Microbiability of meat quality and carcass composition traits in swine

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Research

Keywords: microbiome, microbiability, heritability, microbial diversity, meat quality and carcass composition traits

Posted Date: April 21st, 2020

DOI: https://doi.org/10.21203/rs.3.rs-22906/v1

Version of Record: A version of this preprint was published at Journal of Animal Breeding and Genetics on September 26th, 2020. See the published version at https://doi.org/10.1111/jbg.12504.

Abstract

Background

Swine gut microbiome constitutes a portion of the whole genome and has potential to affect different phenotypes. More recently, research is more directed towards association of gut microbiome and different traits in swine. However, the contribution of microbial composition to the phenotypic variation of meat quality and carcass composition traits in pigs has not been explored yet. The objectives of this study are to estimate the microbiabilities for different meat quality and carcass composition traits; to investigate the impact of intestinal microbiome on heritability estimates; to estimate the correlation between microbial diversity and meat quality and carcass composition traits; and to estimate the microbial correlation between the meat quality and carcass composition traits in a commercial swine population.

Results

The contribution of the microbiome to carcass composition and meat quality traits was prominent although it varied over time, increasing from weaning to off test for most traits. Microbiability estimates of carcass composition traits were greater than that of meat quality traits. Among all of the traits analyzed, belly weight had higher microbiability estimate (0.29 ± 0.04). Adding microbiome information did not affect the estimates of genomic heritability of meat quality traits but affected the estimates of carcass composition traits. Fat depth had greater decrease (10%) in genomic heritability. High microbial correlations were found among several traits. This suggested that genomic correlation was partially contributed by genetic similarity of microbiome composition.

Conclusions

Results indicate that better understanding of microbial composition could aid the improvement of complex traits, particularly the carcass composition traits in swine by inclusion of microbiome information in the genetic evaluation process.

Background

The mammalian gastrointestinal tract is a home of a diverse microbiota population which serve various biological functions of the host [1]. Gut microbiota has recently been the target of many research efforts resulting from the rapid development in molecular technologies and led to a vast influx of “omics” studies [2]. The importance of gut microbiota is widely accepted [3], with commensal bacteria often being called the “forgotten organ” of the host [4], impacting hosts in a multitude of ways. For example, microbial composition helps in promoting the gastrointestinal health through metabolites, postnatal development, degradation of short chain fatty acids and stimulation of immune system[5–7].

Gut microbiome constitutes a portion of the whole genome [8, 9] and has the potential to affect numerous biological activities that the hosts lack [10]. Different researchers reported that microbiome has considerable effect on human health and traits [11–13]. For example, differences in bacterial species diversity and gene counts between lean and obese individuals have been found [14]. The microbial diversity of intestine accounted for significant amount of phenotypic variation for any trait in human and should be accounted when assessing the heritability not only in human but also in plants and livestock [15]. In livestock, Difford et al. [16] termed “microbiability” as the proportion of total variance explained by microbiome for performance traits of dairy cattle. Difford et al. [17] reported the effect of microbiota variation in methane production in dairy cows while, Mach et al. [18] reported the impact of gut microbiome at early life on phenotypes of pig. Gut microbiome also has a significant impact on porcine fatness [19]. Camarinha-Silva et al. [20] reported the presence of a significant effect of microbial composition on daily gain, feed intake and feed conversion rate in swine. Until recently, selection of different traits in pigs has been done with the use of pedigree and genomic information, yet the advantage of incorporating microbial information in the genetic evaluation processes has not been assessed. Few studies have described the relationship of microbial diversity and host e.g. [21, 22], however these were mostly from a nutritional perspective.

Specifically, the contribution of microbial composition to the phenotypic variation of meat quality and carcass composition traits in pigs has yet to be explored and no studies to date have been conducted on the effect of microbial composition at different stages of production on growth and carcass composition. Therefore, the objectives of this study are to estimate the microbiabilities for different meat quality and carcass composition traits; to investigate the impact of intestinal microbiome on heritability estimates; to estimate the correlation between microbial diversity and meat quality and carcass composition traits; and to estimate the microbial correlation between the meat quality and carcass composition traits in a commercial swine population.

Methods

Due to technical limitations, the Methods section is only available as a download in the supplemental files section

Result And Discussions

Data summary, distribution of alpha diversities and variance contributed by each sample

Mean and standard deviation for each meat quality and carcass composition trait are provided in Table 1. There were 9 meat quality and 6 carcass composition traits. The number of individual samples with complete genotypic, phenotypic and microbiome information at each stage was 1,123, which was used for further analyses. The distribution of OTU at weaning, Mid-test and Off-test is given in Figure. 1A. Of a total 1,755 OTU, there were 1,580 OTU in common between weaning, Mid-test and Off-test. There

were 1,685 OTU in common between Mid-test and Off-test, while between weaning and Mid-test were 1,626 and between weaning and Off-test were 1590.

Alpha diversity is a measure of within-sample diversity. It measures the richness of species and is measured as the number of species in a sample of standard size [35]. Distribution of alpha diversity among weaning, Mid-test and Off-test is given in Fig. 1B. Mean alpha diversity at Off-test, Mid-test and Wean was 4.63 ± 0.01, 4.53 ± 0.01 and 3.85 ± 0.02 respectively. Results from Mann-Whitney tests showed that alpha diversity at all stages were different ($P < 0.001$) from each other. This was in accordance with similar studies in pigs and other organisms [1, 2, 24]. The increase in alpha diversity with age was similar to what previously found [3, 36–38]. The change in the diets in piglets from sow's milk to complete feed-based diet partially explains the shift in microbial diversity after weaning. Different researchers [1, 39] reported that change in the diet impacted significantly the microbiota composition in the gut. Piglets are exposed to a large number of stressors during weaning which triggered the physiological change in structure and function of intestine [2]. This change caused the microbial shift after weaning transition [40] and microbial succession continues until microbiota composition reaches to climax community [38] which consists of microbes that are stable in composition. Further higher granularity results on the characterization of the microbial composition in the individuals of the current study can be found in Lu et al [24].

Microbiability estimates

The proportion of variance explained by each random term for meat quality and carcass composition traits is presented in Fig. 2 and Fig. 3, respectively. The estimates of microbiability and variance components along with their respective standard errors are provided (see additional File 4). The variance component estimates from the model which contain only the microbiome information and pen are also provided. The results identified several traits with significant microbiability.

The microbiability of carcass composition traits were higher than those of meat quality traits. In all cases microbiabilities for both meat quality and carcass composition traits at weaning were negligible and ranged from zero for several traits to a maximum of 0.06 ± 0.03 (estimate ± SE) for CADG. Three of the 9 meat quality traits investigated showed significant microbiability at Mid-test, with estimates of 0.07 ± 0.02 for SMARB, 0.08 ± 0.03 for SFIRM and 0.10 ± 0.04 for SSF. At Off-test, 4 meat quality traits had significant microbiability, with estimates of 0.06 ± 0.02 for IMF, 0.09 ± 0.02 for MINA, 0.11 ± 0.04 for MINB and 0.13 ± 0.04 for SFIRM. For carcass composition traits, we found that 5 out of 6 traits were significantly affected by microbiome at Mid-test and Off-test. The microbiability of carcass composition traits at Mid-test ranged from 0.12 ± 0.04 for LOIN and FD to 0.20 ± 0.04 for BEL. The microbiability of carcass composition traits at Off-test ranged from 0.13 ± 0.05 for LOIN to 0.29 ± 0.05 for BEL. In our study, the microbiome did not contribute significantly to loin depth variability. In most of the cases microbiome at weaning did not contribute to trait variation, however, microbiome at Mid-test and Off-test contributed significantly to trait variation. This might have several causes including the sudden change of microbiome composition shortly after the diet switch occurring at weaning as well as other environmental factors like, stress. To our knowledge this is the first attempt to obtain microbiability estimates for meat

quality and carcass composition traits. We did not find any literature to compare the estimates with previous research. Our results suggest that later measures of microbial composition might be more informative for selection purposes, but further research would be needed to clarify this aspect.

Among meat quality traits, microbial variance explained a larger proportion of phenotypic variance than additive genetic for SFIRM and MINB at Off-test (Fig. 2). Among carcass composition traits, BEL, HAM, and CADG at Off-test had higher proportion of phenotypic variation explained by microbiome than by additive genetic (Fig. 3). These results indicated that a significant proportion of total variance is explained by the microbiome, in some cases larger than the additive genetics and that prediction for these traits could be improved by accounting for the effect of variability in gut microbiome composition. The variation in gut microbiome could be fitted as the systematic environmental effect in model.

In the current study we observed a decrease in genomic heritability for most of the carcass composition traits at Off-test when microbiome information was added. The decrease in heritability ranged from 1% for LD to about 10% for FD. At Mid-test, the decrease in heritability ranged from 0% for CADG, BEL, HAM and LOIN to 4% for FD. No change in genomic heritability were observed at weaning. The decrease in heritability for FD was similar to that found by Lu et al [24] for similar traits. He et al. [19] also reported the significant contribution of microbiome for porcine fatness. These results suggested that part of the resemblance among individuals captured by genetic effects in breeding values prediction, might be in fact a resemblance among microbial composition and genetic parameters might not be accurate.

In contrast, for most of the meat quality traits considered, the inclusion of microbial composition did not affect the estimates of genomic heritability, thus suggesting that at least for meat quality traits, gut microbial composition is mostly an environmental factor. The decrease in genomic heritability when we included the microbiome composition in the models was previously observed by Sandoval-Motta et al [15] who reported the possibility of overestimation of heritability values with the use of genetic similarities by kinship information. The authors also suggested that inclusion of genetic diversity of individual microbiome will most likely increase the accuracy of heritability of various traits. The heritability and microbiability estimation of daily gain, feed intake and feed conversion ratio in swine [20] and methane emission in cattle [17] strongly suggested a significant contribution of microbiome to the total variation in the complex phenotypes of livestock. In human, Richards et al [41] reported that host genes are affected by the microbiome composition. These previous studies agreed with our results. Our results also agreed with the concept of “hologenome” of evolution [42], where the animal or plant along with associated microorganisms are the unit of selection in evolution.

Correlation of meat quality and carcass composition traits with alpha diversity at different stages

Host genetics plays a major role in shaping the intestinal microbiota of mice and humans [43–45]. Different studies [24, 46, 47] reported the impact of host genetics on development of gut microbiota in pigs. So, the alpha diversities at weaning, Mid-test and Off-test were considered as separate phenotypic records and genetic correlations were estimated between different alpha diversities and other traits

measured. The results are presented in Table 2 suggesting very weak correlations for alpha_w for all traits measured. Weak correlations were estimated between meat quality traits and alpha_mid with the exception of MINA (-0.45 ± 0.19) where greater alpha diversity seems linked to a paler red color of meat given that MINA is related to the amount of myoglobin in muscle. We obtained weak correlations between alpha_mid and carcass composition traits except for CADG (-0.43 ± 0.19), suggesting that an increase in microbial diversity would decrease CADG. This was in contrast with general opinion that the diversity will increase the metabolite production from different microbiota [40, 48] and increase the weight of host. However, this was in agreement with what found by Lu et al [24]. Alpha diversity could be used as a potential indicator trait in CADG selection. In all cases correlations of alpha_off with growth, carcass and meat quality traits were weak (Table 2).

This study is the first to estimate the genetic and phenotypic correlation between alpha diversity, and carcass and meat quality traits. Our results suggested that diversity at weaning might not be an accurate predictor of growth, carcass and meat quality traits which agreed with Huttenhower et al [13]. Alpha diversity was reported to be associated with gut health of animal and associated with the normal physiology of host animals [2]. The major role could include the normal function of gut, enhance immune response and play active role in digestion and utilization of nutrients. Our results presented weak correlation in terms of magnitude and direction at different stages. So, for routine use of the alpha diversity as indicator trait, further investigation of alpha diversity after weaning of piglets is warranted.

Correlation among traits

In the discussion of correlation, we only focus on microbial correlations. Genomic correlations are only discussed if the genomic correlations changed due to inclusion of microbiome information in the model. The genomic correlations without inclusion of microbiome in the model are presented in additional file 5.

Correlations among meat quality and carcass composition traits at mid test

Overall there were 3 meat quality traits and 5 carcass composition traits having variance of microbiome composition greater than 3%. Microbial correlations among meat quality and carcass composition traits at Mid-test are presented in Table 3. Most of the microbial correlations were significant. Subjective marbling score was moderately positively correlated (0.46 ± 0.24) with FD. This suggested that shifting of microbiota for high marbled meat would results in higher fat depth. Shear force is the measure of tenderness. In this study, the microbial composition of SSF was highly negatively correlated with SMARB, SFIRM, FD, CADG, LOIN and BEL which ranged from − 0.93 ± 0.11 for SSF and SFIRM to -0.50 ± 0.25 for SSF and LOIN. High positive correlations of SFIRM were found with CADG, HAM, LOIN and BEL which ranged from 0.58 ± 0.26 between SFIRM and LOIN to 0.87 ± 0.16 between SFIRM and BEL. There were moderate to high correlations of microbial composition of FD with CADG, HAM, LOIN and BEL which ranged from 0.44 ± 0.21 between FD and LOIN to 0.74 ± 0.11 between FD and BEL. High positive correlations were found between CADG and HAM, LOIN and BEL. Belly weight was highly positively

correlated with HAM (0.96 ± 0.03) and LOIN (0.94 ± 0.06). We did not find any other estimates to compare our values with microbial correlation between meat quality and carcass composition traits.

Correlation between meat quality traits and carcass composition traits at off test

There were six meat quality traits and five carcass composition for which variance of microbiome composition was greater than 3%. The microbial and genomic correlations among meat quality traits at Off-test are presented in Table 4. pH had high positive microbial correlation (0.90 ± 0.25) with SCOL and SFIRM (0.73 ± 0.35). This is in partial agreement with results from Ratzke and Gore [49], that reported the specific bacteria which is responsible for building lactic acid in the muscle results in the anaerobic breakdown of glucose and glycogen, which eventually loosens the myofibril, thus scattering more light making the muscle pale [50]. Furthermore, increasing pH causes swelling of myofibrils [51] which ultimately makes the muscle firmer. High positive microbial correlation was found between IMF and SFIRM (0.91 ± 0.17), MINA (0.55 ± 0.28) and MINB (0.75 ± 0.27). This agrees with [52] who reported that gut bacteria involved in energy metabolism and intramuscular fat content in pig also regulate the muscle composition and muscle fibers. Higher microbial correlation of IMF with minolta color measurements and SFIRM indicated that microbial composition increasing IMF would make the muscle paler and firmer. High microbial correlation of MINA and MINB (0.78 ± 0.16) suggests that microbiota responsible for redness of meat also contribute to the yellowness in the meat. This agreed with Kim et al [53] who reported the positive correlation of yellowness and redness in the muscle of pig.

The microbial and genomic correlations among carcass composition traits at Off-test are presented in Table 5. The microbial correlation of carcass composition traits was highly and positively correlated to each other ranging from 0.55 ± 0.17 between FD and LOIN to 0.97 ± 0.02 between CADG and HAM. McCormack et al [22] reported a positive correlation between gut microbiota and feed efficiency in swine. Gut microbiota has considerable effect on feed intake, final body weight [47] and growth traits [54]. All these studies suggested that microbial composition has considerable effects on many carcass composition traits, with positive correlations between them. These high correlations indicated that all the traits could be simultaneously improved through the same microbial composition.

The microbial correlations for meat quality traits and carcass composition traits at Off-test are presented in Table 6. Intramuscular fat was highly correlated with FD (0.90 ± 0.14) and BEL (0.73 ± 0.18). Firmness score was positively correlated with BEL (0.50 ± 0.18). Moderate positive correlation was found between MINA and BEL (0.41 ± 0.21) and high positive correlation was found between MINA and FD (0.53 ± 0.18), and MINA and CADG (0.66 ± 0.17). Minolta b* had moderate positive correlation with FD (0.43 ± 0.19) and high positive correlation with CADG (0.58 ± 0.18): suggesting that increase in microbiota for lean meat and high daily gain of carcass would make the meat more yellowish.

Change in genomic correlation with the inclusion of microbiome information

In this study, we observed a decrease in genomic correlations among meat quality and carcass composition traits when microbiome information was included in the model. The genomic correlations without the inclusion of microbiome in model are provided in Additional file 5. At Mid-test, the decrease in genomic correlation ranged from 0% among majority of meat quality traits to 18% for BEL and LOIN. The genomic correlation of BEL with FD and HAM decreased by 5% and 16%, respectively. The genomic correlation of FD with SMARB and SSF decreased by 7% and 4%, respectively.

At Off-test, the genomic correlation between PH and SCOL (0.91 ± 0.29), SFIRM and IMF (0.36 ± 0.15), FD and CADG (0.27 ± 0.13), and BEL and HAM (0.58 ± 0.19) became non-significant with the inclusion of microbiome. Among carcass traits, the decrease in genomic correlation ranged from 1% between BEL and CADG to 30% between BEL and LOIN. The genomic correlation of BEL with FD, CADG with HAM, CADG with LOIN, FD with IMF, FD with MINB, BEL with IMF, and BEL with SFIRM decreased by 13%, 4%, 2%, 9%, 6%, 13% and 8%, respectively. Among meat quality and carcass traits, the decrease in genomic correlations ranged from 1% for FD and SFIRM to 9% for BEL and IMF. We observed a decrease in genomic correlations with the inclusion of microbiome, particularly of any other traits with fat related traits e.g. (BEL, FD, IMF). This could be due to the greater influence of gut microbiome on fat deposition. Furthermore, we observed that there was a decrease in genomic correlation for those traits which had higher microbial correlation. High microbial correlations among different traits suggested that genomic correlations among traits are partially contributed by the correlations among the gut microbiota composition. The covariance among microbiome for different traits might have contributed to the genetic covariance and hence the genomic correlation. We observed that the decrease in the genomic correlation was higher at Off-test than at Mid-test. This was due to high variability accounted by microbiome composition at Off-test in comparison to Mid-test.

This is the first study to evaluate the variance accounted by microbiome and estimate the microbial correlations for meat quality and carcass traits in swine. So, we have explored the model sequentially, first with inclusion of genomic information and then addition of microbiome information at different stages. Variance component estimates of different random effects with inclusion of interaction of genotype-by-microbiome in the model is recommended for future studies.

Conclusions

This study was conducted on crossbred pigs to investigate the impact of intestinal microbiota through different stages (weaning, Mid-test and Off-test) of production. To our knowledge this study is the first attempt to investigate the impact of microbiome on the meat quality and carcass composition traits at a large scale in swine. The contribution of microbiome to all traits was significant although it varied over time with an increase from weaning to Off-test for most of the traits. Adding microbiome information did not affect the estimates of genomic heritability of meat quality traits but changed the estimate of carcass composition traits suggesting that portion of genomic variance was contributed by gut microbiome. Alpha diversity at Mid-test was strongly correlated with carcass average daily gain and minolta a* color score. A better understanding of microbial composition could aid the improvement of complex traits,

particularly the carcass composition traits in swine by inclusion of microbiome information in the genetic evaluation process. High microbial correlations were found among different traits, particularly with traits related to fat deposition. Adding microbiome information decreased the genomic correlation for those traits which had higher microbial correlation suggesting that portion of genomic correlation was due to genetic covariance among microbiome composition affecting those traits. Based on the results we can conclude that microbial composition could be altered to improve a given trait. To obtain optimum microbial composition, manipulation of gut microbiota could be done using specific bacterial composition as probiotics or increasing the relative abundance through prebiotics, feed additives supplements and fecal microbiota transplantation could also be done. The estimated parameters provide a reference value for further research on gut microbial contribution to complex phenotypes in pigs. These results may lead to establish a newer approach of genetic evaluation process through the addition of gut microbial information.

Abbreviations

Wean
Weaning
Mid-test
15 weeks post weaning
Off-test
End of test
IMF
Intramuscular far
MINA
Minolta a*
MINB
Minolta b*
MINL
Minolta L*
SCOL
Subjective color score
SMARB
Subjective marbling score
SFIRM
Subjective firmness score
SSF
Shearing force
BEL
Belly weight
HAM

Ham weight
LOIN
Loin weight
FD
Fat depth
LD
Loin depth
CADG
Carcass average daily gain
alpha_w
Alpha diversity at weaning
alpha_mid
Alpha diversity at mid-test
alpha_off
Alpha diversity at off-test
OTU
Operational taxonomic units

Declarations

Ethics approval and consent to participate

Animal welfare approval was not needed for this study since all data came from animals raised in a commercial setting by The Maschhoffs, LLC (Carlyle, IL, USA). All pigs were harvested in commercial facilities under the supervision of USDA Food Safety and Inspection Service.

Consent for publication

Not applicable

Availability of data and materials

The data that support the findings of this study are available from MATATU, but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. Data are however available from the authors upon reasonable request and with permission of MATATU.

Competing interests

The authors declare that they have no competing interests.

Funding

This study is a part of the project “Re-defining growth efficiency accounting for the interaction between host genome and commensal gut bacteria” funded by The National Pork Board Association and part of the project “From Host to Guest and back” funded by The Maschhoffs, LLC and North Carolina State University.

Author’s contribution

PK carried all analyses, as well as interpreted the results and drafted the manuscripts. CS and JF were involved in designing the experiment and helped in interpretation of results. CM and FT were involved in designing the experiment and providing consultation for the analyses. All co-authors provided feedback for the manuscript. All authors have read and approved the final manuscript.

Acknowledgements

We would like to thank Jessica Hoisington-Lopez from the DNA sequencing Innovation Lab at the Center for Genome Sciences and Systems Biology at Washington University in St. Loius for her sequencing expertise and Nicholas S. Grohmann for phenotype and sample collection.

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Tables

Table 1. Descriptive statistics of carcass composition and meat quality traits: acronym, means, standard deviation (SD) values.

Traits	Acronym	Mean	SD
Carcass composition traits			
Loin depth, mm	LD	67.99	7.21
Back fat depth, mm	FD	22.07	5.24
Carcass average daily gain, g/day	CADG	552.90	73.93
Ham weight, kg	HAM	25.19	2.34
Loin Weight, kg	LOIN	20.01	1.88
Belly weight, kg	BEL	15.88	2.55
Meat quality			
Intramuscular fat, %	IMF	2.71	1.01
Minolta a*	MINA	3.77	1.16
Minolta b*	MINB	-0.16	0.87
Minolta L*	MINL	45.37	5.76
Ultimate pH	PH	5.64	0.22
Subjective color	SCOL	2.72	0.57
Subjective marbling	SMARB	3.10	0.91
Subjective firmness	SFIRM	3.05	1.04
Slice shear force, N	SSF	156.96	41.99

Table 2. Genetic correlation of carcass composition traits and meat quality traits with alpha diversity at weaning (alpha_w), week 15 (alpha_mid) and end of test (alpha_off).

Traits[1]	alpha_w	alpha_mid	alpha_off
Carcass composition			
FD	0.54±0.39	-0.22±0.15	-0.30±0.19
LD	0.16±0.48	-0.15±0.24	-0.30±0.29
CADG	0.36±0.39	**-0.43±0.19**	-0.25±0.24
HAM	-0.13±0.50	-0.13±0.22	0.04±0.26
LOIN	-0.65±0.60	0.16±0.20	0.13±0.24
BEL	0.02±0.43	-0.31±0.20	-0.41±0.23
Meat quality			
SCOL	0.31±0.44	-0.09±0.17	-0.25±0.21
SFIRM	0.50±0.42	-0.21±0.22	-0.22±0.27
SSF	0.01±0.39	0.11±0.18	0.10±0.22
IMF	0.14±0.32	-0.13±0.15	0.001±0.18
SMARB	0.17±0.37	-0.15±0.18	-0.21±0.21
MINA	0.78±0.76	**-0.45±0.19**	-0.30±0.25
MINB	0.66±0.48	-0.03±0.27	0.50±0.31
MINL	-0.22±0.46	0.05±0.19	0.14±0.23
PH	0.88±0.60	0.007±0.33	0.43±0.39

[1]LD = Loin depth; FD = Fat depth, CADG = Carcass average daily gain, HAM = Ham weight; LOIN = Loin weight; BEL = Belly weight, SCOL = Subjective color score, SFIRM = Subjective firmness score, SSF = Slice shear force, IMF = Intramuscular fat percent, SMARB = Subjective marbling score, MINA = Minolta a*, MINB = Minolta b*, MINL = Minolta L*, PH = Ultimate pH;

Numbers in bold are significant

Table 3. Estimates of microbial correlation (above diagonal) and genomic correlation (below diagonal) at Mid-test among meat quality and carcass composition traits.

	[1]SMARB	SFIRM	SSF	FD	CADG	HAM	LOIN	BEL
RB		0.39±0.33	**-0.72±0.28**	**0.46±0.24**	-0.21±0.28	-0.27±0.29	-0.34±0.32	-0.02±0.26
M	**0.42±0.18**		**-0.93±0.11**	NC[2]	**0.86±0.17**	**0.62±0.24**	**0.58±0.26**	**0.87±0.16**
	0.08±0.16	-0.23±0.21		**-0.70±0.21**	**-0.68±0.22**	-0.45±0.25	**-0.50±0.25**	**-0.55±0.24**
	0.22±0.11	NC	**-0.44±0.13**		**0.68±0.15**	**0.50±0.19**	**0.44±0.21**	**0.74±0.11**
	0.02±0.17	0.03±0.23	0.19±0.18	0.21±0.15		**0.98±0.02**	**0.95±0.03**	**0.98±0.01**
	-0.13±0.18	0.11±0.24	0.27±0.20	0.01±0.15	**0.67±0.11**		NE[3]	**0.96±0.03**
	-0.09±0.17	0.10±0.23	0.11±0.18	-0.14±0.15	**0.69±0.09**	**0.53±0.11**		**0.94±0.06**
	0.31±0.17	0.35±0.23	0.18±0.15	**0.57±0.11**	**0.79±0.06**	**0.42±0.17**	**0.42±0.15**	

[1]SMARB = Subjective marbling score, SFIRM = Subjective firmness score, SSF = Slice shear force, FD = Fat depth, CADG = Carcass average daily gain, HAM = Ham weight; LOIN = Loin weight; BEL = Belly weight;

[2]Not Converged; [3]Not estimable; Numbers in bold are significant

Table 4. Estimates of microbial correlation (above diagonal) and genomic correlation (below diagonal) at Off-test among meat quality traits.

	[1]SCOL	IMF	SFIRM	MINA	MINB	PH
SCOL		-0.28±0.57	0.07±0.31	0.29±0.44	-0.26±0.39	**0.90±0.25**
IMF	-0.22±0.13		**0.91±0.17**	**0.55±0.28**	**0.75±0.27**	0.10±0.47
SFIRM	0.18±0.19	0.29±0.17		0.26±0.27	0.12±0.26	**0.73±0.35**
MINA	**0.45±0.16**	**0.29±0.14**	-0.53±0.28		**0.78±0.16**	0.33±0.36
MINB	**-0.94±0.22**	**0.78±0.16**	-0.03±0.32	-0.10±0.27		0.38±0.38
PH	0.13±0.50	-0.18±0.25	0.44±0.36	-0.04±0.33	-0.47±0.42	

[1]SCOL = Subjective color score, SFIRM = Subjective firmness score, IMF = Intramuscular fat percent, MINA = Minolta a*, MINB = Minolta b*, PH = Ultimate pH;

Numbers in bold are significant.

Table 5. Estimates of microbial correlation (above diagonal) and genomic correlation (below diagonal) at Off-test among carcass composition traits.

	[1]FD	CADG	HAM	LOIN	BEL
FD		**0.71±0.11**	**0.59±0.16**	**0.55±0.17**	**0.94±0.05**
CADG	0.14±0.15		**0.97±0.02**	**0.91±0.05**	**0.94±0.03**
HAM	-0.10±0.17	**0.63±0.13**		[2]NE	**0.87±0.06**
LOIN	-0.13±0.15	**0.67±0.10**	**0.54±0.19**		**0.82±0.08**
BEL	**0.49±0.13**	**0.78±0.07**	0.34±0.19	**0.40±0.16**	

[1]FD = Fat depth, CADG = Carcass average daily gain, HAM = Ham weight; LOIN = Loin weight; BEL = Belly weight;

[2]Non estimable; Numbers in bold are significant.

Table 6. Estimates of microbial correlation between meat quality traits and carcass composition traits at Off test.

	[1]FD	CADG	HAM	LOIN	BEL
SCOL	-0.29±0.37	-0.09±0.35	0.16±0.38	-0.25±0.35	-0.32±0.37
IMF	**0.90±0.14**	0.43±0.33	0.29±0.27	0.21±0.30	**0.73±0.18**
SFIRM	NE[2]	0.31±0.19	0.18±0.24	-0.01±0.20	**0.50±0.18**
MINA	**0.53±0.18**	**0.66±0.17**	0.11±0.27	0.08±0.30	**0.41±0.21**
MINB	**0.43±0.19**	**0.58±0.18**	0.12±0.25	-0.13±0.28	0.35±0.20
PH	0.17±0.31	0.27±0.35	NC[3]	NC	0.11±0.32

[1]FD = Fat depth, CADG = Carcass average daily gain, HAM = Ham weight, LOIN = Loin weight, BEL = Belly weight;

[2]Non estimable; [3]Not converged; Numbers in bold are significant.

Figures

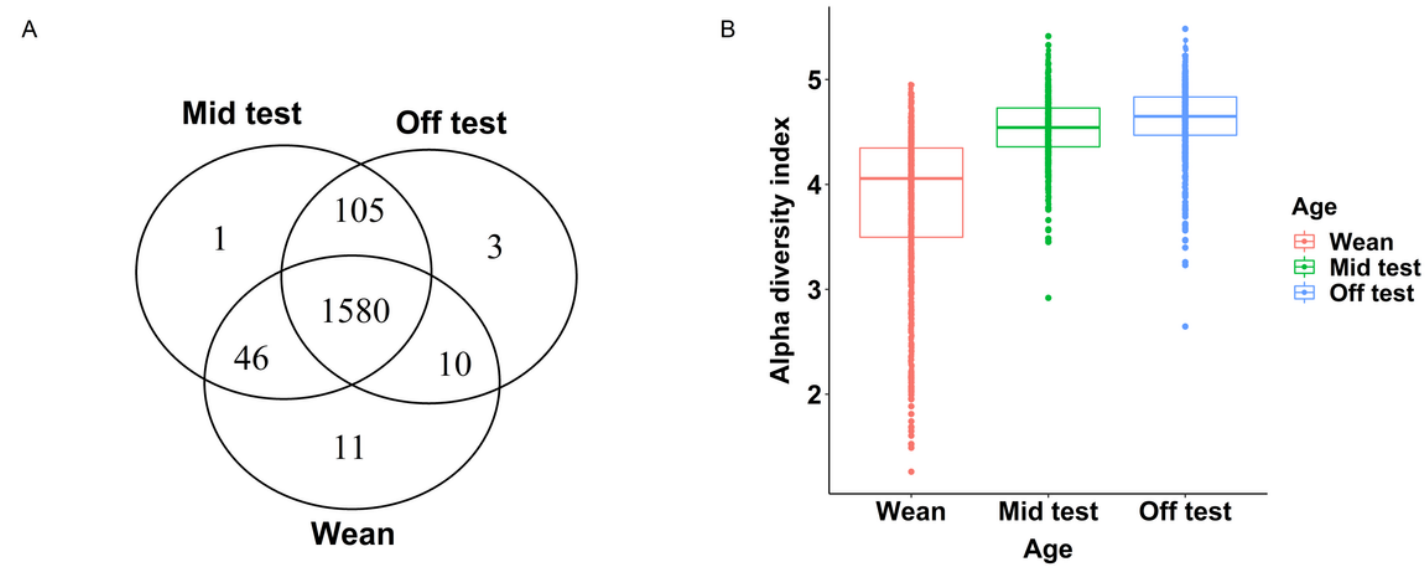

Figure 1

(A) Venn diagram with the numbers of common operational taxonomic units (OTU) among weaning, mid test and off test. (B) Distribution of alpha diversity index among weaning, mid test and off test. X- axis represents the different age group and Y-axis represent the alpha diversity index of each sample for each group.

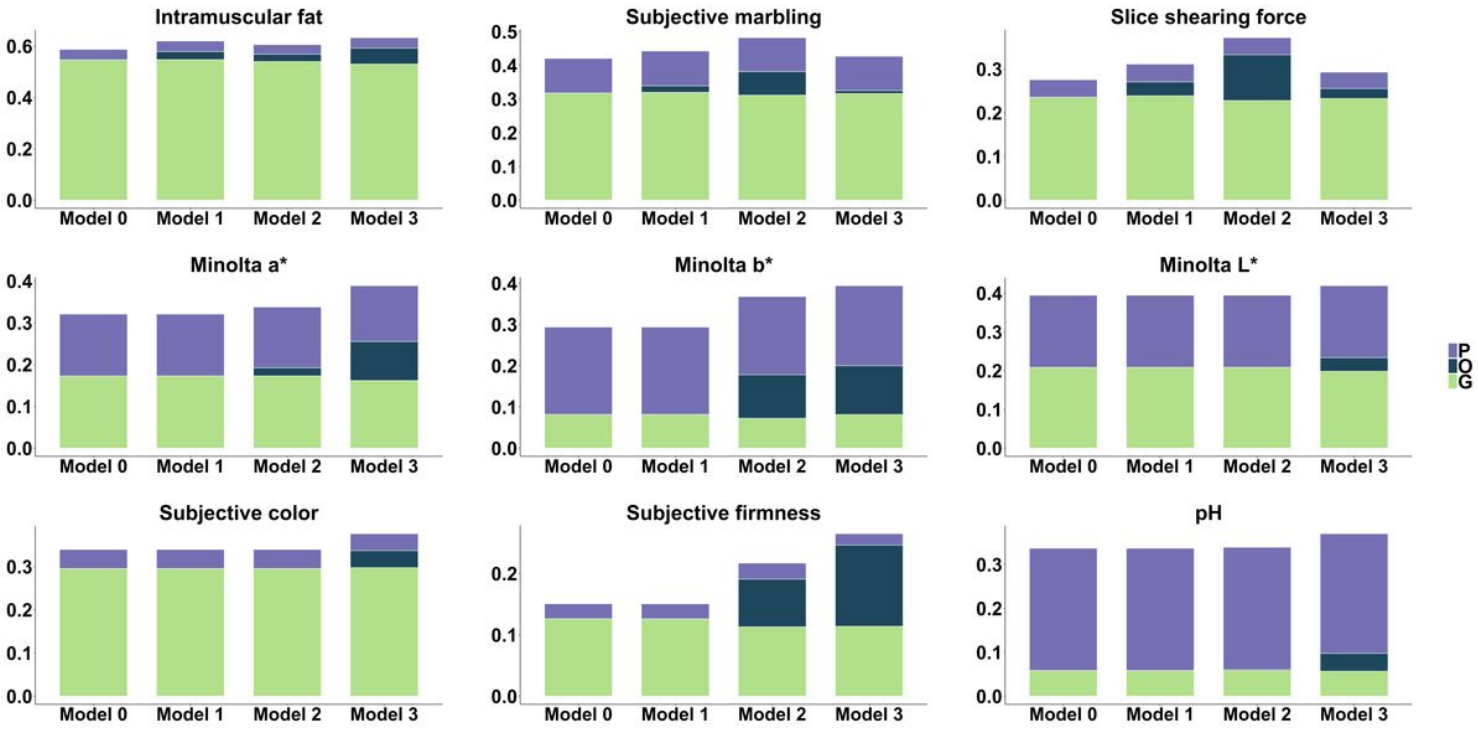

Figure 2

Proportion of variance explained by microbiome relationship matrix (O), genomic relationship matrix (G) and pen (P) for meat quality traits. Model 0 contains G matrix and pen effect as random effect, Model 1,

Model 2 and Model 3 contains O matrix at weaning, Mid-test and Off-test in addition to G matrix and pen effect.

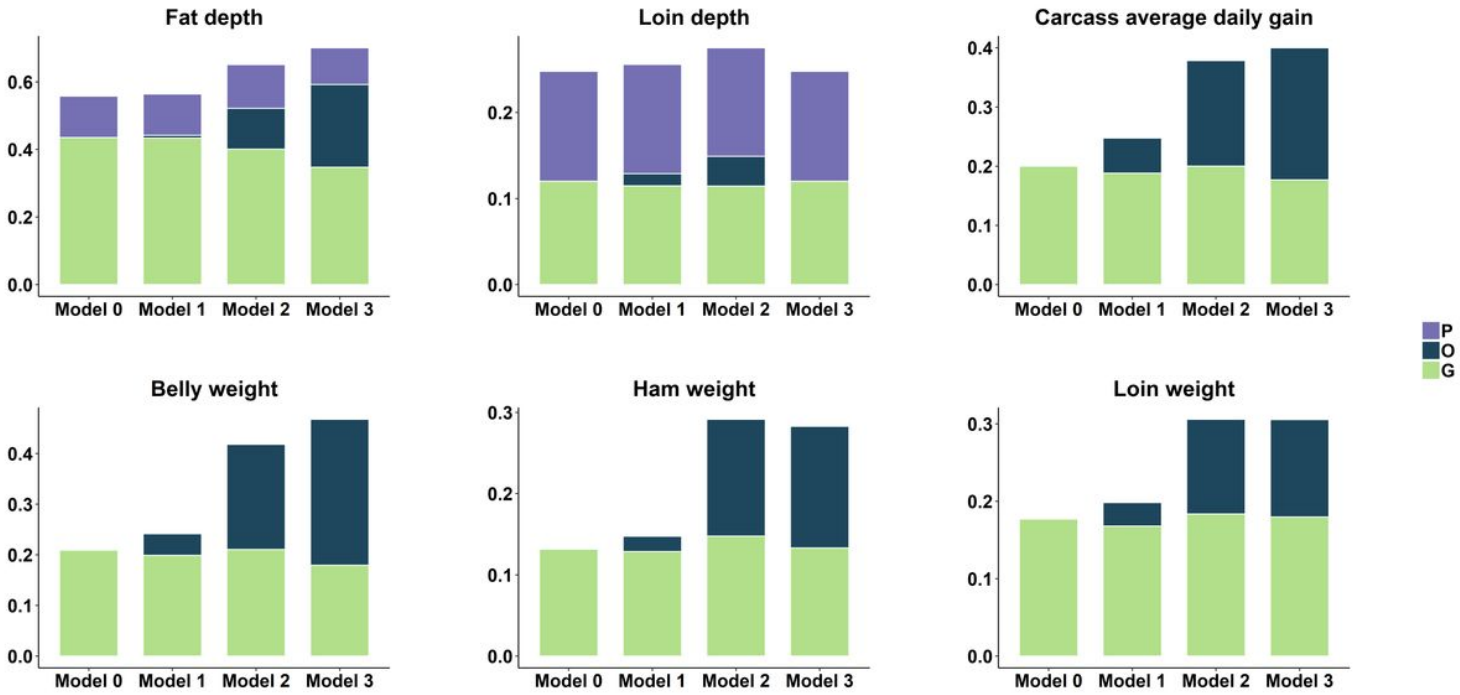

Figure 3

Proportion of variance explained by microbiome relationship matrix (O), genomic relationship matrix (G) and pen (P) for carcass composition traits. Model 0 contains G matrix and pen effect as random effect, Model 1, Model 2 and Model 3 contains O matrix at weaning, Mid-test and Off-test in addition to G matrix and pen effect.

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