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Oncorhynchus mykiss silage improves meat fatty acids profile, blood parameters, intestinal histomorphometry, productive performance, and modulates the cecal microbiota of *Cavia porcellus*

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The use of rainbow trout silage represents an alternative for the feeding of domestic species such as guinea pigs with a circular economy approach. The objective of this study was to evaluate the effect of *Oncorhynchus mykiss* silage in the diet of *Cavia porcellus* on the fatty acid profile of the meat, blood parameters, intestinal histomorphometry, productive performance, and cecal microbiota. Thirty-three weaned male guinea pigs of the Peru breed were used, distributed in three treatments: T0 (0%), T1 (4%), and T2 (8% silage inclusion in the diet), with 11 replicates each. The inclusion of silage in the diets significantly modified the lipid profile of the meat, increasing monounsaturated fatty acids and docosahexaenoic acid (DHA, C22:6) ($p < 0.001$) compared to T0. No changes were observed in most hematological and biochemical parameters, with the exception of mean platelet volume (MPV) ($p = 0.020$) and total cholesterol (TC) ($p < 0.001$). Higher silage inclusion favored the development of crypt depth ($p = 0.047$). The alpha diversity of cecal microbiota did not vary ($p > 0.05$), but beta diversity revealed compositional changes associated with silage consumption (Bray–Curtis, $p = 0.006$; Jaccard,

$p = 0.017$). Productive performance, such as weight gain increased in T2 ($p = 0.050$) and feed conversion factor, decreased with silage inclusion ($p < 0.001$), without affecting intake. In conclusion, trout silage represents a sustainable alternative ingredient in the use of fish by-products that improves the nutritional quality of guinea pig meat and optimizes feed efficiency, without compromising animal health or performance.

KEYWORDS

domestic guinea pig, fish hydrolysate, circular economy, meat quality, genomic sequencing, productive performance, health

1 Introduction

Cavia porcellus is a South American rodent species of the family Caviidae and genus *Cavia* (1). Its breeding plays a very important role in rural families in Peru, Ecuador, Colombia, and Bolivia, where it is deeply rooted as a cultural practice, contributes to food security, and serves as a source of economic income (2, 3). Peru stands out as the primary producer (17.4 million animals) and per capita consumer of guinea pigs (0.66 kg/person/year), increasing over the years (4). The consumption of guinea pig meat is due to its high protein content and biological value (5).

Traditionally, guinea pig have been fed kitchen by-products and pasture as supplements (6). The growing demand for guinea pig meat requires the optimization of feeding and management programs, for which it is essential to determine nutritional requirements and evaluate the nutritional value of available feed inputs (7). The guinea pig has the capacity to adapt to diverse climatic conditions and ecosystems, due to its physiological capacities as a herbivorous species, its short reproductive cycle, and its versatile diet (2). The transition to more intensive breeding systems, the use of improved genetic lines, and the use of balanced feeds make the guinea pig activity more essential to meet their nutritional needs (8). Consequently, the need to produce naturally dense feeds with high nutritional content has led to the use of agricultural and industrial by-products, which are essential for maintaining productivity without increasing production costs (9), while also contributing to environmental sustainability (10).

Among the by-products of the fishing industry, fish silage has emerged as a promising ingredient. It contains bioactive compounds, fatty acids such as omega (ω)-3, hydrolyzed proteins, small peptides, and free amino acids that are rapidly digested and absorbed (11–13).

There is evidence on the use of silage sources as a dietary supplement in various species, observing positive impacts on growth, intestinal health, and lipid composition of meat (14–16). For example, in tilapia (*Oreochromis mossambicus*), the inclusion of rainbow trout (*Oncorhynchus mykiss*) silage oil effectively replaced fish oil by not affecting the composition of ω -3 polyunsaturated fatty acid (ω -3 PUFA) levels in fillets (17). Similarly, in South African abalone (*Haliotis midae*), the inclusion of *O. mykiss* silage oil in the feeding of has been shown to have no significant effects on immune function, proximal composition, and fatty acid profile of abalone muscle (18).

Furthermore, Güllü et al. (19) found that it is possible to replace up to 20% fish meal with fish silage in *O. mykiss* feed without negatively affecting growth, fatty acid composition, and serum biochemical parameters. Fish silage can promote a more optimal intestinal morphology by stimulating intestinal mucosal folds that are deeper and more regular, as well as maintaining the integrity of

microvilli. This contributes to a better health status in fish, which is reflected in specific hematological parameters in tilapia (20).

Despite its demonstrated benefits in feeding aquaculture species, the use of fish silage in herbivorous animals such as guinea pigs has not yet been explored. This study provides new evidence on how trout silage can benefit the feeding of herbivorous monogastric animals, such as guinea pigs, with enzymatic digestion in the stomach and bacterial digestion in the cecum (2). Although *C. porcellus* has a herbivorous digestive physiology and relies on cecal fermentation to obtain energy from structural carbohydrates, fish possess a more active gastric phase and higher levels of pancreatic proteases and lipases (21). Therefore, the incorporation of marine-derived lipids or peptides from silage could have species-specific physiological consequences.

In recent years, the characterization of the intestinal microbiota in animals of zootechnical interest has advanced considerably due to modern molecular tools (22). The use of high-throughput sequencing platforms has facilitated a more accurate and in-depth view of bacterial diversity (23, 24). Sequencing of hypervariable regions of the 16S rRNA gene provides insight into how different factors, such as intestinal inflammation, parental offspring, and diet, can modify the microbial composition, potentially influencing intestinal health and productive efficiency in animals of zootechnical interest (25–27). Given the growing demand for functional foods of animal origin and the interest in increasingly sustainable production systems, it is pertinent to explore alternative ingredients that simultaneously improve the nutritional quality of the meat, the physiological parameters of the animal, and the productive efficiency. Despite the evidence accumulated in other species, the knowledge of the effects of fish silage, particularly of *O. mykiss* on *C. porcellus*, is scarce; therefore, the objective of this research was to evaluate the effect of *O. mykiss* silage on meat fatty acids, blood parameters, productive performance, intestinal histomorphometry, and cecal microbiota of guinea pigs of the Peruvian breed.

2 Materials and methods

2.1 Ethical statement

Animal welfare was ensured at all times during the research. The euthanasia process followed the guidelines of ARRIVE 2.0 and the AVMA Guide: 2020 Edition (28, 29). The study was approved by the Institutional Research Ethics Committee of the University Nacional Toribio Rodríguez de Mendoza of Amazonas, through code CIEI-N°0061.

2.2 Place of study

The research was carried out in the guinea pig module of the Chachapoyas Experimental Station of the Livestock and Biotechnology Research Institute of the Universidad Nacional Toribio Rodríguez de Mendoza de Amazonas (UNTRM), located in the southern hemisphere of the province of Chachapoyas, Amazonas region. The city of Chachapoyas is located in the northern Andes of Peru, at an altitude of 2,338 m.a.s.l., with an average annual rainfall of 800 mm and an average temperature of 15.6 °C. There is a very low annual thermal variation, with 1 °C in average monthly temperatures. The lowest monthly minimum temperature values (10.5 °C) are reported between June and August, while the highest monthly maximum temperature values (25.8 °C) occur from August to December (30).

2.3 Animals and management

Thirty-three weaned male guinea pigs of the Peru breed were selected, 15 ± 2 days old with an average weight of 248.35 ± 3.65 g, distributed in three treatments (T0: 0% inclusion of trout silage in the diet, T1: 4% inclusion of trout silage in the diet, and T2: 8% inclusion of trout silage in the diet) with 11 replicates each. The research period lasted 11 weeks. A maximum of 8% trout silage was used, as this provided the energy balance in the diet. Each animal was identified with numbers engraved on aluminum earrings and placed on the animal's right ear pinna; they were individually placed in a pool with brick walls lined with cement, chip floor, measuring 0.8 m × 0.9 m × 0.45 m in width, length, and height, respectively. The area provided was more than enough for each animal for both the rearing and fattening stages (31). Feed supply (alfalfa + balanced feed) was provided once a day at 8 a.m. The balanced feed was supplied in clay feeders placed in the center of each pool, while the grass was thrown directly into each pen at 20% of each animal's live weight (fresh basis). The supply of grass was maintained at 20% of each animal's live weight to encourage the consumption of balanced feed; thus, adjustments were made weekly (32). All animals always had water freely available through an automatic nipple type waterer. Silage preparation was performed in an artisanal manner following the guidelines of Toppe et al. (33). The viscera of rainbow trout sold at the municipal market in Chachapoyas were collected, chopped into 3 cm pieces, washed with drinking water to remove food and fecal matter, and stored for 30 days in 20-L airtight containers with 3% of 85% formic acid added (Spectrum Chemical Mfg. Corp., USA). Chemical analysis was performed by standard procedures of the Association of Official Analytical Chemists (34). The composition and nutritional values of the experimental diets, pasture, and trout silage are presented in Table 1. The fatty acid profile of the trout silage was analyzed according to the official method 996.06 of the Association of Official Agricultural Chemists (35).

2.4 Productive performance

Daily feed intake (g) was calculated by subtracting the feed fed on the previous day minus the residual feed, and the feed conversion factor (kg) was calculated as the ratio of total feed consumed on a fresh basis to total weight gained (36). Cumulative weight gain (g) was

determined by the difference between the initial and the final live weights.

2.5 Hematological and biochemical analysis

The hematological analysis was performed at week 9 after starting the experiment. After a minimum fasting period of 10 h, 1.5 mL of blood was collected from the cranial vena cava, without prior anesthesia, into vacutainer tubes containing EDTA as anticoagulant (37). The following parameters were analyzed: white blood cell count, lymphocyte number, monocyte number, granulocyte number, lymphocyte percentage, red blood cell count, hemoglobin concentration, hematocrit, mean corpuscular volume, mean corpuscular hemoglobin, mean corpuscular hemoglobin concentration, platelet count, mean platelet volume, and procalcitonin at the Domestic Animal Infectious and Parasitic Diseases Laboratory. Samples were processed on a VH30 automated veterinary hematology analyzer (Shenzhen, China) following the methodology proposed by El-Moghazy et al. (38). For biochemical profiling, blood was collected in week 11 into tubes with clot activator (39). Serum was obtained by centrifugation at 825 × g for 10 min at room temperature (Rotofix 32A, Hettich, Germany). Within 5 days, the following were assessed using commercial kits (Química Clínica Aplicada, Amposta, Spain): high-density lipoproteins (HDL), low-density lipoproteins (LDL), liquid triglycerides (TL), lipase, total proteins (TP), and total cholesterol (TC), using a GENESYS 10S UV-Vis spectrophotometer (Thermo scientific, Wisconsin, USA).

2.6 Meat fatty acid analysis

After completing the experiment, all guinea pigs in each experimental group were sacrificed at 13 weeks of age by cervical dislocation and cutting of the jugular vein, with exsanguination performed immediately thereafter (40). Tissue samples were obtained from the abdominal muscle, stored at -80 °C for 24 h, and then dried at -81 °C in a Labconco™ FreeZone™ freeze dryer (Fisher Scientific, Madrid, Spain). Total lipid was extracted from 0.2 g of muscle mixed with 50 mL of chloroform-methanol on a magnetic stirrer for 1–2 h. The fatty acid was converted to methyl ester by acetyl chloride; the internal standard was methyl undecanoate (41). Fatty acids were determined by La Molina Calidad Total Laboratorios (Lima, Peru) by gas chromatography coupled to a mass spectrometer (Agilent-7890-MS-5975C, Agilent Technologies, USA), following the guidelines of the bb official method 996.06 of the Association of Official Agricultural Chemists (35).

2.7 Intestinal histomorphometry

Tissues were taken from the middle section of the jejunum following the guidelines of Yuan et al. (42) with some modifications. Samples were fixed in 10% formaldehyde for 24 h, dehydrated in ethanol (70–80%–96–100%) for 1 h each, sectioned into 3–5 μm slices, stained with hematoxylin and eosin, and observed with an Olympus optical microscope, BX53F (Tokyo, Japan). In each field, 8–10 villi were

TABLE 1 Composition and nutritional values of the experimental diets, forage, and trout silage.

Ingredients (Kg)	T0	T1	T2	Alfalfa	Trout silage
Wheat bran	63.15	57.00	52.70	–	–
Corn	16.00	21.10	21.80	–	–
Molasses	2.00	2.00	2.00	–	–
Soybean cake	15.00	13.00	12.70	–	–
Soybean oil	1.00	0.00	0.00	–	–
Trout silage	0.00	4.00	8.00	–	–
DL-Methionine (99%)	0.12	0.15	0.18	–	–
L-Lysine (98.5%)	0.00	0.00	0.04	–	–
Calcium carbonate	2.30	2.30	2.30	–	–
Premix vitamins ^a	0.10	0.10	0.10	–	–
Choline chloride (60%)	0.10	0.10	0.10	–	–
Common salt	0.20	0.20	0.20	–	–
Vitamin C	0.03	0.03	0.03	–	–
Total	100.0	100.0	100.0	–	–
<i>Nutrient</i>	<i>Analyzed chemical composition^b</i>				
Dry matter %	88.45	80.77	74.83	20.5	93.16
Ashes %	8.29	9.26	6.37	8.68	4.22
Crude fat %	3.29	3.40	4.32	3.02	52.58
Crude protein %	12.76	13.66	14.3	19.17	33.38
Crude fiber %	13.05	7.05	6.75	24.84	n.d.
Nitrogen free extract %	53.83	50.48	45.22	40.45	n.d.
<i>Trout silage fatty acid profile (%)^c</i>	<i>Composition</i>				
Caprylic acid (C8:0)	0.2				
Myristic acid (C14:0)	0.99				
Palmitic acid (C16:0)	10.13				
Palmitoleic acid (C16:1)	1.5				
Heptadecanoic acid (C17:0)	0.12				
Stearic acid (C18:0)	3.32				
Oleic acid (C18:1 n9c)	12.63				
Linoleic acid (C18:2 n6c)	8.3				
Arachidic acid (C20:0)	0.13				
Eicosenoic acid (C20:1 Cis 11)	0.45				
Linolenic acid (C18:3 n3)	0.51				
Eicosadienoic acid (C20:2)	0.53				
Behenic acid (C22:0)	0.1				
Eicosatrienoic acid (C20:3)	0.19				
Nervonic acid (C24:1)	0.16				
Docosahexaenoic acid (C22:6)	0.38				
Total fat	41.74				
Saturated fats	15.08				
Monounsaturated fats	15.11				
Polyunsaturated fats	9.91				

^aPer kg of feed: 104 International Units (IU) Vitamin A; 2,500 IU Vitamin D3; 15 mg Vitamin E; 3 mg Vitamin K3; 1 mg Vitamin B1; 4 mg Vitamin B2; 3 mg Vitamin B6; 15 mg Vitamin B12; 8 mg Pantothenic Ac. B5; 0.5 mg Folic Acid (Vit. B9); 30 mg Nicotinic Acid (Vit. B3); 25 mcg biotin (Vit. B7); 7 mg choline; 5 mg copper; 25 mg iron; 60 mg manganese; 0.2 mg selenium; 0.5 mg iodine; 60 mg zinc; 1.3 g methionine.

^bLaboratory of Animal Nutrition and Food Bromatology—National University Toribio Rodriguez of Mendoza of Amazonas.

^cLa Molina Total Quality Laboratories, National Agrarian University La Molina.

n.d., not determined.

selected. The total villi (length and width) and the depths of the Lieberkühn crypts were measured at 10× magnification with the help of cellSens Standard. Ink software. Villus length was measured from the apex of the villus to the apex of the crypt entrance, villus width was measured at the vertical midpoint of the chosen villus, and crypt depth was measured from the crypt entrance to the basal area of the crypt (43).

2.8 Metagenomic sequencing and bioinformatic analysis

2.8.1 DNA extraction and library construction

For the extraction of metagenomic DNA collected from the cecal mucosa, the Quick-DNA™ Fungal/Bacterial Miniprep Kit (Zymo Research, USA) was used following the manufacturer's instructions. DNA quantification and purity were performed using a NanoDrop One Microvolume UV-Vis (Thermo Fisher Scientific, USA) and a Qubit 3 Fluorometer (ThermoFisher Scientific, USA). Paired-end metabarcoding sequencing (2 × 150 bp) of the V3 and V4 hypervariable regions of the bacterial 16S rRNA was performed in a commercial genomic facility, generating approximately 250-bp amplicons.

2.8.2 Bioinformatic analysis

FASTQ files were grouped according to experimental group (T0, T1, and T2). Analysis was performed using the nf-core/Ampliseq v2.9.0 (44) pipeline, run with Nextflow v4.2.1 (45) using the Singularity container. Quality control was performed with FastQC and MultiQC (46, 47). Adapter trimming was performed with Cutadapt (48). Demultiplexing of reads, chimera removal, and amplicon sequence variant (ASV) generation were performed with DADA2 v1.26.0 (49) and QIIME2 (50). ASVs with low sequencing depth were filtered based on rarefaction curves. Taxonomic assignment was performed using the SILVA v138 reference database (51). Sequences identified as chloroplasts, mitochondria, and archaea were removed from the dataset. The rarefaction curve and alpha diversity were assessed via Phyloseq. Modified scripts were performed using the Microeco and MicrobiotaProcess libraries (52, 53). Indices such as Shannon, Pielou's Uniformity, and the number of OTUs observed were used. Between-group comparisons were performed using the Kruskal–Wallis non-parametric test, applying the Bonferroni correction for multiple comparisons. Beta diversity was assessed by principal coordinate analysis (PCoA) using weighted and unweighted Bray–Curtis, Jaccard, and UniFrac distance metrics, using R v4.4.1. Significant differences were tested by PERMANOVA. Functional taxa and metabolic pathways were analyzed with the differential abundance test (DESeq2) and non-parametric Wilcoxon tests with Bonferroni correction.

2.9 Data analysis

Data were analyzed under a completely randomized design with three treatments (T0, T1, and T2). The homogeneity of variances test was performed with Levene's test ($p > 0.05$). An analysis of variance was performed to determine the significance ($p < 0.05$) and to determine the effects of the diet on the fatty acid profile of the meat, blood parameters, intestinal histomorphometry, productive

performance, and traits of sacrifice. The comparison of means was performed with Dunnett's statistical test ($p < 0.05$), considering T0 as control or without silage inclusion. These data were processed in R v4.3.3 software using the Agricolae library. For principal component analysis, the ggplot2 (54) and Phyloseq (55) libraries were used. The alpha diversity indices (Shannon, Pielou, and Observed Features) were compared using the Kruskal–Wallis test followed by pairwise Wilcoxon rank-sum tests with multiple-test corrections. Beta diversity differences based on Bray–Curtis, Jaccard, and UniFrac distance matrices were evaluated using PERMANOVA (999 permutations). Taxonomic differential abundance was assessed using DESeq2 and non-parametric Wilcoxon tests.

3 Results

3.1 Meat fatty acid profile

The fatty acid profile of the guinea pig pectoral muscle is presented in Table 2. Inclusion of *O. mykiss* silage significantly ($p < 0.001$) modified most fatty acids, with the exception of heptadecenoic/margaloleic acid, arachidonic acid, and unsaturated fatty acids in *C. porcellus* meat. Diets with silage inclusion resulted in a significant increase ($p < 0.001$) in docosahexaenoic acid (DHA) (C22:6) with respect to T0. Along the same line, total meat fat was also increased at T1 and T2 ($p < 0.001$). Silage supplementation also affected the lipid profile of meat by increasing ω -6 and ω -9 content ($p = 0.001$, $p < 0.001$, respectively). The only fatty acids that decreased ($p < 0.001$) as silage inclusion in the diets increased were γ -linolenic acid (C18:3 n6), arachidic acid (C20:0), and ω -3.

3.2 Blood parameters

3.2.1 Hematological parameters

Table 3 shows the average values of the analysis of hematological variables of the guinea pigs. The total white blood cell count (WBC) presented a decreasing trend from T0 to T2 ($p = 0.050$). The number of lymphocytes (Lym#) was significantly higher at T0 compared to T2 ($p = 0.037$), while the number of monocytes (Mid#) showed no significant difference ($p = 0.673$). On the other hand, red blood cell count (RBC), hemoglobin concentration (HGB), hematocrit (HCT), mean corpuscular volume (MCV), mean corpuscular hemoglobin (MCH), platelets (PLT), and procalcitonin (PCT) remained without significant changes between treatments ($p > 0.05$). Similarly, mean corpuscular hemoglobin concentration (MCHC) decreased significantly from T0 to T2 ($p < 0.001$). In contrast, mean platelet volume (MPV) showed significant differences, being higher at T2 ($p = 0.020$) with respect to the other treatments.

3.2.2 Biochemical parameters

The serum biochemical parameters evaluated in *C. porcellus* showed no significant differences between treatments, with the exception of total cholesterol (TC) ($p < 0.001$) (Table 4). We observed that, when 4% silage was included in the diet, the LC increased with respect to the samples of *C. porcellus* that represented the control group. As for lipoproteins, both high-density lipoproteins

TABLE 2 Fatty acid profile of guinea pig pectoral muscle (g/100 g of muscle).

Fatty acid	T0	T1	T2	p-value
Lauric acid (C12:0)	0.058 ± 0.003 ^b	0.06 ± 0.003 ^b	0.07 ± 0.003 ^a	0.006
Myristoleic acid (C14:1)	0.24 ± 0.003 ^c	0.27 ± 0.003 ^b	0.34 ± 0.003 ^a	<0.001
Palmitoleic acid (C16:1)	3.89 ± 0.003 ^c	4.27 ± 0.003 ^b	4.76 ± 0.018 ^a	<0.001
Heptadecanoic/margaric acid (C17:0)	0.12 ± 0.003 ^b	0.12 ± 0.003 ^b	0.18 ± 0.003 ^a	<0.001
Heptadecenoic/margaleic acid (C17:1)	0.13 ± 0.003 ^a	0.12 ± 0.003 ^b	0.12 ± 0.003 ^b	0.030
Trans-linoleic acid (C18:1 t)	1.22 ± 0.003 ^c	1.30 ± 0.003 ^b	1.46 ± 0.003 ^a	<0.001
Trans-linoleic acid (C18:2 t)	2.62 ± 0.003 ^b	2.55 ± 0.003 ^c	3.14 ± 0.003 ^a	<0.001
-γ-linolenic acid (C18:3 n6)	3.52 ± 0.003 ^a	3.26 ± 0.003 ^b	3.03 ± 0.003 ^c	<0.001
Arachidic acid (C20:0)	0.17 ± 0.003 ^a	0.16 ± 0.003 ^b	0.10 ± 0.003 ^c	<0.001
Eicosenoic acid (C20:1 Cis11)	0.00 ± 0.000 ^b	0.00 ± 0.000 ^b	0.06 ± 0.003 ^a	<0.001
Arachidonic acid (C20:4 n6)	0.21 ± 0.003 ^b	0.22 ± 0.003 ^a	0.21 ± 0.003 ^b	0.030
Docosahexaenoic acid (C22:6)	0.00 ± 0.000 ^c	0.09 ± 0.003 ^b	0.17 ± 0.003 ^a	<0.001
Total fat	12.96 ± 0.003 ^c	13.25 ± 0.003 ^b	14.55 ± 0.003 ^a	<0.001
Saturated fats	0.46 ± 0.003 ^b	0.45 ± 0.003 ^c	0.49 ± 0.003 ^a	<0.001
Unsaturated fats	8.08 ± 0.003	8.37 ± 0.003	8.83 ± 0.003	0.252
Monounsaturated fats	4.34 ± 0.003 ^c	4.76 ± 0.003 ^b	5.35 ± 0.003 ^a	<0.001
Polyunsaturated fats	3.84 ± 0.003 ^a	3.61 ± 0.003 ^b	3.49 ± 0.003 ^c	<0.001
Trans fats	3.84 ± 0.003 ^c	3.85 ± 0.003 ^b	4.59 ± 0.003 ^a	<0.001
Trans-11 isomers (18:0 2)	2.62 ± 0.003 ^b	2.55 ± 0.003 ^c	3.14 ± 0.003 ^a	<0.001
Trans-9 isomers (18:0 1)	1.22 ± 0.003 ^c	1.30 ± 0.003 ^b	1.47 ± 0.003 ^a	<0.001
ω-3 total	3.52 ± 0.003 ^a	3.35 ± 0.003 ^b	3.22 ± 0.003 ^c	<0.001
ω-6 total	0.21 ± 0.003 ^b	0.23 ± 0.003 ^a	0.23 ± 0.003 ^a	0.001
ω-9 total	0.06 ± 0.003 ^b	0.06 ± 0.003 ^b	0.09 ± 0.003 ^a	<0.001
ω-6/ω-3 ratio	0.06 ± 0.002 ^b	0.06 ± 0.002 ^b	0.07 ± 0.002 ^a	<0.001

γ, gamma; ω, omega.

Mean values ± standard deviation, a,b,c = different letters in each row indicate significant differences at $p < 0.05$.

TABLE 3 Hematological parameters of guinea pigs according to treatment.

Hematological variables	T0	T1	T2	p-value
WBC ($\times 10^9/L$)	3.62 ± 1.24 ^a	3.46 ± 0.54 ^{a,b}	2.78 ± 0.45 ^b	0.050
Lym# ($\times 10^9/L$)	2.18 ± 0.55 ^b	2.66 ± 0.46 ^a	2.15 ± 0.47 ^b	0.037
Mid# ($\times 10^9/L$)	0.41 ± 0.20	0.30 ± 0.11	0.44 ± 0.62	0.673
Neu# ($\times 10^9/L$)	1.03 ± 1.17 ^a	0.50 ± 0.24 ^{a,b}	0.38 ± 0.16 ^b	0.007
Lym (%)	64.68 ± 20.01	77.00 ± 7.97	74.09 ± 9.25	0.100
RBC ($10^{12}/L$)	4.89 ± 0.35	5.02 ± 0.32	4.96 ± 0.30	0.614
HGB (g/dL)	15.35 ± 0.60	15.24 ± 0.98	14.69 ± 1.10	0.218
HCT (%)	36.24 ± 1.81	37.41 ± 2.15	36.67 ± 2.87	0.479
MCV (fL)	74.31 ± 3.78	74.52 ± 1.98	73.93 ± 2.15	0.879
MCH (pg)	31.50 ± 1.78	36.68 ± 20.93	29.67 ± 1.09	0.385
MCHC (g/dL)	42.38 ± 0.75 ^a	40.67 ± 1.05 ^b	40.08 ± 0.76 ^b	<0.001
PLT ($\times 10^9/L$)	453.55 ± 102.92	457.36 ± 52.99	427.64 ± 73.34	0.636
MPV (fL)	5.62 ± 0.25 ^b	5.94 ± 0.35 ^{a,b}	6.09 ± 0.49 ^a	0.020
PCT (%)	0.25 ± 0.06	0.27 ± 0.03	0.27 ± 0.06	0.679

WBC, white blood cell count; Lym#, number of lymphocytes; Mid#, number of monocytes; Neu#, number of granulocytes; Lym%, percentage of lymphocytes; RBC, red blood cell count; HGB, hemoglobin concentration; HCT, hematocrit; MCV, mean corpuscular volume; MCH, mean corpuscular hemoglobin; MCHC, mean corpuscular hemoglobin concentration; PLT, platelet count; MPV, mean platelet volume; PCT, procalcitonin.

Mean values ± standard deviation, a,b = different letters in each row indicate significant differences at $p < 0.05$.

TABLE 4 Serum biochemical values of guinea pigs according to treatment.

Variables	T0	T1	T2	p-value
HDL (mg/dL)	57.43 ± 64.79	91.59 ± 74.90	60.54 ± 42.03	0.374
LDL (mg/dL)	297.89 ± 797.24	43.08 ± 40.37	129.33 ± 118.56	0.437
TL (mg/dL)	99.12 ± 68.22	99.90 ± 46.51	110.28 ± 84.50	0.913
Lipase (U/L)	41.78 ± 25.11	55.46 ± 13.09	46.57 ± 17.73	0.256
TP (g/dL)	4.67 ± 1.47	3.74 ± 1.25	4.32 ± 1.20	0.263
TC (mg/dL)	36.42 ± 8.51 ^b	49.51 ± 14.64 ^b	81.78 ± 24.68 ^a	<0.001

HDL, high-density lipoproteins; LDL, low-density lipoproteins; TL, triglycerides; TP, total proteins; LC, total cholesterol. Mean values ± standard deviation, a,b = different letters in each row indicate significant differences at $p < 0.05$.

TABLE 5 Intestinal histomorphometry of the jejunum.

Variable	T0	T1	T2	p-value
VW (μm)	73.63 ± 34.28	71.93 ± 49.41	83.66 ± 20.80	0.723
VH (μm)	510.33 ± 200.33	494.74 ± 236.57	602.70 ± 149.10	0.398
DC (μm)	170.85 ± 55.19 ^{a,b}	124.60 ± 64.26 ^b	204.07 ± 91.50 ^a	0.047
VH/DC (μm)	3.42 ± 2.26	4.17 ± 2.86	3.23 ± 1.00	0.570

VW, villus width; VH, villus height; DC, depth of the crypt.

Mean values ± standard deviation, a,b = different letters in each row indicate significant differences at $p < 0.05$.

(HDL) and low-density lipoproteins (LDL) did not show statistically significant variations between treatments ($p = 0.374$ and $p = 0.437$, respectively), although higher values were observed at T1 for HDL and at T0 for LDL-C. Similarly, liquid triglycerides (TL), lipase, and total proteins remained stable ($p = 0.913$, $p = 0.256$, $p = 0.263$, respectively), with values close to and without relevant changes between treatments.

3.3 Intestinal histomorphometry

Table 5 shows data on villus height (VH) and width (VW) measurements, as well as crypt depth (DC) and ratio (VH/DC). No significant differences were found in (VH) and (VW), or VH/DC between treatments ($p > 0.05$). However, DC presented significant differences ($p = 0.047$), showing that T2 animals registered a higher value compared to T1, while T0 showed an intermediate value.

3.4 Cecal microbiota

3.4.1 Rarefaction curve

A total of 3,747,446 raw reads were obtained after sequencing of the V3 and V4 regions of the 16S rRNA gene from 33 samples. Quality filtering was then performed, yielding 2,190,184 clean reads. A total of 22,912 amplicon sequence variants (ASVs) were identified as part of the bacterial community present in guinea pig cecal samples. Rarefaction analysis based on three alpha diversity indices: ACE, Chao1, and Observed Features (observed richness), generated by QIIME2 is shown in Figure 1. The rarefaction curves revealed that the sequencing depth was sufficient to capture the microbial diversity in the guinea pig cecal microbiota, with a plateau reached between 25,000 and 40,000 reads for T0 and T1, where approximately 1,600–1,800 ASVs were observed. In contrast, T2 showed a sustained increase in richness, reaching approximately 2,000 ASV at greater

depth, suggesting a greater presence of treatment-influenced taxa (Supplementary Figure S1).

3.4.2 Alpha diversity analysis

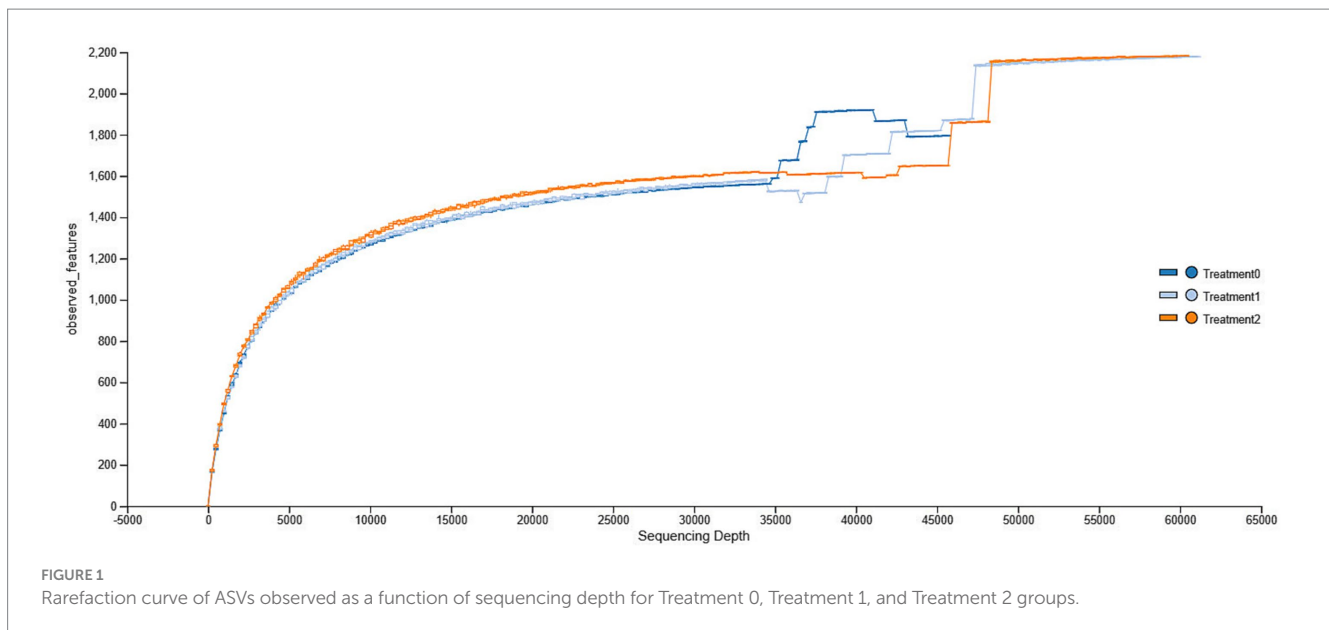
The alpha diversity analysis, evaluated by Shannon's index, showed that the microbial diversity of the cecal microbiota was similar between T0, T1, and T2. The distributions, represented in violin plots, evidenced a slight tendency for the median to increase at T2; however, these differences were not statistically significant ($p > 0.05$) (Figure 2A). The Kruskal–Wallis test confirmed this absence of relevant differences ($H = 0.265$ and $p = 0.875$) (Supplementary Table S1), while paired comparisons also showed no significance (Supplementary Table S2).

The Pielou Evenness index (Figure 2B) indicated an equal distribution of ASV abundances among treatments, with no statistically significant differences ($p > 0.05$). The Kruskal–Wallis test ($H = 0.317$ and $p = 0.853$) (Supplementary Table S3) and paired analyses ($p = 0.630$, 0.630 , and 0.895 for T0 to T1, T0 to T2, and T1 to T2 comparisons, respectively) (Supplementary Table S4) confirmed homogeneity between groups, with adjusted q -values of 0.895.

The Observed Features index showed that microbial richness was similar between T0 and T1, with a slight non-significant reduction at T2 ($p > 0.05$), possibly associated with the dominance of certain microbial groups (Figure 2C). The Kruskal–Wallis test ($H = 0.358$; $p = 0.836$) (Supplementary Table S5) and adjusted values ($q = 0.847$) confirmed the absence of relevant changes, while paired comparisons also showed no significant differences ($p = 0.847$, 0.564 , 0.691 for T0, T1, and T2, respectively) (Supplementary Table S6).

3.4.3 Beta diversity analysis

The absence of significant changes in the alpha diversity analyses does not imply that the microbial composition was unchanged, as shown in Table 6. Beta diversity analysis, evaluated by Bray–Curtis (Figure 3A), Jaccard (Figure 3B), and Weighted UniFrac distances



(Figure 3C), evidenced that the composition of the cecal microbiota did undergo modifications associated with silage consumption. Bray–Curtis (pseudo- $F = 1.247$, $p = 0.006$) and Jaccard (pseudo- $F = 1.089$, $p = 0.017$) metrics showed statistically significant differences between the control group and both silage treatments in both relative abundance and the presence/absence of ASV. In contrast, the Weighted UniFrac distance, which incorporates phylogenetic information, did not detect significant differences ($p = 0.136$).

Finally, Supplementary Table S7 presents the results of the PERMANOVA analysis applied to the Bray–Curtis, Jaccard, and Weighted UniFrac distances in order to evaluate differences in microbial composition between treatments. The methods based on Bray–Curtis and Jaccard revealed significant differences ($p < 0.05$) between T0 with T1 and T0 with T2, while no differences were observed between T1 with T2 ($p > 0.05$). In contrast, analysis with Weighted UniFrac showed no statistically significant differences between any of the pairs compared, suggesting that the variations detected are mainly associated with differences in the presence/absence and relative abundance of taxa, rather than with the phylogenetic structure of the communities.

3.4.4 Taxonomic composition

Analysis of the cecal microbiota showed that, at the Phylum level (Figure 4A), Firmicutes was the dominant group in all treatments (40–60%), followed by Bacteroidetes (30–50%); however, a clear trend was observed in the progressive increase in Bacteroidetes at T0 with respect to T2, while Firmicutes decreased. Other phyla, such as Verrucomicrobiota, Actinobacteria, and Proteobacteria, presented lower abundances (3–10%) (Supplementary Figure S2), but Verrucomicrobiota showed a marked increase at T2.

At the order level (Figure 4B), Bacteroidales and Oscillospirales concentrated the highest proportion of readings, although Bacteroidales increased markedly at T2. This increase was accompanied by an increase in Verrucomicrobiales, Fibrobacteriales, and Spirochaetales, all of which are Orders linked to the degradation

of structural polysaccharides and adaptations to changes in the protein-rich diet (Supplementary Figure S3).

At the family level (Figure 5A), Lachnospiraceae and Prevotellaceae were dominant in the three treatments (18–30%, 15–25%, respectively), although Prevotellaceae increased in abundance, especially at T2, as did Synergistaceae and Ruminococcaceae, which also showed notable increases in the same treatment (Supplementary Figure S4).

Genus-level analysis (Supplementary Figure 5B) showed dominance of d5_Muribulaceae with consistent distribution across individuals. Other major genera included Akkermansia, Lachnospiraceae, and Bifidobacterium, with variable proportions, but without markedly differential changes between treatments (Supplementary Figure S5).

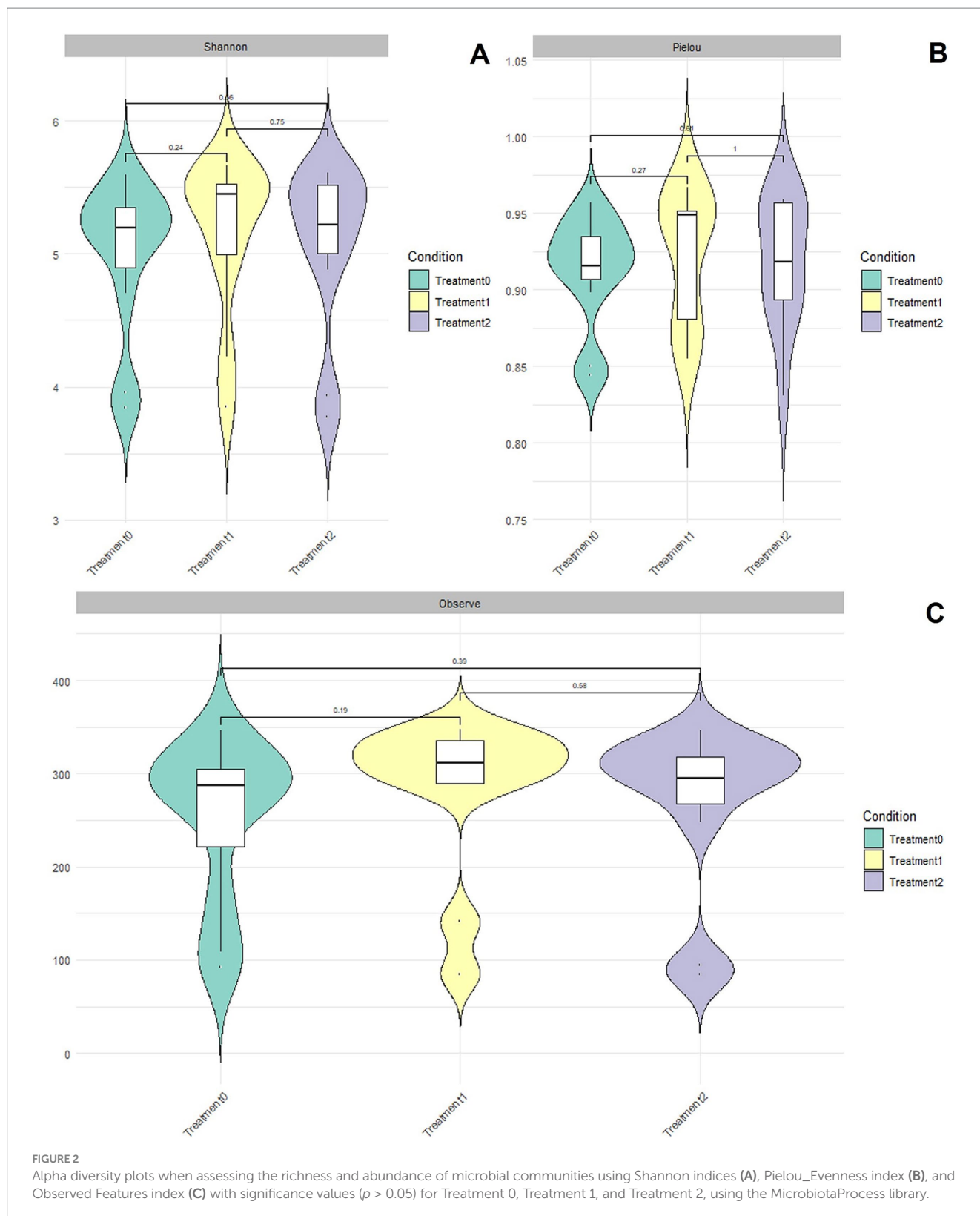
Biplot analysis at the phylum level showed that microbial communities did not vary dramatically between treatments, although a slight separation of T2 samples was detected to be associated with the increase in Verrucomicrobia (Figure 6). Most phylum, such as Firmicutes and Bacteroidota, were located near the center of the graph, reflecting their common presence in all groups without significant influence.

Differential abundance analyses (DESeq2) and non-parametric Wilcoxon tests with Bonferroni correction on the 10 most abundant functional taxa confirmed that several bacterial groups and metabolic pathways were significantly enriched or decreased, depending on the treatment ($p < 0.05$) (Supplementary Tables S8, S9).

Evaluation of the cecal microbial structure revealed distinctive patterns in both the composition and exclusivity of the microbiota. The Venn diagram constructed from the amplicon sequences (ASVs) showed the existence of a conserved microbial core of 1,889 ASVs present in the three treatments (Figure 7).

3.4.5 Functional profile

Analysis of the predicted functional profiles of the cecal microbiota showed a remarkably homogeneous distribution among



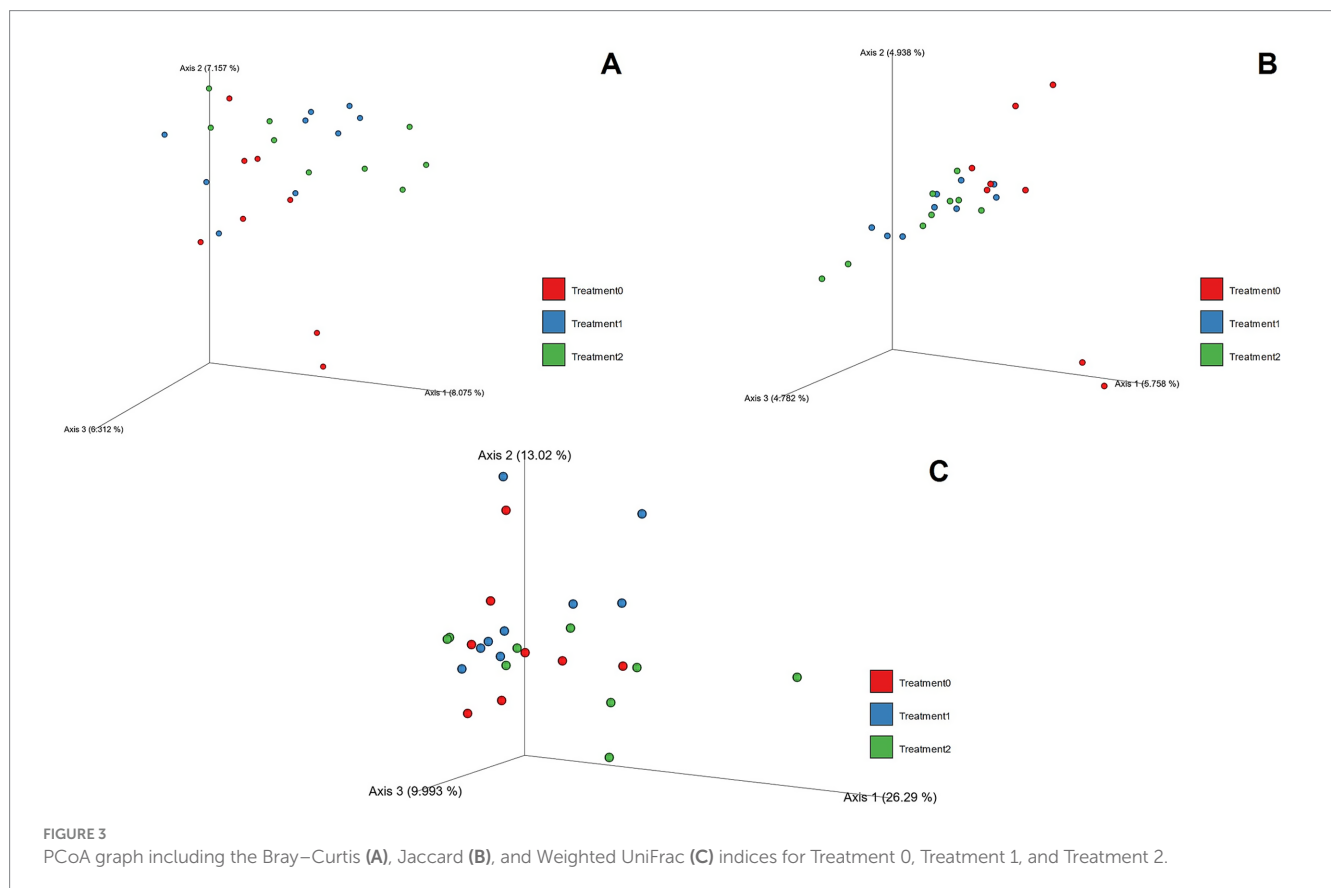
the T0, T1, and T2 groups, with no distinct clustering patterns or abundance gradients suggesting diet-induced alterations (Figure 8). The most representative metabolic pathways included the Calvin–Benson–Bascham cycle, branched-chain amino acid biosynthesis (L-isoleucine, L-valine), glycolysis, oxidative and non-oxidative

pentose phosphate pathways, peptidoglycan biosynthesis, and coenzyme A biosynthesis. Hierarchical clustering of ASVs and heat map color intensity confirmed that differences between treatments were minimal and did not show consistent patterns of functional increase or reduction. This interpretation was supported by

TABLE 6 PERMANOVA statistical analysis for Bray–Curtis, Jaccard, and Weighted UniFrac distances.

Distances	PERMANOVA results			
	Test statistic name	Test statistic	<i>p</i> -value	Number of permutations
Bray–Curtis distance	pseudo-F	1.247	0.006 ^a	999
Jaccard distance	pseudo-F	1.089	0.017 ^a	999
Weighted UniFrac	pseudo-F	1.297	0.136 ^b	999

a,b = different letters in each column indicate significant differences at $p < 0.05$.



non-parametric statistical tests (Supplementary Table S10), where all paired comparisons reported $p > 0.05$, indicating no significant differences in the relative abundance of the metabolic pathways evaluated. Taken together, these results suggest that the cecal microbiota maintained functional resilience, preserving its core metabolic repertoire in the face of variations in the level of inclusion of *O. mykiss* silage in the diet.

3.5 Productive performance

The productive performance data are presented in Table 7. There were no significant differences ($p > 0.05$) in daily concentrate intake (DCI) or daily pasture intake (DPI) among treatments. However, cumulative weight gain (CWG) was significantly higher in the group with higher silage inclusion T2 compared to the group that did not receive trout silage T0 and T1 ($p = 0.050$). Similarly, the feed conversion factor (FCF) improved significantly ($p < 0.001$) in the

animals supplemented with trout silage (T1 and T2), being more efficient in T2.

4 Discussion

Underutilized parts of fish such as viscera, skin, and others could be valuable sources of edible proteins and other nitrogenous compounds such as peptides, amino acids, hydrolysates, and lipids, among other bioactive compounds (56). The utilization of these by-products can reduce raw material costs, increase industrial productivity, and minimize environmental pollution (10).

In this study, the inclusion of silage in guinea pig diets modified the lipid profile of the meat. The results suggest that the inclusion of trout silage modifies the lipid profile of the pectoral muscle, increasing mainly monounsaturated fatty acids and certain long-chain fatty acids such as DHA (C22:6). To date, numerous investigations have been conducted to evaluate the possible production of a functional feed by

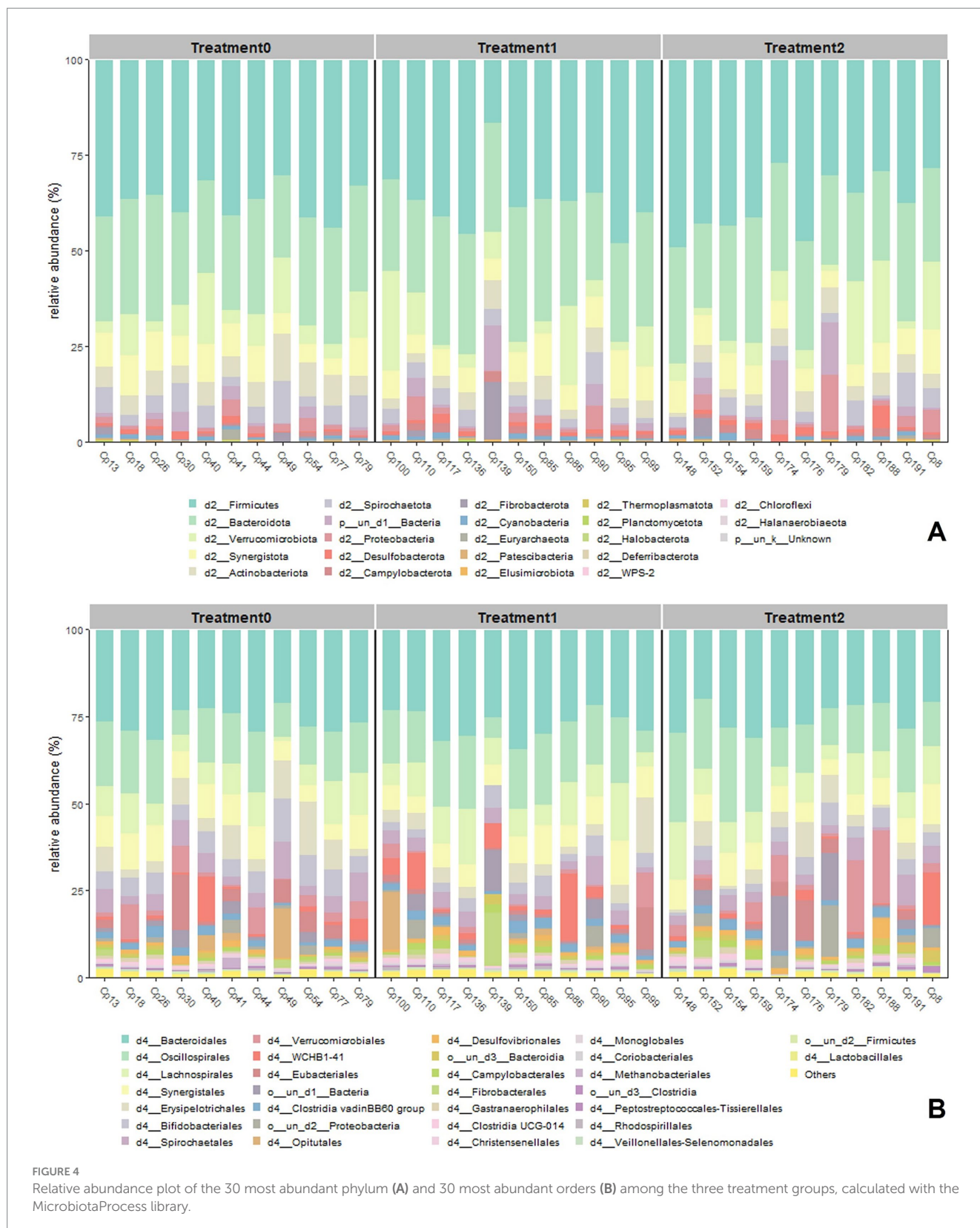


FIGURE 4 Relative abundance plot of the 30 most abundant phylum (A) and 30 most abundant orders (B) among the three treatment groups, calculated with the MicrobiotaProcess library.

administering diets enriched with ω -3 PUFA. For example, Rodriguez et al. (57) evaluated the inclusion of fish oil as a source of fatty acids in rabbit feed, and they found that the total PUFA content and the ratio of ω -6/ ω -3 were lower in the samples of rabbits with enriched diets. This could be primarily due to its content and capacity to

transform DHA from fish oil (58). Arachidonic acid (C20:4 ω -6) is one of the precursors of prostaglandins and thromboxanes, in addition to regulating body homeostasis (59). DHA (C22:6) is a major constituent of membrane phospholipids in the retina, brain, reproductive tissues, and gametes; therefore, meat from guinea pigs



FIGURE 5 Relative abundance graph of the 30 most abundant family (A) and 30 most abundant genus (B) among the three treatment groups, calculated with the MicrobiotaProcess library.

fed trout silage may represent a good source of DHA. The main sources of ω -3 PUFA for humans are fish and marine algae, while the requirements of ω -6 PUFA are satisfied by meat intake (60). This leads to infer that the production and consumption of PUFA-enriched functional foods, especially guinea pig meat, could be a new complementary strategy to reduce the incidence of several pathologies and improve human health (61). Bouzaida et al. (62) and Scerra et al. (63) found similar results for PUFA ω -6 and ω -3 in rabbits fed diets

containing 20% grape pomace and 10% grape seeds, respectively. The data from our study also show that there was a slight decreasing trend of PUFA ω -3, while PUFA ω -6 tended to increase. This led to an undesirable increase in the ω -6/ ω -3 ratio; however, this ratio did not even exceed one-fourth of the maximum recommended dietary value of 4 (64). On the other hand, we also found that the content of monounsaturated fatty acids increased as the percentage of silage inclusion in the diets increased. Monounsaturated fatty acids can

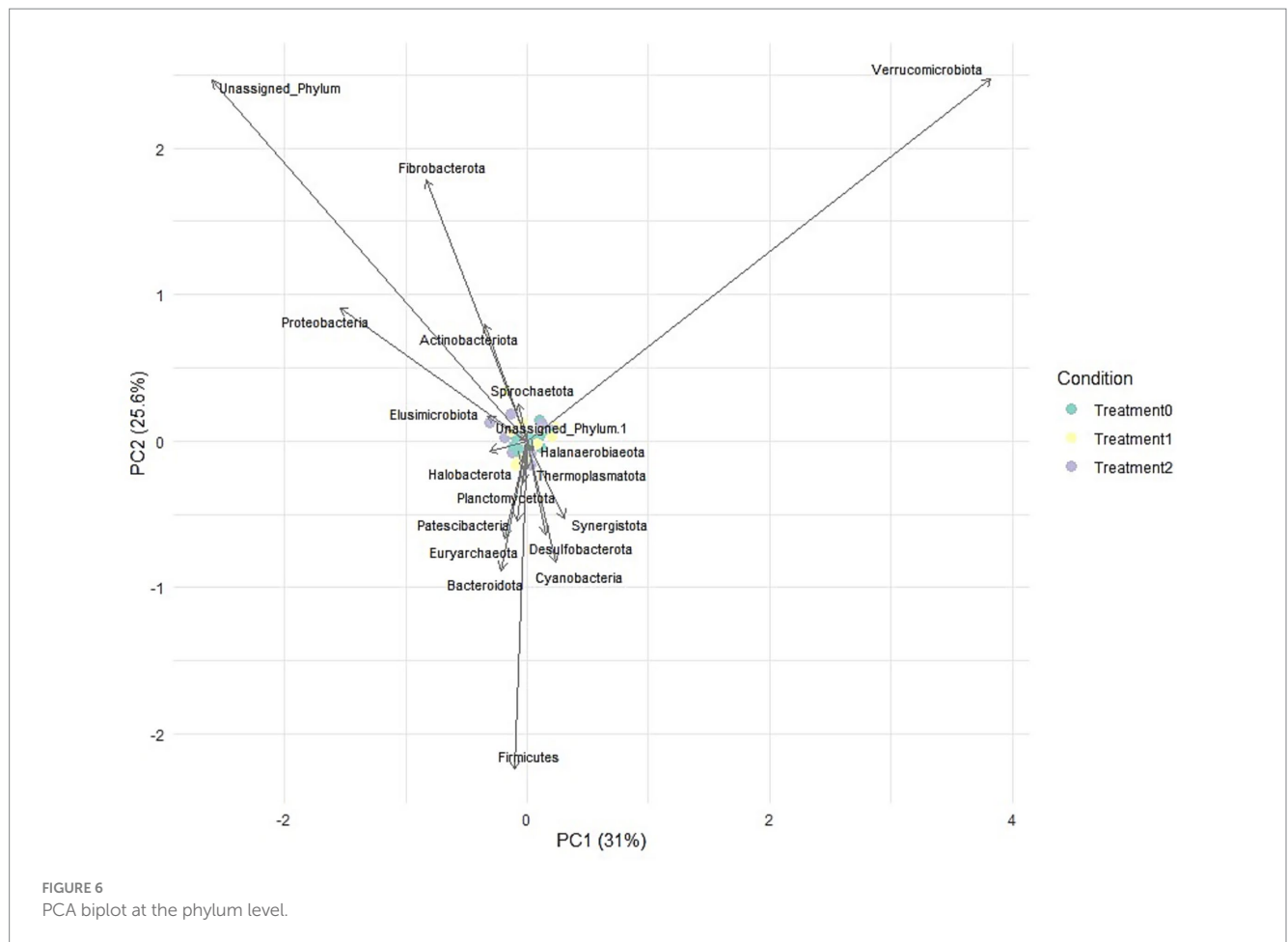


FIGURE 6
PCA biplot at the phylum level.

improve the lipid profile by increasing HDL and reducing LDL and triglycerides (65). There are communities in the world that consume diets rich in monounsaturated fatty acids, such as the Mediterranean. These habits are associated with a lower risk of cardiovascular disease, improved insulin sensitivity, decreased risk of certain types of cancer, and positive effects on cognition, in addition to being considered as one of the world diets for the prevention and treatment of type 2 diabetes (66).

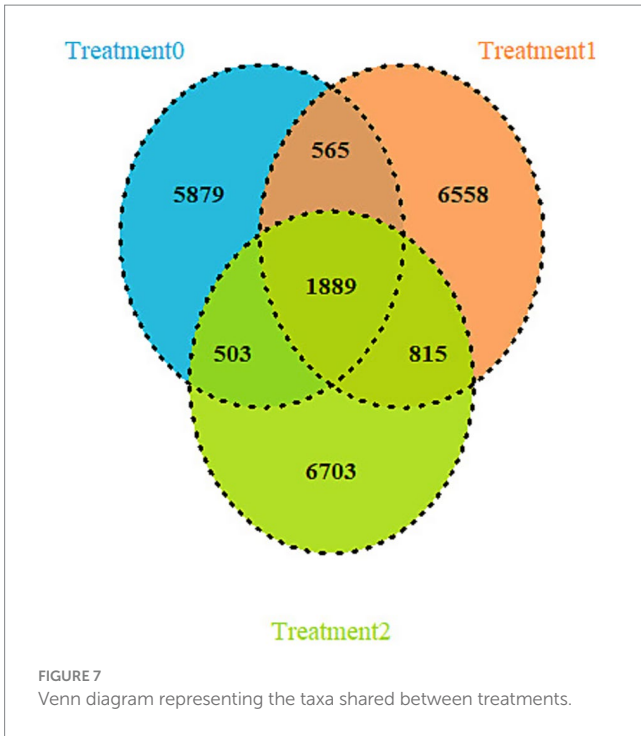
In our research, treatments that had trout silage in the diets modified some of the hematological parameters. Previous studies also indicate that fish silage contains active biopeptides that interfere with the values of different blood parameters (67). Goosen et al (17), who evaluated the inclusion of rainbow trout silage oil in Mozambique tilapia diet and found no differences in the means of hematocrit and red blood cell count, reported similar increases in mean platelet volume values. Although some parameters decreased at higher silage inclusion, their values remained above those reported for native guinea pigs and those raised in humid tropical conditions (68, 69).

Our findings found no significant changes in most of the biochemical values, coinciding with those reported by Ardó et al. (70), who also found no differences when evaluating the incorporation of *Astragalus membranaceus* and *Lonicera japonica* in the serum protein of Nile tilapia. The parameter that did show a statistical difference is total cholesterol, which tends to increase as the incorporation of trout silage in the diet increases. This result differs from that reported by Zamora et al. (71), who found no differences in serum total cholesterol

values when increasing levels of sacha inchi oil were incorporated in diets for laying hens. Similarly, Wang et al. (72) found no differences in total cholesterol in pigs. These differences between what was reported are possibly due to the difference in the animal species used in the study and to the different source of food ingredients. No statistical differences were observed in most of the histomorphometric measurements performed, with the exception of crypt depth, where it is shown that, as the inclusion dose of trout silage increases, its depth also increases; this could be due to its properties on the improvement of digestion, absorption, and the functioning of the immune system of animals that consume trout silage (73), besides standing out for having good antioxidant, antithrombotic, antihypertensive, and antibacterial qualities (67).

The guinea pig cecum, a key organ for feed fermentation, harbors a dense and complex microbiota dominated by phyla such as Firmicutes and Bacteroidota, mainly adapted to the digestion of fibrous plant material (74). In this study, the results suggest that the addition of trout silage does not substantially alter the alpha diversity of guinea pig cecal microbiota with respect to the control group. This is consistent with previous observations reporting that high-protein diets promote the proliferation of proteolytic bacteria in the distal gut without substantial changes in microbial composition (75).

Beta diversity analysis indicates that diet reshaped the identity and relative abundance of certain taxa, favoring those better adapted to metabolize the nutrients present in trout silage, possibly with greater proteolytic and lipolytic capacity (75, 76). The lack of significance in



the Weighted UniFrac analysis suggests that changes occurred primarily among phylogenetically close taxa, at the species or genus level, within the same bacterial families, without substantial modifications in the larger lineages.

The reduction in Spirochaetaceae between T0 and T1 could be associated with competition for easily fermentable substrates present in the silage, as well as a decrease in intestinal pH, which could affect their growth (77). On the other hand, the increase in Lachnospiraceae and Ruminococcaceae indicates a strengthening of the fermentative capacity of complex fibers and an increased production of short-chain fatty acids (SCFA), particularly butyrate, which is consistent with that reported by Choy et al. (78) and Louis and Flint (79). In addition, the increase in Prevotellaceae suggests that silage treatment may be favoring fiber fermentation, while the reduction in Bacteroidota could signal a shift in microbiome dynamics toward a composition that favors SCFA production.

The Venn diagram indicates a stable community probably composed of generalist taxa well adapted to the basal gut environment (80, 81). However, a high number of exclusive ASVs per treatment was detected, suggesting a marked process of environmental filtering that promoted the formation of specific and specialized ecological niches (82). This phenomenon, in which a dietary intervention significantly alters microbial structure, has been documented in diverse gut

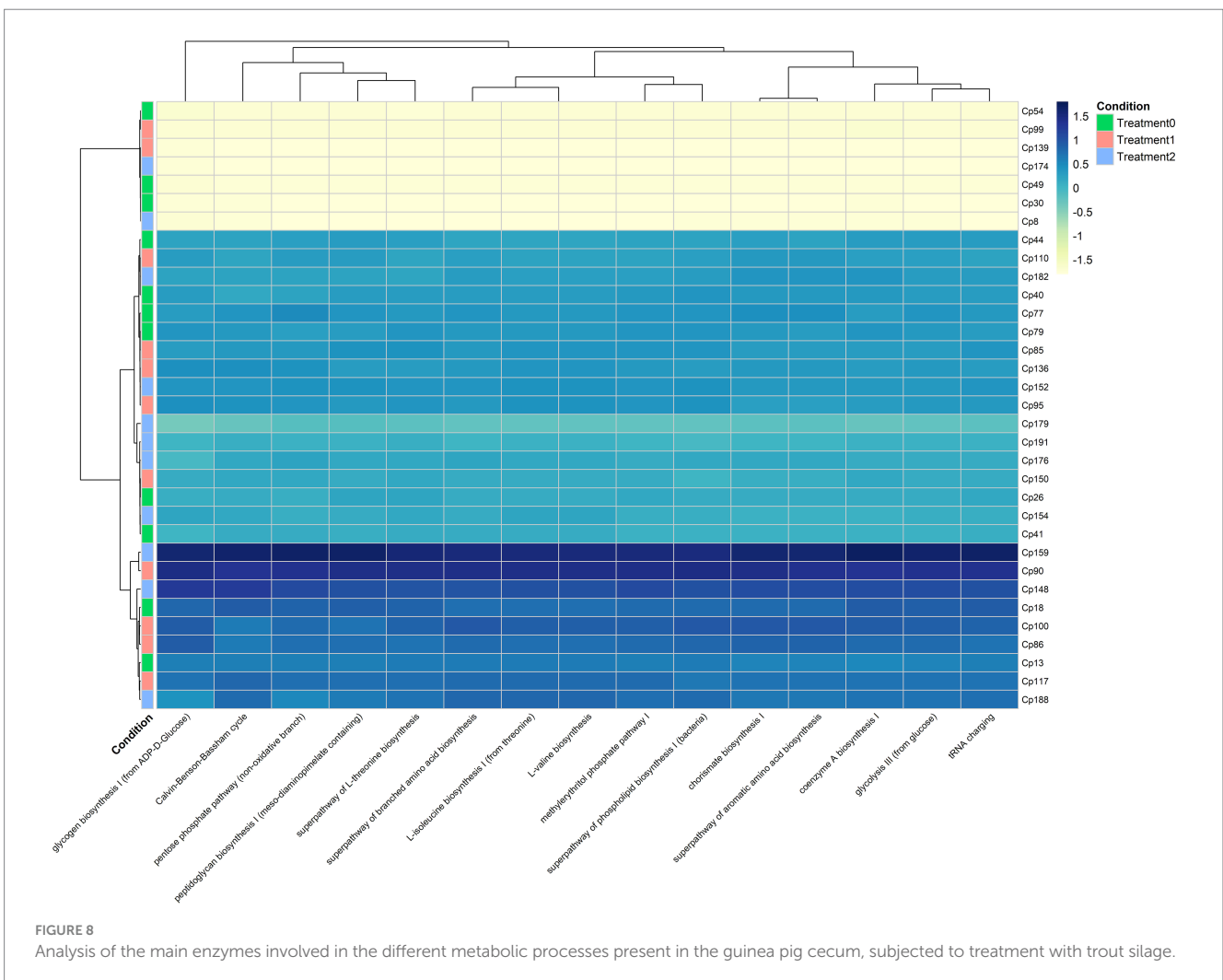


TABLE 7 Productive performance of guinea pigs according to treatment.

Parameter	T0	T1	T2	p-value
DCI (g)	26.24 ± 5.49	26.45 ± 3.20	29.58 ± 3.43	0.126
DPI (g)	114.53 ± 6.48	111.17 ± 6.91	116.58 ± 7.45	0.200
CWG (g)	788.27 ± 110.28 ^b	790.18 ± 97.35 ^b	884.36 ± 121.26 ^a	0.050
FCF (Kg)	4.49 ± 0.22 ^c	4.24 ± 0.28 ^b	3.94 ± 0.29 ^a	<0.001

DCI, daily concentrate intake; DPI, daily pasture intake; CWG, cumulative weight gain; FCF, feed conversion factor. Mean values ± standard deviation, a,b,c = different letters in each row indicate significant differences at $p < 0.05$.

ecosystems, where selective pressures modify diversity and favor taxa adapted to particular conditions (83, 84). The greatest intersection of ASV was observed between T1 and T2, indicating that both treatments exerted similar selective pressures, although without fully converging in composition.

Although none of the predicted metabolic pathways showed significant differences between treatments, this study suggests that the cecal microbiota of guinea pigs maintains a highly conserved functional core, regardless of dietary variations. The stability of these pathways is consistent with the concept of functional redundancy, where different taxa can sustain equivalent metabolic functions even when the microbial structure fluctuates (85). The persistence of central pathways such as glycolysis and pentose phosphate is consistent with their universal role in obtaining energy and generating biosynthetic precursors necessary for bacterial proliferation (86). The stability of peptidoglycan biosynthesis and coenzyme A pathways supports the idea that the microbial community maintains essential structural functions necessary for bacterial cell wall and energy metabolism (87, 88). Taken together, these findings indicate that the cecal community of *C. porcellus* responds to the progressive inclusion of *O. mykiss* silage, an important source of bioactive compounds, peptides, vitamins, and DHA, through compositional reorganizations that preserve core functional potential, a pattern of resilience that is physiologically consistent with the fermentative role of the cecum and the need to maintain the production of key metabolites such as short-chain fatty acids (SCFA) for the host.

Regarding productive performance, concentrate intake per day, pasture intake per day, and cumulative weight gain did not show differences. These results differ from those reported by Shabani et al. (89), who did find differences for weight gain values in broilers fed 30, 60, 90, and 120 g/kg levels of fish silage. This could be primarily attributed to the higher protein quality, the biological values of fish silage, and the species under study, although chickens differ from guinea pigs in their digestive system (90). The only parameter that presents statistical difference in our study is the feed conversion factor (FCF), contrary to our results reported (91), who found no differences when evaluating the partial substitution of fish meal for trout viscera silage in red tilapia. Similarly, Vélez and Cadavid (92) reported that the inclusion of red tilapia viscera silage does not affect feed conversion in rabbits, which have a digestive system similar to that of guinea pigs. The positive results for this parameter in our study can be attributed to the balanced nutritional composition of the diets, the high solubility of the silage, and the presence of several fatty acids in the silage (93, 94).

5 Conclusion

The findings of this study demonstrate that the inclusion of rainbow trout silage in the guinea pig diet significantly modified the

lipid profile of the meat, increasing monounsaturated fatty acids and the DHA content, thereby suggesting its potential for obtaining meat with functional characteristics for human health. On the other hand, the addition of silage did not alter most hematological and biochemical indicators, except for serum cholesterol and some cellular values, which remained within physiological ranges reported for the species. Intestinal histomorphometry showed a greater depth of crypts, which was linked to a better digestive capacity reflected in better feed and immune conversion. Regarding cecal microbiota, although no relevant changes in alpha diversity were evidenced, modifications in beta diversity and taxonomic composition were observed, indicating an adaptive reorganization of the microbial community in the face of silage without compromising its functional stability. From a productive point of view, silage did not significantly affect feed intake or weight gain, but improved the feed conversion factor, reflecting a more efficient use of nutrients. Overall, these results demonstrate that trout silage constitutes a viable alternative ingredient, capable of improving the nutritional quality of meat and favoring sustainability parameters in guinea pig production, without adverse effects on the health and productive performance of the animals.

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 in the article/Supplementary material.

Ethics statement

The animal study was approved by Universidad Nacional Toribio Rodríguez de Mendoza de Amazonas, Comité Institucional de Ética de la Investigación. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

MA: Validation, Supervision, Writing – review & editing, Writing – original draft, Methodology, Conceptualization, Investigation, Data curation. SZ-H: Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition, Validation. JS-U: Writing – review & editing, Formal analysis, Software, Data curation. PF-C: Writing – original draft, Formal analysis, Software, Data curation. NM: Conceptualization, Writing – original draft, Methodology, Investigation. LV: Investigation, Writing – original draft. JS: Writing – original draft, Investigation. DA: Investigation, Writing – original draft. RL:

Investigation, Writing – review & editing. CT: Writing – original draft, Methodology, Investigation. YL: Resources, Writing – original draft. HV: Writing – review & editing, Resources. JM: Writing – review & editing, Funding acquisition. WB: Project administration, Methodology, Writing – review & editing, Investigation, Validation, Funding acquisition, Resources.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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