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# Assessment of the influence on *Hypsizygus marmoreus* stem waste as a sustainable alternative to corn in Holdobagy geese dietary

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The processing of edible mushrooms generates a large amount of mushroom residue. How to handle this mushroom residue in a way that avoids environmental pollution and maximizes effective utilization is a current issue that needs to be explored. This study aimed to investigate the effects of substituting dietary corn with *Hypsizygus marmoreus* mushroom stem waste (HSW) in the diet of geese. The control group was fed with a basal diet (BD), and the other groups were fed the basal diet to which 12% (HSW12 group), 24% (HSW24 group), or 32% (HSW32 group) of HSW were added to replace the equivalent proportion of corn. The test lasted 28 days. The results showed that the average daily feed intake (ADFI) of the HSW12 and HSW24 groups at 35–49 d, and the HSW12 and HSW32 groups at 35–63 d, was significantly higher compared to the BD group ( $p < 0.05$ ). The average daily gain (ADG) of the HSW12 group was significantly higher than BD at 35–49 d ( $p < 0.05$ ), but there was no significant difference in the feed/gain (F/G) among the groups. The levels of serum total protein (TP), albumin (ALB), globulin (GLOB), glutathione peroxidase (GSH-Px), and catalase (CAT) in HSW24 group were significantly higher than those in the BD group ( $p < 0.05$ ). Total cholesterol (TC), triglycerides (TG), low-density lipoprotein cholesterol (LDL-C), and malondialdehyde (MDA) decreased significantly, and there were no significant differences in carcass traits and meat quality. As 24% HSW supplementation had the best overall effect on the growth performance, serum biochemical indicators, meat quality, and carcass traits of geese, gut microbiota analysis was only performed on this group. The microbiota  $\alpha$ -diversity of the cecum and ileum did not differ significantly between the BD and HSW24 groups. Principal coordinate analysis (PCoA) indicated that the difference in the cecum was significant in the  $\beta$ -diversity ( $p < 0.05$ ). Short chain fatty acid-producing bacteria and decomposing protein and carbohydrate bacteria (*Prevotella*) were enriched in the cecum in the HSW24 group. Gut immune regulating and nutritional bacteria, *Lactococcus* and *Bacillus*, respectively, were enriched in the ileum in HSW24 group. Spearman's analysis indicated that *Bacillus*, *Prevotella*, and *Clostridium* were positively associated with serum protein and lipid metabolism. These results indicate that 24% HSW substitution of corn could improve goose serum ALB and fat metabolism, and increase serum antioxidant capacity, which may be caused by the improvement of goose cecal microbiota.

## KEYWORDS

diet, growth, lipids, microorganisms, mushrooms, nutrition, proteins

## Introduction

Corn is nutritionally balanced and an important part of animal husbandry (Limba et al., 2019; Williams, 2022). However, owing to the impact of COVID-19 and wars in recent years, the international price of corn has increased sharply (Lv and Xu, 2022; Xu and Zhang, 2022). Simultaneously, the supply of corn has recently been insufficient, increasing the cost of animal husbandry and limiting its development (Jim, 2020; Jacqueline, 2021). Therefore, it has become necessary to find alternate, unconventional feeds to replace corn, depending on the available local resources. Studies have found that corn in animal diets can be partially replaced without changing growth performance (Kim et al., 2021; Jeong et al., 2022), while improving the gut microbiome (Gheorghie et al., 2017).

The production and export of edible fungi in China has always been in the forefront of the world, ranking among the top five in terms of agricultural output (Li and Xu, 2022). *H. marmoreus* accounts for a large proportion of the edible fungus industry, and is widely planted worldwide (Yamanaka, 1997). The cultivation substrate of *H. marmoreus* mainly consists of corn cobs, rice bran, wheat bran, soybean husks, and sorghum flour. The production cycle of *H. marmoreus* is 110 to 120 days. In 2019, the total daily production capacity of *H. marmoreus* in China's commercial mushroom farms reached 930 tons. Its roots, stems, and caps have similar nutritional components, and are rich in crude protein, crude fiber, amino acids, and umami peptides, making it rich in nutrients and giving it a high edibility value. However, during processing or picking, the lower half of the stem is usually treated as waste, which causes environmental pollution while being wasted (Wu et al., 2019). Mushroom waste stems are considered a type of prebiotic and contain hemicellulose and polysaccharides (Singdevsachan et al., 2016). Studies have shown that adding mushroom waste stems to the diet of pigs is beneficial for growth, and can increase short-chain fatty acids in the gut (Liu et al., 2020). Studies have also shown that mushroom waste stems can improve the antioxidant capacity, immunity, and apparent digestibility of animals (Chen et al., 2018; Sun and Li, 2021). The *in vitro* immune activity of mushroom polysaccharides can provide a theoretical basis for determining the growth and health status of animals (Guo et al., 2003). Mushrooms contain high levels of cellulose (Liu et al., 2020), which cannot be directly digested and absorbed by many animals. However, geese, compared to other poultry, have well-developed ceca (Zhang et al., 2022), which provide a larger volume and longer retention time, allowing more time for interaction between the digesta and the microorganisms in the ceca. Research has shown that geese rely on cellulose-degrading bacteria in the ceca to decompose cellulose (Volk and Lacy, 2017), thereby releasing nutrients such as organic acids and short-chain fatty acids.

Therefore, in this experiment, the HWS were used as an unconventional feed to replace part of the corn-based diet of geese, and its growth performance, serum biochemical indices, slaughter performance and gut microbiome were evaluated.

## Materials and methods

### Animal ethics

Animal care and procedures were performed according to the Chinese Animal Welfare Guidelines. This research was approved by

the Laboratory Animal Ethics Committee of the Shanghai Academy of Agricultural Sciences (SAASPZ0522046).

### Animals and experimental design

HMS were provided by the Zhuanghang Comprehensive Experimental Station of Shanghai Academy of Agriculture Sciences (Shanghai, China) and processed at Shengwang Feed Co., Ltd. (Shanghai, China). Specifically, fresh HMS was dried using a three-stage rotary drum dryer (Lunji, Shandong, China) at 65°C, then pulverized using a grinder (Jishun, Shandong, China) and sieved through a 2-millimeter mesh to obtain a powdered form, which was subsequently incorporated into the daily ration. The same batch of HMS was used for all experiments. The nutritional and amino acid composition of HMS are presented in Table 1.

The geese used in the experiment were purchased from the Xiangtiange Family Farm, Ma'anshan City, Anhui Province, China. A total of 192 35-day-old Hordobagy geese from the same batch were randomly allocated into four groups. Each group had six replicates

TABLE 1 Nutrient level of HSW (air-dried basis) %<sup>a</sup>.

| Items       | Content % |
|-------------|-----------|
| EE          | 0.83      |
| Ash         | 12.35     |
| CF          | 19.87     |
| CP          | 8.00      |
| ME (MJ/kg)  | 13.98     |
| Ca          | 0.78      |
| P           | 0.73      |
| Amino Acids |           |
| Asn         | 0.51      |
| Thr         | 0.27      |
| Ser         | 0.27      |
| Glu         | 0.78      |
| Gly         | 0.31      |
| Ala         | 0.33      |
| Cys         | 0.19      |
| Val         | 0.30      |
| Met         | 0.10      |
| Ile         | 0.21      |
| Leu         | 0.36      |
| Tyr         | 0.14      |
| Phe         | 0.22      |
| Lys         | 0.27      |
| His         | 0.12      |
| Trp         | 0.03      |
| Arg         | 0.25      |
| Pro         | 0.33      |

<sup>a</sup>All indicators are measured values.

with eight geese (half males and half females). The control group was fed a basal diet (BD) comprising corn, the other groups were fed a mixture of the basal diet with 12% (HSW12 group), 24% (HSW24 group), or 32% (HSW32 group) dry mass of HSW, included to replace the same proportion of corn. The test period was 28 days. The basal diet group was based on the NRC1994 standard and adjusted according to the nutritional status of Chinese geese (Table 2). Each replicate of eight geese was housed in an individual mesh cage (80 × 80 × 80 cm) in a naturally ventilated windowed shed at a temperature between 10–15°C. Only natural light was provided, and the light time of each cage was the same throughout the experiment. Feed and water were provided *ad libitum*. Disinfection and administration of vaccines progressed on schedule, as for other geese on the farm.

### Growth performance

At the beginning (35 d), middle (49 d), and end (63 d) of the experiment, the body weight and feed consumption of each goose were measured, and its ADG, ADFI and F/G were calculated. The geese were fasted for 12 h before weighing.

$$ADFI = \text{total feed intake} / (\text{test days} \times \text{total number of test geese}).$$

$$ADG = (\text{final body weight} - \text{initial body weight}) / \text{test days}.$$

$$F / G = ADFI / ADG.$$

### Serum collection and analysis

Blood samples were collected at the end of the experiment. One male goose from each cage was chose and draw 4 mL of blood from the wing vein, stored in vacuum-sealed blood collection tubes at 37°C for 1 h, and centrifuged at 4,500 rpm for 15 min. Then collected the serum for further analysis. Serum biochemical parameters, including total protein (TP), albumin (ALB), globulin (GLOB), glucose (GLU), burea nitrogen (BUN), total cholesterol (TC), Triglycerides (TG), low-density lipoprotein cholesterol (LDL-C), high-density lipoprotein cholesterol (HDL-C), alanine aminotransferase (ALT), aspartate aminotransferase (AST), and alkaline phosphatase (AKP) were detected using an automatic biochemical analyzer (HITACHI 7180, Japan). Malondialdehyde (MDA), superoxide dismutase (SOD), glutathione peroxidase (GSH-Px), catalase (CAT), and total antioxidant capacity (T-AOC) were detected by ELISA (DENLEY DRAGON Wellscan MK 3, Finland), with the appropriate test kit purchased from Nanjing Jiancheng Biotechnology Co., Ltd., China.

TABLE 2 Composition and nutrient level of experiment diets (air-dry basis).

| Items                   | Treatment |        |        |        |
|-------------------------|-----------|--------|--------|--------|
|                         | BD        | HSW12  | HSW24  | HSW32  |
| Ingredients             |           |        |        |        |
| Corn                    | 67.92     | 55.99  | 43.99  | 36.08  |
| Soybean meal            | 24.90     | 24.80  | 24.80  | 24.70  |
| HSW                     | 0.00      | 12.00  | 24.00  | 32.00  |
| Soybean oil             | 2.00      | 2.00   | 2.00   | 2.00   |
| Lys                     | 0.09      | 0.09   | 0.08   | 0.08   |
| Met                     | 0.09      | 0.11   | 0.12   | 0.13   |
| Thr                     | 0.00      | 0.05   | 0.05   | 0.05   |
| Premix <sup>a</sup>     | 5.00      | 5.00   | 5.00   | 5.00   |
| Total                   | 100.00    | 100.00 | 100.00 | 100.00 |
| Nutrient level          |           |        |        |        |
| CP                      | 16.00     | 15.99  | 16.02  | 16.00  |
| ME (MJ/kg) <sup>b</sup> | 12.40     | 11.63  | 11.50  | 12.09  |
| CF                      | 2.56      | 4.74   | 6.94   | 8.39   |
| Ca                      | 0.79      | 0.79   | 0.78   | 0.79   |
| P                       | 0.51      | 0.50   | 0.51   | 0.52   |
| Lys                     | 0.90      | 0.90   | 0.90   | 0.90   |
| Met+Cys                 | 0.66      | 0.66   | 0.66   | 0.66   |
| Thr                     | 0.63      | 0.63   | 0.63   | 0.63   |

<sup>a</sup>One kilogram of the premix contained the following: Fe 100 mg, Cu 8 mg, Mn 120 mg, Zn 100 mg, Se 0.4 mg, Co 1.0 mg, I 0.4 mg, VA 8330 IU, VB1 2.0 mg, VB2.8 mg, VB6 1.2 mg, VB12 0.03 mg, VD31440 IU, VE 30 IU, biotin 0.2 mg, folic acid 2.0 mg, pantothenic acid 20 mg, niacin acid 40 mg.

<sup>b</sup>Nutrient levels were all calculated values.

### Carcass traits and meat quality

After the experiment, geese were fasted for 12 h and deprived of water for 2 h. One goose was selected closed to the average body weight of each replicate. After weighing, the jugular vein was cut and the goose bled to death. The measurement and calculation of carcass traits is reference to Zhai et al. (2020).

According to the method in “Determination of Meat Quality of Livestock and Poultry” (NY/T 823–2004), a colorimeter (Chroma Meter CR-410, Konica Metanon Corporation, Japan) was used to measure the chest muscle and leg muscle. The tissue pH was measured using a Testo-205 pH-measuring instrument.

### 16S rDNA sequencing

After slaughtering, the ileum and cecum were retrieved. Using cotton thread, both ends were ligated. Approximately 1 g of digesta from the middle portion was collected in a 2 mL centrifuge tube. The samples were rapidly frozen using liquid nitrogen and stored at -80°C. The DNA of microorganisms in ileal and cecal digesta was extracted using a DNA extraction kit (Tiangen, Beijing, China). The concentration of DNA was measured with a UV spectrophotometer (NanoDrop 2000, ThermoFisher, MA, United States). The purity of the DNA was checked by 1% agarose gel electrophoresis. DNA is used as a template for PCR amplification and the products are purified, quantified and normalized to form a sequencing library. The library was sequenced after dilution and quantification (NovaSeq 6,000, San Diego, United States), and the amplicon sequence variants, diversity and difference analysis was performed on the sequence information.

TABLE 3 Effect of HSW on growth performance<sup>a</sup>.

| Items                          | Treatment            |                      |                      |                     | SEM   | p-value |
|--------------------------------|----------------------|----------------------|----------------------|---------------------|-------|---------|
|                                | BD                   | HSW12                | HSW24                | HSW32               |       |         |
| Body weight, g                 |                      |                      |                      |                     |       |         |
| 35d                            | 3612.38              | 3609.46              | 3600.22              | 3614.85             | 22.24 | 0.996   |
| 49d                            | 4054.50              | 4106.19              | 4087.04              | 4003.14             | 24.79 | 0.481   |
| 63d                            | 4627.25              | 4737.19              | 4793.06              | 4694.98             | 34.12 | 0.371   |
| Average daily feed intake, g/d |                      |                      |                      |                     |       |         |
| 35–49d                         | 192.12 <sup>b</sup>  | 206.38 <sup>a</sup>  | 204.89 <sup>a</sup>  | 187.26 <sup>b</sup> | 2.00  | <0.05   |
| 49–63d                         | 295.06 <sup>ab</sup> | 332.37 <sup>b</sup>  | 313.39 <sup>bc</sup> | 378.19 <sup>a</sup> | 8.02  | <0.05   |
| 35–63d                         | 243.59 <sup>c</sup>  | 269.37 <sup>ab</sup> | 259.14 <sup>bc</sup> | 282.73 <sup>a</sup> | 3.95  | <0.05   |
| Average daily gain, g          |                      |                      |                      |                     |       |         |
| 35–49d                         | 31.58 <sup>b</sup>   | 35.48 <sup>a</sup>   | 34.77 <sup>ab</sup>  | 27.72 <sup>c</sup>  | 0.63  | <0.05   |
| 49–63d                         | 40.91                | 45.07                | 50.43                | 49.42               | 1.84  | 0.238   |
| 35–63d                         | 36.25                | 40.28                | 42.60                | 38.58               | 0.97  | 0.123   |
| F/G                            |                      |                      |                      |                     |       |         |
| 35–49d                         | 6.20                 | 5.98                 | 5.91                 | 6.78                | 0.13  | 0.063   |
| 49–63d                         | 7.42                 | 7.75                 | 7.74                 | 7.67                | 0.26  | 0.972   |
| 35–63d                         | 6.76                 | 6.87                 | 6.74                 | 7.34                | 0.13  | 0.349   |

<sup>a</sup>Different lowercase letters with the same column date meant significant difference ( $p < 0.05$ ).

## Statistical analysis

The raw data on growth performance, serum biochemical indicators, and slaughter performance were organized using Microsoft Excel 2007, and one-way ANOVA analysis of variance and Duncan's multiple range test were conducted using SPSS 25.0 software (IBM, New York, United States). Significant differences were indicated by  $p < 0.05$ . The raw gut microbiota sequencing data were quality controlled using QIIME 2.0 software. Optimized sequences were obtained by sequence trimming, filtering, and chimera removal. Clustering analysis of amplicon sequence variants (ASV) was performed using USEARCH 7.0 software. Classification analysis of ASV sequences was conducted using the greengene gene database, and the community composition of each sample was analyzed at the phylum, class, order, family, genus, and species levels. Principal coordinate analysis (PCoA) of the cecal microbiota was performed using R language, and data visualization was conducted using STAMP 2.1.3 software. -diversity indices were calculated using Mothur 1.2 software. Spearman analysis was performed using GeneCloud.<sup>1</sup>

## Results

### Growth performance

Compared with the BD group, there was no difference in body weight between groups at 49 d and 63 d (Table 3), but the ADFI of the

HSW12 and HSW24 groups at 35–49 d, and of the HSW12 and HSW32 groups at 35–63 d, increased significantly ( $p < 0.05$ ). The ADG of the HSW12 group increased significantly compared to the control at 35–49 d ( $p < 0.05$ ), but there was no significant difference in the F/G between groups.

### Serum biochemical indicators

Compared with the BD group, there was no significant difference in the levels of GLU, BUN, UA, HDL-C, ALT, AST, and AKP (Table 4). However, the levels of TP, ALB, and GLOB in the HSW24 group increased significantly. In contrast, the levels of TG, TC, and LDL-C decreased significantly ( $p < 0.05$ ).

### Serum antioxidant indicators

There were significant differences among the other indexes between the groups: MDA levels decreased significantly in the HSW24 and HSW32 groups ( $p < 0.05$ ), the levels of CAT and GSH-Px increased significantly in the HSW12 and HSW24 groups ( $p < 0.05$ ), and the T-AOC levels were significantly higher in the HSW32 group (Table 5).

### Carcass traits and meat quality

There were no significant differences in carcass traits or meat quality (Table 6). However, the pH of the breast muscle in the HSW24 group tended to increase slightly, but not significantly ( $p < 0.10$ ).

<sup>1</sup> <https://www.genescloud.cn/>

TABLE 4 Effect of HSW on serum biochemical indexes<sup>a</sup>.

| Items         | Treatment          |                     |                    |                     | SEM   | P-value |
|---------------|--------------------|---------------------|--------------------|---------------------|-------|---------|
|               | BD                 | HSW12               | HSW24              | HSW32               |       |         |
| TP, g/L       | 29.53 <sup>b</sup> | 34.80 <sup>ab</sup> | 39.53 <sup>a</sup> | 32.62 <sup>b</sup>  | 1.28  | 0.031   |
| ALB, g/L      | 9.62 <sup>b</sup>  | 11.67 <sup>a</sup>  | 12.25 <sup>a</sup> | 10.72 <sup>ab</sup> | 0.36  | 0.041   |
| GLOB, g/L     | 19.91 <sup>b</sup> | 23.13 <sup>a</sup>  | 28.95 <sup>a</sup> | 21.90 <sup>b</sup>  | 1.06  | 0.008   |
| GLU, mmol/L   | 8.80               | 8.60                | 7.83               | 8.60                | 0.28  | 0.399   |
| BUN, mmol/L   | 0.67               | 0.47                | 0.62               | 0.71                | 0.04  | 0.114   |
| UA, umol/L    | 152.17             | 143.83              | 105.83             | 132.67              | 9.47  | 0.350   |
| TC, mmol/L    | 4.25 <sup>a</sup>  | 3.28 <sup>ab</sup>  | 2.83 <sup>b</sup>  | 3.06 <sup>b</sup>   | 0.20  | 0.045   |
| TG, mmol/L    | 1.07 <sup>a</sup>  | 0.60 <sup>b</sup>   | 0.61 <sup>b</sup>  | 0.74 <sup>b</sup>   | 0.05  | 0.002   |
| HDL-C, mmol/L | 1.78               | 2.00                | 2.87               | 2.08                | 0.16  | 0.084   |
| LDL-C, mmol/L | 1.42 <sup>a</sup>  | 0.91 <sup>b</sup>   | 0.73 <sup>b</sup>  | 0.99 <sup>ab</sup>  | 0.09  | 0.033   |
| ALT, IU/L     | 9.67               | 12.83               | 12.50              | 10.00               | 0.79  | 0.372   |
| AST, IU/L     | 35.33              | 30.33               | 26.33              | 21.83               | 2.30  | 0.197   |
| AKP, IU/L     | 470.67             | 445.67              | 570.16             | 426.33              | 27.15 | 0.253   |

<sup>a</sup>Different lowercase letters with the same column date meant significant difference ( $p < 0.05$ ).

TABLE 5 Effect of HSW on serum antioxidant indexes<sup>a</sup>.

| Items         | Treatment          |                     |                     |                     | SEM  | P-value |
|---------------|--------------------|---------------------|---------------------|---------------------|------|---------|
|               | BD                 | HSW12               | HSW24               | HSW32               |      |         |
| MDA, ng/mL    | 58.50 <sup>a</sup> | 47.15 <sup>ab</sup> | 33.00 <sup>b</sup>  | 30.45 <sup>b</sup>  | 3.70 | 0.054   |
| SOD, ug/mL    | 6.23               | 6.95                | 6.59                | 5.80                | 0.26 | 0.465   |
| GSH-Px, ug/mL | 5.99 <sup>b</sup>  | 8.94 <sup>a</sup>   | 11.07 <sup>a</sup>  | 10.20 <sup>a</sup>  | 0.53 | 0.001   |
| CAT, ug/mL    | 22.71 <sup>b</sup> | 31.33 <sup>a</sup>  | 32.80 <sup>a</sup>  | 28.71 <sup>ab</sup> | 1.42 | 0.048   |
| T-AOC, ug/mL  | 11.33 <sup>b</sup> | 15.38 <sup>b</sup>  | 16.06 <sup>ab</sup> | 18.56 <sup>a</sup>  | 0.95 | 0.045   |

<sup>a</sup>Different lowercase letters with the same column date meant significant difference ( $p < 0.05$ ).

## Gut microbiome composition

In summary, we believe that adding 24% HSW to the diet had the best overall effect on growth performance, serum biochemical indicators, meat quality, and carcass traits of geese. Therefore, we further investigated the differences in gut microbiota composition between the BD and HSW24 groups.

In the ileum (Figure 1A), the dominant phyla (top 10) were Proteobacteria, Firmicutes, Bacteroidetes, Actinobacteria (Thermi), Cyanobacteria, Tenericutes, Acidobacteria, Verrucomicrobia, Planctomycetes, and the dominant genera (top 10) were *Cupriavidus*, *Lactobacillus*, *Ochrobactrum*, *Sphingomonas*, *Pseudomonas*, *Acinetobacter*, *Lachnospiraceae\_Clostridium*, *Pelomonas*, *Subdoligranulum*, and *Enterococcus*. The dominant phyla in the cecum (top 10) are Firmicutes, Proteobacteria, Bacteroidetes, Verrucomicrobia, Actinobacteria, Tenericutes, Cyanobacteria, Synergistetes, Elusimicrobia, Fusobacteria, with the dominant genera (top 10) being *Desulfovibrio*, *Bacteroidaceae\_Bacteroides*, *Subdoligranulum*, *Oscillospira*, *Phascolarctobacterium*, *Akkermansia*, (*Prevotella*), *Faecalibacterium*, *Barnesiella*, and *Ruminococcus* (Figure 1B).

## Gut microbial diversity

There was no significant difference in the microbial  $\alpha$ -diversity index between the ileum and cecum ( $p > 0.05$ ), as shown in Figure 2. The  $\beta$ -diversity based on PCoA showed that the flora of the BD group and the HSW24 group, there was no obvious clustering in the ileum ( $p > 0.05$ ) (Figure 3A), but the clustering was more obvious in the cecum ( $p < 0.05$ ) (Figure 3B), indicating that the diversity of the flora was more similar in the ileum and more dissimilar in the cecum.

## Gut microbial biomarker

The biomarkers of different groups were determined by Linear discriminant analysis Effect Size (LEfSe). *Hymenobacter*, *Bacillus*, *Tetragenococcus*, *Lactococcus*, *Asticcacaulis*, *Ochrobactrum*, *Agrobacterium*, *Sphingobium*, *Acidovorax*, *Aquabacterium*, *Pelomonas*, *Ralstonia*, and *Bdellovibrio* were the biomarkers of the ileum of the HSW24 group, and *g\_Butyricimonas* was the biomarker of the ileum of the BD group

TABLE 6 Effect of HSW on carcass traits and meat quality<sup>a</sup>.

| Items              | Treatment          |                     |                    |                     | SEM  | P-value |
|--------------------|--------------------|---------------------|--------------------|---------------------|------|---------|
|                    | BD                 | HSW12               | HSW24              | HSW32               |      |         |
| Slaughter rate     | 0.87               | 0.87                | 0.88               | 0.88                | 0.01 | 0.739   |
| Half-bore rate     | 0.93               | 0.91                | 0.94               | 0.91                | 0.01 | 0.560   |
| Full-bore rate     | 0.83               | 0.80                | 0.83               | 0.81                | 0.01 | 0.800   |
| Breast muscle rate | 0.11               | 0.11                | 0.10               | 0.10                | 0.01 | 0.314   |
| Leg muscle rate    | 0.11               | 0.10                | 0.12               | 0.11                | 0.01 | 0.593   |
| Abdominal fat rate | 0.03               | 0.04                | 0.03               | 0.03                | 0.01 | 0.236   |
| Breast muscle      |                    |                     |                    |                     |      |         |
| L*                 | 40.86              | 40.44               | 41.09              | 40.44               | 0.76 | 0.075   |
| a*                 | 9.24               | 8.95                | 9.63               | 12.27               | 0.46 | 0.989   |
| b*                 | 7.05               | 6.48                | 7.73               | 8.04                | 0.40 | 0.536   |
| pH                 | 5.63               | 5.74                | 6.07               | 5.71                | 0.07 | 0.062   |
| Leg muscle         |                    |                     |                    |                     |      |         |
| L*                 | 41.32 <sup>b</sup> | 40.13 <sup>ab</sup> | 41.46 <sup>a</sup> | 39.23 <sup>ab</sup> | 1.20 | 0.914   |
| a*                 | 8.38               | 8.75                | 8.95               | 8.88                | 0.41 | 0.958   |
| b*                 | 8.51               | 8.89                | 9.33               | 9.03                | 0.37 | 0.970   |
| pH                 | 6.13               | 6.31                | 6.50               | 6.40                | 0.05 | 0.838   |

<sup>a</sup>Different lowercase letters with the same column date meant significant difference ( $P < 0.05$ ).

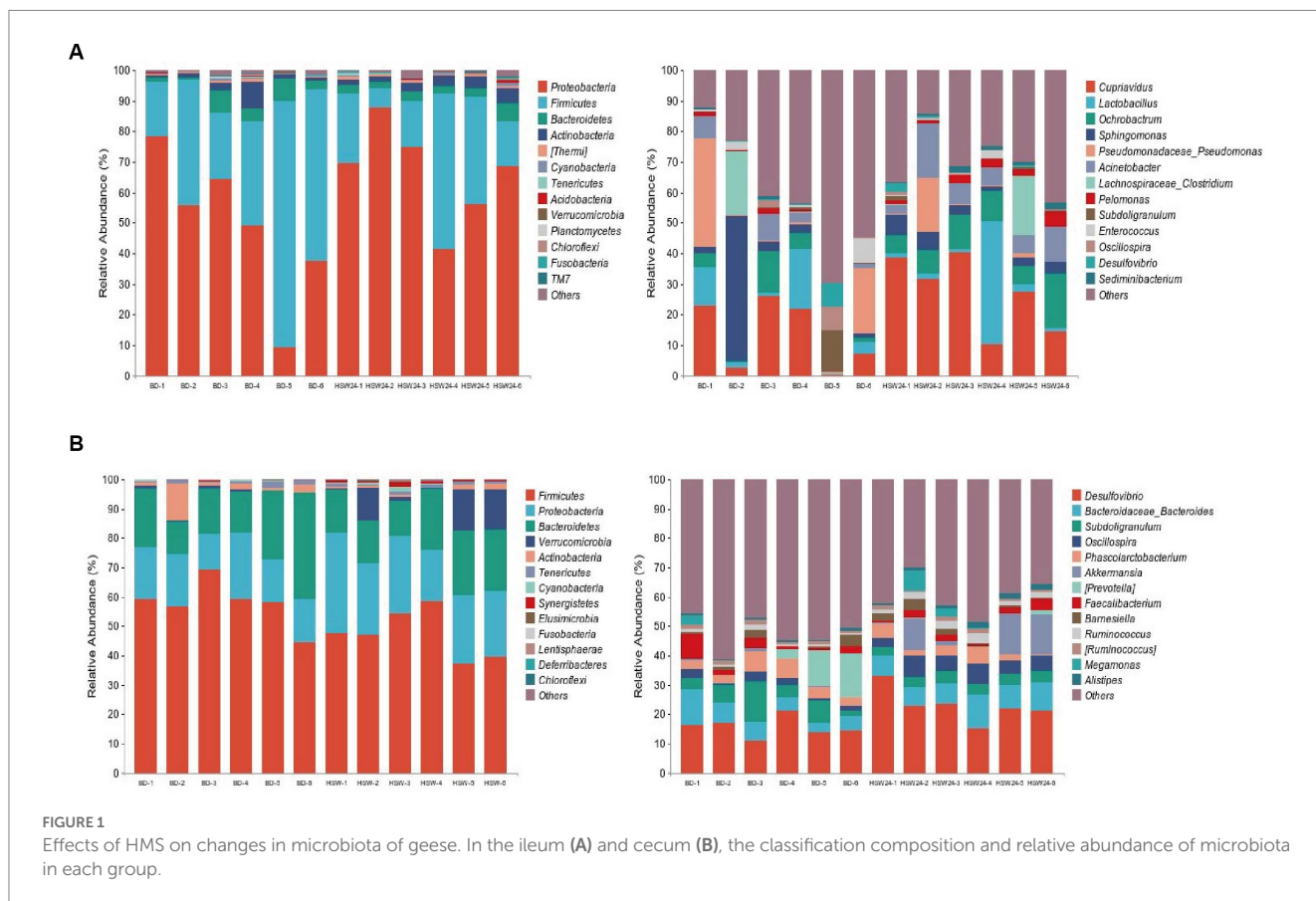
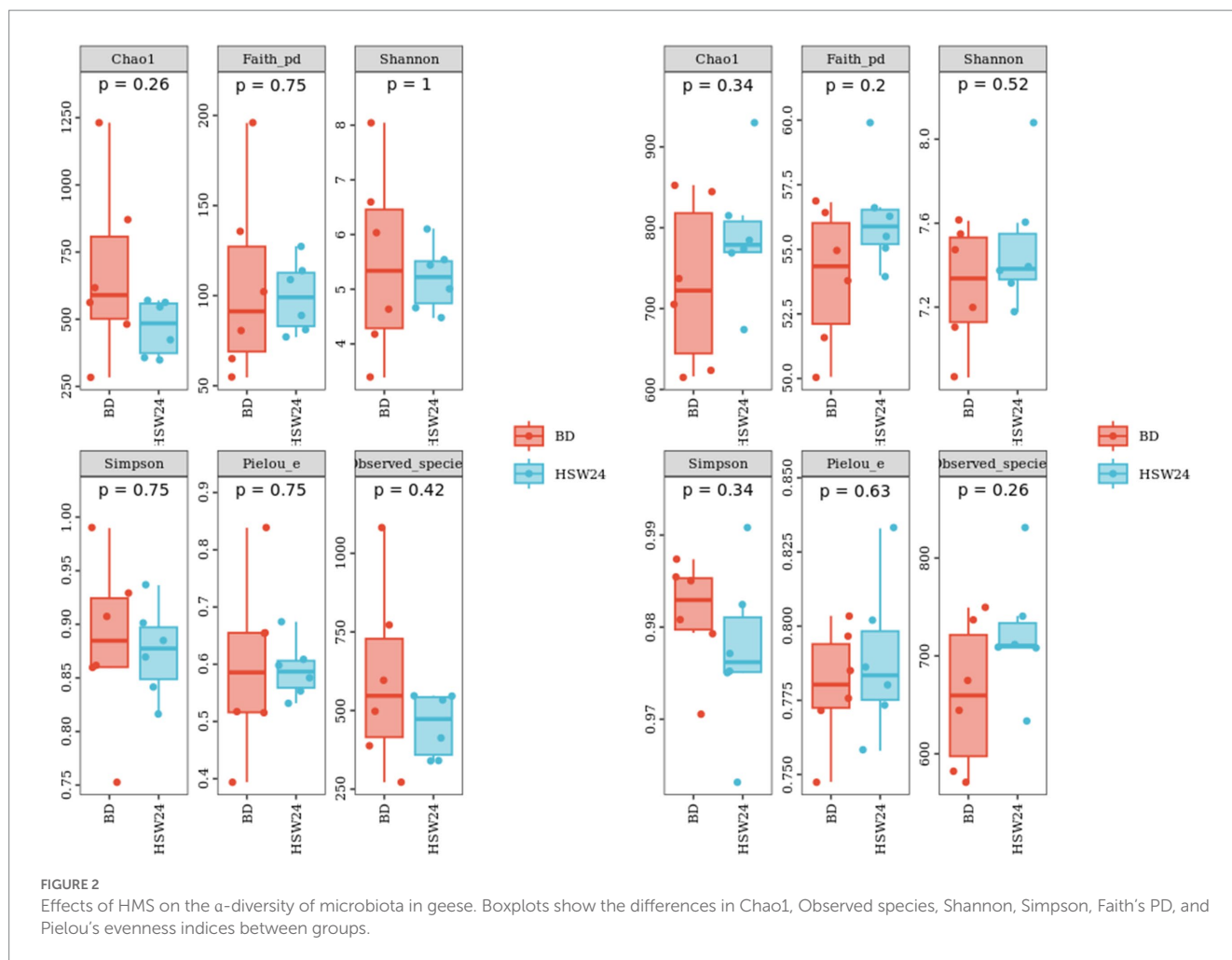


FIGURE 1 Effects of HMS on changes in microbiota of geese. In the ileum (A) and cecum (B), the classification composition and relative abundance of microbiota in each group.

(Figure 4A). In the cecum, *Prevotella*, AF12, *Alistipes*, f-Ruminococcaceae, g-*Clostridium*, *Oscillospira*, *Ruminococcus*, *Sutterella*, *Desulfovibrio* were the biomarkers of the

HSW24 group (Figure 4B), while YRC22, *Megasphaera*, *Lactobacillus*, *Dorea*, *Turicibacter* were biomarkers for the BD group.



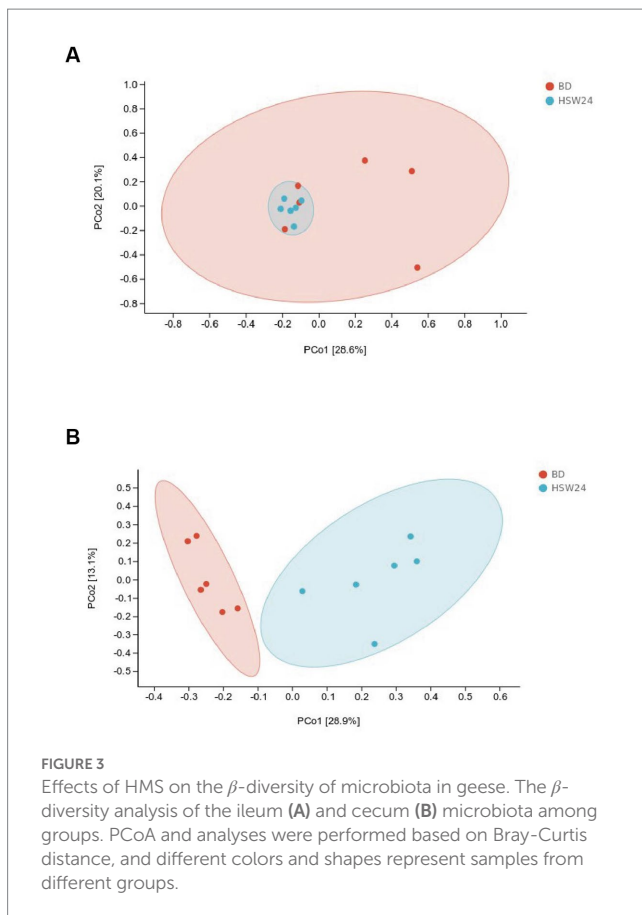
## Correlation between microbiota and parameters

By Spearman analysis, we found among the ileum biomarkers (Figure 5A), *Ochrobactrum* was positively associated with ADG and CAT, and negatively associated with ALT and MDA. *Pelomonas* was positively associated with ADG, CAT, GSH-Px, and T-AOC, and negatively associated with ALT. *Agrobacterium* was positively associated with ADG, CAT, and T-AOC, and negatively associated with ALT and MDA. *Butyricoccus* was negatively associated with BUN and AST; *Lactococcus* was negatively associated with TG; *Bacillus* was positively associated with ADG, TP, ALB, GLOB, HDL-C, and AKP, and negatively associated with TC. *Sphingobium* was positively associated with ADFI, GLOB, CAT, GSH-Px, and T-AOC. Among the biomarkers of the cecum (Figure 5B), *Desulfovibrio* was positively associated with ADG, ALB, GLOB, and HDL-C, and negatively associated with UA, TC, TG, and LDL-C. *Oscillospira* was positively associated with GSH-Px and CAT, and negatively associated with UA; *Alistipes* was positively associated with CAT; *Butyricoccus* was positively associated with TG. YRC22 was positively associated with TG and AST, and negatively associated with GSH-Px and T-AOC. *Megasphaera* was positively associated with TG, LDL-C, and MDA, and negatively associated with GLOB, CAT, GSH-Px, and T-AOC. *Prevotella* was positively associated with

ADFI, GSH-Px, and CAT, and negatively associated with LDL-C levels. *Dorea* was negatively associated with GSH-Px, and positively associated with TG. *AF12* was positively associated with TP, CAT, GSH-Px, and T-AOC and negatively associated with TG. *Sutterella* was positively associated with T-AOC and negatively associated with UA, ALT, and MDA. *Clostridium* was positively associated with ADG, ADFI, TP, ALB, GLOB, HDL-C, CAT, GSH-Px, and T-AOC, and negatively associated with TC, TG, and LDL-C.

## Discussion

Palatability refers to the positive response of animals to the taste of particular foods. In animal husbandry, the average daily feed intake is the main index reflecting food palatability, which is usually used to evaluate feed quality (Kondo et al., 1988; Brown et al., 2016). Animal feed intake is mainly affected by the degree of feed crushing and crude fiber level (Ginindza et al., 2017; Sagols et al., 2019). In poultry, smell and taste are important factors affecting feed intake (Niknafs and Roura, 2018). Mushroom aroma is mainly derived from volatile aldehydes, acids, ketones, and esters. The umami taste of mushrooms originates from guanylates, taste amino acids, and umami peptides (Shen et al., 2023). Some studies have found that using waste stems from edible fungi (Hwangbo, 2014; Zheng et al., 2022) can improve



the feed intake of animals, which is similar to the results of the present study, possibly because mushrooms contain different polysaccharides, such as chitin, hemicellulose, mannan,  $\alpha$ -glucan,  $\beta$ -glucan, galactan, and xylan (Singdevsachan et al., 2016). The gut contains various bacteria that are capable of hydrolyzing polysaccharides and converting them from macromolecular polymers to small molecules, thereby promoting host health (Shang et al., 2018; Sun et al., 2018). Although adding HSW can improve feed intake and average daily gain from 35 to 49 days, we also noticed that there was no difference in the final body mass among the groups, and the feed-to-weight ratio of the HSW32 group was 8.6% higher than that of the BD group. This could be attributed to the crude fiber levels of 8.39% in the HSW32 group and 2.56% in the BD group. The production performance of geese is best when the crude fiber level is 4–7% (Li et al., 2022; Zheng et al., 2022). Although the goose has a more developed cecum compared to other poultry, its ability to decompose cellulose is not well developed, therefore we think that adding 32% HSW has a negative effect on the F/G.

TP, ALB, and serum levels are related to liver physiological function and body protein metabolism (Tasharofi et al., 2018). GLOB is an important indicator of the immune ability of the body. An increase in its content is indicative of the body's immunity (Tsang et al., 2011). In this study, we found that TP, ALB, and GLOB increased with an increase in HSW addition, and the effect was the best when the HSW addition was 24%. Previous studies have found that adding fermented *Flammulina velutipes* mycelia can improve crude protein digestibility (Lee et al., 2014), and that adding mushroom powder to diets can improve nitrogen digestibility. This may be the reason for the

increased serum protein content. Simultaneously, we found that HSW had a positive effect on reducing TC and TG levels in goose serum. It is possible that HSW has a higher level of crude fiber, which improves lipid metabolism and lowers TC levels (Massa et al., 2022). An appropriate amount of crude fiber can improve serum TC levels, and studies have shown that 10% crude fiber in broiler diets can cause a significant reduction (Sethi and Sikka, 2013). Elevated levels of serum TG and LDL-C have been shown associated with an increased risk of disease, such as increased abdominal fat and liver fat (Sun et al., 2007). Adding mushroom powder to the diet of broilers can reduce serum TC content (Daneshmand et al., 2012; Shang et al., 2014; Fanhani et al., 2016), which is consistent with the results of this study.

Mushrooms contain various phenolic compounds, which are generally believed to be related to antioxidant activity (Bayram and Karabacak, 2022; Moazzen et al., 2022), with phenolic compounds in mushrooms reportedly possessing the ability to remove LDL-C (Tang et al., 2016). Mushrooms also contain vitamin C and selenium, which have antioxidant properties (Lauridsen et al., 2021; Rathore et al., 2022). Six antioxidants can be extracted from *H. marmoreus* (Cai et al., 2020), and polysaccharides extracted from *H. marmoreus* can improve the antioxidant status by enhancing CAT, SOD, GSH-Px, and T-AOC, and reducing MDA (Liu et al., 2018). Nowadays, the antioxidant properties of mushrooms are widely used in animal husbandry. For example, adding mushrooms (*Hericium caput-medusae*) to the diet of broiler chickens can increase the levels of SOD, GSH-PX, and CAT in serum, liver, and breast muscle, and reduce MDA (Shang et al., 2016). Adding *Agaricus bisporus* stem residues to the diet of laying hens can increase the levels of SOD and GSH-PX in the serum (Yang et al., 2021). Adding mushroom residues to broiler diets resulted in higher expression of the Nrf2 and SOD-1 antioxidant genes (Chuang et al., 2020, 2021). Therefore, we believe that adding HSW to the diet improves the antioxidant activity of the serum.

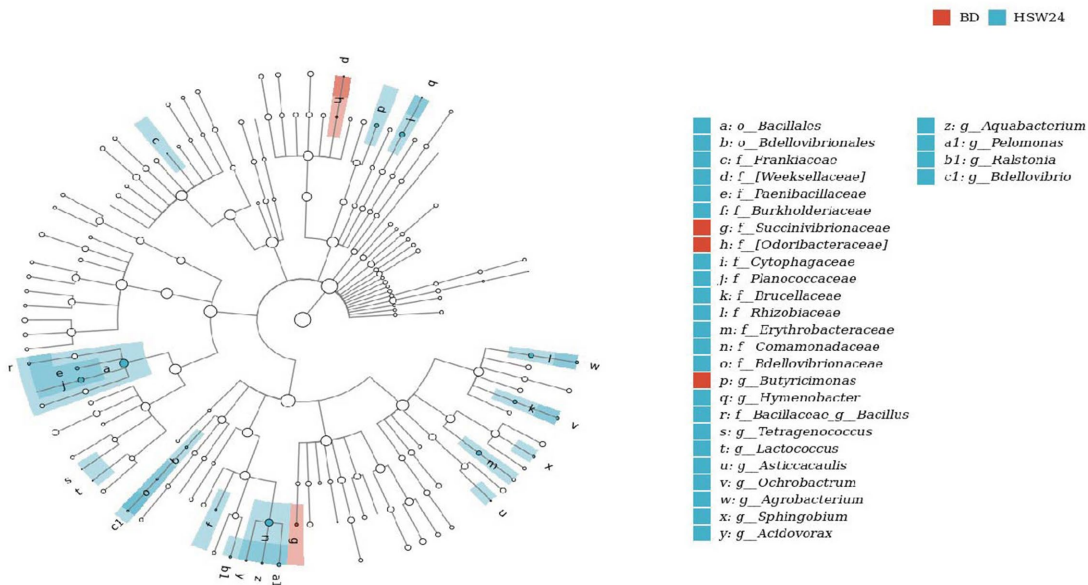
Carcass traits and meat quality are important indicators of animal health and breeding benefits, and diet composition and nutritional level are important factors (Meel et al., 2021; Sallam et al., 2021). Adding *A. bisporus* dry powder to broiler diets does not improve carcass traits (Kavyani et al., 2012), and the addition of *F. velutipes* residues to the diets of finishing pigs had no significant effect on their meat color (Liu et al., 2020). The results of our experiments showed that adding 32% HSW to the diet did not affect the quality of breast and leg muscles of geese.

The intestinal microbes of animals play important roles in nutrient digestion and absorption, immune status and gut homeostasis (Peng et al., 2021; Kogut and Fernández-Miyakawa, 2022; Norozi et al., 2022). The cecum is an ideal habitat for the microbes and has the highest density in the goose gut. The ileum has a unique microbiome, with fewer microbiota than the cecum. However, they can shape epithelial gene expression, gut physiology, nutrition, and molecular exchange between microbes (Yilmaz et al., 2022). In this study, Firmicutes, Bacteroidetes, and Proteobacteria were the dominant phyla in the goose cecum and ileum, which is similar to previous studies (Li et al., 2018; Xu et al., 2022). Many members of Firmicutes were highly positively associated with blood lipid levels and fat storage capacity (Turnbaugh et al., 2006; Zhang et al., 2020), which is also consistent with the TC and TG levels in serum. We noticed a decrease in the ratio of Firmicutes to Bacteroidetes in both the ileum and cecum, suggesting that F/B may be a factor in obesity in animals (Indiani et al., 2018). *Lactobacillus* and *Bacteroides* were the dominant



A

The current LDA threshold is 2



B

The current LDA threshold is 2

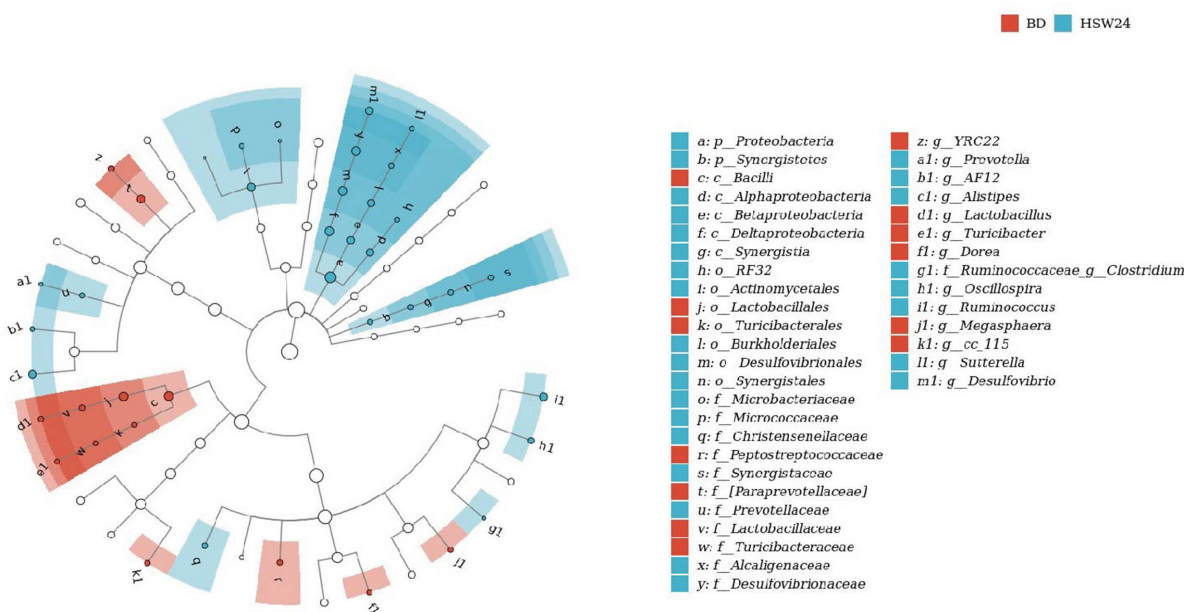


FIGURE 4 Effects of HMS on changes in ileum (A) and cecum (B) microbiota of geese. Linear discriminant analysis (LDA) (LDA>2.0,  $p < 0.05$ ) of cecal microbiomes.

bacterial genera in the ileum and cecum, and the abundance of the HSW24 group was higher than that of the BD group. These bacteria can break down complex polysaccharides, proteins, and lipids, thereby supporting the growth of other bacteria and maintaining intestinal homeostasis (Brown et al., 2019). *Lactobacillus* has a strong ability to metabolize carbohydrates to produce acid, synthesize glucan and heteropolysaccharides, and ferment sugars to produce lactic acid and

acetic acid (Moestedt et al., 2020). Furthermore, they antagonize pathogenic bacteria and help maintain immune function at the same time (Wang et al., 2022).

Through LEfSe analysis, we found biomarkers in the ileum and cecum of the HSW24 group. *Prevotella* has been extensively studied for its ability to break down the cellulosic hemicellulose, secreting cellulase enzymes that help the host gut digest fiber (Dao et al.,

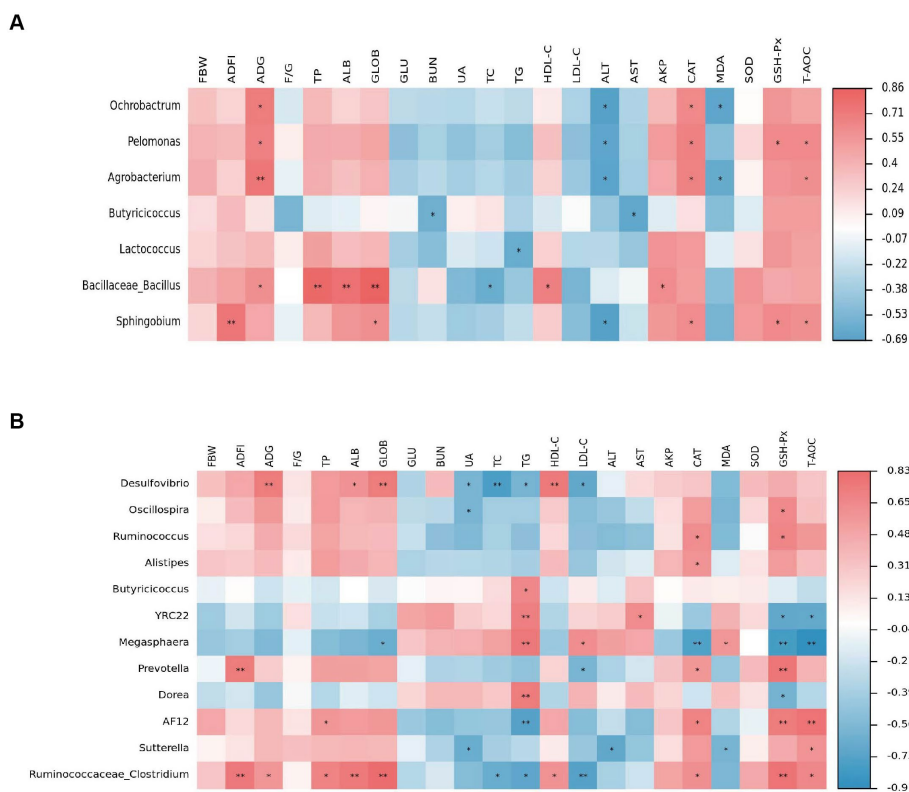


FIGURE 5 Relationships between main parameters and genera in the ileum (A) and cecum (B). Red represents positive correlation, blue represents negative correlation, and \* $p < 0.05$  and \*\* $p < 0.01$  represent significant correlations.

2021). This may explain why its abundance was positively related with the ADFI in this study. *Prevotella* is a bacterium associated with health status (Du et al., 2022). Adding mushrooms or selenium-enriched mushroom powder to pig diets increased the abundance of *Prevotella*, which is the main SCFA-producing bacterium that metabolizes succinate and acetate (Shkoporov et al., 2015). Although *Alistipes* was not associated with serum lipid metabolism in this experiment, it is fatty acid utilizable (Radka et al., 2020) and inversely associated with obesity (Dai et al., 2022). *Desulfovibrio* is a sulfate-reducing bacterium, it was positively associated with serum immune-related GLOB in this study, probably due to its bioremedial potential (Rowan et al., 2010). In the gut of pigs, *Desulfovibrio* was also positively associated with the health state and growth performance (Jiang et al., 2022). *Oscillospira* are widely found in the digestive tracts of herbivores (Mackie et al., 2003; Ren et al., 2017), and from metagenomic and metabolic characterization, this organism was able to mediate butyrate kinase-mediated, which was indicated that *Oscillospira* are butyrate producers. Like *Alistipes*, *Oscillospira* are negatively associated with obesity (Shen et al., 2021). It is the dominant bacterium in the intestinal of chicken, which is a manifestation of animal production performance and intestinal function (Keerqin et al., 2021). We observed that although *Oscillospira* is not directly related to protein metabolism in the serum in this study, it is negatively associated with serum UA level, which is the main metabolite of birds and reptiles. High levels of UA in serum respond to abnormal kidney and liver metabolism in animals (Yustisia et al., 2022).

*Bacillus* has a variety of probiotic functions, similar to *Bacillus amyloliquefaciens* and *Bacillus subtilis*, which are widely used as probiotics in animal husbandry (Jiang et al., 2022; Xu et al., 2022). *Bacillus* can induce *Oscillospira* to become a dominant genus (Keerqin et al., 2021) and can be used to treat diarrhea in pigs (Jinno et al., 2022). In this experiment, *Bacillus* was positively associated with growth performance, serum protein content, and antioxidant level, and negatively associated with serum fat and TC, as consistent with previous studies. The addition of *B. subtilis* to broiler diets can reduce TC and LDL-C levels (Mohamed et al., 2022). *Ruminococcus* obtains nutrients by decomposing cellulose in the host's digestive system, making it is one of the most efficient bacterial genera for decomposing carbohydrates (Iakiviak et al., 2016). It is the key bacterium for degrading resistant starch (Sun et al., 2016), and members of the genus *Sutterella* are important commensals in the gut. *Sutterella*, which is abundant in the duodenum of healthy adults, has been found to increase the abundance of feces in mice fed prebiotics (Nowak et al., 2018). Therefore, we conclude that HSW-supplemented diets have a positive gut response in geese.

### Conclusion

Partial substitution of corn with HSW in geese diets had no negative effects on growth performance, carcass traits, and meat quality. The addition of 24% HSW improved serum lipid metabolism

and antioxidant levels, which may be related to the increased abundance of probiotics such as *Prevotella*, *Oscillospira*, *Alistipes*, and *Ruminococcus* in the cecum. However, the functions of these bacteria require further investigation to verify the links between HSW and intestinal bacteria. Further research is also needed to determine the underlying mechanism of HSW in lipid metabolism in geese.

## Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: <https://www.ncbi.nlm.nih.gov/PRJNA935563>.

## Ethics statement

The animal study was reviewed and approved by the Laboratory Animal Ethics Committee of the Shanghai Academy of Agricultural Sciences.

## Author contributions

GL, YL, XW, DH, and HW contributed to the design of this study. GL, YL, CW, YY, and SG participated in the sample collection and data

analysis. DH and HW provided the funding and analytical tools. GL wrote the original draft. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

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