pig farm located in Heyuan City, Guangdong Province, China which is affiliated with Guangdong Foodstuffs Import & Export (group) Co., Ltd. A total of 80 multiparous sows (Landrace × Large White) were randomly assigned into two dietary treatments (40 replicates per treatment) according to parity, backfat thickness, and historical reproductive performance as follows: 1) CON group fed with a basal diet; 2) GML group fed a basal diet supplemented with 1000 mg/kg GML. The GML product was provided by Guangdong Cardlo Biotechnology Co., Ltd (https://www.cardlo.cn/). The active ingredients of the product were α-GML, β-GML, dilaurin, and silicon dioxide carrier. Among them, α-GML content was more than 90%, and β-GML accounted for approximately 2% of the total. The feeding experiment lasted from d 85 of gestation (G85) to d 23 of lactation (L23). The basal diet was formulated to meet or exceed the nutritional needs of sows during gestation and lactation based on National Research Council guidelines (NRC, 2012). The ingredient and nutritional composition of the control basal diet is shown in Table 1.

All sows were housed in individual gestation stalls during late gestation (2.1 m × 0.6 m). Each sow was provided restricted feeding (3.0-3.5 kg/d) and fed twice at 07:00 and 15:00. All sows were moved to the individual farrowing crates on d 107 of gestation (G107). After parturition, the diet was gradually increased by 1.0 kg/d until fed ad libitum. The temperature of the farrowing house was maintained at around 23 °C in summer. Warming lamps were installed above farrowing crates to maintain the temperature for newborn piglets. After farrowing, the reproductive and litter performance of sows (without colostrum consumption) were recorded. In order to comply with the farm epidemic prevention policy, the neonates were only cross-fostered within the treatment on d 3 of lactation (L3). Animals were provided ad libitum water in the entire trial. Piglets were weaned on L23 and had no access to creep feed. The daily feed consumption of every sow was registered to calculate ADFI during lactation. Moreover, the fasting body weight (BW) of piglets as well as litter performance were documented after cross-fostered on L3 and at weaning on L23 to calculate the average daily gain (ADG) during lactation. The sow oestrus rate was registered within 7 d after weaning. Backfat thickness was detected at the 10th rib using a digital device on G110 and L23.

2.3. Feed chemical analyses

The chemical analyses of the pregnant and lactating diets were executed to measure actual nutritional levels. The crude protein content in diets was measured as N × 6.25, using a FOSS Kjeltec 8400 (FOSS Inc., Eden Prairie, MN) according to Kjeldahl method (GB/T 6432-2018; China National Standard, 2018a). The values of crude fiber (GB/T 6434-2022; China National Standard, 2022), crude fat (GB/T 6433-2006; China National Standard, 2006), crude ash (GB/T 6438-2007; China National Standard, 2007), total calcium (GB/T 6436-2018; China National Standard, 2018b) and total phosphorus (GB/T 6437-2018; China National Standard, 2018c) in diet were measured based on the China National Standard (GB/T 39235-2020; China National Standard, 2020), respectively. The

Table 1
Ingredient composition and nutritional levels of the basic diet (air-dried basis, %).

Item	Pregnant diet	Lactating diet
Ingredients		
Corn	20.50	34.10
Soybean meal	16.50	15.00
Wheat	16.00	12.00
Barley	26.90	8.00
Extruded soybean		20.00
Soybean sheet	15.00	3.00
Fish meal	0.80	2.50
Soybean oil	0.60	1.80
Dicalcium phosphate	1.40	1.20
Limestone	0.58	0.78
Salt	0.30	0.30
Choline chloride (50%)	0.12	0.12
Pregnant vitamin and mineral premix [1]	1.20	
Lactating vitamin and mineral premix [2]		1.10
Mold inhibitor	0.10	0.10
Total	100.00	100.00
Nutritional levels [3]		
Digestible energy, MJ/kg	12.76	14.26
Crude protein	13.90	17.50
Crude fiber	8.30	5.21
Crude fat	4.45	6.96
Ash	5.52	5.30
Calcium	0.80	0.90
Total phosphorus	0.60	0.60
Available phosphorus	0.48	0.52
SID Lys	0.76	0.95
SID Met + Cys	0.45	0.53
SID Thr	0.49	0.62
SID Trp	0.14	0.18

[1] Pregnant vitamin and mineral premix provide per kilogram of complete diet: 13,000 IU, vitamin A, 4000 IU, vitamin D_3, 30 IU, vitamin E, 4 mg vitamin K_3, 4 mg vitamin B_1, 10 mg vitamin B_2, 4.8 mg vitamin B_6, 0.034 mg vitamin B_{12}, 0.14 mg I (CaI_2O_6), 0.30 mg Se (Na_2SeO_3), 40 mg niacin, 20 mg D-pantothenate, 2.0 mg folic acid, 0.16 mg D-biotin, 80.0 mg Zn ($ZnSO_4 \cdot H_2O$), 100.0 mg Fe ($FeSO_4 \cdot H_2O$), 45.0 mg Mn ($MnSO_4 \cdot H_2O$), 15.0 mg Cu ($CuSO_4 \cdot 5H_2O$).
[2] Lactating vitamin and mineral premix provide per kilogram of complete diet: 13,000 IU, vitamin A, 4000 IU, vitamin D_3, 30 IU, vitamin E, 4 mg vitamin K_3, 4 mg vitamin B_1, 10 mg vitamin B_2, 4.8 mg vitamin B_6, 0.034 mg vitamin B_{12}, 0.14 mg I (CaI_2O_6), 0.3 mg Se (Na_2SeO_3), 40 mg niacin, 20 mg D-pantothenate, 2.0 mg folic acid, 0.16 mg D-biotin, 80.0 mg Zn ($ZnSO_4 \cdot H_2O$), 100.0 mg Fe ($FeSO_4 \cdot H_2O$), 45.0 mg Mn ($MnSO_4 \cdot H_2O$), 15.0 mg Cu ($CuSO_4 \cdot 5H_2O$).
[3] The digestible energy, standardized ileal digestibility (SID) amino acids, and available phosphorus are calculated values, and all other nutritional levels are measured values.

calculated values of digestible energy (DE) and standardized ileal digestibility (SID) amino acids were also referred to China National Standard (GB/T 39235-2020; China National Standard, 2020).

2.4. Sample collection

2.4.1. Plasma sampling of sows and piglets

On d 1 of lactation (L1) and L21, ten sows ($n = 10$) and six weaned piglets ($n = 6$) per treatment were chosen to collect samples. Fasting blood samples (10 mL) were collected from sows *via* the ear vein and from piglets *via* the anterior vena cava using EDTA vacutainers. After centrifugation at 3000 × *g* for 20 min, the plasma samples were transferred to a 1.5-mL cryovial and stored at −20 °C.

2.4.2. Colostrum and milk samplings of sows

Within 12 h after the first piglet parturition, colostrum samples of 10 sows per treatment were manually obtained on L1. Milk samples were collected after 2 mL oxytocin intramuscular injection on L21. The sow colostrum and milk samples were subsequently stored at −20 °C until further analysis.

2.4.3. Feces sampling of sows

On L1 and L21, 10 sows per treatment were selected to obtain feces through rectal palpation. Fecal samples were obtained within two collection days and stored at −80 °C for subsequent 16S rRNA analysis.

2.4.4. Small intestine mucosal sampling of piglets

After fasting, piglets from two treatments ($n = 6$ per group) were selected and sacrificed by electrocution after weaning on L23. Middle duodenal and jejunal samples as well as posterior ileal samples (3 cm segments) were collected, and the chyme was washed away by saline solution. Immediately, mucosal samples were collected by scraping with glass slides and placed into liquid nitrogen, and finally frozen at -80 °C for protein isolation.

2.5. Laboratory analysis

2.5.1. Colostrum and milk composition

A 10-mL milk sample was mixed with the same volume of double distilled water. Then, the composition (solids-not-fat, fat, protein, and lactose) of the milk was detected using a milk composition analyzer machine (Milko-Scan, Foss Company, Denmark).

2.5.2. Determination of fatty acid profile of sow plasma and milk

The fatty acids were extracted and measured in the sow plasma, colostrum, and milk samples according to the method described in the literature (Jang et al., 2020). Plasma and colostrum samples (100 μL) were mixed with 1 mL methanol and 2 mL methanolic–HCl. Finally, the total fatty acids were analyzed using a gas chromatography (Agilent 7890 B, Agilent Technologies, Palo Alto, USA) installed with a column (30 m × 200 μm × 0.35 μm film thickness, Varian Co., Palo Alto, USA).

2.5.3. Evaluation of immune and redox status indices in plasma and milk of sows and piglets

The levels of immune indices, including immunoglobulin (Ig) A and IgG in plasma, colostrum, and milk of sows and piglets were detected using commercial ultrasensitive ELISA kits following the manufacturer's instructions (Cusabio, Wuhan, China). Besides, the levels of malondialdehyde (MDA), glutathione (GSH), total antioxidant capacity (T-AOC), and superoxide dismutase (SOD) in plasma of sows and piglets, colostrum, and milk were analyzed using respective commercially available kits (Nanjing Jiancheng Institute of Bio-engineering, Jiangsu, China).

2.5.4. Analysis of fecal microbiota of sows

After the extraction of microbial genomic DNA from the sow fecal samples, the bacterial 16S rDNA high-throughput amplicon sequencing was performed by Majorbio Co. Ltd. (Shanghai, China). The region V3–V4 was amplified using barcode-specific primers pair 338F (5′- CCTGATAGACAGCAG-3′) and 806R (5′-GGACTAGGGTCTAAT-3′). Pan operational taxonomic unit (OTU) analysis was evaluated to determine whether the number of fecal samples in this sequencing is sufficient or not according to the flatness of the Pan species curve. Alpha diversity indices (abundance-based coverage estimators [ACE] and Chao1 multiplicity; Shannon and Simpson richness) at the level of OTU reads were analyzed by the QIIME2 software. The multidimensional scaling-principal coordinates analysis (PCoA) based on the unweighted UniFrac as bacterial β-diversity was used to distinguish the microbial community variation discrepancy. The differential biomarker bacteria at the genera level were identified using linear discriminant analysis (LDA) effect size (LEfSe) analysis (LDA score > 2.0, $P < 0.05$). In LEfSe analysis, the non-parametric factorial Mann–Whitney *U*-test

was used to detect significant differential biomarkers and investigate biological consistency among subclasses. Spearman's correlation between IgA and IgG in plasma and milk with fecal differential bacteria was calculated using the R package ggplot 23.3.1.

2.5.5. Small intestinal morphological examination of piglets

Formalin-fixed, paraffin-embedded small intestinal samples were stained using hematoxylin and eosin (H&E) and then sealed to obtain intestine pieces. To examine intestinal morphology, the images were captured using a microscopy system (Nikon DS-U3, Nikon, Tokyo, Japan). After morphological examination, the intestinal villus height (VH), crypt depth (CD), and VH:CD ratio (VCR) were assessed and calculated.

2.5.6. Analysis of relative protein abundances

Piglet small intestinal mucosal protein was homogenized in RIPA lysis containing 1% PMSF and phosphatase inhibitors. Protein concentration was detected using the BCA kit (Beyotime Biotechnology, Shanghai, China), then the extractive protein was boiled. Then, the denatured protein was divided using SDS-PAGE gel, followed by a transfer onto the polyvinylidene fluoride (PVDF) membrane (Millipore). The membranes were blocked with a blocking buffer, followed by probing with primary antibodies against β-actin (#4970, CST), G protein-coupled receptor 84 (GPR84; bs-15353R, Bioss), proliferating cell nuclear antigen (PCNA; #ab92552, Abcam), cyclin D1 (#ab134175, Abcam), phosphatidylinositol 3-kinase (PI3K; #4249, CST), p-PI3K (#17366, CST), protein kinase B (Akt; #4691, CST), and p-Akt (#4060, CST) at 4 °C overnight. After washing, the foregoing membranes were incubated using horseradish peroxidase-conjugated secondary antibodies. Following visualization of protein bands using a Tanon chemiluminescence imaging system, the relative intensity of target proteins was normalized against β-actin using ImageJ Software.

2.6. Statistical analyses

Significant statistical difference between the two treatments were evaluated by the Student's *t*-test using the SPSS v22.0 (SPSS Inc., Chicago, IL, USA). Each sow and litter were considered to be the individual experimental units for the analysis of reproductive performance data. All analysis results were expressed as means ± standard error of the mean (SEM). $P < 0.05$ and $0.05 \leq P < 0.10$ were used as the criterion of the significance difference value and a trend toward difference, respectively. Alpha diversity and relative bacterial abundances based on phylum and genus levels were analyzed using the Mann–Whitney *U*-test method. Correlation heatmap analysis was performed using the R package (version 3.3.1).

3. Results

3.1. Sow reproductive performance

As shown in Table 2, the number of total, alive, and healthy born, as well as stillbirths and mummies in piglets were not affected by maternal GML supplementation during late gestation ($P > 0.05$). No significant treatment effect was observed at birth on litter weight, piglet body weight, healthy weight, and stillborn weight ($P > 0.05$). Additionally, dietary GML addition showed no effect on placental weight or placental weight per piglet ($P > 0.05$).

Table 2
Effect of maternal GML supplementation on reproductive and litter performance of sows ($n = 40$).

Litter characteristics	Treatments		*P*-value
	CON	GML	
Total born number	11.26 ± 0.382	11.60 ± 0.370	0.529
Alive born number	10.38 ± 0.338	10.66 ± 0.362	0.332
Healthy born number	9.94 ± 0.326	9.97 ± 0.341	0.208
Stillbirths	0.88 ± 0.240	0.94 ± 0.178	0.634
Mummies	0.06 ± 0.019	0.09 ± 0.015	0.672
Birth weight of litter, kg	17.20 ± 0.560	17.03 ± 0.532	0.561
Birth weight of piglet, kg	1.67 ± 0.047	1.63 ± 0.041	0.791
Healthy weight, kg	1.70 ± 0.042	1.69 ± 0.033	0.901
Stillborn weight, kg	1.21 ± 0.025	1.22 ± 0.022	0.885
Placental weight, kg	1.64 ± 0.145	1.85 ± 0.175	0.363
Placental weight per piglet, kg	0.12 ± 0.012	0.17 ± 0.021	0.145

GML = glycerol monolaurate.
All values are expressed as means ± standard error of the mean (SEM). Control (CON) group, sows fed basal diet; GML, group, sows fed basal diet supplemented with 1000 mg/kg GML.

3.2. GML supplementation improved lactation performance of sows

As summarized in Table 3, maternal GML supplementation significantly increased the litter weight of piglets during the entire lactation ($P < 0.05$). In addition, dietary GML supplementation significantly increased average weight in the third week ($P = 0.048$) and ADG in the third week ($P = 0.018$) and first to third week ($P = 0.048$) of lactating piglets. Maternal GML supplementation tended to increase the preweaning survival during lactation ($P = 0.063$).

3.3. GML supplementation regulated feed intake and backfat thickness of sows

As shown in Table 4, the ADFIs of the second week ($P = 0.080$), third week ($P = 0.036$) and first to third week ($P = 0.032$) were higher in the GML group than those in the CON group. Dietary GML supplementation had no effect on the sow backfat thickness loss during lactation ($P > 0.05$).

3.4. GML supplementation optimized compositions of colostrum and milk

The compositions of colostrum and milk on L21 are presented in Table 5. Dietary GML addition tended to increase colostrum fat ($P = 0.056$), and significantly improved the milk fat content on L21 ($P = 0.005$).

3.5. GML supplementation regulated fatty acid profiles in sow plasma

Fatty acid profiles in the plasma of sows on L1 and L21 are presented in Tables 6 and 7, respectively. Compared with the CON group, the amounts of C12:0 on L1 ($P = 0.024$) and L21 ($P = 0.031$) as well as C20:5n-3 on L1 ($P = 0.004$) in plasma were higher in the GML group. Besides, the levels of total polyunsaturated fatty acids (PUFA) significantly decreased ($P = 0.035$) on L21 in the GML group compared to the Control group.

3.6. GML supplementation regulated fatty acid profiles in colostrum and milk

Fatty acid profiles in sow colostrum and milk on L21 are summarized in Tables 8 and 9, respectively. The concentrations of C12:0 ($P = 0.022$), C16:0 ($P = 0.001$), C22:6n-3 ($P = 0.047$), and total saturated fatty acids (SFA) ($P = 0.006$) in colostrum as well as C8:0 ($P = 0.041$), C12:0 ($P = 0.001$), and C24:0 ($P = 0.047$) in milk were significantly higher, whereas the n-6:n-3 PUFA ratio in milk

Table 3
Effect of maternal GML supplementation on growth performance of offspring piglets during lactation ($n = 40$).

Item	Treatments		*P*-value
	CON	GML	
Litter size (*n*)			
After cross-fostering	9.50 ± 0.182	9.51 ± 0.191	0.966
First week	9.03 ± 0.218	9.34 ± 0.207	0.281
Second week	8.73 ± 0.232	9.17 ± 0.228	0.160
Third week	8.65 ± 0.245	9.12 ± 0.222	0.151
Preweaning survival, %	91.44 ± 2.036	95.8 ± 1.145	0.063
Litter weight, kg			
After cross-fostering	19.37 ± 0.635	19.68 ± 0.701	0.739
First week	29.29 ± 0.842	31.68 ± 0.722*	0.034
Second week	43.13 ± 1.41	47.66 ± 1.155*	0.015
Third week	59.15 ± 1.885	66.80 ± 1.463*	0.002
Average weight of piglets, kg			
After cross-fostering	2.05 ± 0.061	2.09 ± 0.081	0.710
First week	3.26 ± 0.077	3.42 ± 0.074	0.132
Second week	4.99 ± 0.142	5.25 ± 0.124	0.174
Third week	6.91 ± 0.192	7.39 ± 0.156*	0.048
ADG of piglets, g/d			
First week	173.68 ± 9.020	189.8 ± 8.052	0.186
Second week	247.23 ± 13.422	261.79 ± 9.642	0.379
Third week	273.85 ± 11.488	306.03 ± 6.897*	0.018
Mean of first to third week	231.27 ± 8.637	252.54 ± 6.204*	0.048

GML = glycerol monolaurate; ADG = average daily gain.
Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML.
All values are expressed as means ± standard error of the mean (SEM). Asterisk (*) denotes a significant difference ($P < 0.05$).

Table 4
Effects of maternal GML supplementation on feed consumption and backfat thickness loss of sows during lactation ($n = 40$).

Item	Treatments		*P*-value
	CON	GML	
ADFI, kg/d			
First week	2.98 ± 0.112	3.15 ± 0.131	0.307
Second week	4.36 ± 0.118	4.71 ± 0.150	0.080
Third week	5.08 ± 0.095	5.35 ± 0.087*	0.036
Mean of the first to third week	4.30 ± 0.074	4.57 ± 0.102*	0.032
Backfat thickness, mm			
Day 110 of gestation	19.46 ± 0.623	18.53 ± 0.481	0.233
Weaning	15.99 ± 0.600	15.33 ± 0.422	0.393
Lactation loss	3.47 ± 0.282	3.19 ± 0.252	0.458
Weaning-to-estrus interval, d	5.78 ± 0.354	5.65 ± 0.313	0.556

GML = glycerol monolaurate; ADFI = average daily feed intake.
Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML.
All values are expressed as means ± standard error of the mean (SEM). Asterisk (*) denotes a significant difference ($P < 0.05$).

($P = 0.031$) was lower in GML group compared to the CON group. In addition, compared with the CON group, the GML group tended to have increased amounts of C16:1n-9 ($P = 0.088$), C18:1n-9 ($P = 0.062$), C22:2n-13 ($P = 0.091$), total monounsaturated fatty acids (MUFA) ($P = 0.087$) in colostrum as well as C17:0 ($P = 0.075$), C20:5n-3 ($P = 0.067$), and n-3 PUFA ($P = 0.086$) in milk; while decreased levels of C24:1n-15 ($P = 0.062$), total PUFA ($P = 0.071$), n-6 PUFA ($P = 0.067$), and n-6:n-3 PUFA ratio ($P = 0.085$) in sow colostrum.

3.7. Maternal GML supplementation improved immunity transfer in the sow-piglet model

The levels of immunoglobulins transfer from sow plasma and milk to offspring plasma on L1 and L21 are shown in Table 10. The

Table 5
Effect of maternal GML supplementation on the colostrum and milk composition ($n = 10$).

Item	Treatments		*P*-value
	CON	GML	
Colostrum, %			
Fat	3.83 ± 0.115	4.51 ± 0.292	0.056
Lactose	4.94 ± 0.113	4.99 ± 0.118	0.742
Protein	7.21 ± 0.300	7.34 ± 0.331	0.775
Solids-not-fat	11.67 ± 0.112	11.9 ± 0.110	0.799
Milk at d 21 of lactation, %			
Fat	6.19 ± 0.092	7.12 ± 0.228*	0.005
Lactose	6.52 ± 0.315	6.81 ± 0.122	0.391
Protein	4.63 ± 0.061	4.82 ± 0.150	0.277
Solids-not-fat	19.21 ± 0.824	19.52 ± 0.893	0.168

GML = glycerol monolaurate.
Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML.
All values are expressed as means ± standard error of the mean (SEM). Asterisk (*) denotes a significant difference ($P < 0.05$).

IgA concentrations in sow on L1 ($P = 0.003$) and piglet plasma on L21 ($P = 0.011$) as well as colostrum ($P = 0.045$) were higher in the GML group than those in the CON group. Besides, the IgG contents in sow colostrum ($P = 0.018$) and milk ($P = 0.019$) as well as piglet plasma on L21 ($P = 0.038$) were significantly higher in the GML group than those in the CON group.

3.8. Maternal GML supplementation improved redox status transfer in sow-piglet model

The redox status transfer from sows to offspring piglets through colostrum and milk intakes on L1 and L21 are shown in Fig. 1. The T-AOC and SOD activities in sow colostrum and milk, T-AOC in offspring plasma on L1 and L21, and GSH content in offspring plasma on L1 were higher in GML group ($P < 0.05$), while the MDA concentration in sow plasma on L1 and L21, colostrum, and piglet plasma on L1 were significantly lower in GML group than those in the CON group ($P < 0.05$).

3.9. GML supplementation altered fecal-associated microbiota community of sows

16S rRNA high-throughput sequencing of sow fecal microbiota was operated to investigate the effect of dietary GML addition on L1 and L21. The Pan curve was flat and approached the saturation plateau, indicating the number of fecal samples was adequate to cover almost all bacterial OTU in sequencing on L1 (Fig. 2A) and L21 (Fig. 3A). The Venn diagram showed OTUs network relation on L1 (Fig. 2B) and L21 (Fig. 3B), 4160 and 3979 microbial OTUs were estimated, of which 1283 (30.84%) and 1099 (27.62%) individual cores OTUs shared between CON and GML groups on L1. Besides, 4001 and 4117 microbial OTUs were found, of which 1269 (31.71%) and 1385 (33.64%) individual cores OTUs were shared between CON and GML groups on L21. The microbial alpha diversity indexes are shown in Figs. 2C and 3C. The Chao1 index was increased in the GML group than in the CON group on L1 and L21 ($P < 0.05$). The microbial beta diversity PCoA analysis was used to find the microbial community differences on L1 (Fig. 2D) and L21 (Fig. 3D). The PCoA analysis showed that the distinct separations in microbial OTU levels between two treatments.

The abundance distribution in sow fecal microbiota and differential microbiota based on the relative abundance on L1 and L21 are plotted in Figs. 4 and 5, respectively. At the phylum level, the top five dominant phyla (Firmicutes, Bacteroidota, Proteobacteria,

Table 6
Effect of maternal GML supplementation on fatty acid profiles of sow plasma on d 1 of lactation ($n = 10$).

Item	Treatments		*P*-value
	CON	GML	
SFA, %			
C4:0	0.35 ± 0.112	0.55 ± 0.128	0.237
C6:0	3.44 ± 0.380	3.25 ± 0.390	0.926
C8:0	0.57 ± 0.213	0.84 ± 0.154	0.303
C12:0	1.06 ± 0.135	1.65 ± 0.183*	0.024
C14:0	0.95 ± 0.392	0.67 ± 0.041	0.492
C16:0	24.11 ± 1.580	24.35 ± 0.780	0.895
C17:0	2.33 ± 0.471	2.09 ± 0.535	0.739
C18:0	17.88 ± 1.612	15.34 ± 0.436	0.158
C20:0	0.79 ± 0.251	0.66 ± 0.150	0.667
C24:0	1.17 ± 0.478	1.21 ± 0.334	0.958
Total SFA	52.66 ± 1.413	50.26 ± 2.355	0.402
MUFA, %			
C16:1n-9	0.59 ± 0.162	0.89 ± 0.075	0.096
C18:1n-9	9.89 ± 0.581	10.17 ± 1.100	0.823
C20:1n-11	0.21 ± 0.097	0.22 ± 0.043	0.227
C24:1n-15	0.54 ± 0.128	0.89 ± 0.252	0.369
Total MUFA	11.12 ± 0.516	12.14 ± 1.265	0.469
PUFA, %			
C18:2n-6	21.07 ± 2.158	23.84 ± 2.014	0.279
C18:3n-3	1.16 ± 0.351	1.01 ± 0.269	0.199
C18:3n-6	1.50 ± 0.550	0.83 ± 0.278	0.914
C20:2n-11	0.28 ± 0.099	1.28 ± 0.727	0.797
C20:3n-8	0.86 ± 0.187	0.94 ± 0.598	0.828
C20:3n-11	0.31 ± 0.068	0.27 ± 0.118	0.966
C20:4n-6	4.90 ± 1.0328	5.23 ± 1.026	0.875
C20:5n-3	0.52 ± 0.109	0.59 ± 0.181*	0.004
C22:2n-13	2.45 ± 0.656	2.31 ± 0.74	0.189
C22:6n-3	0.54 ± 0.112	1.47 ± 0.235	0.499
Total PUFA	33.16 ± 2.915	37.65 ± 1.300	0.189
n-3 PUFA	2.22 ± 0.340	3.13 ± 0.445	0.132
n-6 PUFA	27.23 ± 2.747	29.90 ± 2.655	0.499
n-6:n-3 PUFA ratio	13.96 ± 2.654	10.76 ± 1.748	0.337

GML = glycerol monolaurate; SFA = saturated fatty acids; PUFA = polyunsaturated fatty acids; MUFA = monounsaturated fatty acids.
Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML.
All values are expressed as means ± standard error of the mean (SEM). Asterisk (*) denotes a significant difference ($P < 0.05$).

Table 7
Effect of maternal GML supplementation on fatty acid profiles of sow plasma on d 21 of lactation ($n = 10$).

Item	Treatments		*P*-value
	CON	GML	
SFA, %			
C4:0	0.49 ± 0.082	0.33 ± 0.032	0.133
C6:0	2.68 ± 1.213	2.25 ± 1.331	0.816
C8:0	0.76 ± 0.195	0.78 ± 0.210	0.969
C12:0	0.98 ± 0.180	1.59 ± 0.162*	0.031
C14:0	0.82 ± 0.095	0.66 ± 0.062	0.178
C16:0	21.13 ± 1.11	22.10 ± 1.100	0.549
C17:0	1.11 ± 0.742	0.16 ± 0.031	0.195
C18:0	18.36 ± 1.703	18.3 ± 0.945	0.973
C20:0	1.05 ± 0.241	0.55 ± 0.100	0.110
C24:0	1.13 ± 0.472	0.76 ± 0.112	0.461
Total SFA	48.32 ± 2.566	47.48 ± 0.260	0.752
MUFA, %			
C16:1n-9	1.21 ± 0.165	1.00 ± 0.143	0.302
C18:1n-9	15.90 ± 3.077	20.07 ± 2.310	0.969
C20:1n-11	0.40 ± 0.092	0.39 ± 0.110	0.101
C24:1n-15	0.97 ± 0.124	0.40 ± 0.112	0.506
Total MUFA	18.47 ± 3.342	21.81 ± 2.421	0.439
PUFA, %			
C18:2n-6	23.56 ± 2.871	19.83 ± 1.441	0.274
C18:3n-3	0.78 ± 0.396	0.67 ± 0.113	0.608
C18:3n-6	1.30 ± 0.513	1.16 ± 0.172	0.243
C20:2n-11	0.50 ± 0.115	0.77 ± 0.081	0.964
C20:3n-8	0.75 ± 0.212	0.42 ± 0.170	0.851
C20:3n-11	0.33 ± 0.050	0.33 ± 0.052	0.722
C20:4n-6	5.31 ± 0.391	5.17 ± 0.537	0.282
C20:5n-3	0.37 ± 0.138	0.31 ± 0.090	0.108
C22:2n-13	2.23 ± 0.717	1.29 ± 0.424	0.114
C22:6n-3	0.83 ± 0.108	0.55 ± 0.180	0.214
Total PUFA	35.96 ± 1.918	30.43 ± 2.152*	0.035
n-3 PUFA	1.98 ± 0.277	1.77 ± 0.164	0.529
n-6 PUFA	30.16 ± 2.724	26.16 ± 1.866	0.478
n-6:n-3 PUFA ratio	13.82 ± 2.085	12.99 ± 1.018	0.724

GML = glycerol monolaurate; SFA = saturated fatty acids; PUFA = polyunsaturated fatty acids; MUFA = monounsaturated fatty acids.
Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML.
All values are expressed as means ± standard error of the mean (SEM). Asterisk (*) denotes a significant difference ($P < 0.05$).

Spirochaetota, and Actinobacteriota) were commonly identified between two treatments of sow fecal microbiota on L1 (Fig. 4A) and L21 (Fig. 5A), which accounted for more than 95%. Besides, the top 20 most dominant abundance distributions in the fecal microbiota on L1 (Fig. 4B) and L21 (Fig. 5B) at the genus level were plotted as a heatmap. Furthermore, the differential (at phylum and genus levels) and biomarker (at genus level) bacterium between the two treatments were identified by LEfSe analysis based on the relative abundance. The differentially abundant microbiota at phylum (top 5 dominant phyla) and genus levels on L1 (Fig. 4C–E) and L21 (Fig. 5C–E) between two treatments were further determined using the Mann–Whitney U-test and LEfSe analysis. At the phylum level, the relative abundances of the top five dominant phyla on L1 and L21 were compared, and the relative abundance of Proteobacteria in the GML group was significantly lower than in the CON group on d 21 of lactation ($P < 0.05$). At the genus level, LEfSe results showed that compared with CON group, the relative abundances of *norank_f_Ruminococcaceae* and *Parabacteroides* were increased in the GML group on L1 and L21, *unclassified_f_Prevotellaceae* and *Caryophanon* were only increased in the GML group on L1, and *unclassified_o_Bacteroidales* were only increased in the GML group on L21 ($P < 0.05$).

3.10. Microbial derived-immunoglobulin transmission from plasma to milk of sows

To explore the correlation of IgA and IgG with fecal microbiota of sows, Spearman's correlation analysis was performed and presented in Fig. 6. Spearman's analysis showed that GML supplementation associated with differential genus *unclassified_f_Prevotellaceae* of microbiota on L1 was positively correlated with L1 plasma IgA and colostrum IgG ($P < 0.05$). Dietary GML supplementation associated *Ruminococcaceae*was positively correlated with L21 plasma IgA and L21 milk IgG ($P < 0.05$). Besides, *Parabacteroides* was also positively correlated with L21 milk IgG ($P < 0.05$). These bacteria might be involved in the derivation of IgA and IgG in plasma and milk.

3.11. Maternal GML supplementation improved the small intestinal morphology of piglets

The effect of maternal GML supplementation on small intestinal VH and CD of suckling piglets were measured and shown in Fig. S1. Maternal GML addition significantly up-regulated the VH value in

Table 8
Effect of maternal GML supplementation on fatty acid profiles of sow colostrum ($n = 10$).

Item	Treatments		*P*-value
	CON	GML	
SFA, %			
C4:0	0.12 ± 0.023	0.15 ± 0.032	0.451
C6:0	0.09 ± 0.012	0.15 ± 0.047	0.171
C8:0	0.11 ± 0.021	0.13 ± 0.034	0.757
C12:0	0.18 ± 0.024	0.28 ± 0.036*	0.022
C14:0	1.30 ± 0.097	1.09 ± 0.241	0.425
C16:0	18.89 ± 0.368	21.58 ± 0.312*	0.001
C17:0	1.18 ± 0.363	0.96 ± 0.087	0.528
C18:0	4.73 ± 0.278	5.19 ± 0.235	0.220
C20:0	0.20 ± 0.042	0.17 ± 0.040	0.589
C24:0	0.53 ± 0.063	0.42 ± 0.123	0.427
Total SFA	27.33 ± 2.666	29.62 ± 2.588*	0.006
MUFA, %			
C16:1n-9	1.92 ± 0.071	2.32 ± 0.217	0.088
C18:1n-9	31.31 ± 1.392	35.61 ± 2.061	0.062
C20:1n-11	0.16 ± 0.035	0.29 ± 0.051	0.370
C24:1n-15	0.19 ± 0.078	0.12 ± 0.048	0.062
Total MUFA	33.58 ± 1.728	38.33 ± 2.196	0.087
PUFA, %			
C18:2n-6	33.20 ± 1.665	26.91 ± 2.517	0.384
C18:3n-3	2.02 ± 0.112	1.62 ± 0.215	0.705
C18:3n-6	0.16 ± 0.068	0.24 ± 0.051	0.204
C20:2n-11	0.81 ± 0.115	0.84 ± 0.053	0.348
C20:3n-8	0.31 ± 0.067	0.44 ± 0.072	0.278
C20:3n-11	0.12 ± 0.024	0.18 ± 0.060	0.641
C20:4n-6	0.86 ± 0.061	0.94 ± 0.022	0.303
C20:5n-3	0.12 ± 0.028	0.14 ± 0.043	0.591
C22:2n-13	0.36 ± 0.115	0.72 ± 0.312	0.091
C22:6n-3	0.34 ± 0.092	0.41 ± 0.110*	0.047
Total PUFA	38.29 ± 1.815	32.38 ± 2.590	0.071
n-3 PUFA	2.48 ± 0.100	2.32 ± 0.162	0.412
n-6 PUFA	34.23 ± 1.694	28.04 ± 2.498	0.067
n-6:n-3 PUFA ratio	13.86 ± 0.574	12.14 ± 0.851	0.085

GML = glycerol monolaurate; SFA = saturated fatty acids; PUFA = polyunsaturated fatty acids; MUFA = monounsaturated fatty acids.
Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML.
All values are expressed as means ± standard error of the mean (SEM). Asterisk (*) denotes a significant difference ($P < 0.05$).

Table 9
Effect of maternal GML supplementation on fatty acid profiles of sow milk on d 21 of lactation ($n = 10$).

Item	Treatments		*P*-value
	CON	GML	
SFA, %			
C4:0	0.09 ± 0.015	0.19 ± 0.050	0.095
C6:0	0.12 ± 0.032	0.17 ± 0.032	0.192
C8:0	0.13 ± 0.031	0.31 ± 0.074*	0.041
C12:0	0.36 ± 0.032	0.65 ± 0.044*	0.001
C14:0	3.18 ± 0.210	3.19 ± 0.116	0.970
C16:0	32.79 ± 1.182	33.09 ± 0.610	0.827
C17:0	0.37 ± 0.021	0.43 ± 0.072	0.075
C18:0	3.59 ± 0.313	3.14 ± 0.230	0.271
C20:0	0.17 ± 0.020	0.21 ± 0.061	0.572
C24:0	0.20 ± 0.052	0.44 ± 0.113*	0.047
Total SFA	40.85 ± 1.187	41.80 ± 0.798	0.515
MUFA, %			
C16:1n-9	8.94 ± 0.797	9.99 ± 0.748	0.411
C18:1n-9	25.53 ± 1.498	23.85 ± 1.269	0.885
C20:1n-11	0.17 ± 0.032	0.17 ± 0.020	0.596
C24:1n-15	0.22 ± 0.076	0.29 ± 0.112	0.216
Total MUFA	34.87 ± 1.049	34.29 ± 1.556	0.766
PUFA, %			
C18:2n-6	20.93 ± 0.620	19.35 ± 1.021	0.284
C18:3n-3	1.51 ± 0.047	1.49 ± 0.068	0.467
C18:3n-6	0.08 ± 0.018	0.17 ± 0.075	0.245
C20:2n-11	0.34 ± 0.072	0.49 ± 0.194	0.577
C20:3n-8	0.16 ± 0.022	0.41 ± 0.194	0.135
C20:3n-11	0.07 ± 0.028	0.11 ± 0.036	0.369
C20:4n-6	0.40 ± 0.056	0.28 ± 0.068	0.394
C20:5n-3	0.10 ± 0.032	0.15 ± 0.043	0.067
C22:2n-13	0.57 ± 0.180	0.84 ± 0.2425	0.731
C22:6n-3	0.26 ± 0.068	0.74 ± 0.235	0.209
Total PUFA	24.38 ± 0.721	23.90 ± 1.138	0.730
n-3 PUFA	1.84 ± 0.074	2.40 ± 0.280	0.086
n-6 PUFA	21.41 ± 0.600	19.79 ± 1.054	0.209
n-6:n-3 PUFA ratio	11.67 ± 0.421	8.80 ± 1.063*	0.031

GML = glycerol monolaurate; SFA = saturated fatty acids; PUFA = polyunsaturated fatty acids; MUFA = monounsaturated fatty acids.
Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML.
All values are expressed as means ± standard error of the mean (SEM). Asterisk (*) denotes a significant difference ($P < 0.05$).

duodenum and jejunum as well as the CD value in the ileum of piglets compared to the CON group ($P < 0.05$).

3.12. Expression of GPR84 and PI3K/Akt signaling pathway in the small intestine of piglets

We further assessed the effects of maternal GML supplementation on the small intestinal proliferation of the offspring piglets through expressions of GPR84, PI3K/Akt signaling pathway, PCNA and cyclin D1. As shown in Fig. 7, compared with the CON group, maternal GML supplementation significantly up-regulated the relative protein expressions of GPR84, PCNA, cyclin D1, the ratio of p-PI3K to PI3K, and the ratio of p-Akt to Akt in the duodenum and jejunum of suckling piglets ($P < 0.05$).

4. Discussion

Sows have high requirements of nutrients during milk production and may account for 70% to 75% of the total energy need during peak lactation (Tian et al., 2022; Wang et al., 2022). Dietary fatty acid supplementation during late pregnancy and lactation is an efficient approach to the supply of high energy density feed in order to improve total energy ingestion and refrain from the negative energy balance of sows (Kong et al., 2021; Mo et al., 2019). Besides, milk fat as a main resource, accounts for more than 50% of energy transfer from mother to offspring piglets (Liu et al., 2021). Although milk fat is crucial for the growth performance of offspring, the impact of diet composition on the milk fatty acid profile, particularly MCFA, is still unclear (Zhe et al., 2023).

Feeding higher levels of lipids during the late pregnancy and lactation stages may be a valid strategy to improve the growth performance of suckling piglets by increasing the available energy from colostrum and milk consumption (Ren et al., 2020; You et al., 2023). Medium-chain fatty acids have antibacterial properties, enhance intestinal integrity, and can serve as an effective energy source for enterocytes (Świątkiewicz et al., 2020). Oxidative stress and an immature immune system have been demonstrated to be vital factors in early fetal abortion (Li et al., 2022b). Therefore, our present study investigated the maternal effect of dietary supplementation of GML during late pregnancy and lactation on reproductive performance, immunity and antioxidant capacity transfer, and gut health of piglets. Consistent with our experimental hypothesis, results in this study revealed that maternal supplementation of GML increased lactation and litter performance, possibly associated with enhanced redox status and immunity transfer, and improved gut health through activation of GPR84 and PI3K/Akt

Table 10
Effect of maternal GML supplementation on the immunoglobulins of plasma and milk of sows ($n = 10$) and plasma of piglets ($n = 6$) (μg/mL).

Item	Treatments		*P*-value
	CON	GML	
Sow			
Plasma, d 1 of lactation			
IgA	675.53 ± 22.524	847.37 ± 43.086*	0.003
IgG	1431.96 ± 79.590	1649.13 ± 56.968	0.260
Plasma, d 21 of lactation			
IgA	348.39 ± 29.167	393.09 ± 39.791	0.383
IgG	344.56 ± 28.224	402.02 ± 27.552	0.421
Colostrum, d 1 of lactation			
IgA	1052.01 ± 124.325	1370.88 ± 76.730*	0.045
IgG	9,793.05 ± 555.342	11,771.94 ± 376.975*	0.018
Milk, d 21 of lactation			
IgA	88.61 ± 7.821	107.07 ± 8.385	0.140
IgG	822.21 ± 38.318	955.25 ± 30.680*	0.019
Piglet			
Plasma, 1 d of age			
IgA	1499.27 ± 66.524	2751.25 ± 225.121*	0.042
IgG	2844.21 ± 196.394	3204.78 ± 175.898	0.201
Plasma, 21 d of age			
IgA	268.65 ± 6.927	291.35 ± 6.553*	0.011
IgG	1539.68 ± 145.412	2444.95 ± 209.772*	0.038

GML = glycerol monolaurate; IgA = immunoglobulin A; IgG = immunoglobulin G. Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML.
All values are expressed as means ± standard error of the mean (SEM). Asterisk (*) denotes a significant difference ($P < 0.05$).

pathway. The present research will supply a reference on the maternal-offspring dietary GML feeding strategy in a sow-piglet model.

Both MCFA and MCFA monoglyceride are efficiently hydrolyzed by gastric and pancreatic lipases and provide fast energy for enterocytes and intermediate liver metabolism, allowing better growth performance in the suckling young (Chen et al., 2019; Świątkiewicz et al., 2020). In this research, GML supplementation in sow diet during late gestation and lactation improved lactation performance, including litter weight, average body weight, ADG, and preweaning survival of piglets. A previous study on the sows and offspring indicated that maternal GML supplementation enhanced litter weight and average body weight at weaning of nursing piglets (Li et al., 2023). Wang et al. (2023) also showed that ADG in weaned piglets was increased linearly by GML supplementation compared with the CON group. It is supposed that GML supplementation during lactation was an efficient nutrition strategy for energy utilization in sows, and regulated absorption and metabolism of milk fat in piglets to support growth.

It is widely recognized that newborn piglets have inadequate immunity and their survival rate is dependent on the passive immunity transfer from mother to offspring through colostrum ingestion especially IgG (Bussy et al., 2019). Besides, milk intake after delivery is vital to accelerate gut development (Curtis and Bourne, 1971). Previous research showed that IgG is the main antibody resource in plasma and colostrum, while IgA predominated in milk of sow (Bourne and Curtis, 1973). Previous studies

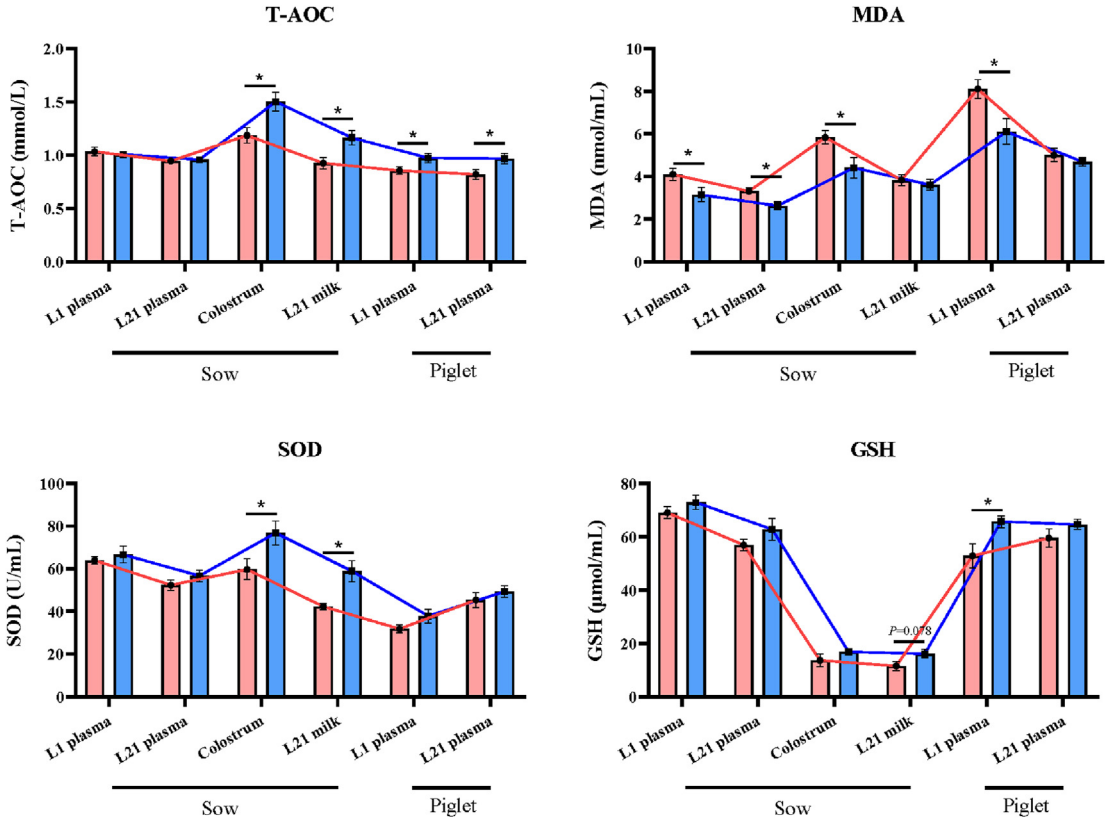

Fig. 1. Effect of dietary GML supplementation on the antioxidative and oxidative indicators of plasma in sows ($n = 10$) and offspring piglets ($n = 6$) on d 1 of lactation (L1) and d 21 of lactation (L21). Asterisk (*) denotes a significant difference ($P < 0.05$). Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML. GML = glycerol monolaurate; GSH = glutathione; MDA = malondialdehyde; SOD = superoxide dismutase; T-AOC = total antioxidant capacity.

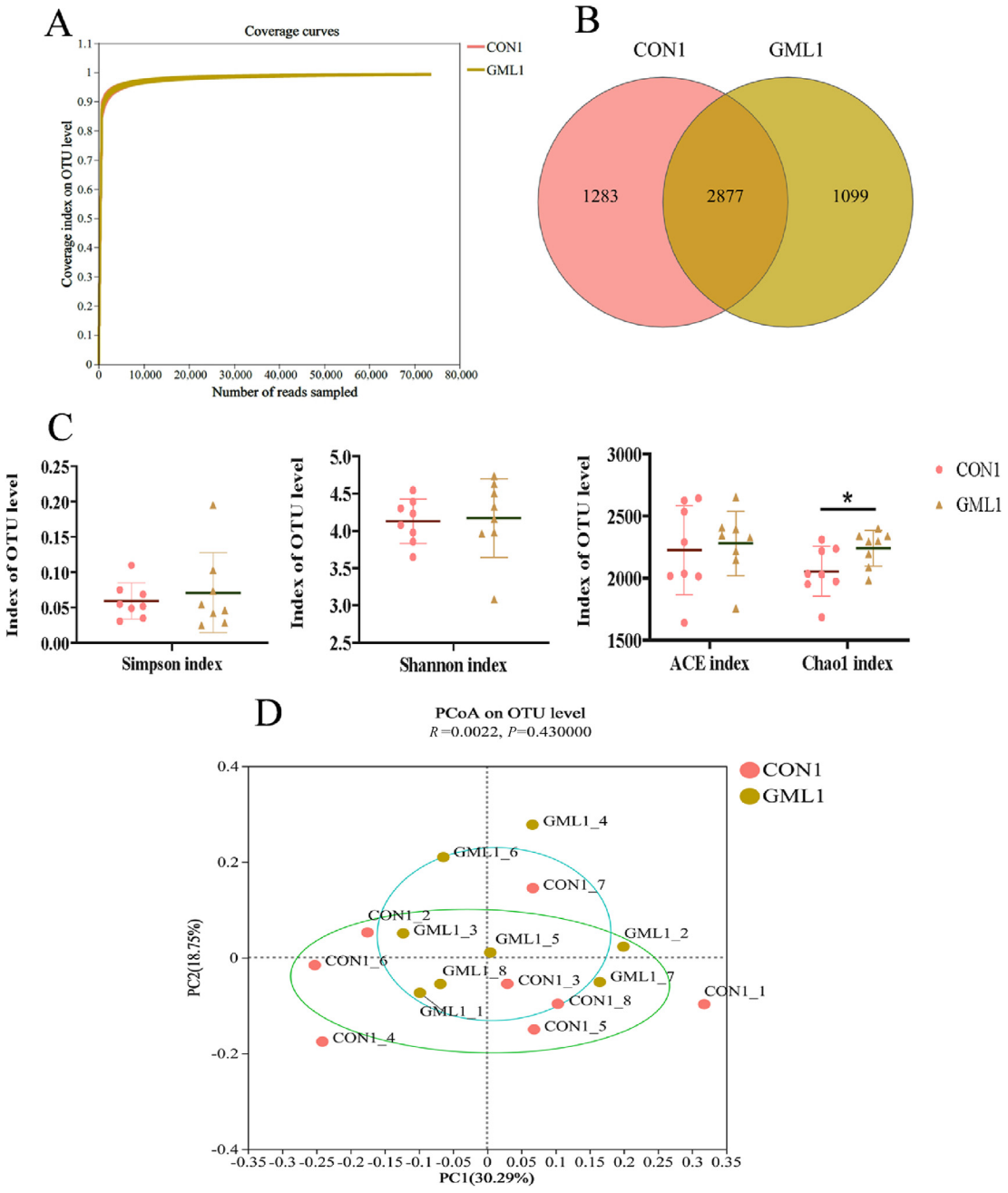

Fig. 2. Effect of dietary GML supplementation on the sow fecal microbial diversity and structure on d 1 of lactation (L1). The coverage curves of 16S rRNA sequencing depth (A). The Venn analysis plot on operational taxonomic unit (OTU) level (B). The microbial alpha diversity, including Shannon, Simpson, ACE, and Chao1 indexes (C). The beta-diversity principal co-ordinates analysis (PCoA) plot based on unweighted UniFrac (D) on microbial OTU level. $n = 8$ per group. Asterisk (*) denotes a significant difference ($P < 0.05$). Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML. CON1 and GML1 means that sow fecal samples from CON group and GML group were collected on L1. GML = glycerol monolaurate; ACE = abundance-based coverage estimators.

showed that increased IgA and IgG levels were also observed in colostrum from sows supplemented with GML (Li et al., 2023). Additionally, Chen et al. (2019) reported that dietary addition of MCFA enhanced the levels of IgA and IgG in the colostrum of sows. In the present study, maternal GML supplementation exhibited higher concentrations of IgA and IgG in plasma, colostrum, and milk of sows and further transmission to the piglets through milk revealed a role of GML for improved passive immunity in offspring.

As expected, the current research showed that GML supplementation in sow diets altered the fatty acid profile of sow plasma, colostrum, and milk, and the effect was mainly seen on colostrum and milk. In terms of SFA, GML treatment significantly increased the LA (C12:0) levels in the plasma (0.18% CON vs 0.28% GML) and colostrum (0.36% CON vs 0.65% GML) of sows, which was consistent with previous finding (Li et al., 2023). The current results also showed that GML treatment significantly increase total SFA (27.33% CON vs 29.62% GML) in colostrum, mainly reflected in fatty acids C16:0 (18.89% CON vs 21.58% GML) and C12:0. In agreement with the findings of Melichar et al. (1975), the proportions of C12:0, C14:0 and C16:0 in sow milk were increased along with the

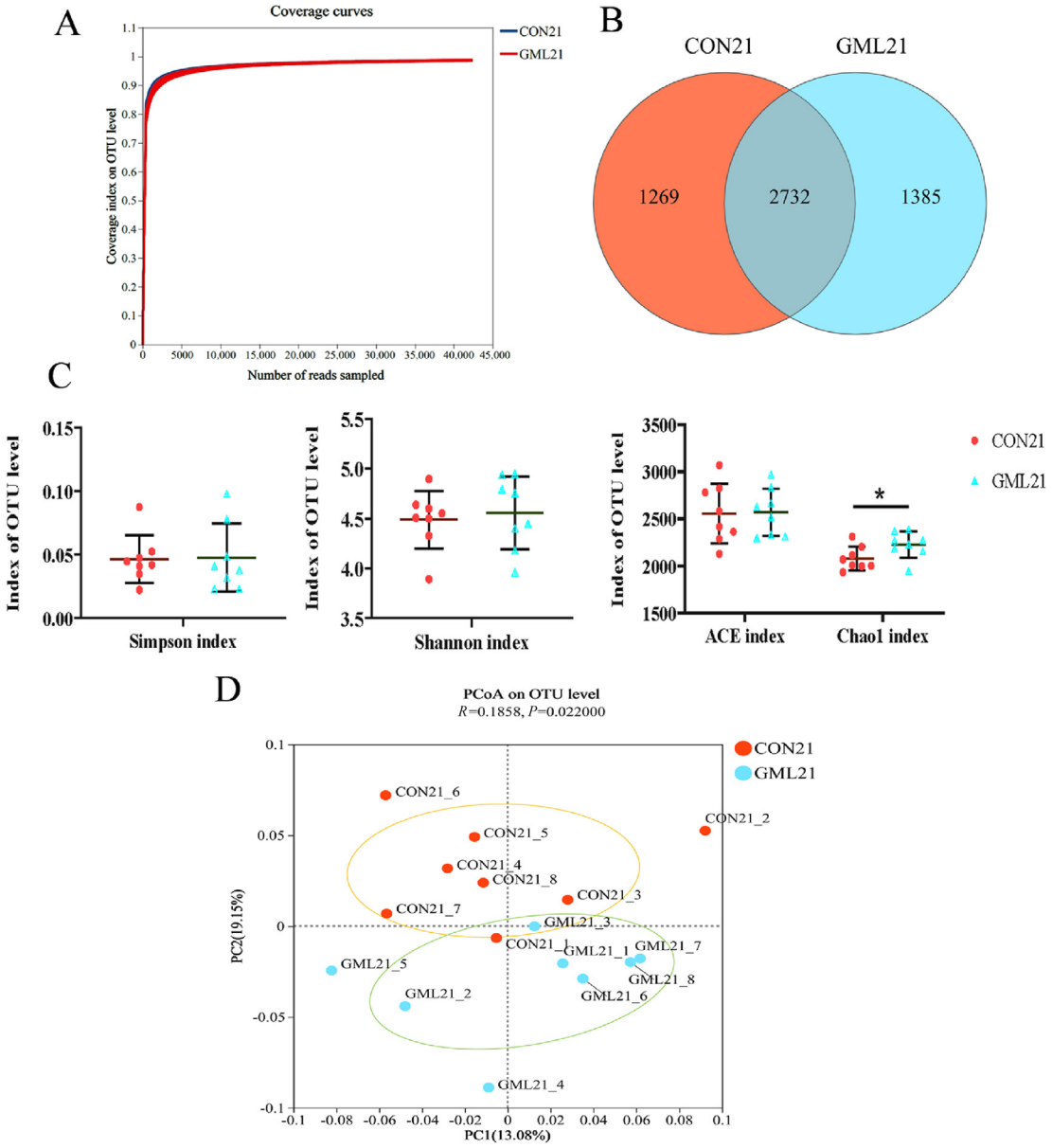

Fig. 3. Effects of dietary GML addition on the sow fecal microbial diversity and structure on d 21 of lactation (L21). The coverage curves of 16S rRNA sequencing depth (A). The Venn analysis plot on operational taxonomic unit (OTU) level (B). The microbial alpha diversity, including Shannon, Simpson, ACE, and Chao1 indexes (C). The beta-diversity principal coordinates analysis (PCoA) plot based on unweighted UniFrac (D) on microbial OTU level. $n = 8$ per group. Asterisk (*) denotes a significant difference ($P < 0.05$). Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML. CON21 and GML21 means that sow fecal samples from CON group and GML group were collected on L21. GML = glycerol monolaurate; ACE = abundance-based coverage estimators.

lactation time. C16:0 as the major SFA in sow milk accounts for 20% to 30% of the total fatty acid profile, which is initially from sow blood and synthesized in sow mammary epithelial cells (Holen et al., 2023). The increased proportion of C16:0 was conducive to milk fat synthesis, which supplied fractional energy for nursery piglet development (Hu et al., 2019). Therefore, we speculated that the increasing SFA in sow milk were associated with the improved offspring growth performance.

In the case of MUFA, GML treatment increased the total MUFA and proportion of C18:1n-9 (31.31% CON vs 35.61% GML) in sow colostrum. Oleic acid (C18:1n-9), similar to all free fatty acids is an energy molecule and cell membrane element. Besides, oleic acid directly participates in the regulation of antioxidant enzyme activity (Santa-María et al., 2023), and suppresses the inflammatory response through inhibition of proinflammatory cytokines synthesis and secretion (Oh et al., 2009). The current study indicated that GML treatment tended to reduce the proportion of total PUFA, n-6 PUFA, and n-6:n-3 PUFA ratio, and increased n-3 PUFA proportion in sow plasma and milk. The present study was the first to find that GML supplementation in the sow diet decreased the total PUFA proportion in milk. Based on lactation milk biology, milk short chain fatty acids (SCFA) and MCFA are synthesized de novo in the mammary gland, while milk LCFA are normally synthesized from lipolysis of maternal body fat reserve or from the mammary gland LCFA absorption (Churakov et al., 2021; Suarez-Trujillo et al., 2021). Thus, we speculated that the decreasing trend in the PUFA

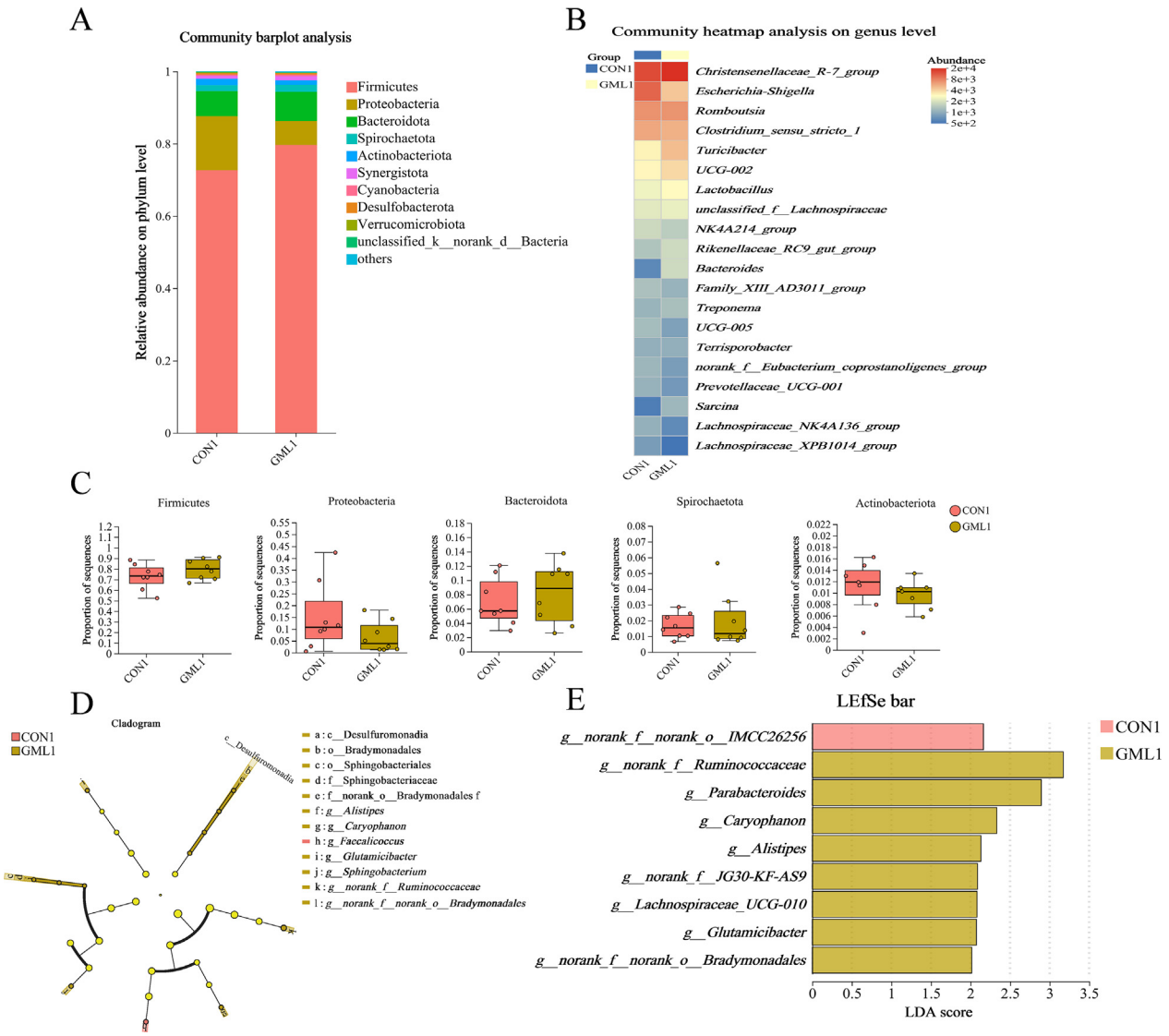

Fig. 4. The fecal microbial communities and differential microbial biomarker based on the relative abundance at phylum and genus levels of sows on d 1 of lactation (L1). The bacteria with proportion greater than 0.1% at phylum level (A) and the top 20 bacteria at genus level (B) were presented. The top 5 bacteria based on average relative abundances of phylum level (C) were listed and compared. The cladogram (D) plotted based on linear discriminant analysis effect size (LEfSe) analysis from the phylum to genus level. Differential biomarker in microbial community between two groups were screened out through LEfSe analysis at genus level (E). $n = 8$ per group. Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML. CON1 and GML1 means that sow fecal samples from CON group and GML group were collected on L1. GML = glycerol monolaurate.

proportion caused by the GML addition in the sow diet might be due to the rapid bioenergy supply of MCFA metabolism, without the demand for mobilizing body fatty acid reserves to synthesize PUFA. It has been widely accepted that a high n-6:n-3 PUFA ratio is the biomarker of increased inflammatory mediator production and metabolic syndrome pathology (Ma et al., 2019; Yang et al., 2016). Many emerging studies indicated that diet intervention strategy mainly focused on n-3 PUFA proportion, including a lower n-6:n-3 PUFA ratio or a higher amount of n-3 PUFA consumption (Bhurosy and Jeewon, 2014; Duan et al., 2014). A recent study reported that lower n-6:n-3 PUFA ratio attenuated LPS-induced oxidative stress and systemic inflammation (Park et al., 2022). The present results revealed that GML treatment improved offspring redox and immune status through reducing n-6 PUFA proportion and n-6:n-3 ratio, whereas increasing oleic acid and n-3 PUFA proportions in sow plasma and colostrum.

Higher alpha diversity contributed to the gut microbiota maturation and host health (Finn, 2024). Alpha diversity is reflected by the richness index (Chao1 and ACE) and the diversity index (Shannon and Simpson). Our results showed that the Chao1 index was higher in the GML group than in the CON group, suggesting that GML improved the diversity and stability of the microbiota in the hind intestine of sows. In the present study, GML treatment significantly decreased the relative abundance of Proteobacteria and increased the abundances of Ruminococcaceae and *Parabacteroides*. The Proteobacteria is associated with intestinal inflammation. A large number of bacteria in this phylum induce intestinal lesions, including *Salmonella* (causes enteritis) (Threlfall, 2002) and *Escherichia coli* (causes diarrhea) (Tenaillon et al., 2010). Ruminococcaceae is extensively demonstrated to have carbohydrate-active enzymes that can degrade undigested cellulose and starch and produce SCFA, improving feed conversion and

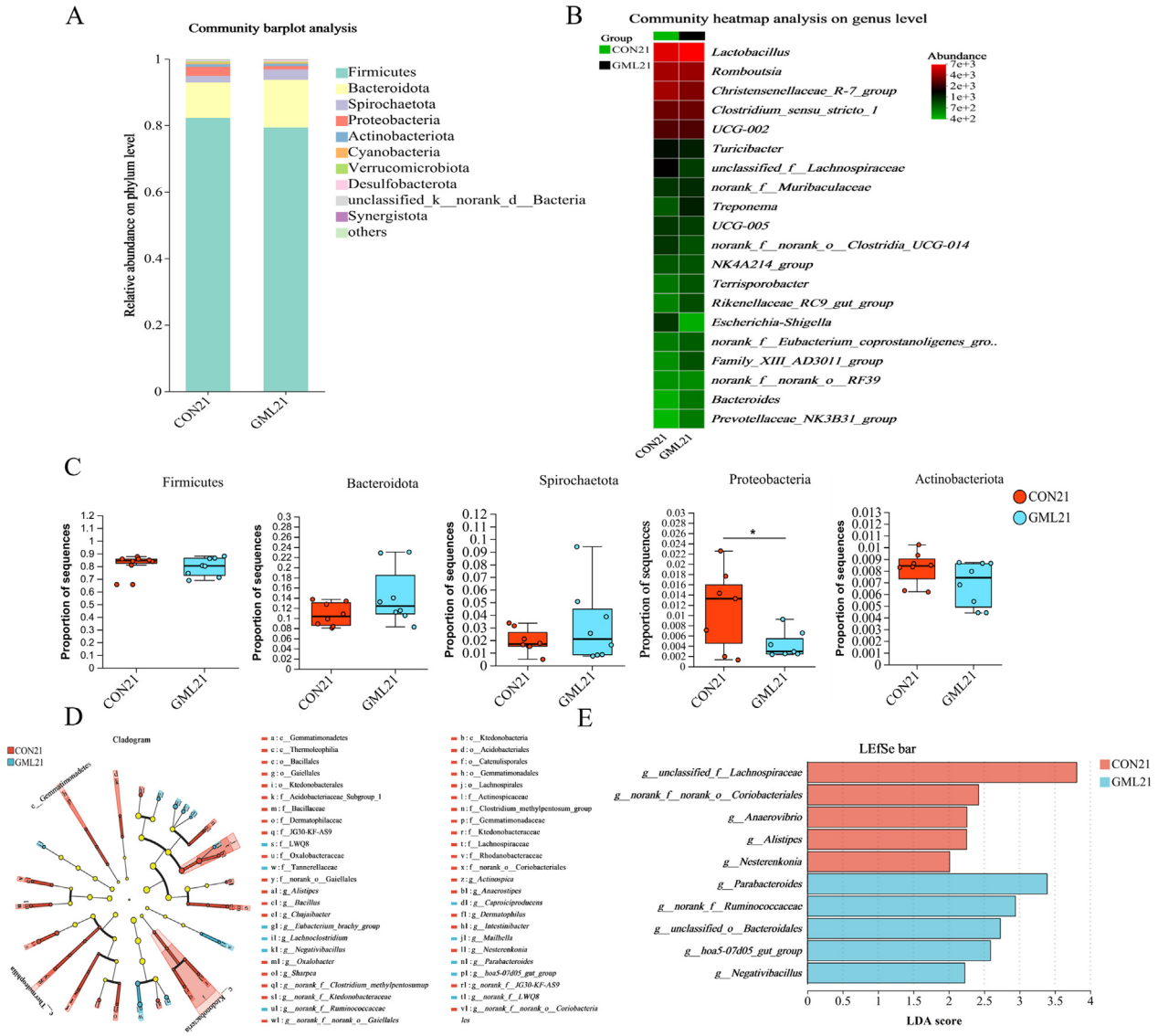

Fig. 5. The fecal microbial communities and differential microbial biomarker based on the relative abundance at phylum and genus levels of sows on d 21 of lactation (L21). The bacteria with proportion greater than 0.1% at phylum level (A) and the top 20 bacteria at genus level (B) were presented. The top 5 bacteria based on average relative abundances of phylum level (C) were listed and compared. The cladogram (D) plotted based on linear discriminant analysis effect size (LEfSe) analysis from the phylum to genus level. Differential biomarker in microbial community between two groups were screened out through LEfSe analysis at genus level (E). $n = 8$ per group. Asterisk (*) denotes a significant difference ($P < 0.05$). Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML. CON21 and GML21 means that sow fecal samples from CON group and GML group were collected on L21. GML = glycerol monolaurate.

growth performance in animals (Liang et al., 2021). Besides, *Parabacteroides* also have the physiological characteristics of carbohydrate metabolism and SCFA secretion (Cui et al., 2022). Thus, our finding revealed that GML supplementation increased the alpha diversity and proliferation of SCFA-producing Ruminococcaceae and *Parabacteroides*, and inhibited harmful Proteobacteria, further promoting the hind intestinal microbiota homeostasis of sows.

To investigate the effect of maternal GML supplementation on the gut health of offspring piglets, we measured the expression of GPR84 and PI3K/Akt pathway as well as proliferation marker proteins PCNA and cyclin D1. GPR84 as an orphan class A G protein-coupled receptor (GPCR) is activated by MCFA and its derivatives (Liu et al., 2023). Research has shown that the PI3K/Akt pathway is an important intracellular signaling pathway involved in mediating epithelial cell proliferation, migration, and apoptosis (Chen et al., 2024; Zhao et al., 2020). Besides, the PI3K/Akt pathway plays a pivotal role in regulating intestinal mucosal injury repair, barrier integrity, and proliferation of IPEC-J2 cells (Yan and Ajuwon, 2017). Until now, there have been no studies of GML on intestinal cells, and in vitro experiments were mostly focused on immune cells. The research on LA (GML derivative) is limited. Only one previous study has reported that LA facilitates the differentiation and proliferation of IPEC-J2 cells with a low range of 0.1 to 0.25 mmol/L (Yang et al., 2020). Besides, a previous report showed that dietary 1% LA stimulated mammary gland development through increasing the expressions of GPR84 and cyclin D1, and activating the GPR84 and PI3K/Akt signaling pathways of pubertal mice (Meng et al., 2017). Meanwhile, the results of cell culture also revealed that the activation of PI3K/Akt was abolished by GPR84 knockdown (Meng et al., 2017). The latest research focusing on the effect of LA on

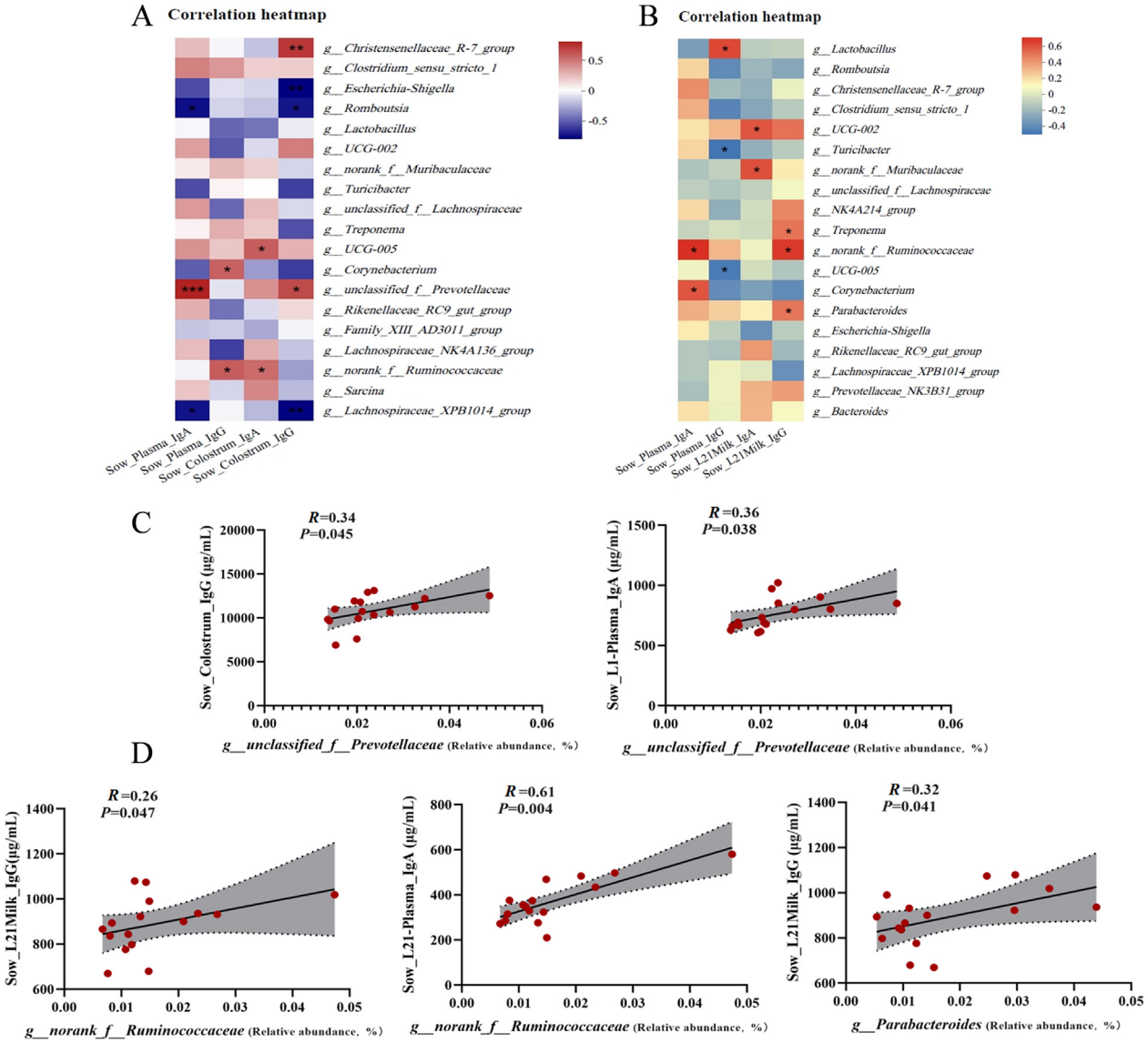

Fig. 6. The dietary GML supplementation associated microbial derived-immunoglobulin in the transmit from plasma to milk of sows. The Spearman's correlation analysis of IgA and IgG from plasma and colostrum on d 1 of lactation (A) as well as d 21 of lactation (B) with top 20 and differential genus bacteria abundances. *$P < 0.05$; **$P < 0.01$; ***$P < 0.01$. Spearman's correlation analysis of biomarker genera *Prevotellaceae*, *Ruminococcaceae*, and *Parabacteroides* abundances with IgA and IgG concentrations of plasma and milk on L1 (C) and L21 (D). GML = glycerol monolaurate; Ig = immunoglobulin.

mammary epithelial cells reported that LA addition stimulated cell proliferation through activation of the GPR84-Akt/mTOR pathway and increasing cyclin A1 and PCNA expressions (Zhang et al., 2024). In line with the previous research, our results showed that maternal GML addition up-regulated the relative protein expressions of GPR84, PCNA, cyclin D1, GPR84, and PI3K/Akt pathways in the duodenum and jejunum of suckling piglets. Besides, the small intestinal morphology results also showed that maternal GML improved the villus height in the duodenum and jejunum. It is worth noting that the effect of maternal GML on the intestinal morphology, expression of proliferation marker proteins, and potential involvement of GPR84 and PI3K/Akt pathways mainly manifested in the proximal part of the small intestine. The possible reason is that the proximal part, duodenum and jejunum were the main absorption sites of fatty acids from milk. However, whether the maternal GML supplementation acted as a fast energy-supplying substrate for sows or the substrate for de novo synthesis of milk SCFA and MCFA remains to be investigated.

5. Conclusion

In conclusion, our study demonstrated that maternal dietary GML supplementation during late gestation and lactation (from G85 to L23) optimized the milk fat and lauric acid profiles and microbiota derived immunoglobulins transfer in sows. Besides, maternal GML supplementation enhanced the piglet growth performance during lactation, which might be attributed to the improvement of gut health through the potential involvement of GPR84 and PI3K/Akt pathways (Fig. 8). The present study offers scientific insight into the swine industry in that dietary GML may

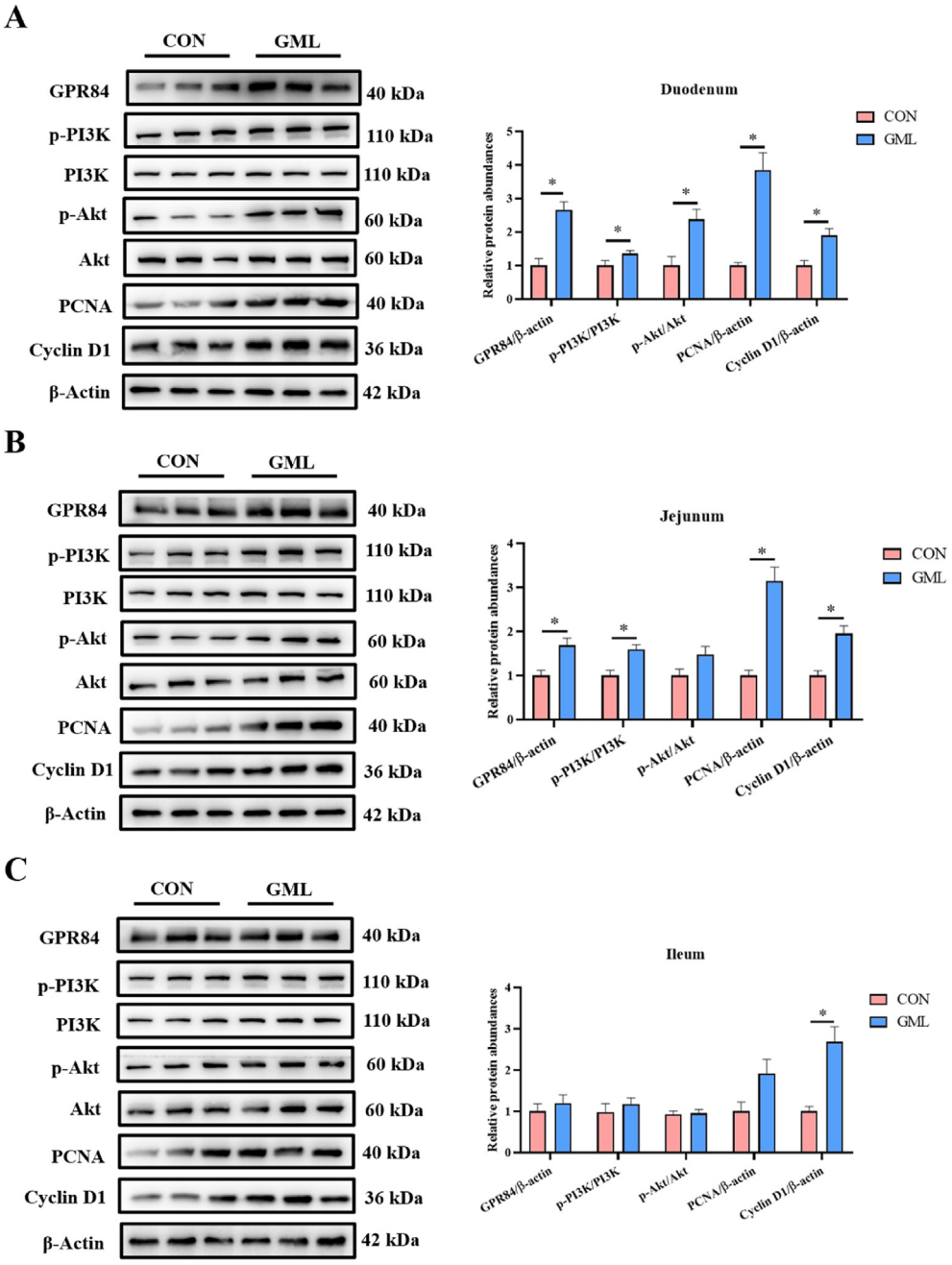

Fig. 7. Effects of maternal GML supplementation on the small intestinal health through potential involvement of GPR84 and PI3K/Akt signaling pathway and proliferation marker protein PCNA as well as cyclin D1 of suckling offspring piglets in the duodenum (A), jejunum (B), and ileum (C). Data are represented as means ± SEM, $n = 6$ per group. Asterisk (*) denotes a significant difference ($P < 0.05$). Control (CON) group, sows fed basal diet; GML group, sows fed basal diet supplemented with 1000 mg/kg GML. Akt = protein kinase B; GML = glycerol monolaurate; GPR84 = G protein-coupled receptor 84; PCNA = proliferating cell nuclear antigen; PI3K = phosphatidylinositol 3-kinase.

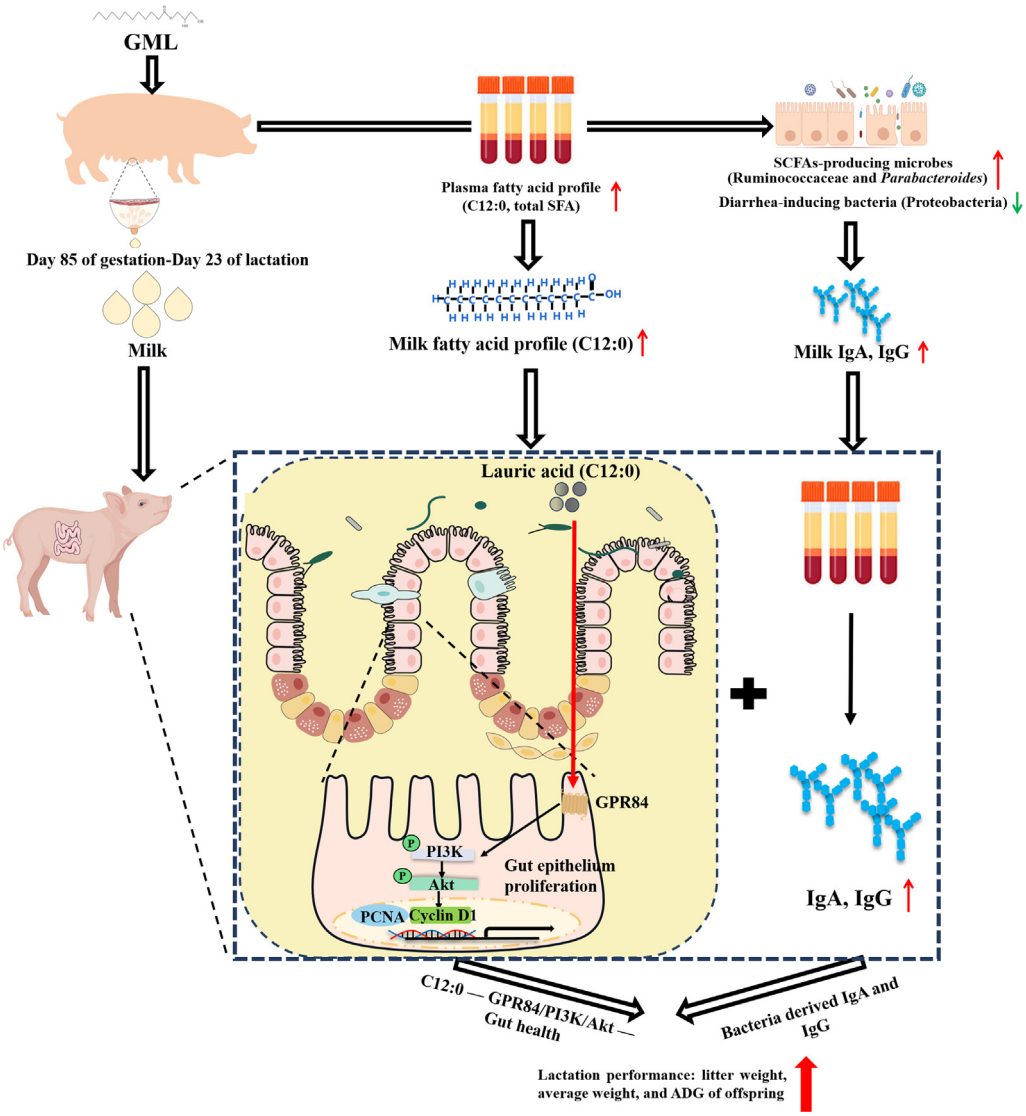

Fig. 8. The graphical representation of maternal GML supplementation enhanced piglet growth performance during lactation. ADG = average daily gain; SFA = saturated fatty acid; SCFA = short-chain fatty acid; Ig = immunoglobulin; GML = glycerol monolaurate; GPR84 = G protein-coupled receptor 84; PI3K = phosphatidylinositol 3-kinase; Akt = protein kinase B.

be used as a maternal nutrition intervention strategy during lactation for improving litter performance.

Credit Author Statement

Liang Xiong: Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Zhijin Zhang:** Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Shiqi Dong:** Visualization, Software, Resources, Methodology, Investigation. **Tongbin Lin:** Software, Investigation, Formal analysis, Data curation. **Xianhuai Yue:** Software, Resources, Methodology, Investigation, Formal analysis. **Fang Chen:** Visualization, Supervision, Software, Project administration. **Wutai Guan:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Shihai Zhang:** Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

Acknowledgments

This study was jointly supported by the Project of the Swine Innovation Team in Guangdong Modern Agricultural Research System (2022KJ126), National Key Research and Development

Program (No. 2021YFD1300401-2). The authors would like to thank our laboratory and Guangdong Foodstuffs Import & Export Group Co., Ltd. for their assistance during the animal experiment.

Appendix A. supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aninu.2024.11.017.

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