Animal Microbiome

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Increasing the level of hemicelluloses in the lactation diet affects the faecal microbiota of sows and their piglets without affecting their performances

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Abstract

Background Specific sources of dietary fibres in sow gestation and lactation diets, such as inulin or wheat bran, have been shown to affect both the sow and its litter health by modulating the piglet's intestinal microbial population and composition. However, only a few studies have reported the effects of some specific fractions of the cell wall of the plants in the sow's lactation diet. Therefore, this study investigates the effect of increasing the level of HCs in a sow's lactation diet on the nutrient apparent total tract digestibility (ATTD), the faecal volatile fatty acid (VFA) profile, the microbiota of the sow and the microbiota and the performances of slow-growing (SG) and fast-growing (FG) piglets.

Results Increasing HCs level increased ($P < 0.05$) the proportions of butyrate and valerate on day 3, and the ATTD of acid detergent fibres (ADF), neutral detergent fibres (NDF), and gross energy and decreased ($P < 0.05$) the proportion of propionate on day 17, and the ATTD of crude protein. The beta diversity was affected ($r^2 = 0.11$; $P = 0.02$) by the maternal dietary treatments with 11 common genera differing ($P < 0.05$) in the sow's faecal microbiota, and five in the piglet's microbiota. Regardless of the maternal dietary treatment, SG piglets had a lower ($P < 0.05$) proportion of isobutyrate and isovalerate, a lower ($P < 0.05$) abundance of *Lachnospiraceae_XPB1014*_group, *Enterococcus*, and *Succinovibrio* genera, and a greater ($P < 0.05$) abundance of *Olsenella* than FG piglets.

Conclusions Increased HCs level in a sow's lactation diet affects the ATTD of nutrients, the faecal VFA and microbiota profiles of the sows with limited effects on SG and FG piglets' faecal microbiota and no effects on the performance or VFA profile of these piglets.

Keywords Dietary fibres, Slow-growing piglets, Swine, Volatile fatty acids, Butyrate, Bacteria

Introduction

Due to the genetic selection for sow prolificacy, litter size has been increasing since the end of last century [43]. Although this commercial choice has brought economic benefits to the pig industry, it has negatively affected the development and health of the offspring [5]. Indeed, the average litter birth weight has been dramatically decreasing, and the birth weight variability between and within litters has been increasing, as has the proportion of low-birthweight piglets [22]. Considering that birthweight is

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one of the main factors affecting pre- and postweaning average daily gain (ADG), these piglets are more prone to slow growth [44]. Slow-growing (SG) piglets are defined as piglets that are lighter than the rest of the litter and that require additional time to reach the targeted slaughter weight [9], they present a management challenge and an additional cost for farmers because they may have a higher mortality and morbidity risk compared with their fast-growing (FG) siblings [28]. Therefore, it is essential to find strategies to ensure that lighter piglets can successfully catch up with their heavier litter mates. In this context, nutritional interventions during the perinatal period might be key factors contributing to piglet's growth and health. Since piglets are strictly in contact with faeces, skin and mucosal and environmental surfaces of the sow during the suckling period, shaping the sow's gut microbiota may be an effective way to influence the microbiota of its offspring. The modulation of sow gut microbiota can be achieved by using dietary fibres (DF) that include cell wall plant components, such as cellulose, hemicelluloses (HCs), lignin, mixed linked β-glucan, pectins, gums and mucilages [12]. In the large intestine, beneficial bacteria such as Lactobacilli and Bifidobacteria ferment DF and produce volatile fatty acids (VFAs), which decrease the pH of gut content, thereby reducing the development of potential pathogenic bacteria such as Clostridium and Salmonella [7]. The use of specific DF sources in sow gestation and lactation diets, such as inulin or wheat bran, has been shown to affect both the sow and its litter health by modulating the piglet's intestinal microbial population [23, 38]. However, to the best of our knowledge, little is known about the effects of some specific fractions of the cell wall of the plants in the sow's lactation diet. In a previous study, low-birthweight piglets exhibited a reduced growth and a higher incidence of postweaning diarrhoea during the second week after weaning, as the level of HCs in the sow's lactation diet increased [40]. We hypothesised that those changes may be mainly driven by the microbiota of the sow, which, in turn, can affect the microbiota of low-birthweight piglets. Therefore, the present study aims at investigating whether an increased HCs level modifies the apparent total tract digestibility (ATTD) of nutrients, the faecal fermentation profile and the faecal microbiota of the sows and ultimately affects the performances and the microbiota of SG and FG piglets during the suckling period. Finally, to the best of our knowledge, few studies have investigated the possible connection between piglet's gut microbiota and growth during the suckling period [16, 25, 26]. Therefore, the present study was also designed to compare the faecal microbiota and VFA profiles of SG and FG piglets during the suckling period.

Results

Apparent total tract digestibility of neutral detergent fibres, acid detergent fibres, gross energy and crude protein and volatile fatty acid profile in sow faeces

Increasing the level of HCs in sow's lactation linearly decreased ($L < 0.05$; $Q < 0.01$) the ATTD of CP and increased (L < 0.05) the ATTD of GE, neutral detergent fibres (NDF) and acid detergent fibres (ADF) (Table 1). In particular, the ATTD of CP was greater ($P < 0.05$) in HC9 and HC8 compared with HC11, with intermediate values for HC13. The ATTD of NDF was the lowest ($P < 0.05$) in the HC8 group and the greatest in the HC11 and HC13 groups.

On day 110 of gestation, a quadratic effect existed for total VFA concentration ($Q = 0.01$) (Table 2). The faeces of HC11 sows had a greater ($P < 0.05$) concentration of total VFA than those of HC13 sows with

Table 1 Apparent total tract digestibility of ADF, NDF, gross energy and crude protein of sow diet with increasing level of hemicelluloses during the lactation period

	†Dietary treatment				SEM	‡*P*-values		
	HC8	HC9	HC11	HC13		T	*L*	*Q*
Apparent total tract digestibility, %								
§ADF	40.3	46.8	49.9	51.7	3.29	0.09	0.02	0.46
°NDF	44.5[a]	54.6[b]	63.0[c]	67.9[c]	2.28	< 0.01	< 0.01	0.23
Gross energy	81.9	82.5	82.0	84.5	0.74	0.07	0.04	0.18
Crude protein	88.1[b]	86.6[b]	83.3[a]	86.2[ab]	0.82	< 0.01	0.02	< 0.01

† Dietary Treatment: HC13 = Sow's lactation diet containing 13% hemicelluloses; HC11 = Sow's lactation diet containing 11% hemicelluloses; HC9 = Sow's lactation diet containing 9% hemicelluloses; HC8 = Sow's lactation diet containing 8% hemicelluloses

‡ *P*-values: The presented *P*-values depict the overall sow dietary treatment (T), linear (L) and quadratic (Q) effects

§ ADF: Acid Detergent Fibres

°NDF: Neutral Detergent Fibres

[a, b,c] For a dietary treatment effect, means with different superscripts within a row differ significantly ($P < 0.05$)

Table 2 Volatile fatty acid profile in the faeces of sow feed with increasing levels of hemicelluloses during lactation period on day 110 of gestation, days 3 and 17 of lactation

	[†]Dietary treatment				SEM	[‡]*P*-values		
	HC8	HC9	HC11	HC13		T	*L*	*Q*
Day 110 of gestation								
Total volatile fatty acids, µmol/g	90.7[ab]	98.0[ab]	108.7[b]	89.5[a]	5.25	0.03	0.77	0.01
Individual VFA, %								
Acetate	60.6	60.1	61.5	62.0	1.47	0.81	0.42	0.73
Propionate	24.3	25.4	23.1	22.7	1.20	0.40	0.21	0.53
Isobutyrate	2.3	2.1	2.0	2.2	0.18	0.59	0.83	0.21
Butyrate	8.5	8.3	9.6	9.0	0.51	0.23	0.27	0.73
Isovalerate	2.8	2.7	2.4	2.6	0.26	0.74	0.52	0.54
Valerate	1.5	1.5	1.5	1.5	0.14	0.96	0.76	0.85
Day 3 of lactation								
Total volatile fatty acids, µmol/g	79.3	115.4	114.9	108.8	10.50	0.05	0.07	0.06
Individual VFA, %								
Acetate	60.8	59.4	58.3	58.5	1.18	0.38	0.14	0.48
Propionate	25.0	25.4	25.0	24.2	1.18	0.92	0.61	0.60
Isobutyrate	2.8	2.4	2.7	2.9	0.20	0.34	0.52	0.10
Butyrate	5.8[a]	7.8[ab]	8.5[b]	8.4[b]	0.65	0.02	< 0.01	0.10
Isovalerate	3.6	3.2	3.4	3.7	0.23	0.38	0.65	0.10
Valerate	1.9	1.8	2.2	2.3	0.14	0.08	0.03	0.34
Day 17 of lactation								
Total volatile fatty acids, µmol/g	112	120	132	137	12.9	0.50	0.14	0.94
Individual VFA, %								
Acetate	56.9	56.7	57.6	57.6	1.24	0.92	0.59	0.94
Propionate	25.0	23.4	22.1	22.0	1.05	0.15	0.04	0.45
Isobutyrate	3.1	2.9	2.9	3.4	0.22	0.32	0.35	0.12
Butyrate	9.3	10.9	11.6	10.5	1.02	0.35	0.33	0.16
Isovalerate	3.6	4.0	3.6	4.1	0.24	0.24	0.38	0.68
Valerate	2.4	2.2	2.2	2.1	0.13	0.38	0.14	0.36

[†] Dietary Treatment: HC13 = Sow's lactation diet containing 13% hemicelluloses; HC11 = Sow's lactation diet containing 11% hemicelluloses; HC9 = Sow's lactation diet containing 9% hemicelluloses; HC8 = Sow's lactation diet containing 8% hemicelluloses

[‡] *P*-values: The presented *P*-values depict the overall sow dietary treatment (T), linear (L) and quadratic (Q) effects

[a, b,c] For a dietary treatment effect, means with different superscripts within a row differ significantly ($P < 0.05$)

intermediate values for those of HC8 and HC9 sows. On day 3 of lactation, the total VFA concentration was affected ($P = 0.05$) by the dietary treatment but the pairwise comparisons could not differentiate the four dietary treatments. Moreover, on the same time point, the proportion of butyrate and valerate linearly increased ($L < 0.05$) when the level of HCs in the sow's lactation diet increased. In particular, the butyrate proportion was higher ($P < 0.05$) in the HC13 and HC11 groups than the HC8 group, with intermediate values for the HC9 group. On day 17 of lactation, the proportion of propionate linearly decreased ($L < 0.05$) when the level of HC in the sow's lactation diet increased.

Faecal microbiota of the sows

The dietary treatments had no effects on the Chao1, Shannon and Simpson alpha diversity indexes (Fig. 1) but did affect ($r^2 = 0.11$; $P = 0.02$) the beta diversity (Fig. 2) in the sow's faeces. However, the pairwise comparisons could not differentiate the four dietary treatments.

At the genus level, 11 common genera differed in the sow's faeces when HC8 diet was compared with HC9, HC11 and HC13 diets: *Angelakisella* and *Lachnospiraceae_UCG-008* were less abundant (*P*-adj < 0.05) while *Erysipelotrichaceae_UCG-006, Faecalicoccus, Hungatella, Parabacteroides, Parasutterella, Pyramidobacter,*

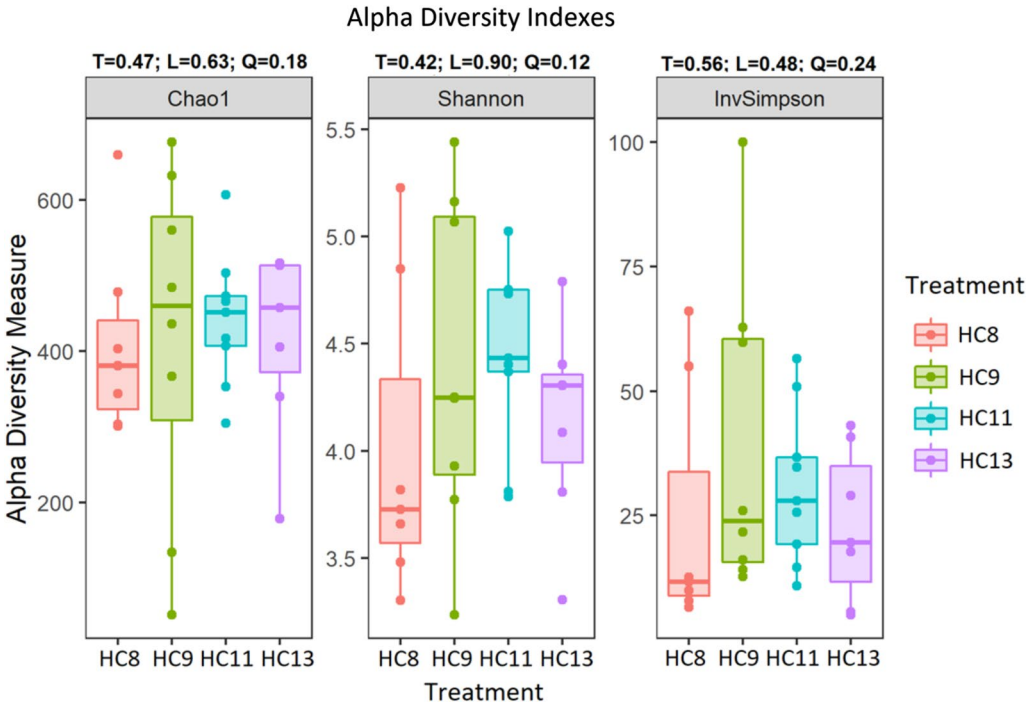

Fig. 1 Box plot showing alpha diversity indexes (Chao1, Shannon and InvSimpson) in faecal microbiota at day 17 of lactation of sows fed increasing dietary levels of hemicelluloses (HC13 = 13%, HC11 = 11%; HC9 = 9%; HC8 = 8%) during the lactation period. The presented *P*-values depict the overall sow dietary treatment (T), linear (L) and quadratic (Q) effects

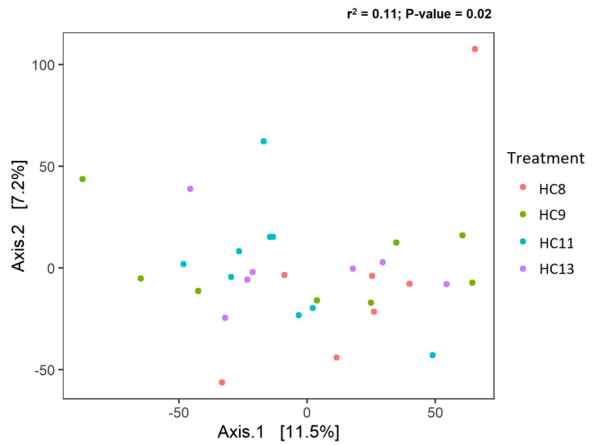

Fig. 2 Principal coordinate analysis plot (PCoA) using an Euclidean distance matrix at the amplicon sequence variant level in faecal microbiota at day 17 of lactation of sows fed increasing levels of hemicelluloses (HC13 = 13%, HC11 = 11%; HC9 = 9%; HC8 = 8%) during the lactation period. Axis 1 and Axis 2, respectively, explained 11.5% and 7.2% of the variance of the abundance of gut microbiota at the amplicon sequence variant level. The present r-square (r^2) and *P*-value depict the overall sow dietary treatment effect

Sutterella, Terrisporobacter, and *Turicibacter* were more abundant (*P*-adj < 0.05) in HC8 compared with HC9, HC11 and HC13 (Table 3).

Volatile fatty acid profile and microbiota in piglet faeces

There were no significant interactions between maternal dietary treatment and growth category for total VFA concentration, VFA profile and microbial profile. Neither the total VFA concentration nor the proportion of each VFA in the piglet's faeces were affected by the increase in HC levels in the maternal diet (Table 4). Similarly, the alpha- and beta-diversities (Figs. 3 and 4, respectively) were not affected by the increase in HC levels in the maternal diet.

However, the comparison of HC8 with HC9, HC11 and HC13 groups revealed five common genera that differed in piglet faeces: *Catenibacterium*, *Lachnospiraceae_CAG-56*, *Lachnospiraceae_UCG-002* and *Succinivibrio* were less abundant (*P*-adj < 0.05), while *Paludibacteraceae*_H1 was more abundant (*P*-adj < 0.05) in the faeces of piglets raised by HC8 sows compared to those of piglets raised by HC9, HC11 and HC13 sows (Table 5).

Regardless of the maternal diet, besides a similar total VFA concentration, the proportion of isobutyrate and isovalerate were 15% and 20% lower (*P* < 0.05), respectively, in the faeces of SG piglets than in those of FG piglets (Table 4). Besides no effects on the alpha- and beta-diversities, there were some taxonomical differences at the genus level between SG and FG piglets (Table 6). *Olsenella* was more abundant (*P*-adj < 0.05) and *Lachnospiraceae_XPB1014_group*, *Enterococcus* and

Table 3 Common taxonomic genera differing on day 17 of lactation in the faeces of sows fed with 8% hemicelluloses compared with 9%, 11% and 13% hemicelluloses during the lactation period

[†]Dietary treatment	HC8 vs								
	HC9			HC11		[¶]*P*-adj	HC13		
	[‡]log2FC	[§]lfcSE	[¶]*P*-adj	[‡]log2FC	[§]lfcSE		[‡]log2FC	[§]lfcSE	[¶]*P*-adj
Angelakisella	−21.93	4.373	< 0.01	−19.47	4.331	< 0.01	−30.00	4.868	< 0.01
Lachnospiraceae_UCG-008	−14.37	4.373	0.01	−27.48	4.314	< 0.01	−19.49	4.892	< 0.01
Erysipelotrichaceae_UCG-006	23.95	4.368	< 0.01	26.09	4.328	< 0.01	15.13	4.887	0.01
Faecalicoccus	23.74	4.367	< 0.01	25.21	4.328	< 0.01	16.07	4.887	0.01
Hungatella	23.95	4.368	< 0.01	26.09	4.328	< 0.01	15.13	4.887	0.01
Parabacteroides	3.02	1.016	0.02	3.74	0.999	< 0.01	3.20	1.129	0.03
Parasutterella	22.17	4.368	< 0.01	25.54	4.329	< 0.01	14.51	4.887	0.02
Pyramidobacter	30.34	4.367	< 0.01	32.76	4.328	< 0.01	18.32	4.887	< 0.01
Sutterella	24.20	4.368	< 0.01	26.87	4.328	< 0.01	16.03	4.887	0.01
Terrisporobacter	1.56	0.561	0.04	1.53	0.556	0.04	1.95	0.628	0.01
Turicibacter	2.46	0.883	0.04	3.51	0.875	< 0.01	3.66	0.988	< 0.01

[†] Dietary treatment: HC13 = Sow's lactation diet containing 13% hemicelluloses; HC11 = Sow's lactation diet containing 11% hemicelluloses; HC9 = Sow's lactation diet containing 9% hemicelluloses; HC8 = Sow's lactation diet containing 8% hemicelluloses

[‡] log2FC: log2 fold change is the effect size estimate

[§] lfcSE: standard error for the log2 fold change estimate

[¶] *P*-adj: *P*-value adjusted for multiple comparison using the false discovery rate method

Table 4 Volatile fatty acid (VFA) profile in the faeces of slow- and fast-growing piglets originating from sows fed increasing levels of hemicelluloses during the lactation period

[†]Dietary treatment	HC8		HC9		HC11		HC13		SEM	[§]*P*-values				
[‡]Growth category	SG	FG	SG	FG	SG	FG	SG	FG		T	G	T x G	*L*	*Q*
Total volatile fatty acids,µmol/g	46.1	47.4	51.7	40.2	41.5	58.8	38.6	42.1	6.70	0.13	0.55	0.12	0.93	0.46
Individual VFA, % of total VFAs														
Acetate	54.9	51.7	54.3	54.3	58.2	55.2	56.6	52.6	3.21	0.83	0.22	0.92	0.81	0.40
Propionate	19.7	19.6	19.8	15.6	17.4	15.2	16.3	17.9	2.01	0.29	0.32	0.39	0.56	0.09
Isobutyrate	3.7	4.8	3.9	4.5	4.5	4.7	4.3	5.3	0.35	0.41	< 0.01	0.36	0.30	0.17
Butyrate	12.5	12.8	12.6	15.2	11.3	14.2	13.0	13.2	1.81	0.75	0.19	0.76	0.96	0.32
Isovalerate	5.2	7.2	5.9	6.8	5.8	7.04	6.0	7.4	0.52	0.84	< 0.01	0.69	0.72	0.42
Valerate	4.0	3.9	3.4	3.7	2.8	3.6	3.9	3.6	0.42	0.94	0.58	0.49	0.57	0.82

[†] Dietary treatment: HC13 = Sow's lactation diet containing 13% hemicelluloses; HC11 = Sow's lactation diet containing 11% hemicelluloses; HC9 = Sow's lactation diet containing 9% hemicelluloses; HC8 = Sow's lactation diet containing 8% hemicelluloses

[‡] Growth category: SG = piglets displaying slow growth (average daily gain: 167 ± 10.1 g/d) from 0 to 16 days of age; FG = piglets displaying fast growth (average daily gain: 280 ± 10.1 g/d) from 0 to 16 days of age

[§] *P*-values: The presented *P*-values depict the overall sow dietary treatment (T), growth category (G), the interaction between sow dietary treatment and growth category (T x G), linear (L) and quadratic (Q) effects

Succinovibrio were less abundant (*P*-adj < 0.05) in SG compared with FG piglets.

Performances of the selected female piglets

There were no significant interactions between the maternal dietary treatment and the growth category for growth performances and occurrence of postweaning diarrhoea (Table 7).

Neither BW, ADG nor the occurrence of diarrhoea were affected by the increase in HC level in the maternal diet (Table 7). However, these measurements were affected ($P < 0.05$) by the growth category during the preweaning and postweaning periods.

Compared to FG piglets, SG piglets were lighter at birth (1.37 ± 0.055 kg *vs* 1.72 ± 0.055 kg), at 5 (1.91 ± 0.080 kg *vs* 2.68 ± 0.080 kg) and 16 (4.04 ± 0.193 kg *vs* 6.20 ± 0.193 kg) days of age, at weaning (5.75 ± 0.289 kg *vs* 8.61 ± 0.289 kg)

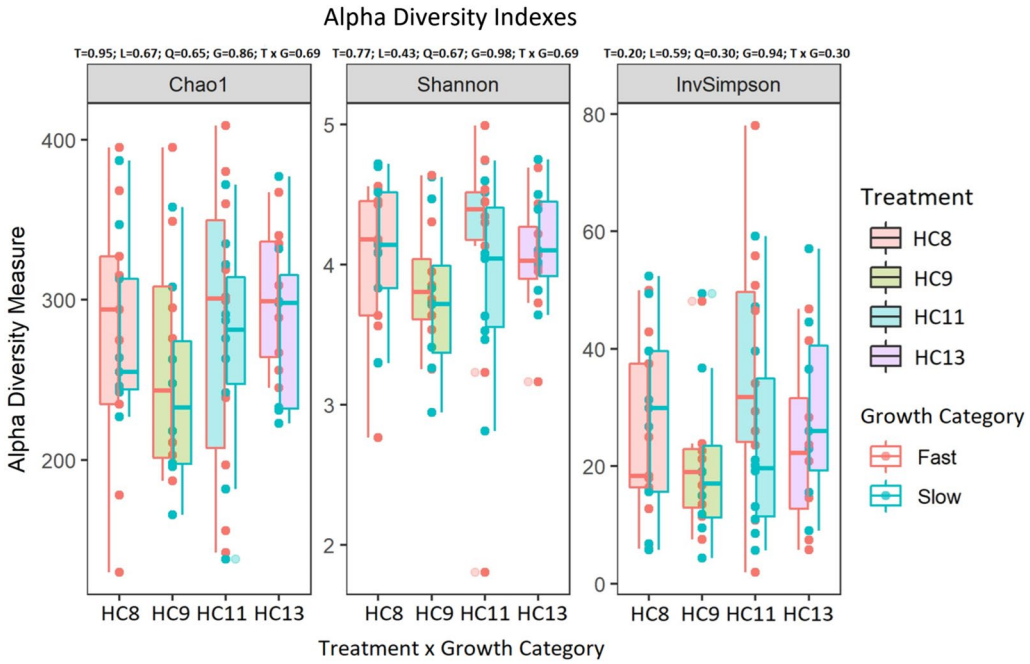

Fig. 3 Box plot showing alpha diversity indexes (Chao1, Shannon and InvSimpson) in faecal microbiota at day 16 of life of piglets displaying slow growth (average daily gain: 167 ± 10.1 g/d) and fast growth (average daily gain: 280 ± 10.1 g/d) from 0 to 16 days of age and originating from sows fed increasing levels of hemicelluloses (HC13 = 13%, HC11 = 11%; HC9 = 9%; HC8 = 8%) during the lactation period. The presented *P*-values depict the overall sow dietary treatment (T), growth category (G), the interaction between sow dietary treatment and growth category (T x G), linear (L) and quadratic (Q) effects

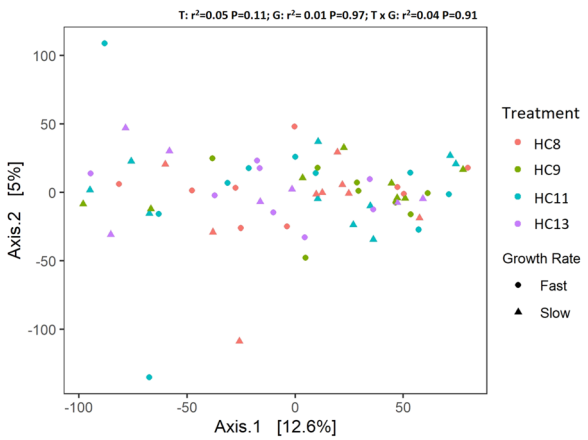

Fig. 4 Principal coordinate analysis plot (PCoA) using an Euclidean distance matrix at the amplicon sequence variant level in faecal microbiota at day 16 of life of piglets displaying slow growth (average daily gain: 167 ± 10.1 g/d) and fast growth (average daily gain: 280 ± 10.1 g/d) from 0 to 16 days of age and originating from sows fed increasing levels of hemicelluloses (HC13 = 13%, HC11 = 11%; HC9 = 9%; HC8 = 8%) during the lactation period. Axis 1 and Axis 2, respectively, explained 12.6% and 5% of the variance of the abundance of gut microbiota at the amplicon sequence variant level. The present r-square (r^2) and *P*-value depict the overall sow dietary treatment (T) growth category (G), the interaction between sow dietary treatment and growth category (T x G) effects

and at one week (6.06 ± 0.294 kg *vs* 8.63 ± 0.294 kg) and two weeks (7.49 ± 0.349 kg *vs* 10.00 ± 0.344 kg) postweaning. As a result, from birth to 5 days of age, from birth to 16 days of age and from birth to weaning, their ADGs were lower ($P < 0.05$) than those of FG piglets. Throughout the experiment, i.e. from birth to two weeks postweaning, SG piglets had a 54 g/d lower ($P < 0.05$) growth rate than FG piglets. Nonetheless, from weaning to the first week postweaning, SG piglets had a 43 g/d-greater ($P < 0.05$) ADG than FG piglets. The occurrence of diarrhoea was not affected by the growth category.

Discussion

Effect of increasing the level of hemicelluloses on sows' faecal apparent total tract digestibility, volatile fatty acid profile and microbial composition

In the present experiment, increasing the level of HCs in the sow's lactation diet increased the ATTD of GE, ADF and NDF. Indeed, DF can have an impact on the digestive process, even before reaching the large intestine [24]. This effect may be related to the type of DF included in the lactation diet and to their physiochemical properties, such as water solubility. Water solubility is defined as the capability of DF to be fully dispersed in water [35]. Regarding HCs, these compounds can be both soluble and insoluble [6]. However, Palumbo et al. [40],

Table 5 Common taxonomic genera differing on day 16 in the faeces of piglets originating from sows fed increasing levels of hemicelluloses during the lactation period

[†]Dietary treatment	HC8 vs								
	HC9			HC11			HC13		
	[‡]log2FC	[§]lfcSE	[¶]*P*-adj	[‡]log2FC	[§]lfcSE	[¶]*P*-adj	[‡]log2FC	[§]lfcSE	[¶]*P*-adj
Catenibacterium	−38.48	5.955	< 0.01	−44.99	5.660	< 0.01	−25.83	6.168	< 0.01
Lachnospiraceae_CAG-56	−15.65	4.566	0.01	−17.22	4.343	< 0.01	−17.91	4.700	< 0.01
Lachnospiraceae_UCG-002	−18.53	5.944	0.02	−21.77	5.653	< 0.01	−21.23	6.144	0.01
Succinivibrio	−45.72	5.930	< 0.01	−34.72	5.663	< 0.01	−27.45	6.166	< 0.01
Paludibacteraceae_H1	27.41	5.963	< 0.01	27.97	5.672	< 0.01	21.59	6.163	0.01

[†] Dietary treatment: HC13 = Sow's lactation diet containing 13% hemicelluloses; HC11 = Sow's lactation diet containing 11% hemicelluloses; HC9 = Sow's lactation diet containing 9% hemicelluloses; HC8 = Sow's lactation diet containing 8% hemicelluloses

[‡] log2FC: log2 fold change is the effect size estimate

[§] lfcSE: standard error for the log2 fold change estimate

[¶] *P*-adj: *P*-value adjusted for multiple comparison using the false discovery rate method

Table 6 Taxonomic differences at the genus level of piglets characterised by slow and fast growth

[†]Growth Category	[‡]log2FC	[§]lfcSE	[¶]*P*-adj
SG vs FG			
Lachnospiraceae_XPB1014_group	−28.00	6.302	< 0.01
Enterococcus	−6.92	1.774	< 0.01
Olsenella	19.74	3.561	< 0.01
Succinivibrio	−27.20	6.299	< 0.01

[†] Growth category: SG = piglets displaying slow growth (average daily gain: 167 ± 10.1 g/d) from 0 to 16 days of age; FG = piglets displaying fast growth (average daily gain: 280 ± 10.1 g/d) from 0 to 16 days of age

[‡] log2FC: log2 fold change is the effect size estimate

[§] lfcSE: standard error for the log2 fold change estimate

[¶] *P*-adj: *P*-value adjusted for multiple comparison using the false discovery rate method

using the same diets as in the present study, observed that increasing the level of HCs in a sow's lactation diet also increased the intake of soluble DF. Soluble DF, when compared with insoluble DF, can be easily fermented at the end of the small intestine [19]. Therefore, one can hypothesise that the greater soluble DF intake might be responsible for the observed effects on the digestibility of the ATTD of GE, ADF and NDF. Renteria-Flores, Johnston, Shurson, and Gallaher [45] similarly reported a positive correlation between the intake of soluble DF and energy digestibility, but no differences were observed in N digestibility. Conversely, the present study reported that increasing the level of HCs in the sow's lactation diet decreased the CP digestibility. In a growing pig model, it has been already reported that increasing the intake of soluble DF can decrease the CP digestibility [46]. This negative effect might be caused by the ability of certain sources of DFsuch as sugar beet pulp to form polysaccharides gel that increase the viscosity of the small intestine, reducing the absorbed amino acids [34]. However, to evaluate the latter parameter, it would have been better to evaluate ileal digestibility rather than ATTD because a certain proportion of amino acids could also be derived from bacterial origin [11]. Moreover, because increasing the level of HCs in sow's diet during lactation improved the degradation of ADF and NDF in the small intestine, it would have been reasonable to find a lower concentration of VFAs in the large intestine due mainly to a lower substrate of fermentation for cellulolytic bacteria in the large intestine [27]. Palumbo et al. [40] showed that increasing the level of HCs in a sow's lactation diet decreased the proportion of butyrate and the total concentration of VFAs in sow milk. As VFAs are absorbed from large intestine to the blood circulation, they might arrive to the mammary glands, where they can be used as source of energy for milk production [50]. Therefore, because of the results of the previous study, one can expect a lower proportion of butyrate and lower concentration of VFAs in the sow's hindgut when HCs level increased. Surprisingly, the present experiment showed that increasing the level of HCs in the sow's lactation diet had an opposite trend regarding the butyrate proportion, hence slightly affecting the total VFA concentration on day 3 of lactation. Nonetheless, attention must be paid when comparing these results because the time after the meal was not considered in either the aforementioned or current study. Indeed, this latter parameter might have affected the kinetics of fermentation in the large intestine and, hence, also the time interval that VFAs need to be transferred to the mammary glands [4]. Therefore, the mechanism underlying the passage of VFAs from the large intestine to the mammary glands should be better understood for further studies. In addition, increasing

Table 7 Growth performance and occurrence of diarrhoea in piglets characterised by slow and fast growth and born from sows fed with increasing levels of hemicelluloses during the lactation period

	HC8		HC9		HC11		HC13		SEM	§*P*-values				
	SG	FG	SG	FG	SG	FG	SG	FG		T	G	T x G	*L*	*Q*
Body weight, kg														
At birth	1.21	1.54	1.48	1.81	1.37	1.79	1.43	1.72	0.111	0.24	< 0.01	0.92	0.30	0.12
5 days postfarrowing	1.79	2.44	2.07	2.82	1.94	2.76	1.85	2.68	0.162	0.29	< 0.01	0.89	0.37	0.14
16 days postfarrowing	3.79	5.67	4.35	6.30	3.99	6.42	4.03	6.41	0.387	0.41	< 0.01	0.68	0.19	0.39
Weaning	5.71	8.20	5.84	8.48	5.69	9.20	5.76	8.57	0.580	0.58	< 0.01	0.65	0.48	0.41
1 week postweaning	5.90	8.12	6.36	8.42	6.23	9.22	5.76	8.76	0.590	0.52	< 0.01	0.65	0.31	0.50
2 week postweaning	7.44	9.70	7.53	9.54	7.51	10.64	7.48	10.13	0.693	0.62	< 0.01	0.76	0.44	0.79
ADG, g/d														
Birth-5 days postfarrowing	116	179	117	202	114	195	83	191	18.9	0.83	< 0.01	0.52	0.73	0.46
Birth-16 days postfarrowing	161	258	179	280	164	289	162	293	20.2	0.58	< 0.01	0.58	0.22	0.62
Birth- Weaning	171	252	174	266	169	289	169	265	20.5	0.56	< 0.01	0.66	0.50	0.34
Weaning-1 week postweaning	27	-11	74	-8	78	2	0	26	32.5	0.87	< 0.01	0.11	0.49	0.60
Weaning-2 weeks postweaning	124	107	120	75	132	106	82	114	30.2	0.77	0.38	0.40	0.44	0.78
Birth-2 week postweaning	154	201	154	197	156	224	153	211	17.0	0.60	< 0.01	0.77	0.44	0.78
Postweaning diarrhoea,%														
1 week postweaning	23.3	30.7	30.6	19.5	32.0	32.1	33.7	25.4	10.64	0.89	0.70	0.74	0.67	0.98
2 weeks postweaning	13.1	15.1	10.2	22.3	18.9	22.6	23.8	5.5	10.78	0.81	0.92	0.26	0.94	0.44
Days in diarrhoea, d														
1 week postweaning	1.77	2.22	2.17	1.42	2.30	2.30	2.43	1.93	0.690	0.88	0.70	0.80	0.63	0.92
2 weeks postweaning	1.22	1.45	0.89	1.76	1.46	1.66	2.01	0.64	0.638	0.97	1.00	0.32	0.92	0.72

† Dietary Treatment: HC13 = Sow's lactation diet containing 13% hemicelluloses; HC11 = Sow's lactation diet containing 11% hemicelluloses; HC9 = Sow's lactation diet containing 9% hemicelluloses; HC8 = Sow's lactation diet containing 8% hemicelluloses

‡ Growth categories: SG = piglets displaying slow growth (average daily gain: 167 ± 10.1 g/d) from 0 to 16 days of age; FG = piglets displaying fast growth (average daily gain: 280 ± 10.1 g/d) from 0 to 16 days of age

§ *P*-values: The presented *P*-values depict the overall sow dietary treatment (T), growth category (G), the interaction between sow dietary treatment and growth category (T x G), linear (L) and quadratic (Q) effects

the level of HCs in the sow's lactation diet increased the proportion of valerate on day 3 of lactation, while it decreased the proportion of propionate on day 17 in faeces. Zhao et al. [56] observed no correlations between the intake of HCs and any proportion of VFAs in growing pig faeces. However, in the present study, different patterns of fermentations were expected because of the better ability of sows to degrade DF [36]. A decreased level of propionate is in contrast to what was observed by Tan et al. [49], who reported that increasing the intake of soluble DF increased the level of propionate in the sow's faeces on day 3 of lactation. Those discrepancies could be explained by the different sources of DF included in the diet and by the sampling day because it is known that microbial composition during lactation is varying, hence changing its products of fermentation [23]. However, because different patterns of fermentation were found in sow faeces during lactation, it is plausible to expect different microbial composition. Interestingly, a positive correlation between genus *Parabacteroides* and propionate concentration has been reported in human faeces [32]. Therefore, the greater *Parabacteroides* abundance in the HC8 group may explain the greater propionate proportion in this group. A lower *Lachnospiraceae_UCG-008* abundance was reported in the HC8 group. Because the family of Lachnospiraceae has been shown to be positively correlated with butyrate production in the large intestine, it could explain the increase in butyrate proportion in the faeces when the level of HCs increased [33].

Effects of the maternal diet on piglet' faecal volatile fatty acid profile, microbial composition, growth performance and intestinal health

The effects of DF sources in sow gestation and lactation diet on the microbiota of the piglets are well known [23, 38]. However, to the best of our knowledge, the present study is the first one to investigate the effect of increasing the level of HCs in sow lactation diet on offspring microbiota. According to the present findings, increasing the level of HCs in the sow's lactation diet induced modifications in the faecal microbiota of the sow and their piglets before weaning. The maternal diet affected

certain genera in piglet faecal microbial composition. When HC8 diet was compared with increasing levels of HCs, a greater abundance of *Paludibacteraceae_H1* and a lower abundance of *Catenibacterium*, *Lachnospiraceae_CAG-56*, *Lachnospiraceae_UCG-002* and *Succinivibrio* were observed. Bacteria from the family of Paludibacteraceae and Catenibacterium are considered potential pathogens. Simultaneously, certain genera of the Succinovibrionaceae family like *Succinovibrio* and the Lachnospiraceae family like *Lachnospiraceae_CAG-56* and *Lachnospiraceae_UCG-002* are well known as fibre-degrading commensal bacteria [30]. As already discussed above, genera belonging to the Lachnospiraceae family are also butyrate-producing bacteria. A similar effect was also observed in the faecal microbiota of the sow, where a higher *Lachnospiraceae_UCG-008* abundance was reported when the level of HCs increased. Therefore, the faecal microbiota of the sow may act as a microbial reservoir for vertical transmission of this family of bacteria to the piglets [52]. By eating or being in contact with the faeces of the mother, piglets may have acquired the faecal microbiota of their mother [37]. However, these modifications, were neither associated with changes in piglet faecal butyrate proportion, nor in intestinal health. In addition, the maternal diet did not have any effect on the overall growth performance of the piglets before and after weaning, which is in agreement with the study of Palumbo et al. [40], in which, using the same diets, the pre- and postweaning growth were not affected by increasing the level of HCs in the sow's lactation diet.

Effects of the growth rate on piglet performance, faecal microbiota and fermentations

Modern sow breeds are characterised by hyperprolificacy that has caused wide variations in birthweight [43]. Piglets with a lower birthweight are more prone to diseases, slow growth and a higher risk of mortality compared with the heavier littermates [28]. In this context, Panzardi et al. [41] showed that piglets born below 1.5 kg have higher odds of a low bodyweight at weaning compared with their heavier littermates. In the present study, SG piglets with a mean birthweight of 1.4 kg were 2 kg lighter at weaning compared with their FG siblings with a mean birthweight of 1.8 kg. After weaning, the first week is crucial to achieve an adequate subsequent growth [51]. In the present study, during the first week postweaning, SG piglets showed a greater ADG compared with FG piglets. This phenomenon might be related to the fact that ADG during the suckling period is affected by milk intake rather than creep feed [18]. Therefore, it can be assumed that FG piglets that might have preferred to consume more milk than creep feed during the preweaning period are less prone to a switch to solid feed compared with their SG siblings [39]. However, no growth differences were observed in the postweaning period between the two growth categories, and the difference in BW was still up to 2.5 kg. Differences in the early establishment of gut microbiota between different birthweight categories and growth rates have been already investigated [16]. The current study showed that, regardless of the maternal diet, the growth rate slightly affected faecal microbiota before weaning. Genera within the family of Lachnospiraceae like *Lachnospiraceae_XPB1014_group* and Succinovibrionaceae like *Succinovibrio* were more abundant in FG piglets compared with SG piglets. Similarly, González-Solé et al. [17] reported a higher abundance of *Lachnospiraceae_XPB1014_group* genus in the faeces of FG piglets at 6 weeks post-weaning. The bacteria belonging to these genera have great abilities to degrade starches and produce VFAs [55]. In fact, these characteristics during the postweaning period might be the driver of a better feed conversion and, by that, also a better ADG until slaughter [53]. Of further interest, genera like *Enterococcus* have been widely associated with improved performance of piglets at weaning and during the growing period [54]. Moreover, bacteria belonging to this genus are also characterised by proteolytic activities [47]. Indeed, isobutyrate and isovalerate originate exclusively from valine and leucine fermentation by gut microbiota, respectively, and can serve as marker of protein fermentation in the large intestine [10]. Therefore, the greater abundance of *Enterococcus* in FG piglets' faeces may have increased the proportions of isobutyrate and isovalerate [14], which has improved the performance of FG piglets, which is in agreement with what was observed by Girard, Tretola and Bee [15].

In conclusion, feeding lactating sows with a similar DF level and increasing the level of HCs affects their faecal microbiota and VFA profile but had limited effects on SG and FG piglets' faecal microbiota and no impact on faecal VFA profile and growth performance. A better understanding of the relationship between gut microbial colonisation and growth during the suckling period would then enable solutions to be developed to homogenise pig weights.

Materials and methods

Diets and feeding

Four pelleted experimental diets, reported in Palumbo et al.'s study (2023) (Supplementary Table 1), were formulated to contain increased level of HCs: HC8 (HC: 8.0%), HC9 (HC: 9.4%), HC11 (HC: 11.4%) and HC13 (HC: 12.7%). The level of HCs was calculated as the difference between NDF and ADF. All the diets were isocaloric and isonitrogenous and 1% (10 g/kg) of Celite® was included as an indigestible marker. Sows were fed the experimental

diets from day 110 of gestation to the end of lactation. The daily feed allowance for each sow was calculated according to the current Swiss feeding recommendations for pigs to cover the sow's requirements based on their weight and litter size [1]. The initial feed allowance was set at 3 kg after farrowing and underwent a gradual increase of 0.3 kg/day for primiparous sows and 0.5 kg/day for multiparous sows, until reaching a plateau close to the ad libitum feeding after approximately 12 days of lactation. Diets were provided to the sows in three equal meals via a computerised feed delivery system (Schauer Spotmix, Schauer Agrotronic GmbH, Austria).

From one week prior weaning (18 ± 0.4 days of age) to 2 weeks postweaning (39 ± 0.4 days of age), the piglets had ad libitum access to creep feed and clean water. The creep feed contained 14 MJ/kg digestible energy, 5% crude fibre, 5.8% fat, 17% crude protein and 0.99% digestible lysine.

Animals, housing and experimental design

From 110 days of gestation until weaning, 35 Swiss Large White sows (7 primiparous and 28 multiparous), distributed across five farrowing series, were housed individually in farrowing crates with free access to water. They received daily moderate amounts of straw bedding. The environmental temperature was kept at 24 °C, and each crate had a total surface of 7.1 m^2 and was furnished with an electronic feeder (Schauer Spotmix, Schauer Agrotronic GmbH, Austria), nipple drinker, moderate amounts of straw bedding and a heated covered area for the piglets. Artificial light was provided from 08.00 to 17.00 h. On day 110 of gestation, 9, 8, 10 and 8 sows were allocated to HC8, HC9, HC11 and HC13 experimental feeding groups, respectively. The groups were balanced for body weight (BW) (286 ± 14.2 kg) and parity (3.4 ± 0.69). When the gestation time exceeded 115 and 116 days for primiparous and multiparous sows, respectively, sows received two intramuscular injections of 0.5 ml (0.25 g/ml) of cloprostenol (Estrumate®, MSD Animal Health GmbH, Luzern, Switzerland) at 24 h intervals to induce parturition. At birth, each piglet was individually weighed, and the temperature of the heating nests was settled at 40 °C and gradually decreasing each day by 0.5 °C until reaching 32 °C. Within the first 24 h following birth, each piglet received an individual ear tag, and an iron injection (Feridex®, AMAG Pharmaceuticals, Inc., Waltham, USA). Piglets weighing less than 800 g were excluded from the study. Within the initial 48 h of life, only male piglets were cross fostered to adjust the litter size to an average of 12 piglets per sow. In the second week of life, male piglets were castrated after anaesthesia. At 16 days of age, piglets from all litters were weighed to establish a baseline growth rate for each piglet. Within each litter, two female piglets showing the lowest and greatest growth rates, classified as SG and FG, were selected based on their average daily gain (ADG) from birth to 16 days. Only females were selected to reduce gender-based variability. After weaning at 25 ± 0.4 days, piglets remained in their respective crates for 2 weeks.

Measurements and sampling

Feed samples collected weekly were pooled for chemical composition analysis for each farrowing series. Faeces were sampled on day 110 of gestation before the morning meal, days 3 and 17 of lactation for all the sows involved in the experimental trial (N = 35) and at day 16 of age for the selected piglets (N = 70). They were sampled directly from the rectum using sterile gloves for sows and defecation in piglets was induced by stimulation with a cotton swab. A first aliquot of faeces was weighed and frozen at − 20 °C with 1 mL of phosphoric acid (25%, w/v) to measure the concentration of VFAs in both sow and piglet faecal samples at each time point. A second aliquot of faeces collected from sows on day 17 of lactation and from piglets at day 16 of age was immediately frozen at − 80 °C for subsequent bacterial DNA extraction. In addition, a third aliquot of faeces collected at the same time point for sows was weighed and stored at -20°C for determination of the ATTD of specific nutrients. The selected female piglets were individually weighed at birth, at 5 and 16 days of age, at weaning (25.7 ± 0.4 days of age) and at 1 and 2 weeks after weaning to calculate the individual ADG. From weaning to two weeks post-weaning, diarrhoea incidence was assessed daily by assigning a binary score of 0 (no diarrhoea) or 1 (diarrhoea). Then, the percentage of diarrhoea was calculated as the sum of these scores on a weekly basis.

Laboratory analysis

Chemical analysis

Feed samples were grounded to pass a 1 mm screen (Brabender rotary mill; Brabender GmbH and Co. KG, Duisburg, Germany) and then analysed for dry matter (DM) by heating at 105 °C for 3 h. Afterwards, incineration at 550 °C was performed to reach a stable mass and determine the ash content according to standard method (ISO 5984:2002; prepASH, Precisa Gravimetrics AG, Dietikon, Switzerland). The concentration of acid insoluble ashes was quantified gravimetrically (ISO 5985:2002) by incineration at 550 °C followed by digestion in hydrochloric acid. Nitrogen content was quantified using the Dumas method (ISO 16634–1:2008), and subsequently, crude protein (CP) content was calculated as 6.25 × N. The crude fibre content was determined gravimetrically (ISO 6865:2000) by acid and alkaline digestion, which was followed by the incineration of residual ashes using

a fibre analyser (Fibretherm Gerhardt FT-12, C. Gerhardt GmbH and Co. KG, Königswinter, Germany). The same fibre analyser was used to analyse NDF (ISO 16472:2006) and ADF (ISO 13906:2008) that were expressed without residual ash. Heat stable amylase and sodium sulphite were used to determine NDF. Total DF content was calculated as the sum of soluble, insoluble, and low-molecular-weight DF using AOAC Method 2011.25. Gross energy (GE) was determined by combustion in a calorimetric vessel under pure oxygen condition using an adiabatic bomb calorimeter (AC600 Semi-Automatic Calorimeter, Leco Corporation, USA) (ISO 9831:1998). After freeze-drying for determination of DM, faecal samples were analysed for quantification of acid insoluble ash, NDF, ADF, GE and CP following the procedures previously described for the chemical analysis of the diets.

Volatile fatty acid profile and bacterial DNA extraction

The VFA profile in the faeces was determined using high-performance liquid chromatography (HPLC, Ultimate 3000, Thermo Fisher Scientific, Reinach, Switzerland) following the method described by Htoo et al. [20]. Total bacterial DNA from sow and piglet faeces was isolated and extracted using a FastDNA SPIN kit (MP Biomedicals, Santa Ana, CA, USA). The concentration and purity of the isolated bacterial DNA were assessed using the NanoDrop spectrophotometer (Fisher Scientific, Schwerte, Germany) based on the absorbance ratios at 260/280 and 260/230. The V3–V4 region of the 16S rRNA gene (~460 bp) was amplified, and amplicons were produced using the universal primers Pro341F: 5'-TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG CCTACGGGNBGCASCAG-3' and Pro805R: 5'-GTC TCGTGGGCTCGGAGATGTGTATAAGAGACAGGA CTACNVGGGTATCTAATC C-3' [48] using the Platinum™ Taq DNA Polymerase High Fidelity (Thermo Fisher Scientific, Monza, Italy),the amplicons were then sequenced using the Illumina MiSeq platform 300×2bp. The libraries were prepared using the standard protocol for MiSeq Reagent Kit V3 and sequenced on the MiSeq platform (Illumina Inc., San Diego, Ca, USA).

Bioinformatic analysis

Amplicon sequence variants (ASVs) were generated using DADA2 1.14.0 [8] running on R 4.0.2,for the taxonomic assignment, the Silva database release 138 [42] was used as a reference. Briefly, primers were trimmed to a consistent length: forward reads were truncated at position 290, and reverse reads were truncated at position 220 to remove low-quality sequences. Four sow faeces samples and one piglet faeces sample were consequently excluded from the analysis as they did not yield sufficient reads. Therefore, 31 subjects for the sows (7 HC8, 8 HC9, 9 HC11and 7 HC13) and 69 for the piglets (15 HC13, 20 HC11, 16 HC9, and 18 HC8/ 34 SG and 35 FG) were included in the analysis. The sequencing process produced 16′949′584 reads (with an average of 54′676) and identified 1′684 ASVs. In sow faeces samples, the identified ASVs belonged to 19 different phyla, mainly Firmicutes (77.72%) and Bacteroidetes (16.11%). At the family and genera levels, 70 families (Lactobacillaceae comprising 13.06% and Clostridiaceae 11.89%) and 178 genera (*Lactobacillus* 13.06% and *Clostridium_sensu_stricto_1* 10.89%) were identified. For piglet faeces samples, the identified ASVs were associated with 19 different phyla, where Firmicutes represented 59.42% and Bacteroidetes 28.71%. At the family and genera levels, 83 families, mainly Lactobacillaceae (17.43%) and Oscillospiraceae (11.49%) and 209 genera, mainly *Lactobacillus* (17.97%) and *Bacteroides* (8.79%) were identified.

Calculation and statistical analysis

The acid insoluble ash concentrations of the dietary treatments and of the faeces were used to calculate the ATTD by using the following equation from Jang et al. [21]:

$$ATTD_N = 100 - \left[100 \times \frac{IM\ in\ feed}{IM\ in\ faeces} \times \frac{N\ in\ faeces}{N\ in\ feed}\right]$$

where IM is the indigestible marker (Celite ®) and N is the nutrient of interest, that is, ADF, NDF, GE and CP. Both IM and N are expressed in g/kg.

All statistical analyses were carried out in R (version 4.0.2 for Windows). The NLME package was used for data related to the digestibility of the diets, the VFA profiles in sow and piglet faeces and the performances of the selected female piglets. The experimental unit was either the sow or the piglet. Linear regression models ('lm' function) were used to fit data related to days in diarrhoea, VFA profile in sow's faeces, and the digestibility of the diets. The statistical model for VFA profiles and the digestibility of the diets included the dietary treatment and the farrowing series as fixed effects. Regarding sow's faecal VFA profile, because faeces collected on day 110 were used as a baseline, day 110 was included as a covariate in the statistical model. The model for days in diarrhoea considered the maternal dietary treatment, the growth category, the interaction maternal dietary treatment×growth category, and the farrowing series. For data related to piglet performances and faecal VFA, linear mixed-effects models ('lme' function) were used with the same fixed affects as previously described and with the random effect of the sow. The percentage of diarrhoea was analysed using a generalized linear mixed

model with penalised quasi-likelihood ('glmmPQL' function). This model included the maternal dietary treatment, the growth category, the interaction maternal dietary treatment × growth category, the farrowing series, and the day as fixed effects, and the piglet as a random effect. The statistical analysis on alpha diversity, beta diversity and taxonomic composition were carried out using the phyloseq [31], Vegan [13] and DESeq2 [29] packages. For the alpha diversity, the Shannon, Simpson and Chao1 indices were calculated, and a Multifactorial ANOVA (MANOVA) model was fitted to test the differences between the treatments. For sows, the effect of the dietary treatment, the farrowing series and the parity were considered. For piglets, the following factors were included in the model: the sequencing depth, the maternal dietary treatment, the growth category, the interaction maternal dietary treatment × growth category, the farrowing series as fixed effects and the sow as random effect. For the beta diversity, sample abundance was normalised using variance stabilising transformation provided by DESeq2 package, and a principal coordinate analysis plot (PCoA) was performed. The Euclidian distance matrix was calculated, and the differences between the maternal dietary treatment and growth categories were tested using a nonparametric PERMANOVA (Adonis) model with 999 permutations. For the piglet and sow, the same factors as for the alpha diversity were included in the model. Pairwise contrast was made using the pairwise Adonis function provided by the pairwise Adonis R package [3]. In addition, to test the homogeneity of dispersion among them, a PERMDISP test was used [2]. The DESeq2 was used to aggregate the data at the genus level and test differences in taxonomic composition between the groups. The *P*-value (*P*) was adjusted for multiple comparison using the false discovery rate method (*P*-adj). As one of the main goals is to assess taxonomic differences between HC8 and HC9, HC11 and HC13, only common genera that differed in HC8 compared to groups HC9, HC11 and HC13 are presented. The remaining taxonomic differences between all the groups are presented in the Supplementary Table 2 for sows and in the Supplementary Table 3 for piglets. Orthogonal polynomial contrasts were implemented to evaluate the linear (*L*) or quadratic (*Q*) effects of increasing the HC level on the Shannon, Simpson and Chao1 indices of alpha diversity, the VFA profile in sow and piglet faeces, the digestibility of the diets and the performance of selected piglet. The results were considered significant at $P \leq 0.05$.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42523-024-00354-z.

Additional file1.

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Author contributions
The study design and substantial funding were secured by M.G. and G.B.. F.P. and M.G. conducted the animal experiment, recorded, processed, and validated the data. F.P. and F.C. performed the bioinformatics and statistical analysis. All authors provided oversight for the analyses, and collectively contributed to the drafting and critical review of the manuscript. All authors reviewed and approved the final version of the manuscript.

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Availability of data and materials
The sequence data have been submitted to the NCBI sequence reads archive (SRA) under accession number PRJNA1031820.

Declarations

Ethical approval
The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to and the appropriate ethical review committee approval has been received. The authors confirm that they have followed Swiss Guidelines for Animal Welfare and for the protection of animals used for scientific purposes. The Swiss Cantonal Committee for Animal Care and Use approved all procedures involving animals (approval number: 2019_25_FR).

Competing interest
The authors declare no competing interests.

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