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Investigating the potential for genetic improvement of nitrogen and phosphorus efficiency in a Swiss large white pig population using chemical analysis

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Abstract

Pig production contributes to environmental pollution through excretion of phosphorus and nitrogenous compounds. European pig production requires annual imports of currently 36 million tons of soya bean, because domestic plant protein sources often do not meet the required protein quality. Most of the mineral phosphate sources are also imported. It is therefore desirable to improve nutrient deposition efficiency through selective breeding, that is to realise similar growth rates and carcass compositions as currently achieved but with a lower intake of dietary crude protein or phosphate. For a preliminary evaluation of the potential of selecting for increased nutrient deposition efficiency, we estimated genetic parameters for nitrogen and phosphorus efficiencies in a Swiss Large White pig population including 294 individuals. Nutrient efficiency phenotypes were obtained from wet-chemistry analyses of pigs of various live weights. Heritability of nitrogen efficiency was estimated at 41%. Heritability of phosphorus efficiency was very low (0.3%), but positive genetic correlations with nitrogen efficiency suggest that breeding for nitrogen efficiency would positively affect phosphorus efficiency. Further studies are needed to improve the quality of estimates and to obtain accurate high-throughput measures of nutrient efficiency to be implemented on farms.

KEYWORDS
dietary protein, environmental pollution, selective breeding, swine

1 | INTRODUCTION

Pig production contributes to environmental pollution through the excretion and emission of nitrogenous compounds and phosphorus (P) (Notarnicola, Tassielli, Renzulli, Castellani, & Sala, 2017; Springmann et al., 2018). Specific legal regulations, such as the Gothenburg Protocol or the Nitrates Directive of the European Commission, strive to close nutrient cycles and reduce adverse effects of manure on sensitive ecosystems. However, closing nutrient cycles can be difficult in areas with both high livestock density and low availability of arable land. The application of pig slurry to agricultural land can also result in excess soil P due to its low N:P ratios (Wienhold, 2005). The ecological impact of livestock production also manifests in large-scale imports of soy, which is a preferred feed component because of its favourable amino acid profile (Bracher, 2019; Wang et al., 2011), from Brazil, Argentina or the USA. The geographical separation of soya bean cultivation and livestock production leads to a

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disturbance of nutrient cycles and dramatic changes in the global patterns of N distribution (Erisman, 2004; Galloway et al., 2008).

In view of these problems, the reduction of N and P supplies in animal diets and the reduction in N and P excretions are clearly desirable goals. A promising approach to achieve a reduction in nutrient supply and nutrient voiding is genetic selection for increased N and P efficiencies in pigs (Merks, Mathur, & Knol, 2012; Millet et al., 2018; Neeteson-van Nieuwenhoven, Knap, & Avendaño, 2013). Nutrient efficiency is defined as the proportion of nutrient uptake in the body to the total intake of dietary nutrients. Selection for this trait aims to achieve comparable growth performances with markedly lower dietary nutrient content. Due to its economic importance, improving the feed conversion ratio (FCR; Wilkinson, 2011) has been a priority. One of the main factors influencing feed intake is energy concentration of the feed (Li & Patience, 2017), and selection for improved FCR or residual feed intake (RFI) has therefore increased energy efficiency rather than nutrient efficiency. Focusing on energy efficiency likely leads to an oversupply of dietary proteins and P so as not to restrict the growth of fattening pigs. Thus, the improvement of nutrient efficiency lags behind improvement of FCR over the last 35 years (Lassaletta et al., 2019). However, both RFI and FCR are expected to be genetically correlated with N and P excretion (Saintilan et al., 2013). Recent life-cycle assessment models indicate a high positive correlation of N excretion with FCR (Monteiro, Brossard, Gilbert, & Dourmad, 2019) and lower environmental impacts for a low-RFI selection line (Soleimani Jevanini & Gilbert, 2019). However, selection for lower residual feed intake with the aim of reducing nutrient excretion in poultry is almost 30% less efficient than selection for the excretion trait itself (de Verdal et al., 2011). Hence, while energy-efficient animals are already likely to excrete less N and P, a focus on excretion and retention traits could further reduce the environmental impact of pig fattening by directly targeting the chemical compounds with the greatest negative effects. To quantify nutrient efficiency, the N and P contents of the feed and the empty body or the carcass as well as the amount of feed consumed by each individual have to be determined. Because of the costs involved in chemical analysis, the N and P contents in the empty body or the carcass are generally estimated. For instance, Saintilan et al. (2013) used prediction equations that relate lean meat content during dissections to nitrogen or phosphorus excretion and Shirali et al. (2013) used the deuterium dilution technique to estimate water content, from which lean meat content can be derived. Saintilan et al. (2013) reported heritabilities of N and P retention between 36%–43% and 30%–41%, respectively, in a range of pig breeds. Reliable knowledge of genetic correlations between N and P efficiencies is important to anticipate possible trade-offs. In poultry, protein and P retention have been found to be positively genetically correlated ($r_G = .74$; de Verdal et al., 2011). However, no such data are currently available for pigs.

The aim of the present study was to evaluate the potential of N and P efficiencies to be implemented in future breeding programmes. We used preliminary data on the dam line of a Swiss Large White pig population that were obtained in the course of a feeding experiment with standard and protein-restricted diets, in which N and P contents of the body and the feed were determined using wet-chemistry analyses. We estimated heritabilities, common environment (litter) effects of efficiency traits, average daily gain (ADG) and FCR, and their genetic, common environment and phenotypic correlations.

2 | MATERIALS AND METHODS

2.1 | Animals and data set

The data sets used for this study were collected by Ruiz-Ascacibar et al. (2017) in four experimental runs from July 2012 to October 2016, including eight farrowing series (Table 1, Table S1). Some of the sows were included in several runs. Two sows were used in one farrowing series of run 1 and run 2 each, and a set of three sows and one boar were used in one farrowing series of run 3 and run 4 each. One sow was included in both run 1 and run 3. All sows (and nine of the boars) belonged to the Swiss Large White dam line herd maintained at Agroscope, and thus, the pedigree of the individuals was well connected (Figures S1 and S2, Table S3). The two boars used in run 1 were from another breed; hence, the pigs tested in this run were not purebred dam line but crossbreeds as are used for fattening pig production in Switzerland (Table 1). The pigs used for this study originated from 17 sires and 56 dams (Table 1). Whereas most of the dams had only one litter, six sows had two litters each in the data set. From each litter, six piglets (two males, two females, two castrates) in runs 1 and 2, four piglets (two females, two castrates) in run 3 and three piglets (entire males only) were chosen based on their birth weights. Littermates were assigned to the dietary treatments and slaughter weight categories so that birth weight, weaning weight and breed were as balanced as possible. Piglets were weaned on average at 27 ± 2 days after birth by removing the sow, after which they remained in the farrowing pen up to an age of 22 to 42 days (mean 28 ± 5 days). Pigs were regrouped and mixed with other litters in starter pens. Littermates were assigned to the same starter pen until the maximum number of 14 piglets/pen was reached, in which case littermates were distributed to different starter pens. In the grower and finisher phase (20–60 and 60–100 kg live weight, respectively), pigs were reared in pens equipped with automated feeders with an individual pig recognition system (Schauer Maschinenfabriken GmbH & Co. KG). Each feeder accommodated 14 pigs. The pigs had ad libitum access to the diets. Between weaning and 20kg

TABLE 1 Overview of data sets used in this study showing the timeline of the experiments, the breeds, the sample size, the number of sires and the number of dams in each experimental run

Experiment	Series	Dates	Breeds	N	Sires	Dams
Run 1	1 & 2	July 2012–April 2013	Premo®[a] × Large White	72	2	17
Run 2	3 & 4	August 2013–May 2014	Large White × Large White	72	5	14
Run 3	5 & 6	August 2014–June 2015	Large White × Large White	88	5	16
Run 4	7 & 8	January 2016–October 2016	Large White × Large White	62	6	16
			Total	294	17[b]	56[b]

[a] PREMO® is the Swiss Large White sire line for fattening piglet production. For more information, see https://www.suisag.ch/rassenueberblick

[b] Due to some overlaps in parent individuals between the different experimental runs, there were only 17 unique sires instead of 18 and 56 dams instead of 63.

live weight, they received a standard starter diet formulated according to the current Swiss recommendations. Between 20 and 60 kg, pigs received grower diets, and between 60 and 100 kg and 100 and 140 kg, they received a finisher I and a finisher II diet (Table S2). Pigs in the control treatment groups were fed grower, finisher I and finisher II diets formulated according to the Swiss feeding recommendations. Pigs in the protein-reduced treatment groups were fed grower, finisher I and finisher II diets containing 80% of digestible crude protein, which was achieved through either a reduction in digestible lysine, methionine, threonine and tryptophan contents only or via a balanced reduction in all essential amino acids of the control diet (see Ruiz-Ascacibar et al., 2017 and section 1 in Appendix S1, Tables S1 and S2 for details on the formulation of the diets). Treatment and control diets were iso-energetic (13.2 MJ digestible energy/kg feed). In the final data set, the numbers of animals in both treatment groups and in the sexes were as follows: $N_{\mathrm{control}} = 135$; $N_{\mathrm{treatment}} = 159$; $N_{\mathrm{females}} = 92$; $N_{\mathrm{castrates}} = 92$; and $N_{\mathrm{entire\ males}} = 110$. Serial slaughtering of the pigs occurred in 20-kg intervals from 20 to 140 kg live weights except for run 4, where only three weight categories, 20, 60 and 100 kg, were sampled ($N_{20\ \mathrm{kg}} = 38$; $N_{40\ \mathrm{kg}} = 32$; $N_{60\ \mathrm{kg}} = 57$, $N_{80\ \mathrm{kg}} = 40$, $N_{100\ \mathrm{kg}} = 84$, $N_{120\ \mathrm{kg}} = 40$ and $N_{140\ \mathrm{kg}} = 39$). Pigs were weighed weekly, and slaughtering was scheduled for the week following the predefined target weight of each slaughter weight category. The day before scheduled slaughtering, the pig was weighed again to ensure it had reached the target weight. In runs 1 and 2, entire males, females and castrates were used and sexes were perfectly balanced across dietary treatments and slaughter categories (Table 2). In run 3, only females and castrates were raised and in run 4 only entire males.

2.2 | Traits in the study

All variables used in the present study are presented in Table 3. We included measurements for the empty body (total body without intestinal and bladder contents) as well as the carcass (total body without viscera and intestine, hair, hooves, blood and bile) representing both biological and economic importance. Pigs entered the experiment at a live weight of 20 kg. From that point on, individual daily feed intake was recorded. Pigs were weighed once a week. The exact N and P contents of the diets were repeatedly controlled during the experiment by using chemical analyses described by Ruiz-Ascacibar et al. (2017). The N and P contents of the empty body (*NEmptyBody* and *PEmptyBody*, respectively) and the carcass (*NCarcass* and *PCarcass*, respectively) were determined through chemical analyses after slaughtering following the protocol described by Ruiz-Ascacibar et al. (2017). To obtain a baseline of N deposition for each sex at the start of the experiment, 38 piglets (12 females, 12 castrates and 14 entire males) were slaughtered at approximately 20 kg live weight (20.98 kg ± 1.85 kg, mean and standard deviation). The average N (or P) content per kg live weight was then multiplied with the actual (precisely weighed) live weight of each individual at the time it entered the experiment to obtain an estimate of its N and P contents before the start of the experiment (*N20kgEB and P20kgEB* or *N20kgCarc and P20kgCarc*). The resulting N and P retention values in the empty body or carcass were then divided by the total dietary N and P intake values. *NIntake* (or *PIntake*) is the total dietary N (or P) intake during the days on feed. The variables of interest, N efficiency of the empty body (*NEffEB*) and N efficiency of the carcass (*NEffCarc*), were calculated following Ruiz-Ascacibar et al. (2017). Thus, the N efficiency of the empty body was calculated as … and the N efficiency of the carcass as (the latter part should be inserted between the formulas).

$$NEffEB = \frac{NEmptyBody - N20\mathrm{kg}EB}{NIntake}$$

$$NEffCarc = \frac{NCarcass - N20\mathrm{kg}Carc}{NIntake}$$

P efficiency of the empty body (*PEffEB)* and P efficiency of the carcass (*PEffCarc*) were calculated in the same way. Since the data set includes individuals of various age and weight classes, it was necessary to include age and live weight as fixed effects (Table 3). However, a previous analysis showed that age was highly correlated with live weight (Spearman's rank

TABLE 2 Distribution of sexes across dietary treatments and slaughter categories were balanced in experimental runs 1 and 2

	Males	Females	Castrated
Run 1			
Total	24	24	24
Control	12	12	12
Treatment	12	12	12
40 kg	4	4	4
60 kg	4	4	4
80 kg	4	4	4
100 kg	4	4	4
120 kg	4	4	4
140 kg	4	4	4
20 kg (baseline)	4	4	4
Run 2			
Total	24	24	24
Control	12	12	12
Treatment	12	12	12
40 kg	4	4	4
60 kg	4	4	4
80 kg	4	4	4
100 kg	4	4	4
120 kg	4	4	4
140 kg	4	4	4
20 kg (baseline)	4	4	4
Run 3			
Total	0	44	44
Control	0	22	22
Treatment	0	22	22
40 kg	0	4	4
60 kg	0	8	8
80 kg	0	8	8
100 kg	0	8	8
120 kg	0	8	8
140 kg	0	8	8
20 kg (baseline)	0	4	4
Run 4			
Total	62	0	0
Control	22	0	0
Treatment	40	0	0
40 kg	0	0	0
60 kg	18	0	0
80 kg	0	0	0
100 kg	44	0	0
120 kg	0	0	0
140 kg	0	0	0
20 kg (baseline)	6	0	0

Note: Females and castrates were used in experimental run 3, and entire males were used in run 4. In run 1, two boars from the PREMO® breed were used to produce crossbred terminal piglets of all sexes.

correlation coefficient $\rho = 0.914$, $p < .001$). We therefore used the residuals of a linear regression of age on live weight (*residuals live weight*) in the present analyses to avoid collinearity between fixed effects. Similarly, we used the residuals of the linear regression of treatment on age (*residuals age*) because age and treatment were weakly correlated (Spearman's rank correlation coefficient $\rho = 0.075$, $p = .200$).

To assess whether trade-offs or potential for co-selection between N efficiency and growth performance existed, we calculated ADG as

$$\mathrm{ADG} = \frac{\text{slaughter weight} - \text{weight at 20 kg}}{\text{slaughter age} - \text{age at 20 kg}}$$

We also estimated genetic parameters for FCR, which was computed as

$$\mathrm{FCR} = \frac{\text{average daily feed intake during days on feed}}{\text{ADG of days on feed}}$$

2.3 | Statistical analyses

2.3.1 | Heritability and litter effect estimation

We used R software V 3.6.0 (R Core Team, 2019) for all statistical analyses. We estimated the genetic and environmental variance components of N and P efficiencies by using a univariate (single-trait) mixed-effect animal model, which allows for variance structures to be associated with pedigrees (Henderson, 1984; Lynch & Walsh, 1998). We used the R package *pedantics* V 1.7 (Morrissey & Wilson, 2010) to construct a multigenerational pedigree including 502 individuals and to compute pedigree statistics, such as inbreeding and pairwise relatedness. For 294 individuals, information on N and P efficiency phenotypes was available, and the remaining 208 individuals provided pedigree links between individuals with efficiency data. None of the individuals with efficiency data had unknown parents. Individual pedigrees went back at least one generation and at most 10 generations (for more details, see Figures S1 and S2, and Table S3). Twenty-four per cent of the pairwise coefficients of relatedness were non-zero, and 7% were greater than or equal to 0.125. The mean relatedness was 0.025 (0.104 excluding coefficients of relatedness equal to zero), and the pedigree contained 672 links between full sibs, 245 between maternal and 315 between paternal half sibs. Thirteen per cent of the individuals had a non-zero coefficient of inbreeding (average 0.001).

We fitted the Gaussian animal models by using the Markov Chain Monte Carlo generalized linear mixed model package in R (MCMCglmm V 2.26; Hadfield, 2010), using the model formula

$$\boldsymbol{y} = \boldsymbol{X}\boldsymbol{b} + \boldsymbol{Z}_a\boldsymbol{a} + \boldsymbol{Z}_c\boldsymbol{c} + \boldsymbol{e}$$

TABLE 3 Variables from the four experiments that were used in this study

Variable	Used in/for	Description
NEffEB	Variable of interest	The proportion of dietary N that was fixed in the empty body during the experimental phase (20 kg live weight to slaughtering)
NEffCarc	Variable of interest	The proportion of dietary N that was fixed in the carcass during the experimental phase
PEffEB	Variable of interest	The proportion of dietary P that was fixed in the empty body during the experimental phase
PEffCarc	Variable of interest	The proportion of dietary P that was fixed in the carcass during the experimental phase
ADG	Variable of interest	Average daily gain (g/day)
FCR	Variable of interest	Feed conversion rate (g feed:g gain)
Sex	Correction factor (biological variation)	Females, entire males and castrates
Residuals age	Covariate to be used instead of age (biological variation; only used for efficiency traits)	Residuals of linear model age ~ treatment to correct for collinearity of live weight, treatment and age at slaughter
Residuals live weight	Covariate to be used instead of live weight at slaughtering (biological variation; only used for efficiency traits)	Residuals of linear model live weight ~ age to correct for collinearity of live weight, treatment and age at slaughter
Experimental run	Correction factor (experimental variation)	Data were collected during four experimental runs, see Table 1. Accounts for different cohorts/farrowing series as well as different genetics
Treatment	Correction factor (experimental variation)	Control diet or protein-reduced diet (80% of digestible protein and digestible essential amino acid content of control)
Individual ID	Link to pedigree (random effect; included in uni- and multivariate animal models)	Individual animal tracing database number
Sibship ID	Common environmental effect (random effect; included only in univariate models)	Litter identity

where $\boldsymbol{y}$ is a vector of observations of N or P efficiency, ADG or FCR, $\boldsymbol{b}$ a vector of fixed effects experimental run, sex, treatment, residual live weight and residual age in the efficiency models and experimental run, sex and treatment in the models for ADG and FCR (see section 3 in Appendix S1 for more information on the choice of covariates). $\boldsymbol{X}$ is an incidence matrix relating records to fixed effects. $\boldsymbol{a}$ is a vector of random additive genetic effects, and $\boldsymbol{Z_a}$ is the corresponding incidence matrix. $\boldsymbol{c}$ is a vector of random litter effects, and $\boldsymbol{Z_c}$ is the corresponding incidence matrix. We included "individual ID" (animal identity link to the pedigree to estimate) and "sibship ID" (litter identity) in all models as random effects. This model enabled us to partition the phenotypic variance (V_{P}) into its components of additive genetic variance (V_{A}), common environment variance (V_{CE}) and residual variance (V_{ε}), which includes effects of the maternal and the early social environment before mixing of the groups in the pens. Thus, the total phenotypic variance for each trait could be described as $V_{\mathrm{P}} = V_{\mathrm{A}} + V_{\mathrm{CE}} + V_{\varepsilon}$. The proportion of variance explained by the additive genetic variance component, heritability, was computed as $h^2 = \frac{V_{\mathrm{A}}}{V_{\mathrm{P}}}$. Following the same principle, we calculated the litter effect as $\mathrm{CE}^2 = \frac{V_{\mathrm{CE}}}{V_{\mathrm{P}}}$. Heritability and litter effect estimates were corrected for the inclusion of fixed effects in some of the models. We used non-informative priors from an inverse Wishart distribution for the variances and covariances and from a normal distribution for fixed effects (see section 3 in Appendix S1 for detailed information on priors). Priors had a variance parameter $V = 1$ and a degree-of-belief parameter $nu = 0.002$ for the random effects and the residual variance (for details on priors see section 4 in Appendix S1). Both N and P efficiency are proportions which are bound between zero and one, and hence not normally distributed. However, because their means ranged between 0.38 and 0.47 and their tails were flat close to zero and one, we treated them as normally distributed (see Figure S3). All traits and all continuous covariates were centred and scaled so that the resulting variable had a mean of zero and a standard deviation of one to facilitate the convergence of models. However, for better readability, we use the untransformed variables to present the influence of fixed effects on the traits. We ran the models with 2,000,000 iterations, of which we discarded the first 100,000 as burn-in and a thinning interval of 1,000. The variance components were estimated as the modes of posterior distributions with 95% credible intervals. We performed visual checks to assess whether the mode of the posterior distribution was clearly separated from zero. Assessing the statistical significance of variance components and derived parameters such as heritability is not trivial, because those effects are bound to be greater than or equal to zero and credible intervals will therefore never be smaller than zero. In addition, in a Bayesian framework, the concept of a clear threshold value for significance does not exist. Thus, in order to aid inference, we computed the percentage of overlap of the posterior distributions with randomly generated null distributions. Null distributions were obtained by randomly permuting the variable vector (Araya-Ajoy & Dingemanse, 2017). We calculated the overlap of the real posterior distribution with the null distributions by subtracting the proportion of differences >0 from 1 to obtain the number of cases when the value of the real posterior distribution was larger than the value of the null distribution. We considered an overlap of <5% as clearly different from zero but note that this is an arbitrary threshold and could thus be defined differently. We have chosen this threshold to be consistent with frequentist hypothesis testing.

We ran each model an additional three times to ensure that the estimates obtained by the original model are replicable under the same model specifications. To ensure model convergence, sufficient length of the posterior distribution and independence of each estimate in the posterior distribution from the previous ones (i.e. no autocorrelation), we first visually assessed the trace plot of the posterior distribution of each model. Second, we performed the Heidelberger and Welch's convergence diagnostic of the R package coda V 0.19-2 (Plummer, Best, Cowles, & Vines, 2006) as a measure of convergence (half-width test passed). Third, we computed the autocorrelation (*autocorr* function in coda) of elements of the chain (lag = 1,000), which we required to be <0.1. Finally, we checked whether the size of the posterior distribution adjusted for autocorrelation, that is after removing autocorrelated items, was >1,000 (*effectiveSize* function in coda). We used code from the multi-platform tool "raincloud plots" (Allen, Poggiali, Whitaker, Marshall, & Kievit, 2018) to produce plots of estimates of traits in Figure 1.

2.3.2 | Genetic and phenotypic correlations

To investigate whether N efficiency was genetically and phenotypically correlated with P efficiency, ADG and FCR, we calculated the additive genetic and common environment covariances from bivariate (two-trait) models, which included animal identity (individual ID) as a random effect. We included the fixed effects experimental run, residual live weight, residual age, sex and dietary treatment in these models, but not their interactions, to avoid over-parameterization. The fixed effects of residual age and residual live weight were not included in the bivariate models containing ADG or FCR. We ran the models with weakly informative parameter-expanded priors (Gelman, 2006) with a variance of 1 for each efficiency trait and each variance component as well as the residual, and a degree-of-belief parameter equal to the dimensions of the variance–covariance matrix ($V = \text{diag}(2)$, $nu = 2$, alpha.mu = c(0,0), alpha.V = diag(2)*1,000) following appendix B in de Villemereuil, Gimenez, and Doligez (2013). Details on priors can be found in the section 4 in Appendix S1. Additive genetic and residual covariances were calculated as the mode of the posterior distribution with 95% credible intervals. Correlations were computed by rescaling covariances by the variances. Because correlation estimates can range from −1 to 1, we considered estimates with 95% credible intervals that did not include zero as clearly positive or negative. We ran all models for a total of 10,000,000 iterations, removed the first 1,500,000 iterations as burn-in to ensure stable chain convergence and sampled every 5,000th iteration, which resulted in a chain length of 1,700. Quality control was done as described for univariate models. To check whether the estimates were robust, we ran each model an additional three times.

3 | RESULTS

3.1 | Descriptive statistics of traits

Descriptive statistics for nutrient efficiency traits are given in Tables 4 and 5. As expected, N efficiency in the carcass was lower than that in the empty body (Welch two-sample t test, $t = 23.138$, $df = 581.07$, $p < .001$). The same was true for P efficiency (Welch two-sample t test, $t = 3.572$, $df = 584.38.31$, $p < .001$). The ADG over all live weight categories was 830 g/day. The ADG continuously increased

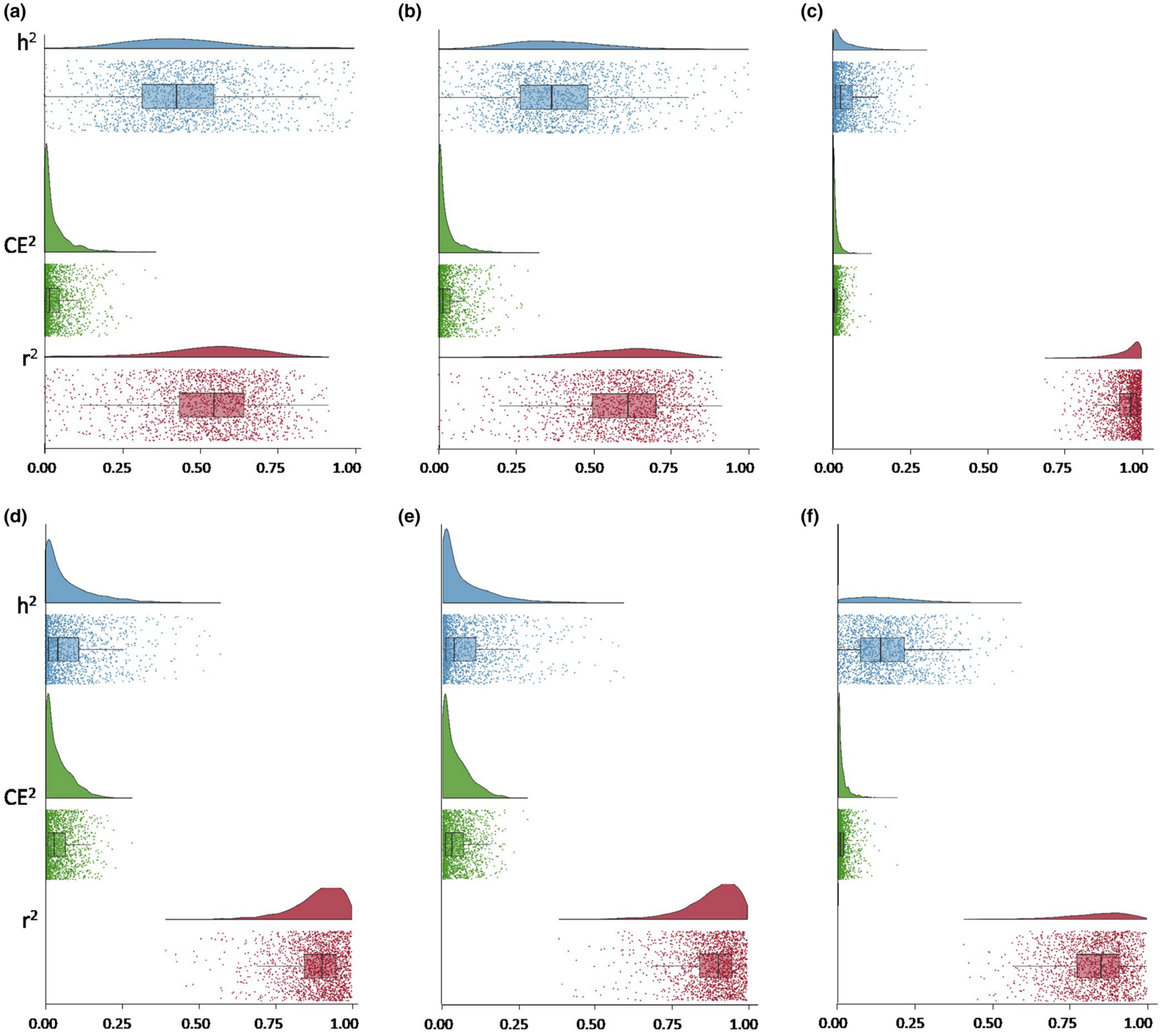

FIGURE 1 Variance decomposition of nitrogen and phosphorus efficiency. Heritability (h^2) is depicted in blue, litter effect, that is common environment effect (CE^2), in green and the proportion of unexplained (residual) variance (r^2) in red. Posterior distributions of the respective variance components are presented as probability density functions (upper part of each panel). Points representing single estimates (mode of posterior distribution) are shown together with a box plot (with median, interquartile range and 5th to 95th percentile range). (a) nitrogen efficiency in the empty body, (b) nitrogen efficiency in the carcass, (c) average daily gain, (d) phosphorus efficiency in the empty body, (e) phosphorus efficiency in the carcass, (f) feed conversion rate

with increasing live weight and peaked at 950 g/day at 140 kg live weight. The average FCR was 2.5 kg feed/kg live weight and continuously increased with increasing live weight (Table 4).

3.2 | Genetic parameters of efficiency and growth traits

All univariate quantitative genetic models fulfilled the quality control criteria, and hence, the estimates could be interpreted. Models that corrected for the inclusion of fixed effects (see section 6 in the Appendix S1 for details) yielded lower estimates than those without the correction (Table S4). However, in order to follow the usual form of reporting, we present uncorrected results below. Most estimates were stable between different runs of the same models, except for N efficiency in the carcass, for which we found the greatest deviations between the original model and the repeated runs and among repeated runs, and FCR, where the absolute difference between runs was 0.08 on average (Table S5, section 7 in Appendix S1). N efficiency of the empty body was

TABLE 4 Descriptive statistics for nitrogen efficiency (*NEff*) and phosphorus efficiency (*PEff*) of the empty body and the carcass for the overall data set and for each category (target weight for slaughter)

			Empty body		Carcass	
Trait	**Category**	***N***	**Mean**	***SD***	**Mean**	***SD***
NEff	Overall	294				
	40	32	0.48	0.07	0.37	0.07
	60	57	0.48	0.05	0.38	0.05
	80	40	0.48	0.04	0.39	0.04
	100	85	0.47	0.04	0.38	0.03
	120	40	0.47	0.04	0.39	0.04
	140	40	0.44	0.05	0.36	0.04
PEff	Overall	294				
	40	32	0.53	0.12	0.49	0.12
	60	57	0.46	0.08	0.44	0.07
	80	40	0.48	0.07	0.46	0.07
	100	85	0.46	0.08	0.44	0.08
	120	40	0.47	0.06	0.45	0.06
	140	40	0.43	0.06	0.42	0.06

Abbreviation: *N*, number of individuals in the respective category.

TABLE 5 Descriptive statistics for average daily gain (ADG) and feed conversion ratio (FCR) for the overall data set and for each category (target weight for slaughter)

Trait	**Category**	***N***	**Mean**	***SD***
ADG (kg/day)	Overall	294		
	40	32	0.68	0.10
	60	57	0.77	0.08
	80	40	0.83	0.12
	100	85	0.83	0.12
	120	40	0.89	0.10
	140	40	0.95	0.10
FCR (g feed:g gain)	Overall	294		
	40	32	2.23	0.27
	60	57	2.34	0.27
	80	40	2.40	0.20
	100	85	2.56	0.31
	120	40	2.66	0.18
	140	40	2.76	0.21

Abbreviation: *N*, number of individuals in the respective category.

clearly heritable ($h^2 = 0.41$ [0.12, 0.87] mode of the posterior distribution and 95% credible intervals in square brackets). The lower limit of the credible interval for N efficiency of the carcass was very close to zero ($h^2 = 0.36$ [0.07, 0.72]). Both posterior distributions were visually clearly separated from zero (Figure 1), and in 98.7%, the real posterior distribution for heritability in the empty body yielded larger values than the null distribution for heritability (98.5% for the carcass (Table 6, Figure 2). The heritability of P efficiencies of empty body and carcass was close to zero (0.003 [4×10^{-4}, 0.27] and 0.003 [3×10^{-4}, 0.26]. The posterior distributions of heritability of P efficiency and ADG were close to zero, and the values of the real and the null posterior distributions were largely overlapping (Figure 2, Table 6). We found evidence for a low heritability of FCR, but its posterior distribution was not clearly separated from zero (Figures 1 and 2, Table 6). For all traits, the litter effect was very small (Figure 1); consequently, the posterior distributions were close to zero and the overlap with a null distribution was large (Table 6; Figure 2).

3.3 | Genetic and environmental correlations

The genetic correlations between N efficiency and P efficiency were generally high and positive but had wide credible intervals that even included zero in the empty body (Table 7A). At the residual level, correlations were moderately positive. Phenotypic correlations were also positive. We found a loose negative phenotypic correlation of N efficiency and ADG, but there was no evidence of a genetic correlation (Table 7B). N efficiency was negatively correlated with FCR genetically, and there was an intermediate negative phenotypic correlation (Table 7C). Repeated runs of correlations yielded consistent results in terms of the sign of the coefficient or whether the credible interval included zero (Table S6).

TABLE 6 Point estimates (modes of the posterior distributions) and 95% credible intervals (highest posterior density intervals) of heritability and litter effect estimates

	Heritability (h^2)		Litter effect (CE^2)	
	Estimate	% Overlap null	Estimate	% Overlap null
NEff empty body	**0.406 [0.117, 0.873]**	**1.33**	0.002 [3×10^{-4}, 0.122]	43.32
NEff carcass	**0.357 [0.072, 0.719]**	**1.48**	0.002 [3×10^{-4}, 0.110]	42.08
PEff empty body	0.003 [4×10^{-4}, 0.266]	35.84	0.002 [3×10^{-4}, 0.128]	32.79
PEff carcass	0.003 [3×10^{-4}, 0.264]	31.88	0.002 [3×10^{-4}, 0.138]	30.28
ADG	0.002 [3×10^{-4}, 0.148]	35.65	0.001 [2×10^{-4}, 0.034]	56.97
FCR	0.103 [3×10^{-4}, 0.341]	12.38	0.001 [3×10^{-4}, 0.053]	54.11

Note: The percentage of overlap, that is the proportion of estimates from the real model that were not larger than the estimates from the null distribution), are presented. Estimates that can be considered clearly different from zero (<5% overlap with null distribution) are printed in bold.

Abbreviations: ADG, average daily gain; FCR, feed conversion ratio; NEff, nitrogen efficiency; PEff, phosphorus efficiency.

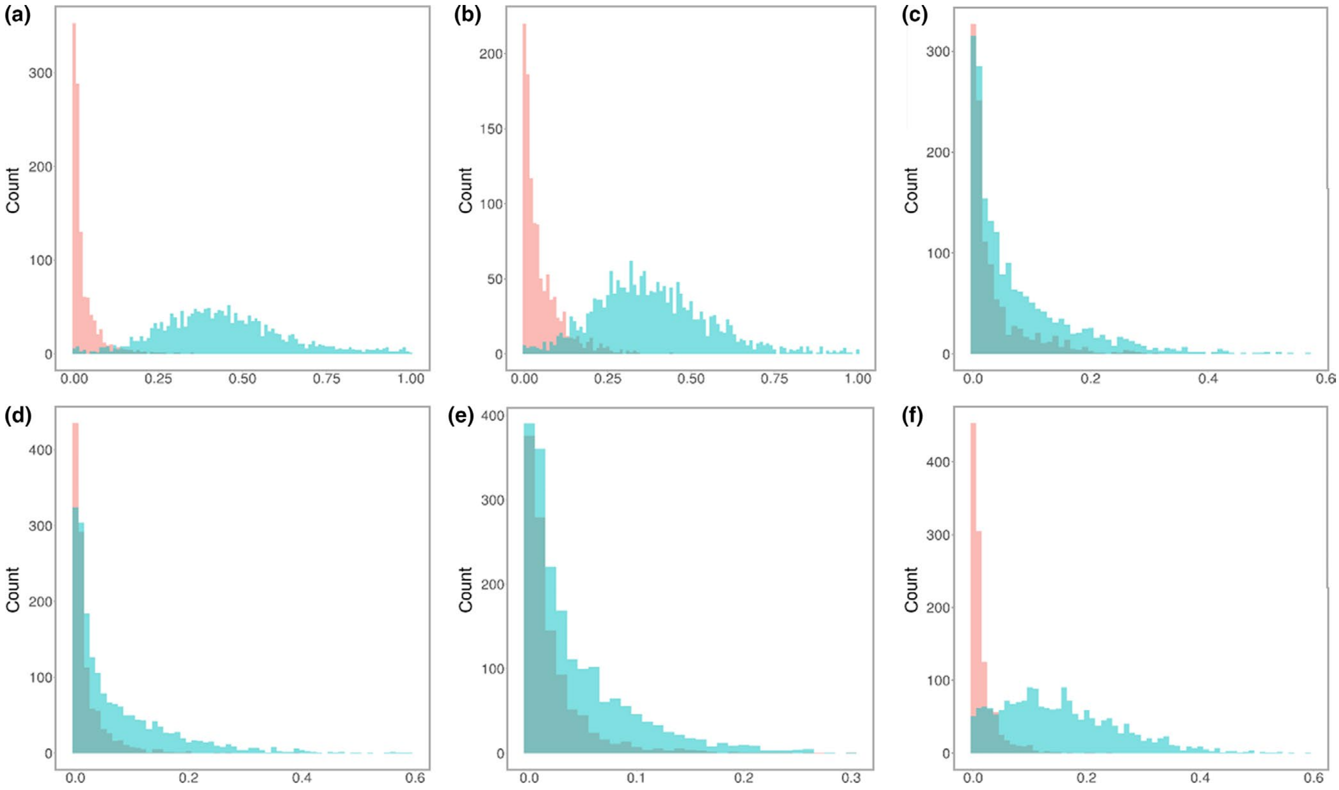

FIGURE 2 Overlap of real distribution (turquoise) and null distribution obtained by permutation of the dependent variable vector (pink). (a) Nitrogen efficiency empty body, (b) nitrogen efficiency carcass, (c) phosphorus efficiency empty body, (d) phosphorus efficiency carcass, (e) average daily gain (ADG), (f) feed conversion ratio (FCR)

4 | DISCUSSION

In this preliminary study, we show a potential to select N-efficient pigs. This finding has important implications for the breeding of more sustainable livestock by reducing the emission of N compounds in pig manure. The predicted increase in the global human population will result in an increased demand and competition for protein sources for humans and livestock (Lassaletta et al., 2019). N-efficient pigs can help to alleviate this conflict. Furthermore, increasing N efficiency in pigs will facilitate conventional and organic pig production by enabling modification of the composition of feed rations to include less raw protein and synthetic amino acids. This could lead to a reduction in demand for protein sources grown specifically for animal feed, such as soya beans. In addition, by-products of human food production could be increasingly used as protein sources in pig feed, for example rapeseed meal. Shifting the focus from FCR to N

TABLE 7 Genetic, litter, residual and phenotypic variances and covariances of nitrogen and phosphorus efficiencies (A). Estimates for the empty body are displayed on the left, those for the carcass on the right. (B, C) Genetic, litter, residual and phenotypic variances and covariances of nitrogen efficiency and average daily gain (ADG) (B) and of nitrogen efficiency and gain-to-feed ratio (FCR) (C). The diagonal shows the standardized variances (e.g. heritability in the case of genetic correlations) and correlations are shown below the diagonal

	Empty body			**Carcass**	
A	***NEff***	***PEff***		***NEff***	***PEff***
Genetic					
NEff	0.112 [0.046, 0.227]	0.002 [−0.035, 0.241]	*NEff*	0.083 [0.028, 0.189]	0.078 [−0.019, 0.244]
PEff	0.725 [−0.109, 0.975]	0.001 [4×10^{-9}, 0.108]	*PEff*	**0.836 [0.034, 0.998]**	0.001 [2×10^{-7}, 0.093]
Residual					
NEff	0.231 [0.141, 0.306]	0.220 [0.074, 0.338]	*NEff*	0.291 [0.167, 0.331]	0.215 [0.082, 0.366]
PEff	**0.333 [0.174, 0.499]**	0.336 [0.244, 0.415]	*PEff*	**0.303 [0.146, 0.473]**	0.323 [0.260, 0.414]
Phenotypicc					
NEff	0.781 [0.683, 1.008]	0.318 [0.197, 0.419]	*NEff*	0.886 [0.727, 1.030]	0.304 [0.207, 0.431]
PEff	**0.379 [0.262, 0.465]**	0.856 [0.710, 1.008]	*PEff*	**0.354 [0.258, 0.461]**	0.892 [0.750, 1.052]
	ADG			**FCR**	
B	***NEff***	**ADG**	**C**	***NEff***	**FCR**
Genetic					
NEff	0.162 [0.083, 0.362]	-1×10^{-4} [−0.173, 0.044]	*NEff*	0.303 [0.151, 0.661]	−0.065 [−0.279, 0.018]
ADG	−0.525 [−0.911, 0.389]	0.001 [3×10^{-7}, 0.111]	FCR	**−0.699 [−0.897, −0.042]**	0.161 [0.012, 0.461]
Residual					
NEff	0.339 [0.199, 0.469]	−0.024 [−0.148, 0.084]	*NEff*	0.726 [0.458, 1.016]	−0.405 [−0.576, −0.274]
ADG	−0.054 [−0.204, 0.131]	0.524 [0.398, 0.619]	FCR	**−0.607 [−0.729, −0.476]**	0.991 [0.700, 1.27]
Phenotypic					
NEff	0.934 [0.756, 1.124]	−0.072 [−0.189, 0.024]	*NEff*	0.9 00 [0.782, 1.124]	−0.502 [−0.675, −0.423]
ADG	**−0.078 [−0.197, 0.024]**	0.917 [0.779, 1.099]	FCR	**−0.565 [−0.648, −0.487]**	0.953 [0.807, 1.135]

Note: Unstandardized covariances are shown above the diagonal. Estimates are the modes of the posterior distributions, and credible intervals (in brackets) are the 95% highest posterior densities. Correlations for which the credible intervals did not span zero are printed in bold.

Abbreviations: ADG, average daily gain; FCR, feed conversion ratio; NEff, nitrogen efficiency; PEff, phosphorus efficiency.

and P efficiencies offers the opportunity to change the paradigm in livestock breeding to take into account the limitation of resources. While in current breeding programmes sufficient nutrients are provided, effort should be directed at selecting animals that cope well with nutrient restriction in future (Stoll & Ruiz-Ascacibar, 2015).

4.1 | Heritability and litter effects

We found that heritabilities of N efficiency in the empty body and in the carcass were intermediate and clearly separated from zero, indicating that this trait has the potential to be implemented in breeding programmes. The heritability estimates of N efficiency for the empty body and the carcass were only slightly different; thus, the environmental variance was equally important in both traits. This contrasts the findings of a previous analysis of the same data set (see section 9 in Appendix S1 for details) in which the heritability in the carcass was half that of the empty body (Table S7; Kasper, Ruiz-Ascacibar, Stoll, & Bee, 2019). In the previous analysis, the means of N efficiency in the empty body and the carcass were clearly different, with a lower value in the carcass. The organs and blood contain an important fraction of proteins and hence N, which is not taken into account in the efficiency measure for the carcass, and their proportion to the carcass changes with live weight (Ruiz-Ascacibar, Stoll, & Bee, 2019). However, the credible intervals of heritability estimates in the current analysis are larger than in the previous analysis (Table 6, Table S7).

We did not detect a notable heritability of P efficiency, neither in the empty body nor in the carcass. The majority of heritability estimates in the posterior distribution, which was heavily right-skewed, were rather low; however, some estimates were as high as 0.78 in the empty body and even 0.99 in the carcass. It might be possible that the heritability of P efficiency was underestimated due to a weaker performance of the models for this variable or a higher impact of measurement error when determining P content, which is around five times lower than N content; thus, measurement error might have more impact on P than on N content. It is also possible that the prior of the Bayesian animal model overly influenced the estimate. In contrast to other studies that reported heritabilities of ADG and FCR in pigs ranging from 0.05 to 0.48 and 0.22 to 0.40 for ADG and FCR, respectively (Kavlak & Uimari, 2019; Nascimento, Nascimento, Dekkers, & Serão, 2019; Saintilan et al., 2013; Shirali, Varley, & Jensen, 2018; Silva, Lopes, Lopes, & Gasparino, 2019), our heritability estimate of ADG was close to zero and the one of FCR was rather low. Several QTLs were identified for ADG (Shirali et al., 2013; Silva et al., 2019) and FCR (Reyer et al., 2017; Silva et al., 2019), indicating a genetic basis of these traits. One possible reason why our estimates for ADG and FCR were comparably low could be the relatively small sample size of our study. The estimates reported above stem from studies with 750 to several thousands of individuals, but a recent study on 71 individuals reported a very low heritability of FCR ($h^2 = 0.019$; Belous, Sermyagin, Kostyunina, Trebunskikh, & Zinovieva, 2018). In general, a lack of power in our study could have caused the modes of the posterior distributions of P efficiency, ADG and FCR to be relatively close to zero. Especially for FCR in our study, the posterior distribution was very wide and some estimates were around 0.62, hinting that an increase in sample size could refine the estimate.

The litter effect in our analysis was close to zero for all traits, which is in contrast to the previous analysis, in which we found a weak but clear effect on N efficiency (Kasper et al., 2019). The small litter effects we found in the previous analysis disappeared after scaling and centring the dependent variable (Table 6, Table S7). It is likely that non-genetic maternal effects, for instance the influence of maternal physiology on the metabolism of the offspring, were distributed over both litter effect and residual variance since there were only six sows with more than one litter in the data set. This means that, beyond genetic effects, pigs growing up in the same preweaning environment were not more similar than those growing up in separate litters. Hence, it can be assumed that environmental influence that is not connected to sharing the same environment is more important than the shared preweaning environment. The gut microbiome has been suggested to be linked to efficiency in terms of lower residual feed intake (McCormack et al., 2017). Here, we cannot assess whether the transfer of gut microbiota between littermates is an important factor shaping efficiency traits. Littermates stayed together during the suckling period and until 22–42 days after birth and were regrouped and mixed with other litters after this time. This period coincides with the developmental phase during which the community structure of the intestinal microbiome consolidates and cohabiting piglets show strong inter-individual similarities of microbial community structure (3–4 weeks after birth; Chen et al., 2017; Thompson, Wang, & Holmes, 2008). Thus, this effect would likely be included in the residual variance in our study.

In future, in addition to improved estimation of genetic parameters, information on the relationship between N efficiency and genetic loci (single nucleotide polymorphisms) will also be needed to accelerate breeding progress through genomic selection. It should be noted that the number of breeding boars and sows in this data set was small, which is noticeable in the relatively wide credible intervals. The estimates should therefore be interpreted with caution, because the small number of different parental genotypes may influence their values. Further experiments with a larger number of individuals and higher genetic variability are therefore necessary for more reliable estimates.

4.2 | Genetic correlations

We found positive phenotypic correlations between N and P efficiencies, and the credible interval of the carcass estimate did not span zero. However, despite their high values, the genetic correlation coefficients had very wide credible intervals. This finding was not surprising because only a small portion of the posterior distribution of P efficiency itself supported evidence of genetic variance (Figure 1c,d). Pigs with high N efficiency had also higher P efficiency; however, it is unclear whether the phenotypic correlations are underlain by genetic ones. N-efficient pigs gained more weight daily, but this positive relationship seemed to be entirely driven by environmental influences, such as dietary treatment, sex, target weight and experimental run (Figure S4). Pigs with high N efficiency were better at converting feed into body mass as indicated by a negative phenotypic correlation of N efficiency and FCR. This relationship was also apparent on the genetic level and supports the life-cycle assessment of the relationship N efficiency–FCR (Monteiro et al., 2019).

4.3 | Influence of dietary treatments on traits

Different diets were fed to the pigs in the experimental runs that supplied the data for this study (details on exact contents can be found in Table S2). These experiments were designed to investigate the effects of a lower-protein/lower essential amino acid diet on growth, N and fat deposition rate and ultimately N efficiency (Ruiz-Ascacibar et al., 2017; Ruiz-Ascacibar, Stoll, & Bee, 2019; Ruiz-Ascacibar, Stoll, Bee, et al., 2019; Ruiz-Ascacibar, Stoll, Kreuzer, & Bee, 2018). In brief, the effect of diet on efficiency and other traits is mediated by sex and live weight. The protein deposition rate of entire males increased with live weight when proteins were supplied as recommended (Ruiz-Ascacibar et al., 2018). By contrast, protein deposition rate decreased with increasing live weight in females and castrates. When fed a protein-reduced diet, entire males had a constant protein deposition rate, which was similar to females and castrates but distinctly lower to entire males fed the control diet. In the current data set, which included also runs 3 and 4, we found a similar pattern for N efficiency and P efficiency (Figure S5, Table S8). ADG was principally influenced by live weight, but sexes responded slightly differently to the dietary treatment, with females and castrates gaining more weight, which was probably due to increased fat deposition (Figure S5; Ruiz-Ascacibar et al., 2018). FCR also increased with weight, with castrates increasing at a steeper rate when protein was not restricted (Figure S5). Taken together, these results suggest that, in addition to selective breeding, nutrient efficiency could be further increased by reducing the protein content of the feed for females and castrates, implementing an optimal slaughter weight and raising entire males (or opting for late immunocastration).

4.4 | Trait measurements

Nutrient efficiency is a trait that is exceptionally difficult to measure because of the high costs and the amount of labour and time involved in chemically determining nutrient content of empty body, carcass or excreta. However, a prerequisite for more robust and precise estimation of heritability and genetic correlations and eventual implementation into breeding programmes is high-throughput phenotyping. Thus, the development of precise, fast and non-invasive methods with low operating costs and low operator bias using proxies is of utmost importance. Body composition can serve as a proxy for N or P content of the carcass since these values can be calculated from lean meat content, which can be obtained from the weight of primal cuts via linear combination (Saintilan et al., 2013), and from bone mass (Skiba, Weremko, Sobol, & Raj, 2015; Teegarden et al., 1998). However, dissections suffer from operator bias (Marcoux, Faucitano, & Pomar, 2005) and are labour-intensive. The use of metabolic cages to measure N or P contents in excreta (de Verdal et al., 2011) poses logistic as well as animal-welfare problems. Deuterium dilution techniques to estimate the empty body water content (Landgraf et al., 2006), from which body composition and protein/nitrogen content can be derived with satisfactory accuracy, has previously been applied to the estimation of genetic parameters of body composition (Mohrmann et al., 2006) and nitrogen excretion in pigs (Shirali et al., 2013). The high costs and the need for specific equipment and rigorous standardization of experimental procedures for this technique could present a serious bottleneck for genetic studies. Imaging techniques, such as computerized tomography (CT), magnetic resonance imaging (MRI) and dual-energy X-ray absorptiometry (DXA), could be a way forward to achieve high-throughput phenotyping of body composition (Scholz, Bünger, Kongsro, Baulain, & Mitchell, 2015). CT is already used in industrial breeding programmes (Scholz et al., 2015), and DXA has been previously applied to assess body protein content of pigs by prediction equations derived from regression of DXA values on values from chemical analysis (Mitchell, Scholz, Pursel, & Evock-Clover, 1998).

5 | CONCLUSION

In this study, we present preliminary estimates of heritability and genetic correlation of N and P efficiencies based on wet-chemistry analyses in a Swiss Large White pig population. Our results indicate a genetic basis of N efficiency, but not P efficiency, which could be exploited in breeding programmes, but results should be interpreted with caution. More individuals with phenotypes are needed to provide more accurate estimates. For the implementation of N efficiency in breeding programmes, a method is needed that is better suited for high-throughput phenotyping than chemical analysis. Pigs are among the most important livestock animals worldwide and have a corresponding share in the environmental impact of agriculture. Selective breeding of nutrient-efficient pigs may help mitigate those problems. Higher N and P efficiencies will require lower dietary crude protein and essential amino acid supply and ultimately reduce costs. Eventually, native fodder plants could cover a higher proportion of the protein requirement of pigs. It should be noted that genetic factors explain at best 41% of N efficiency variation and that almost 60% of this variation is influenced by environmental factors. Thus, despite implementing a successful selection for protein efficient pig breeds, efforts must be made in improving management practises like adaption of feed formulations and implementation of precision feeding.

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CONFLICT OF INTEREST

We declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo (Kasper, Ruiz-Ascacibar, Stoll, & Bee, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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