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The gut microbiota as a predictor of feed efficiency and feeding behavior in Iberian pigs

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Abstract

In recent years, the production system of Iberian pigs has been significantly intensified, with new technologies playing a crucial role in recording traits such as feed efficiency. These advances also allow the study of different traits related to feeding behavior. In addition, the composition of the gut microbiota has previously been associated with animal health and performance. This study evaluated the relationship between the host genetics, the gut microbiota, and traits of feed efficiency and feeding behavior up to 180 d of age. First, we quantified the phenotypic variance explained by the host genetics and the gut microbiota using fecal samples collected at 2-time points: 140 and 180 d. Second, we evaluated whether the microbiota at 140 d could serve as an early predictor of phenotypes measured at 180 d. Identifying accurate early predictors may serve as a valuable tool to support future strategies aimed at reducing testing duration in the nucleus of selection. Our results indicate that microbiota accounts for a low to moderate proportion of total phenotypic variance and improves model fit for feed efficiency traits when included. Furthermore, the inclusion of microbiota data at 140 d improved the prediction of feed efficiency traits at 180 d but did not improve predictions for feeding behavior. This study provides valuable insights into variance component estimation for feed efficiency and feeding behavior traits in Iberian pigs fed with automatic feeders and highlights new opportunities to explore the role of microbiota in feed efficiency.

Lay Summary

In modern pig farming, new technologies are helping farmers better understand how pigs grow and use their feed. One key area of interest is feed efficiency, which considers the animal's ability to convert feed into body weight. Another important factor is feeding behavior, which has been linked to feed efficiency. In addition, current research is focusing on the gut microbiota to assess how it influences animal health and growth. Here, we explored how genetics and gut microbiota contribute to differences in feed efficiency and feeding behavior in Iberian pigs. We analyzed gut microbiota collected from fecal samples at 140 and 180 d of age to see how much variation in feed efficiency and feeding behavior could be explained by genetics and microbiota. Our results show that gut bacteria play a moderate role in shaping both feed efficiency and feeding behavior. These findings suggest that gut bacteria may be a useful tool for improving feed efficiency in pigs. However, microbiota did not significantly improve predictions for feeding behavior. This research opens new opportunities to better understand how gut microbiota and genetics impact animal growth, behavior, and overall farm efficiency.

Key words: cross-validation, feeding behavior, feed efficiency, gut microbiota, Iberian pigs, prediction

Abbreviations: ADFI, average daily feed intake; ADG, average daily gain; ASV, amplicon sequence variant; $BM^{0.6}$, body weight raised to 0.6; BW180,body weight at 180 d; CLR, centered log-ratio transformation; DIC, deviance information criterion; EBV, estimated breeding value; EMV, estimated microbiota value; FCR, feed conversion ratio; FPV, feed intake per visit; FR, feeding rate; h^2, heritability; m^2, microbiability; NVD, number of visits per day; RFI, residual feed intake; TPV, time spent in feeding per day; y^*, adjusted phenotype

Introduction

The Iberian pig is one of the most important livestock breeds in Spain. This breed is characterized by the high quality of its cured products (Mesías et al., 2009). Iberian pigs have traditionally been reared under extensive conditions in the southwest of the Iberian Peninsula, where they are adapted to pasture ecosystems known as *Dehesas* (Lopez-Bote, 1998). However, in recent years, Iberian production has been intensified to increase feed efficiency and reduce the length of the growing period (Nieto et al., 2019). Feed efficiency is a key factor in the profitability of pig farms, as feed costs account for more than 60% of total costs (Patience et al., 2015). Measuring feed efficiency was a challenge in the past, mainly because of the difficulty in measuring individual feed intake. However, with the advent of electronic feeders, it is now possible to assess feed efficiency and feeding behavior traits

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for breeding and management purposes (Chen et al., 2009; Labroue et al., 1999; Lu et al., 2017; Núñez et al., 2023; Piles et al., 2024; Casto-Rebollo et al., 2025).

The pig gut microbiota has been linked to different traits, including immunity (Calle-García et al., 2023; Ramayo-Caldas et al., 2021), meat quality (Sebastià et al., 2023; Khanal et al., 2020), resilience (Mancin et al., 2024), and feed efficiency (Camarinha-Silva et al., 2017; Bergamaschi et al., 2020; Aliakbari et al., 2021; Déru et al., 2022). Differences in gut microbiota composition have been found between pigs selected for high and low feed efficiency (Aliakbari et al., 2021). Furthermore, the pig gut microbiota has been used as a potential predictor of phenotypes (Camarinha-Silva et al., 2017; Aliakbari et al., 2022; Calle-García et al., 2023; Déru et al., 2024). The proportion of the phenotypic variance explained by the microbiota, namely microbiability (Difford et al., 2016), was reported to be around 0.20 for feed efficiency traits (Camarinha-Silva et al., 2017; Aliakbari et al., 2021) and feeding behavior traits (He et al., 2022). Both genetic and microbiota information can be included in the traditional selection models to explore their relationship with economically relevant phenotypes in pigs (Camarinha-Silva et al., 2017; Crespo-Piazuelo et al., 2018; Bergamaschi et al., 2020; Aliakbari et al., 2021; Nuñez et al., 2025).

However, no studies to date have investigated the relationship between the gut microbiota and phenotypes of growth, feed efficiency and feeding behaviour in Iberian pigs. This breed differs significantly from conventional white pigs in terms of productive traits, which may also be linked to differences in gut microbiota composition. Iberian pigs exhibit lower feed efficiency and are subject to specific regulations, which contribute to longer fattening periods and older animals with greater body weights at slaughter (around 150 kg), in contrast to white pigs, which are typically slaughtered at an around 6 months of age and 110 kg of body weight. The differences between Iberian and white pigs complicate the extrapolation of results, making it necessary to explore this breed specifically. Despite the unique characteristics of the Iberian pig, very few studies have examined its gut microbiota composition. For instance, López-García et al. (2021) compared gut microbiota composition and reported higher richness in Iberian pigs compared with Duroc. More recently, Heras-Molina et al. (2024) and Azouggagh et al. (2025) reported important effects of genetic line and age on the microbiota composition.suggested that some taxa associated with genetic line are implicated in short-chain fatty acid production and lipid metabolism, which may influence fat composition in Iberian pigs. However, to the best of our knowledge, no previous studies have investigated the potential of gut microbiota to improve phenotypic predictions of feed efficiency and feeding behavior traits in Iberian pigs. Even though feeding behavior traits do not have a direct economic interest, previous research has shown that they have high heritability and, when correlated, they can provide useful information to predict feed efficiency (Hall et al., 1999; Núñez et al., 2023).

The goal of this study was to evaluate the contribution of gut microbiota to phenotypic variance and its potential as an early predictor of feed efficiency and feeding behavior traits measured at 180 d in intensively reared Iberian pigs. Specifically, we quantified the proportion of phenotypic variance explained by host genetics and gut microbiota using fecal samples collected at both 140 and 180 d. We assessed the predictive ability of the microbiota composition at 140 d as an early indicator of later phenotypes, and used the microbiota at 180 d as a reference point to evaluate the relative accuracy of early predictions. This approach allowed us to explore whether early-life microbial data can serve as a useful tool for predicting productive traits, while also examining how predictive accuracy may vary depending on the timing of microbiota sampling. Based on the observed prediction ability, early gut microbiota composition could serve as a potential tool to shorten the testing period, thereby reducing the time and costs associated with phenotyping in pig breeding programs.

Materials and Methods

Ethical review

All farm management practices were approved by the Ethics and Animal Welfare Committee of the Polytechnic University of Valencia, in accordance with Council Directives 98/58/EC and 2010/63/EU (reference number 2017/VSC/PEA/00212).

Phenotypes

The animals used in this study belonged to 2 Iberian purebred pig strains (Retinto, Entrepelado) and their reciprocal crosses from the Iberian Test Center (IngaFood S.A., Extremadura, Spain). The animals were randomly housed in groups of 12 pigs per pen and were fed ad libitum by automatic feeders. The diet contained 2.50% crude fat, 13.5% crude protein, 6.50% crude fiber, and 5.6% crude ash. More information on the diet composition is shown in Supplementary Table S1. A total of 177,989 records from 156 animals up to 180 d of age were used to generate feed efficiency and feeding behavior traits. Data quality filtering of automatic feeder records was performed to remove visits without ID, feed intake equal to zero, and all the visits of the first week, as they represented an adaptation period to the feeding system. After an exploratory analysis, we removed visits with feed intake higher than 3 kg and duration lower than 2 s. Animals with less than 20 total days in the test were discarded. We computed feed efficiency traits, namely average daily feed intake (ADFI), average daily gain (ADG), body weight at 180 d (BW180), feed conversion rate (FCR), and residual feed intake (RFI). The ADFI was calculated as the sum of the individual feed intakes for each animal divided by the number of days that each animal had at least one visit to the feeder. This approach ensures that we do not include days in which some animals were isolated for veterinary treatment, particularly in cases where feed intake data was not recorded. The animals treated with antibiotics were removed from the study. The ADG was obtained as the total weight gain during the testing period divided by the total number of days. The FCR was obtained as the ratio ADFI/ADG. RFI is the difference between observed and predicted ADFI based on the main energy sinks. We obtained RFI as the residual value of the following multiple linear regression:

$$ADFI_i = b_1 BW_i^{0.6} + b_2 ADG_i + e_i$$

where $BW^{0.6}$ is the metabolic body weight raised to 0.6, and b_1 and b_2 are the regression coefficients of $BW^{0.6}$ and ADG, respectively. The feeding behavior traits were the average feed intake per visit (FPV), average feeding rate (FR), average number of visits per day (NVD), and average duration per visit (TPV). After the filtering process, the final table

contained 156 animals with phenotypes of feed efficiency and feeding behavior.

Pedigree

The pedigree information for the purebred Iberian pigs, up to 5 generations, has 561 animals, including 156 pigs with phenotypes of feed efficiency and feeding behavior, as well as microbiota information.

Gut microbiota

Fecal samples were collected from all 156 pigs at 140 and 180 d of age in the Iberian Test Center between May 2021 and June 2022. The details on sample collection, as well as the information on specific primers and bioinformatic analyses, are explained in Nuñez et al. (2025). Here, we included a summarized description of the process. The gut bacterial DNA was initially extracted, and the 16S rRNA gene was amplified using specific primers for the V3 to V4 region. The resulting amplicons were sequenced on an Illumina MiSeq sequencing platform with 2 × 300 base pair reads. The FASTQC software (Andrews, 2010) was used to assess the quality of reads. The posterior bioinformatic analyses, which included filtering, denoising, merging, chimera removal, and taxonomy assignment, were performed with the pipeline *ampliseq 2.11.0* (Straub et al., 2020) from Nextflow (Di Tommaso et al., 2017). After the bioinformatic process, an average of 69,799 reads per sample were kept, representing 70% of the initial reads. The length of the merged reads ranged from 400 to 485 base pairs. Sequences were assigned to amplicon sequence variants (ASV). We performed the ASV taxonomic classification using the database SILVA v138 (Quast et al., 2013). After this step, we obtained 2 tables of ASV corresponding to the samples of 140 and 180 d. The number of ASV was 9,979 for 140 d and 10,705 ASV for 180 d. All the ASVs present in less than 50% of the samples and those representing less than 0.01% of the total abundance (<1,176 counts for 140 d and <1,191 counts for 180 d) were discarded. After this process, 609 ASVs for 140 and 610 ASVs 180 d were retained. Note that these ASVs represent 90% of the initial reads for both 140 (10,651,500 from 11,764,765) and 180 d (10,766,753 from 11,915,197). The zeros represented 13% of the 2 databases. We performed the ASV taxonomic classification using the database SILVA v138 (Quast et al., 2013). No presence of Archaea and Eukaryotes was detected after the filtering process. Once the filtered table was obtained, the ASV abundances were transformed using a centered log-ratio transformation (CLR) to consider the compositional nature of microbiota (Aitchison, 1982).

Statistical analysis

We used 3 models to estimate the variance components of feed efficiency traits, namely, ADFI, ADG, BW180, FCR, and RFI; and feeding behavior traits, namely, FPV, NVD, and TPV. The models were based on assumptions about the factors shaping the phenotype: (a) only the additive genetic effect (Equation 1; model G), (b) only the microbiota effect (Equation 2; model M), and (c) both genetic and microbiota effects (Equation 3; model GM). The models were implemented as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_{\mathbf{pen}}\mathbf{p} + \mathbf{Z}_{\mathbf{a}}\mathbf{a} + \mathbf{e} \quad (1)$$

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_{\mathbf{pen}}\mathbf{p} + \mathbf{Wm} + \mathbf{e} \quad (2)$$

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_{\mathbf{pen}}\mathbf{p} + \mathbf{Z}_{\mathbf{a}}\mathbf{a} + \mathbf{Wm} + \mathbf{e} \quad (3)$$

where $\mathbf{y}$ is a vector of phenotypic observations for each trait; $\mathbf{X}$ is an incidence matrix relating the phenotypic data with the systematic effects $\mathbf{b}$, which included the phenotypic mean and the age at the beginning of the test period (covariate); $\mathbf{Z}_{\mathbf{pen}}$ corresponds to the incidence matrix of random pen effects $\mathbf{p}$; $\mathbf{Z}_{\mathbf{a}}$ corresponds to the incidence matrix of random additive genetic effects $\mathbf{a}$; $\mathbf{W}$ corresponds to the incidence matrix of random microbiota effect $\mathbf{m}$, and $\mathbf{e}$ is a random vector of residual effects. Normal distributions were assumed for $\mathbf{p}$, $\mathbf{a}$, $\mathbf{m}$, and $\mathbf{e}$ effects; $\mathbf{p}|\ \sigma^2_{pen} \sim N\left(0, \mathbf{I_p}\sigma^2_{pen}\right)$, $\mathbf{a}|\ \sigma^2_a \sim N\left(0, \mathbf{A}\sigma^2_a\right)$, $\mathbf{m}|\sigma^2_m \sim N\left(0, \mathbf{M}\sigma^2_m\right)$, and $\mathbf{e}|\sigma^2_e \sim N\left(0, \mathbf{I_e}\sigma^2_e\right)$, respectively, where $\mathbf{I}_p$ and $\mathbf{I}_e$ are the identity matrices of appropriate dimensions, $\mathbf{A}$ is the relationship matrix between individuals, $\mathbf{M}$ is the microbial co(variance) matrix, created as $\mathbf{M} = \frac{\mathbf{BB}'}{n_b}$ (Difford et al., 2016), being $\mathbf{B}$ the CLR-transformed matrix of ASV abundances and n_b the total number of ASV. The terms σ^2_{pen}, σ^2_a, σ^2_m and σ^2_e are the variances for the pen effect, the additive genetic effect, the microbiota effect, and the residual effect, respectively. Model M and model GM were applied using microbiota data collected at both 140 and 180 d. To assess the similarity between the resulting $\mathbf{M}$ matrices ($\mathbf{M}_{140}$ and $\mathbf{M}_{180}$), we used cosine similarity as described by Lu et al. (2023). Specifically, the lower triangle, including the diagonal of each matrix, was flattened into a long vector, and the cosine similarity was computed as the scalar product of these vectors divided by the product of their magnitudes

A single chain was run with a total of 1,000,000 iterations. Inferences were based on 100,000 samples obtained after discarding the first 500,000 as burn-in and using a thinning interval of 5. All the models were implemented in a Bayesian framework via Markov chain Monte Carlo using the R package Bayesian Generalized Linear Regression (Pérez and de los Campos, 2014). We used the method Bayesian Ridge Regression (model = 'BRR') for pen effects, and Reproducing Kernel Hilbert Space (model = 'RKHS') for genetic and microbiota effects. The posterior distributions of the heritability (h^2), microbiability (m^2), and the variance explained by the pen effect (p^2)were obtained as $h^2 = \sigma^2_a/\sigma^2_{phe}$, $m^2 = \sigma^2_m/\sigma^2_{phe}$ and $p^2 = \sigma^2_{pen}/\sigma^2_{phe}$, respectively; being σ^2_{phe} the phenotypic variance. Specifically, σ^2_{phe} is defined as $\sigma^2_{phe} = \sigma^2_{pen} + \sigma^2_a + \sigma^2_e$ in Model G, $\sigma^2_{phe} = \sigma^2_{pen} + \sigma^2_m + \sigma^2_e$ in Model M, and $\sigma^2_{phe} = \sigma^2_{pen} + \sigma^2_a + \sigma^2_m + \sigma^2_e$ in Model GM. Convergence was visually checked for each estimation. We compared models using the deviance information criterion (DIC; Spiegelhalter et al., 2002). The DIC measures the goodness of fit of a model, considering the complexity given by the number of parameters. When different models are used for the same trait, the best goodness of fit will be indicated by the lowest DIC.

Predictive ability of the models

We evaluated the predictive ability of the 3 models described above to predict the phenotypes measured at 180 d using microbiota information from 140 and 180 d. We performed group-stratified cross-validation by selecting one animal per pen (15 levels) for the test set, ensuring balanced representation across pens. This sampling method was repeated 100 times, with 10% of the total data used as the testing set and the remaining 90% as the training set in each iteration. The training set was used to estimate the effects of the models, while the testing set was used to evaluate the predictive ability of the models. The predictive ability was assessed by calculating the mean squared error of prediction and the Pearson correlation coefficient between the adjusted phenotype (y^*) and the

predictor, which varied depending on the model used (Table 1). The prediction ability was computed for each iteration, and the mean and standard deviation were then calculated across 100 iterations. In model G, the predictive ability was estimated as the correlation between y^* and the estimated breeding value (EBV). In model M, we computed the correlation between y^* and the estimated microbiota value. For model GM, we estimated the correlation between y^* and (EBV + estimated microbiota value). To assess the significance of the differences in predictive ability between models G and GM, we performed a simple paired *t*-test. Additionally, to provide a more practically meaningful interpretation, we also calculated the percentage of increase in predictive ability from G to GM.

Results

Descriptive analysis

From the bioinformatic process, we kept 609 ASV for the microbiota at 140 d and 610 ASV for the microbiota at 180 d. These ASVs represented 90% of the initial reads after quality control. In 140 d, the relative abundance ranged from 0.01% to 24%, being *Lactobacillus* the most abundant genus (24%), followed by *Streptoccocus* (12%) and *Clostridium sensu stricto* (8%). At 180, the most abundant was *Streptoccocus* (23%), followed by *Lactobacillus* (16%) and *Clostridium sensu stricto* (10%). Interestingly, the same 8 genera represent more than 66% of the total abundance at 140 and 180 d of age (Figure 1). However, the cosine similarity between the microbial matrices (M_{140} and M_{180}) was 0.33, indicating weak directional similarity, but differences in composition still exist between the 2 time points.

Table 1. Summarize of the predictors and the Pearson correlations (r) used to estimate prediction ability according to the model used

Model	Vector of prediction	Prediction ability
G	$\mathbf{EBV_G}$	$r(y^*, \mathbf{EBV_G})$
M	$\mathbf{EMV_M}$	$r(y^*, \mathbf{EMV_M})$
GM.	$\mathbf{EBV_{GM}} + \mathbf{EMV_{GM}}$	$r(y^*, \mathbf{EBV_{GM}} + \mathbf{EMV_{GM}})$

G, genetic model; M, microbiota model; GM, genetic + microbiota model. $y^* = y - (\mathbf{Xb} + \mathbf{Z_p p})$; $\mathbf{EBV_G}$, estimated breeding value from G model; $\mathbf{EBV_{GM}}$, estimated breeding value from GM model; $\mathbf{EMV_M}$, estimated microbial value from M model; $\mathbf{EMV_{GM}}$, estimated microbiota value from GM mol; y, vector of phenotypes; X, incidence matrix of systematic effects; b, vector of fixed effects; $\mathbf{Z_p}$, incidence matrix of pen effects; **p**, vector of pen effects.

Heritability, microbiability, and pen effect estimates

We used 3 models to estimate h^2, m^2, and p^2 for all the traits using microbiota from 140 and 180 d of age (Tables 2 and 3). The proportion of the phenotypic variance explained by genetics, microbiota, and pen effects are visually shown in Figure 2 for feed efficiency traits and in Figure 3 for behavioral traits. The p^2 values ranged from 0.09 (TPV) to 0.20 (BW180) for most of the traits, the only exception being FR, where the estimates ranged around 0.30 depending on the model used. For clarity, we described the results of h^2 and m^2 separately for feed efficiency and behavioral traits. The h^2 values obtained with the G model ranged from 0.21 (FCR) to 0.40 (ADG) for productive traits, and from 0.23 (FR) to 0.43 (FPV) for feeding behavior traits. The m^2 results with the M and GM models were estimated using microbiota from both 140 and 180 d. The m^2 values obtained with the M model for productive traits ranged from 0.16 (FCR) to 0.34 (BW180) using microbiota samples from 140 d and from 0.17 (FCR) to 0.29 (BW180) using microbiota from 180 d. For feeding behavior, m^2 ranged from 0.18 (TPV) to 0.25 (FPV) with microbiota at 140 d, and from 0.16 (TPV) to 0.23 (FPV). Interestingly, in the GM model, h^2 and m^2 were lower than their respective values from the G and M models. The h^2 estimates from GM models were similar at 140 and 180 d (Tables 2 and 3), with a range between 0.15

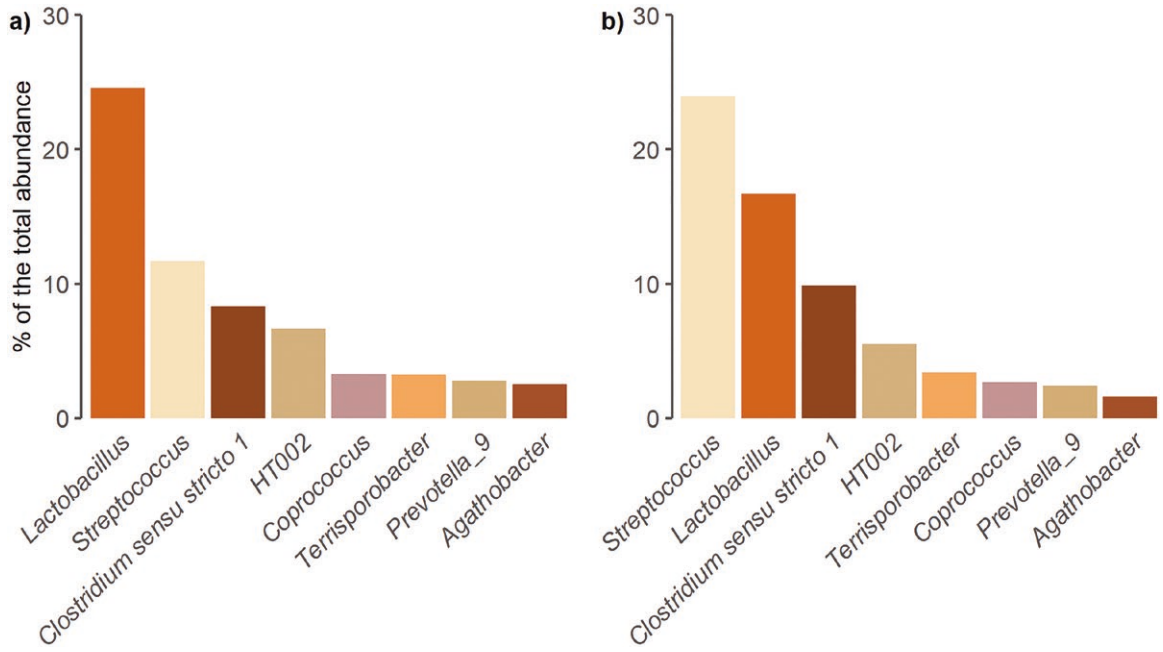

Figure 1. Relative genera abundance obtained from 610 amplicon sequence variants. The plot shows the 8 most abundant genera present in fecal samples from 140-d-old (A) and 180-d-old Iberian pigs (B).

(RFI) to 0.31 (ADG) for productive traits and 0.19 (FR) to 0.37 (TPV) for feeding behavior traits. The m^2 for productive traits were slightly different for the 2 points, ranging between 0.13 (FCR) to 0.25 (BW180) using 140 d and from 0.15 (RFI, FCR, and DFI) to 0.22 (BW180) using microbiota at 180 d. For behavioral traits, the m^2 values varied between 0.11 (TPV) and 0.15 (FPV and NVD) for both time points.

The goodness of fit of the models were assessed using DIC values. The model GM showed lower DIC values than models G and M for most of the traits. The difference in DIC values between the GM model and G model was more important in the case of ADFI (−10%) and RFI (−333%), indicating better goodness-of-fit when genetic and microbiota effects were included together (Tables 2 and 3).

Table 2. Genetic parameters for feed efficiency traits, including only genetic, only microbiota, or both effects, with the 95% highest posterior density (in brackets) using microbiota at 140 d of age

	Model G		Model M		Model GM		
Trait	h^2	DIC	m^2	DIC	h^2	m^2	DIC
ADG	0.40 [0.17, 0.62]	−395	0.23 [0.08, 0.43]	−352	0.30 [0.09, 0.53]	0.16 [0.04, 0.30]	−396
ADFI	0.28 [0.08, 0.51]	65	0.20 [0.07, 0.37]	79	0.21 [0.05, 0.41]	0.16 [0.05, 0.31]	58
FCR	0.21 [0.06, 0.39]	232	0.16 [0.06, 0.30]	238	0.16 [0.05, 0.33]	0.13 [0.04, 0.25]	229
BW180	0.36 [0.16, 0.57]	1,096	0.34 [0.15, 0.55]	1,113	0.24 [0.07, 0.42]	0.25 [0.09, 0.43]	1,082
RFI	0.21 [0.06, 0.40]	1.27	0.17 [0.06, 0.31]	4.95	0.15 [0.04, 0.31]	0.14 [0.04, 0.26]	−2.96
FPV	0.43 [0.23, 0.63]	1,576	0.25 [0.08, 0.44]	1,632	0.35 [0.15, 0.55]	0.15 [0.05, 0.28]	1,570
FR	0.23 [0.08, 0.39]	992	0.19 [0.06, 0.35]	1,015	0.19 [0.06, 0.35]	0.14 [0.04, 0.28]	990
NVD	0.34 [0.14, 0.55]	783	0.21 [0.07, 0.39]	810	0.26 [0.08, 0.46]	0.15 [0.05, 0.28]	776
TPV	0.42 [0.22, 0.62]	1,822	0.18 [0.06, 0.33]	1,883	0.36 [0.15, 0.57]	0.11 [0.04, 0.21]	1,824

h^2, heritability;m^2, microbiability;h^2_d, direct heritability; ADG, average daily gain; ADFI, daily feed intake; FCR, feed conversion ratio; BW180, body weight at 180 d; RFI, residual feed intake; FPV, feed intake per visit; FR, feeding rate; NVD, number of visits per day; TPV, time spent in feeding per visit; DIC, deviance information criterion.

Table 3. Genetic parameters for feed efficiency traits, including only genetic, only microbiota, or both effects, with the 95% highest posterior density (in brackets) using microbiota at 180 d of age

	Model G		Model M		Model GM		
Trait	h^2	DIC	m^2	DIC	h^2	m^2	DIC
ADG	0.40 [0.18, 0.62]	−395	0.23 [0.08, 0.41]	−354	0.31 [0.05, 0.40]	0.16 [0.05, 0.30]	−401
ADFI	0.29 [0.09, 0.53]	65	0.19 [0.06, 0.34]	85	0.21 [0.04, 0.43]	0.15 [0.04, 0.28]	63
FCR	0.21 [0.06, 0.39]	232	0.17 [0.06, 0.32]	235	0.17 [0.04, 0.34]	0.15 [0.05, 0.28]	223
BW180	0.36 [0.16, 0.57]	1,096	0.29 [0.12, 0.48]	1,122	0.26 [0.08, 0.45]	0.22 [0.08, 0.38]	1,085
RFI	0.21 [0.06, 0.40]	1.27	0.18 [0.06, 0.33]	3.75	0.16 [0.04, 0.32]	0.15 [0.05, 0.29]	−6.20
FPV	0.43 [0.23, 0.63]	1,576	0.23 [0.07, 0.40]	1,633	0.36 [0.15, 0.57]	0.14 [0.04, 0.26]	1,571
FR	0.23 [0.08, 0.39]	992	0.17 [0.05, 0.32]	1,016	0.19 [0.05, 0.34]	0.13 [0.04, 0.25]	994
NVD	0.33 [0.13, 0.54]	783	0.22 [0.08, 0.38]	806	0.26 [0.08, 0.46]	0.15 [0.05, 0.28]	772
TPV	0.42 [0.22, 0.62]	1,822	0.16 [0.06, 0.29]	1,883	0.37 [0.16, 0.58]	0.11 [0.04, 0.20]	1,821

h^2, heritability;m^2, microbiability;h^2_d, direct heritability; ADG, average daily gain; ADFI, daily feed intake; FCR, feed conversion ratio; BW180, body weight at 180 d; RFI, residual feed intake; FPV, feed intake per visit; FR, feeding rate; NVD, number of visits per day; TPV, time spent in feeding per visit; DIC, deviance information criterion.

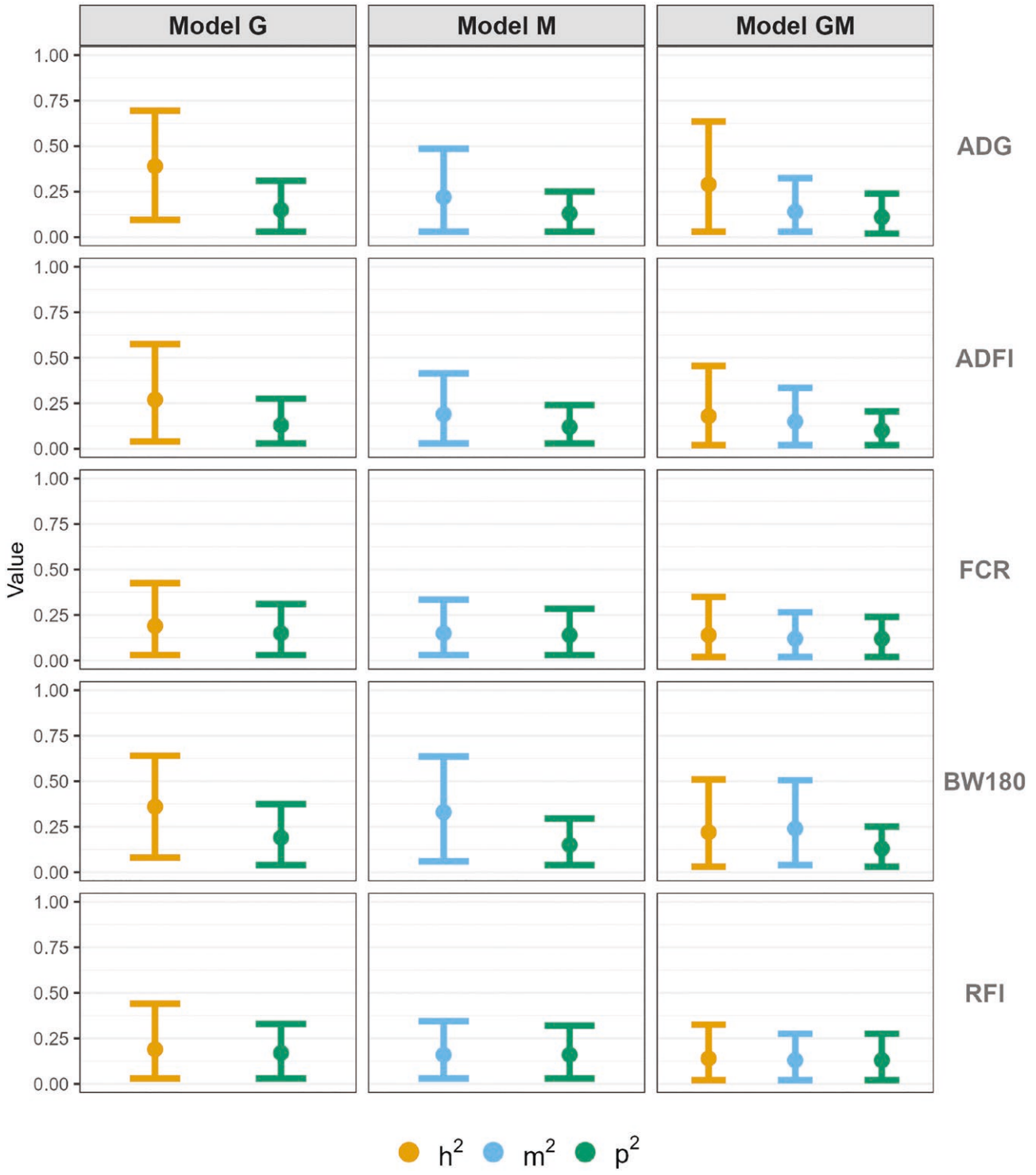

Figure 2. Estimates of heritabilities (h^2), microbiabilities (m^2), and the proportion of the phenotypic variance explained by the pen effect (p^2), with genetic model (G), microbiota model (M) or genetic and microbiota model (GM) for the productive traits using microbiota from 140 d: ADG, average daily gain; ADFI, average daily feed intake; BW180, body weight at 180 d; FCR, feed conversion rate; RFI, residual feed intake.

Predictive ability evaluation

We evaluated the ability of the 3 models (G, M, and GM) to predict phenotypes at 180 d of age. Specifically, our main goal was to estimate the increase in predictive ability when microbiota information from 140 d was added to genetic models (Table 4). Thus, the next results are only focused on microbiota from 140 d. Despite that, we included the Supplementary Table S2 with the prediction abilities using microbiota from 180 d. The predictive ability for model G varied between 0.06 (FCR) and 0.36 (BW180) for feed efficiency traits and from 0.20 (FR) to 0.48 (TPV) for behavioral traits. With model M, the predictive ability ranged from 0.17 (FCR) to 0.43 (BW180) for productive traits and from 0.13 (FR) to 0.33 (FPV) for behavioral traits. With model GM, the predictive

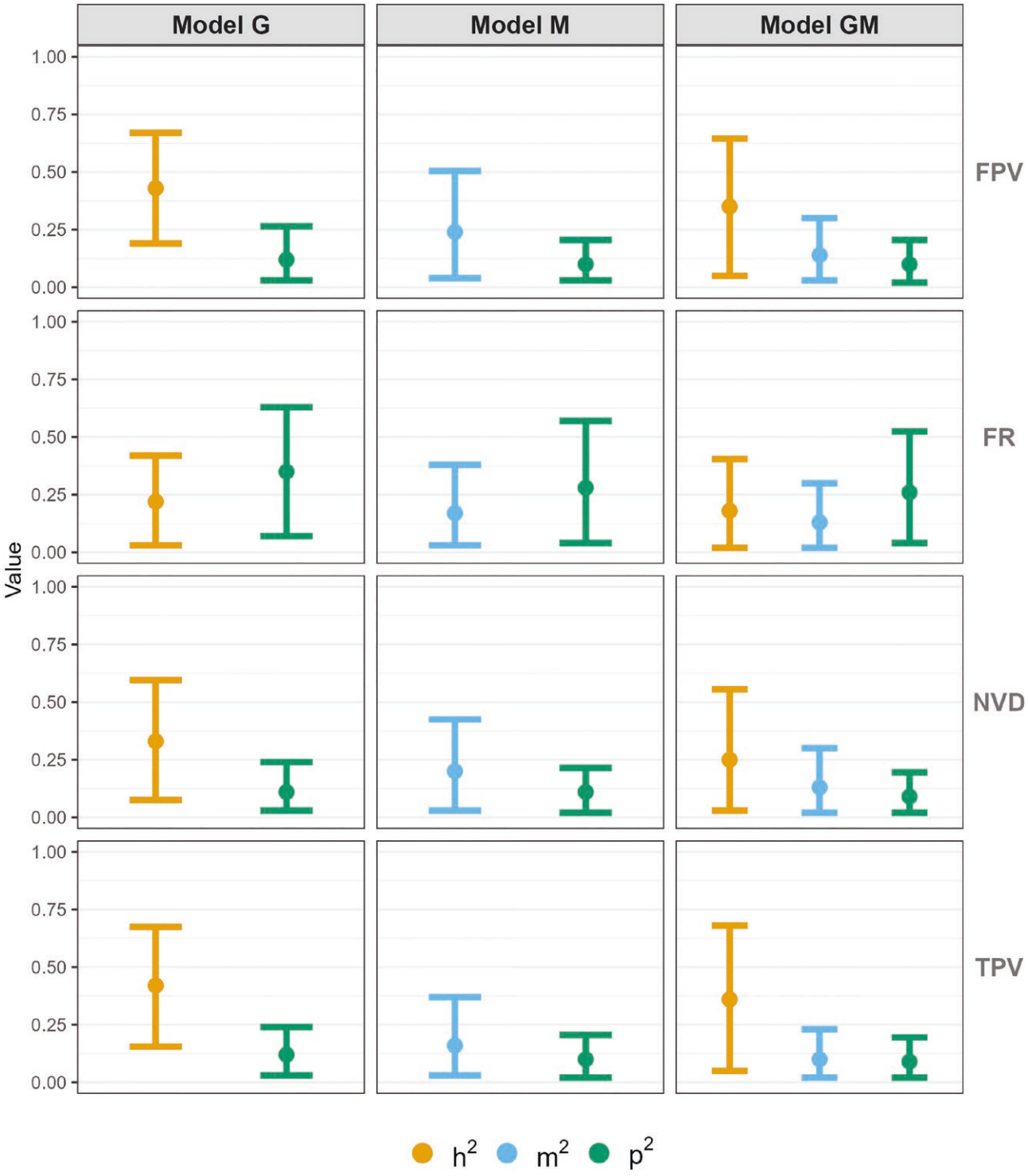

Figure 3. Estimates of heritabilities (h^2), microbiabilities (m^2), and the proportion of the phenotypic variance explained by the pen effect (p^2), with genetic model (G), microbiota model (M) or genetic and microbiota model (GM) for behavioral traits using microbiota from 140 d: FPV, average feed intake per visit; FR, average feeding rate per visit; NVD, average number of visits per day; TPV, average time spent per visit.

ability ranged from 0.14 (FCR) to 0.48 (BW180) for feed efficiency traits, and from 0.23 (FR) to 0.51 (FPV) for behavioral traits. We evaluated whether the predictive ability of the GM model increased compared to the G model. We observed an important increase in the case of FCR (from 0.06 to 0.14), BW180 (from 0.36 to 0.48), and RFI (from 0.07 to 0.25; Table 4). On the other hand, slight to negligible increases were observed for behavior traits (from 0 to 0.04; Table 4).

Table 4. Predictive ability and standard deviations of kernel-based models, including genetic effects (model G), microbiota effects (model M), and both genetics and microbiota (model GM), using microbiota at 140 d

		Model G		Model M		Model GM	
Trait	Unit	$\rho(y^*, EBV)$	MSEP	$\rho(y^*, EMV)$	MSEP	$\rho(y^*, EBV + EMV)$	MSEP
ADG	g	0.34±0.22	0.006 ± 0.002	0.25±0.25	0.006 ± 0.002	0.38±0.22	0.006 ± 0.002
ADFI	kg	0.22±0.24	0.100 ± 0.032	0.22±0.24	0.100 ± 0.031	0.27±0.23	0.100 ± 0.031
FCR	kg/kg	0.06±0.26	0.294 ± 0.185	0.17±0.22	0.288 ± 0.181	0.14±0.23	0.291 ± 0.182
BW180	kg	0.36±0.23	86.14 ± 29.93	0.43±0.23	86.04 ± 28.24	0.48±0.22	80.66 ± 27.52
RFI	kg	0.07±0.26	0.067 ± 0.033	0.28±0.21	0.063 ± 0.030	0.25±0.22	0.061 ± 0.031
FPV	g	0.47±0.22	1666 ± 657.7	0.33±0.24	1915 ± 853.0	0.51±0.20	1615 ± 650.8
FR	g/min	0.20±0.25	42.32 ± 13.61	0.13±0.27	44.98 ± 16.18	0.23±0.21	43.17 ± 14.43
NVD	visits/day	0.40±0.26	9.033 ± 5.298	0.32±0.25	9.605 ± 5.233	0.44±0.25	8.777 ± 5.048
TPV	sec/visit	0.48±0.20	7374 ± 5457	0.20±0.24	9260 ± 7551	0.44±0.20	7687 ± 5804

ADG, average daily gain; ADFI, daily feed intake; FCR, feed conversion ratio; BW180, body weight at 180 d; RFI, residual feed intake; FPV, feed intake per visit; FR, feeding rate; NVD, number of visits per day; TPV, time spent in feeding per visit;
$\rho(y^*, EBV)$ = correlation between adjusted phenotype and estimated breeding value; $\rho(y^*, EMV)$ = correlation between adjusted phenotype and estimated microbiota value; MSEP, mean squared error of prediction.

Discussion

In this study, we first evaluated the proportion of the phenotypic variance explained by the genetics, the microbiota, and the genetics and microbiota. Then, we estimated the ability of the gut microbiota measured at 140 d to predict phenotypes at 180 d. Our microbiability estimates support the hypothesis that gut microbiota accounts for a low to moderate proportion of the phenotypic variance, with similar values observed using microbiota from both 140 and 180 d. Previous studies in pigs have reported m^2 values of approximately 0.20 for feed efficiency and growth traits (Camarinha-Silva et al., 2017; Aliakbari et al., 2022; Déru et al., 2022). He et al. (2022) found values ranging from 0.10 to 0.31 for behavioral traits, depending on breed and timepoint. Although direct comparisons are challenging due to differences in breed, management, diet, season, and age (all of which can affect microbiota composition), our results are in line with these previous studies.

When we included genetics and microbiota effects in the GM model, the estimates of m^2 were lower than those from the M model, which included only microbiota. The same happened with the h^2, which was lower in the GM model compared with the h^2 from G model. This reduction in h^2 and m^2 with model GM has been observed in previous studies (Déru et al., 2022; Martinez Boggio et al., 2024), and may indicate potential confounding effects between genetics and microbiota (Weishaar et al., 2020; Christensen et al., 2021). Including both genetic and microbiota effects leads to a better partitioning of variance component estimates. However, it is important to note that this study was limited to estimating the genetic and microbiota effects without considering the potential covariance between them. Ignoring this covariance could introduce biases in the partitioning of variance components, potentially misattributing genetic and microbiota contributions to the phenotype. In this regard, Martinez Boggio et al. (2024) proposed a method to include the interaction between the host genetic and the microbiota using a linear kernel composed of the Hadamard product of matrices A and M. They assessed this model for RFI in dairy cows, showing that the interaction explained 0.13 of the phenotypic variance, and both h^2 and m^2 decreased from 0.19 to 0.16 and from 0.18 to 0.15, respectively, when the interaction was incorporated.

However, incorporating these covariances into the model could significantly increase computational demands and require larger datasets to obtain reliable estimates.

The GM model yielded a lower DIC for ADFI and RFI compared to the G Model (–10% for ADFI and –333% for RFI), which indicates a better goodness of fit. However, the changes observed in the rest of feed efficiency traits (BW180, FCR, and ADG) were minor (up to 2%), being null in the case of behavioral traits (Tables 2 and 3). These results indicate that the addition of microbiota information benefits the goodness of fit, particularly of ADFI and RFI, with no improvement for behavioral traits. Previous values comparing model fit of growth and feed efficiency traits were reported in Déru et al. (2024), where model GM showed the best numeric performances but these changes represented less than 1% compared with G model.

Our analysis showed that gut microbiota accounts for a relevant percentage of the variance in growth, feed efficiency, and feeding behavior traits. To assess its potential as a predictor, we evaluated the ability of microbiota samples collected at 140 and 180 d to predict phenotypes at 180 d. The basis for using microbiota at 140 days is that, if the predictive performance is sufficiently accurate, it could support strategies aimed at shortening the testing period. Our results showed that microbiota at 140 d provided predictions comparable to those at 180 days, making it a potential criterion for earlier selection. Our discussion focuses on predictions based solely on microbiota from 140 d. However, we also calculated predictions from 180 d (Supplementary Table S2) to compare how consistent the predictions are across time.

The predictive ability for all models and traits were low to moderate, in line with those obtained in growth and feed efficiency traits by Déru et al. (2024) and Camarinha-Silva et al. (2017) in Large white and Pietrain pigs, respectively. Note that we define the predictive ability as the correlation between the EBV and the adjusted phenotype. For instance, in model G, adjusted phenotypes are obtained as $y^* = y_i - X_i b - p_i = a_i + e_i$. In this context, the correlation between (y^*, EBV) is equivalent

to the correlation between (EBV + e, EBV). Therefore, even when the correlation values are low to moderate, they are capturing genetic values. The incorporation of the gut microbiota information (GM model) improved the predictive ability for ADFI, FCR, BW180, and RFI compared with G model. Significant differences ($P < 0.05$) were observed between the GM and G models for the prediction of FCR, RFI, and BW180, whereas no significant differences were found for ADG, ADFI, and the behavioral traits. However, it is important to note that a lack of significance does not necessarily mean the result lacks biological or economic relevance; similarly, a statistically significant result may not always be practically meaningful. To provide a clearer picture of the impact, we also expressed the differences in prediction accuracy as percentages of improvement. This offers a practical measure of the extent to which predictive performance has improved. We observed an increase from 0.22 to 0.27 for ADFI (22%), from 0.36 to 0.48 for BW180 (33%), from 0.06 to 0.14 for FCR (133%), and from 0.07 to 0.25 for RFI (257%). These results suggest that microbiota information explains part of the variability that is not explained by genetics. In this respect, Aliakbari et al. (2022) also reported an improvement in prediction accuracies by combining microbiota and genetic information for ADFI, FCR, and RFI. However, we found no relevant increase for ADG and feeding behavior traits. The lack of improvement in ADG and behavioral traits may be explained by a relatively low m^2 (such as FR, where$m^2 = 0.13$) or by confounding between genetics and microbiota. Overall, our findings indicate that gut microbiota at 140 d can enhance the prediction of RFI, FCR, BW180, and ADFI in Iberian pigs at 180 d of age. Further analyses with larger datasets are needed to deepen our understanding of the relationship between gut microbiota, host genetics, and feed efficiency and feeding behavior traits.

Conclusions

In this study, we evaluated the proportion of the phenotypic variance explained by genetics, gut microbiota, and genetics and gut microbiota. Our results support the hypothesis that the early gut microbiota composition from 140-d-old pigs explains a low to moderate proportion of the phenotypic variance, and a very similar proportion was found when microbiota at 180 d was employed. Our results suggest that the inclusion of early gut microbiota composition in animal models can be used to increase the prediction accuracy of RFI, FCR, and body weight at 180 d. Our findings provide new insights into the relationship between the gut microbiota and key phenotypes in Iberian pigs raised under intensive conditions.

Supplementary Data

Supplementary data are available at the *Journal of Animal Science* online.

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Conflict of Interest Statement

None.

Author Contributions

Pedro Nuñez (Data curation, Formal analysis, Investigation, Methodology, Writing - original draft), Cristina Casto-Rebollo (Data curation, Formal analysis, Supervision, Writing - review & editing), Guillermo Martinez-Boggio (Methodology, Supervision, Writing - review & editing), Sara Negro Rama (Conceptualization, Writing - review & editing), Joaquim Casellas (Project administration, Validation, Writing - review & editing), Luis Varona (Formal analysis, Project administration, Validation, Writing - review & editing), Romi Pena (Methodology, Writing - review & editing), Francisco Peñagaricano (Formal analysis, Investigation, Methodology, Supervision, Validation, Writing - review & editing), and Noelia Ibañez-Escriche (Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Validation, Writing - review & editing).

Data Availability

The 16S sequences used in this study are available on Zenodo. org/records/14013900.

Declaration of generative AI and AI-assisted technologies in the writing process.

During the preparation of this work, the authors used DeepL Write and Grammarly for language editing. After using these tools, the authors reviewed and edited the content, taking full responsibility for the content of the publication.

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