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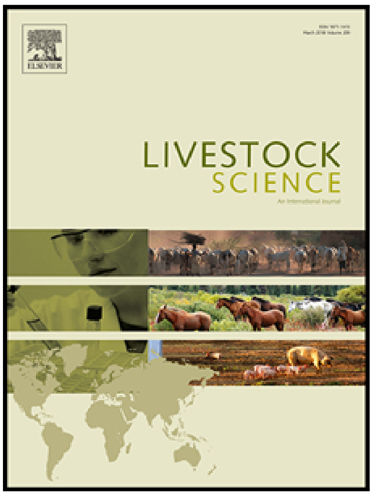

Pedigree relatedness and pseudo-phenotypes as a first approach to assess and maintain genetic diversity of the Walloon Piétrain pig population

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Highlights

- The genetic diversity of the Walloon Piétrain population is still preserved.
- Measures should be implemented to conserve it.
- Multi-dimensional scaling gives insight of genetic links among animals.
- Principal component analysis provides information about breeding objectives.
- Conservation programs should use pedigree, phenotypes and genotypes to succeed.

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Pedigree relatedness and pseudo-phenotypes as a first approach to assess and maintain genetic diversity of the Walloon Piétrain pig population

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Abstract: The breeding of pure Piétrain animals is currently performed in two different contexts: industrial lines and individual breeders. As one of the four main pig breeds worldwide, the Piétrain breed might not be considered to be endangered. However, in Wallonia (southern Belgium), even though the Belgian Piétrain programme aims to preserve the Walloon Piétrain population through cryopreservation of semen of relevant boars, only 10 pure Piétrain breeders remain and produce traditional breeding stock. Current breeders are retiring and no new breeders are replacing them. Moreover, the genetic diversity of the pigs from these individual breeders may highly contribute to the global gene pool of the breed, therefore it is important to assess this diversity. This was done on a local level by using pedigree relatedness but also differences in phenotypes. Pedigree parameters such as effective population size, genetic diversity and inbreeding coefficients were estimated for 219 boars from which offspring performances were recorded at the Walloon test station. A multi-dimensional scaling (**MDS**) was performed based on genetic distances. Considering the current owners of the boars, a principal component analysis (**PCA**) was made on deregressed breeding values (pseudo-phenotypes) based on the performances of their crossbred offspring at the test station. The effective population size was 223, the genetic diversity parameter was 97.96%, while the mean inbreeding coefficient was 2.74%. The MDS identified four main clusters of boars. Two principal components indicated two major directions of selection: growth or meat traits. Genetically close boars did not necessarily show similar performances in their offspring. Different performances for genetically linked animals should reflect the breeding objectives of their owner, a practice that was confirmed by most owners during interviews. Pedigree, phenotypes and genotypes provide complementary information and therefore should be used simultaneously in the implementation of conservation programmes. These first results also showed that the genetic diversity of the Walloon Piétrain population is so far well preserved. However, recommendations need to be developed in order to maintain

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it. For example, boars provided to the progeny-testing scheme should come from equally contributing breeders, allowing the Belgian Piétrain programme to sample boars from a larger variety of animals taking into account genetic and phenotypic diversity. Finally, in-situ preservation of Piétrain diversity will require the development of new tools and mating schemes.

Keywords: breed conservation, deregressed breeding values, genetic distances, principal components

1. Introduction

Modern selection of pigs started between the 18th and 19th centuries through crosses between English indigenous and Chinese pigs. These crosses are the origin of some well-known breeds such as Large White, Landrace and Berkshire (Yang et al., 2017). In the late 19th century, English breeds started to be imported to Belgium to improve local animals. However, the precise origin of the Piétrain pig is still not clear. It is thought to originate from Berkshire and White breeds (e.g. Large White and Landrace) in the first decades of the 20th century in Piétrain, a small town in Wallonia, Belgium (Camerlynck and Brankaer, 1958; Marcq and Lahaye, 1941). The development and extension of the Piétrain breed was driven by the market evolution towards lean meat. In Belgium, during the last decades of the 20th century, this evolution was especially pronounced.

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In current industrial crossbreeding schemes, the Piétrain breed is used almost worldwide as a terminal sire because it confers high leanness and muscling as well as good conformation to its offspring. Piétrain joined other major pig breeds such as Landrace, Large White and Duroc that are intensively used to produce finishing pigs through crossbreeding. The breeding of purebred animals needed for crossbreeding purposes is currently performed in two different contexts: 1) by breeding companies that keep private industrial lines of limited size, 2) by the remaining individual breeders in many countries, which have been strongly decreasing in number, especially during the last decades (e.g. Welsh et al., 2010).

Although the Piétrain breed is normally not considered to be endangered (Henson, 1992), Piétrain populations raised outside of breeding companies are scarce. The genetic diversity of the pigs of these individual breeders may highly contribute to the global gene pool of the breed. This diversity is important to assess because the reduction of this local population could lead to inbreeding depression and dramatic loss of diversity (Robertson, 1961) for the whole breed. Moreover, this limited purebred breeding stock could be at high risk in the case of epizootics (Herrero-Medrano et al., 2013). One example is the current situation in Wallonia, where the small purebred Piétrain population has been threatened since September 2018 by an outbreak of African Swine Fever. In November 2018, an "infected zone" (in the province of Luxembourg, extreme south of Belgium) was defined and divided into two zones according to the identified risk. From the outbreak until December 2019, only cases of infected wild boars have been reported and there are no cases of infected domestic swine. However, all domestic pigs from the "infected zone" were eradicated, as a precautionary measure. Fortunately, this zone did not contain Piétrain pig breeders.

Based on all these elements, we aimed to assess the Walloon Piétrain pig population diversity and to suggest measures to preserve it. The assessment of diversity and the development of conservation programmes can be assessed through pedigree, phenotypes and genotypes. In this study the first two elements were analysed together, while genotypes will be the subject of a second, later, study.

2. Materials and Methods

2.1. Walloon Piétrain breeding

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In Wallonia, purebred Piétrain pigs are traditionally kept in small breeding farms who sell purebred boars to be used in crossbreeding. In this study, each studied boar was assigned to two groups according to its breeder (hereafter called breeder-group) and its current owner (hereafter called owner-group). The hypothesis was that breeders are responsible for mating choices leading to a given animal, i.e., the genetic history of boars. However, breeding objectives are reflected in owners' choices, as they act as nominators for progeny-testing, explained in the next section. In order to clarify identities, an identical breeder- or owner-group number represented the same person, group of persons or company in its role as breeder or owner. Based on available information, the breeders and current owners of progeny-tested boars were determined. Table 1 gives more information about breeders/owners and boars provided to progeny-testing.

Additionally, to correctly interpret the different analyses, Walloon pure Piétrain breeders and owners were interviewed in a semi-directive manner about their policy to provide animals to progeny-testing and their transfers of animals within Wallonia and also across other regions of Europe.

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2.2. Progeny-testing scheme and Belgian Piétrain programme

The current progeny-testing scheme of Piétrain boars was set up in 2009. This programme is run by the Walloon Breeding Association (**awé**) jointly with the Walloon Agricultural Research Centre (**CRA-W**) and Gembloux Agro-Bio Tech, in close collaboration with owners. For this progeny-testing scheme, crossbred progeny of Landrace sows from the CRA-W and Piétrain boars are raised at the station and several traits are recorded. Purebred Piétrain boars whose progeny are to be recorded are nominated by their owners and should reflect their breeding objectives. This was confirmed by interviews with all owners, except owner 1 who nominated a large group of boars without preselection for testing. Selected boars had semen samples taken and mating plans were organised for two recurring groups of Landrace sows from CRA-W with the objective to obtain 18 descendants per boar to be tested at a given moment in time. Offspring were recorded for carcass weight (kg), average daily gain (kg/d), backfat thickness (mm), consumption index (defined as ratio of intake over average daily gain), conformation index and meat percentage. On-farm recording (progeny-tested boars and close relatives) was also performed for live weight (kg), backfat thickness (mm), meat percentage and loin muscle depth (mm). Based on the aforementioned strategy, a total of 10 traits were available for the 219 progeny-tested boars: six recorded on crossbred offspring and four based on on-farm recording. Different models are currently used to generate estimated breeding values (**EBV**) for these progeny-tested boars (Dufrasne et al., 2011). Besides the progeny-testing scheme established in 2009, the awé launched the Belgian Piétrain programme in 2017. This is based on cryopreservation of semen of Walloon Piétrain boars (awé, 2019). For the purpose of this study, the Belgian Piétrain programme was considered to be a boar's owner as they determined which kinds of boars were selected by the programme during the first year of its existence.

2.3. Pedigree analysis

We studied the whole available pedigree of the Piétrain breed in Belgium and, for recent years, in the Walloon region of Belgium. Because of the reorganisation and regionalisation of Belgian agriculture, the Walloon and Flemish parts of the Belgian pigbook were separated, which explains why we only have access to the Walloon pedigree since 2003. Moreover, overall pedigree records were not expected to be very complete before 1980, when the electronic pigbook recording started in Belgium.

Pedigree can be used to assess different parameters such as effective population size (**N_e**) or inbreeding coefficients. The knowledge of these parameters is the first step in defining

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conservation measures (Bosse et al., 2012; Eding et al., 2002). The Piétrain pig pedigree was provided by awé. Total pedigree number of animals, sires, dams, founders, number of generations, mean number of equivalent complete generations and inbreeding coefficient distribution were computed via CFC v1.0 software (Sargolzaei et al., 2006).

In a second part of the pedigree analysis, we studied the specific pedigree of progeny-tested boars. As the progeny-testing scheme was launched in 2009, the objective of this second part of the pedigree study was to estimate different parameters as indicators of recent diversity of Walloon Piétrains. Thus, a total of 219 progeny-tested boars were used for further analysis. The last batch of piglets sired by 5 of these 219 boars entered the station on March 8th, 2018 and they were slaughtered between 175 and 212 days of age. All 219 boars were distributed among breeder-groups, i.e., the person responsible for the mating choice that finally gave birth to them. Number of pigs in the pedigree of progeny-tested boars, maximum and average inbreeding coefficients per breeder-group as well as mean kinship coefficients per breeder-group were also computed via CFC v1.0 software (Sargolzaei et al., 2006). For all progeny-tested boars, the parameters assessed using the optiSel R package (Wellman, 2018) were: number of generations, mean number of equivalent complete generations, mean index of pedigree completeness (**PCI**), kinship coefficients, average inbreeding coefficient, N_e and genetic diversity parameter.

The number of equivalent complete generations was characterised as the sum of the proportion of known ancestors over all traced generations (Wellman, 2018). The PCI was defined as proposed by MacCluer et al. (1983):

$$\frac{2 \times C_{sire} \times C_{dam}}{C_{sire} + C_{dam}} \tag{1}$$

and,

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$$C = \frac{1}{d} \sum_{i=1}^{d} g_i , \tag{2}$$

where C is the contribution of sire or dam, g_i is the proportion of ancestors present in generation i, and d is the total number of generations. In this study, d was fixed to four generations as proposed by Wellman (2018). Parameters linked to pedigree completeness, such as the number of generations, mean number of equivalent complete generations and PCI, are very important for assessments: if ancestors are sufficiently known, other parameters such as genetic diversity or kinship coefficients would be more reliable (Li et al., 2011).

Inbreeding coefficients were defined as the probability that two alleles, randomly chosen from sire and dam, are identical by descent (**IBD)** whereas kinship coefficients were defined as the probability that two alleles, randomly chosen from two individuals, are IBD (Eding et al., 2002; Wellman, 2018). The genetic diversity parameter was computed as 1 minus the mean of kinship coefficients. Finally, the effective population size, N_e, was based on the estimated mean rate of increases in coancestry (Cervantes et al., 2011) by computing:

$$\mathrm{Ne} = \frac{1}{2\overline{\Delta \mathrm{c}}} , \tag{3}$$

where $\overline{\Delta \mathrm{c}}$ was the average of $\Delta \mathrm{c}_{\mathrm{ij}}$ defined as:

$$\Delta \mathrm{c}_{\mathrm{ij}} = 1 - \sqrt[\frac{\mathrm{g_i} + \mathrm{g_j}}{2}]{1 - \mathrm{c}_{\mathrm{ij}}} , \tag{4}$$

with c_{ij} being the kinship between i and j, and $\mathrm{g_i}$,$\mathrm{g_j}$ being the numbers of equivalent complete generations of individuals i and j (Wellman, 2018). Several assumptions were made for N_e: 1) the population is isolated; 2) mating is panmictic; 3) the population growth is linear (Herrero-Medrano et al., 2013).

A classical multi-dimensional scaling (**MDS**) analysis was performed using the cmdscale R function (Gower, 1966). MDS allows the population within and among farms to be structured

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(François et al., 2017). Genetic diversity might be accessed by using an opposite function of kinship coefficients as long as they reflect genetic distances between animals (Laval et al., 2000). In this study, we performed the MDS analysis on a dissimilarity matrix reflecting genetic distances defined as 1 minus the kinship coefficient.

2.4. Pseudo-phenotype analysis

Although pedigree analysis allows us to detect past gene flow, it does not illustrate current breeding decisions that reflect breeding objectives. One possibility is to analyse EBV of boars (n=219) that were nominated in the progeny-testing scheme. As explained previously, with the exception of owner 1, all owners had a policy to nominate boars that corresponded to their breeding objectives. Therefore, according to their current owner, boars were distributed among owner-groups. An identical number for breeder- and owner-group refers to the same physical person or group of persons. The Porcine Artificial Insemination Centre of the Province of Liège (**CIAP**) and the Belgian Piétrain programme were considered to be distinct owners as they are also responsible for nominating animals for progeny-testing. Assessing which types of boars were chosen by the Belgian Piétrain programme during its first year of existence was of particular interest. It was also possible to provide advice to this programme regarding the choice of boars, taking into account the results of this study.

Direct phenotypes of purebred boars were not directly usable for two reasons: 1) they are not always directly recorded on farm and 2) they do not reflect performances in crossbreeding. Moreover, in order to avoid any bias due to differences in reliability due to the regressed nature of EBV, corrected phenotypes should be used. To overcome these limitations, EBV based on performances in crossbreeding were deregressed; i.e., they were divided by their reliabilities (Garrick et al., 2009) in order to obtain pseudo-phenotypes.

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By using the FactoMineR R package (Lê et al., 2008), PCA was further performed to assess the distribution of owner-groups according to pseudo-phenotype values of boars they provided for progeny-testing. The objective of this PCA was to segregate the different owners according to their breeding objectives. Determining which kinds of boars were selected by the CIAP and the Belgian Piétrain programme was also of particular interest. For the PCA, only six pseudo-phenotypes were exploited, i.e., those based on offspring performances. This allowed the use of data that were more uniformly tested and more reliable. For each animal, we took its mean reliability for the six pseudo-phenotypes to be further used in a weighted PCA. Weighting was applied because, even if values were on the same scale after deregression, there were still some major differences in information contents due to differences in reliabilities.

The separation power of the six different pseudo-phenotypes was finally computed to determine on which pseudo-phenotypes the different owners were the most dissimilar. Separation power was defined as the variance among owner-groups divided by the variance within owner-groups (Coghlan, 2019). This analysis was performed using the MASS R package (Ripley, 2019).

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3. Results and Discussion

3.1. Pedigree analysis

In the first part of this study we analysed the available overall Piétrain pedigree. The number of animals in this overall pedigree was 777,321. As expected because of the introduction of electronic pedigree record keeping in 1980, the animals included in the overall pedigree were born between 1970 and 2018, with very few born before 1980. Among these 777,321 pigs, 12,148 boars and 45,307 sows had offspring. We observed that the number of animals registered annually increased up to 1992 when a decreasing trend began to be observed. This may be the first indicator of the start of the decline in purebreeding activity. This behaviour was also reported by Welsh et al. (2010) working with several pedigrees from different pig breeds in the USA. This could indicate a worldwide trend in pig production, probably due to the emergence of breeding companies. In 2003, there was a sharp decrease of the number of animals registered in the part of the Belgian pigbook we had access to. As explained before, this decrease was due to the schism between the Walloon and Flemish parts of the Belgian pigbook. Between 2011 and 2014 a slight increase was observed, likely due to healthy economic conditions (SPF Economie, 2015), but also to good dynamics in Walloon pig breeding. From 2014 to 2017, most likely due to low income earned by breeders (SPF Economie, 2015), the number of animals registered annually decreased from 2,144 to 1,181. Therefore, the Walloon Piétrain population is currently undergoing a strong bottleneck. Supplementary Figure 1 provides the distribution of registered Piétrain pigs from 1970 to 2017.

In the overall pedigree, a total of 10,557 animals were founders, of which 8,031 had offspring (2,220 boars and 5,811 sows). For the non-founders, more than 99% of animals had both known sires and dams. None of the animals had an inbreeding coefficient higher than 41%, and ~99% had inbreeding coefficients smaller than 20%. The maximum level of inbreeding was small compared to other breeds reported by Welsh et al. (2010) for the USA, with 51% for Landrace and 65% for Large White. In our population the average inbreeding was estimated to 4.15%. These values indicate that inbreeding may not yet be an issue in the studied population. However, our pedigree was incomplete before the 1980s, so inbreeding levels may be underestimated. The analysis of the number of generations indicated that there were, on average, 10.48 generations of animals with a range from 0 (founders) to 29 generations (longest ancestral path). The longest ancestral path was greater than the number of generations for breeds reported in other studies (e.g. 17-19 range in Welsh et al., 2010).

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The mean number of equivalent complete generations ranged from 0 to 16.72 with a mean of 5.78.

The extracted pedigree for the 219 progeny-tested boars consisted of 7, 333 animals. The mean PCI for the 219 boars was 95.14% (ranging from 25% to 100%). The distribution of the PCI is provided in Supplementary Figure 2. The vast majority of these boars had a PCI higher than 60%, which was considered sufficient for a pedigree study according to Li et al. (2011). However, some boars had limited pedigree information, especially imported ones. The known number of generations ranged from 1 to 28 (longest ancestral path) with a mean of 22.11. On average, the mean number of equivalent complete generations for progeny-tested boars was 9.97 (ranging from 1.0 to 15.3). The mean number of equivalent complete generations seemed to be appropriate for a pedigree completeness investigation (Wellman, 2018). The means of number of generations and of mean number of equivalent complete generations indicated that the pedigree of progeny-tested boars is more complete, on average, than those obtained from the overall pedigree.

There were 19 breeder-groups of boars: five from Flemish breeders (n=12 animals), one from Germany (n=4 animals) whose different German breeders were not individually identified in the database, and 13 from Walloon breeders (n=213 animals). Flemish and German breeder-groups were kept to determine relationships of these populations with Walloon Piétrain pigs. The average kinship coefficients within each breeder-group, by excluding self-relationships, ranged from 1.11% to 40.00%. The mean inbreeding coefficient for the boars was relatively small (2.74%). All breeder-groups had average inbreeding coefficients under 10%. However, by looking at the maximum inbreeding coefficient, five out of 19 breeder-groups (2, 4, 7, 8 and 13) provided boars with inbreeding coefficients equal to or higher than 10%, with the maximum inbreeding coefficient equal to 21% (breeder-group 4, n=11 boars). This means that some breeders, intentionally or not, lean towards higher levels of inbreeding. This fact can be

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seen to be a management strategy since breeders may tend to send optimal boars for crossbreeding. In this situation, a high individual inbreeding coefficient of the parent would not be apparent in the offspring. Moreover, pedigree information from 1950 to 1970 were not available, which could underestimate inbreeding coefficients. A study from Hanset (1973) assessed the inbreeding coefficient of animals in this earlier part of the pedigree. For boars of which both sire and maternal grand-sire were known, it decreased from 15.62% in 1951 to 5.28% in 1960. At the beginning, two remarkable boars (Max 7B1 and its son Robert 8B43) were intensively used by breeders leading to high levels of inbreeding. Then, in the 1960s other boars, related to Max and Robert but to a lesser extent, were used as sires which lead to decreased levels of inbreeding. The level of inbreeding found during the 1950s, at the start of pedigree registrations, was however smaller than those reported for other breeds (e.g. Large White, Danish Landrace, Berkshire) at their origin.

The genetic diversity parameter among progeny-tested boars was 97.96%. The effective population size was 223, inside the minimum range of 31-250 suggested by Meuwissen and Woolliams (1994b) for sufficient fitness. The genetic diversity parameter and the N_e can be considered to be reliable values because the values of the different parameters of pedigree completeness were considered to be sufficiently high, as explained above. Therefore, it seems that high genetic diversity still exists in the Walloon Piétrain population. However, as 55% of the progeny-tested boars originated from the same breeder (but this breeder did not breed 55% of all available Walloon boars), the overall existing diversity was potentially not captured. Ideally, approximately 10% (n=10 breeders) of the progeny-tested boars should originate from each of these breeders. This proposal can be derived empirically, based on formulas developed by Wray and Thompson (1990) relating expected rate of inbreeding to the sum of the quadratic long-term contribution from each ancestor to its descendants. It can be very easily shown that for unrelated ancestors the rate of inbreeding is minimised with even

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contributions. Empirically, this is absolutely logical as a minimum rate of inbreeding is expected when all available alleles are transmitted in a balanced manner. We can postulate that under the hypothesis that all Walloon breeders have specific Piétrain alleles in their herds, their boars should contribute evenly to the next generation. This point is crucial for breed preservation, and especially for the success of the Belgian Piétrain programme as one of its objectives is preserving the diversity of the Walloon Piétrain population. This programme should be able to have access to the most diverse boars as well as to a balanced number of animals coming from different farms.

3.2. Multi-dimensional scaling analysis of progeny-tested boars

One way to check the uniqueness of progeny-tested boars bred by different breeder-groups is through an MDS analysis. Figure 1 shows the results from the MDS study based on available pedigrees. This figure highlights four main clusters (A, B, C and D) of boars. In general, genetic relationships between clusters fitted well with statements from interviewed breeders. The first cluster (cluster A) presented the greatest diversity even though all boars came from the same breeder. Through his interview we know that this breeder purposely nominated a large variety of boars, not only the ones he considered the best. Our results confirmed his statement. We also know that this breeder had exchanges with Germany. Influences from German boars on some of his animals were expected and were visible because some of his animals were placed close to breeder-group 14 (different German breeders not individually identified in the database).

Cluster B was composed of animals from two main breeder-groups (8 and 13). Some animals from breeder-groups 1, 7, 16 and 19 seemed to have links with animals from this cluster.

In general, cluster C was composed of breeders that seemed to have genetic links within them mainly due to transfers. Cluster C can be divided into two sub-clusters (breeder-groups 2 and

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10 vs. breeder groups 4 and 7) that did not transfer animals between them directly, but were somehow linked to the core cluster (cluster D) through deeper pedigrees.

Finally, we observed a core cluster, cluster D, that grouped Walloon breeders (groups 3, 6 and 9), Flemish breeders (groups 5, 12, 16, 17 and 18) and German breeders. The core cluster would indicate higher rates of inbreeding as different boars from different groups were very close to each other, which would imply higher genetic proximity and thus higher inbreeding levels. However, by looking at the maximum inbreeding coefficients of these breeder-groups (from 0.00%, for boars of limited pedigree, to 3.96%), in general, it did not seem that boars from these groups were particularly inbred. Note that the first two components had a goodness of fit of 7.14%. This small percentage was expected since a 219 × 219 matrix was reduced to a two-dimensional one. This could explain why these breeder-groups did not express high inbreeding levels. They only seemed to be close in the first two-dimensional plan.

Currently, some members from all four clusters are active, though breeders 7, 11, 13 and 15 have stopped their activities. Results from our MDS analysis can help us to develop conservation measures regarding genetic diversity and relationships between farms (Herrero-Medrano et al., 2013). It would be important to preserve diversity from each cluster. Formulas developed by Wray and Thompson (1990) and research by Sonesson and Meuwissen (2001) showed strategies to optimise long-term contributions from related ancestors to descendants in small populations. These strategies could use the information regarding genetic diversity and relationships among farms obtained from the MDS study to select boars of interest. As mentioned previously, the MDS may only be a glimpse of the genetic diversity existing in the Walloon Piétrain pig population as certain breeders sent more animals than others. Moreover, breeders did not send all the diversity of their boars to progeny-testing but only boars they considered to be superior. Breeder 1 was the only exception since he seemed to send almost

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all his boars to progeny-testing. This fact has to be considered when studying the results from the PCA of pseudo-phenotypes.

3.3. Transfers of animals between farms

Figure 2 depicts transfers of animals from breeders to owners. To recap, in this study we consider breeders to be the person responsible for the breeding leading to the boar, whereas owners are responsible for the selection of a boar to progeny-testing; identical numbers are used to identify the same person, or group of persons, therefore the same number is used for breeder and owner; the CIAP and the Belgian Piétrain programme were considered to be owners only as they do not breed boars but can nominate them for progeny-testing.

As illustrated in Figure 2, transfers from a Walloon breeder to a different Walloon owner were almost non-existent. Only one transfer appeared in the data between breeder 13 and owner 6. By combining this information with semi-directed interviews we can infer that, while transfers of pigs have occurred between Walloon farms during the last years, this was relatively scarce. In addition, it seemed that owners/breeders have bought/sold animals from/to the same breeders/owners. This was confirmed in the MDS study: some nuclei of breeders appeared (Fig.1).

On the other hand, some owners have bought boars in Flanders, and therefore, it seemed that there were two types of situation in Wallonia: 1) breeders who have not transferred animals (or very few); 2) breeders/owners who have sometimes sold/bought animals in Flanders. These two strategies were also seen in the MDS (Fig.1) where breeders from type two were in the core cluster (cluster D) whereas breeders from type one were spread out (clusters A, B and C). The fact that transfers were an uncommon practice can explain the great diversity previously found in the studied population. As each Walloon farm seemed to own specific pigs that they did not frequently transfer to another farm, each breeder/owner seemed to keep

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its own specificity and to contribute significantly to the overall diversity of the Walloon Piétrain population. However, the genetic diversity at the farm level may be relatively poor if the number of pigs on the farm was low and if inbreeding levels were high.

In a considered manner, transfers of animals between Walloon farms may increase genetic variability among them (Gomes Arandas et al., 2017). One way to lead these transfers would be through breeding circles (Windig and Kaal, 2008). An increase of genetic diversity in each farm would therefore be expected as different boars would be added to each farm pedigree while the overall N_e of boars would decrease as boars sent to progeny-testing will share more ancestors. This N_e decrease would allow better genetic progress (Meuwissen and Woolliams, 1994a).

Current low transfers also partially explain the high N_e observed. Some farms showed relatively high levels of inbreeding (data not shown) which involved fewer heterozygotes. As transfers were not frequent, progeny-tested boars were expected to be used in a balanced manner in the population. Thus, even if the population is currently undergoing a bottleneck, a low genetic drift could be inferred from these two latter facts (fewer heterozygotes and balanced use of boars) resulting in high N_e (Caballero & Toro, 2000).

The specificity of the Walloon population may however be under threat by transfers from Flanders. As shown in Figure 2, the Belgian Piétrain programme is avoiding these animals, since its main objective is to maintain the genetic diversity of the Walloon Piétrain population germplasm. However, Figure 2 also shows that Flemish breeders have regularly sold boars to the CIAP.

Besides transfers between breeders and owners, another type of gene flow could exist in purebred Piétrains due to artificial insemination (**AI**). Although we had no direct information about the use of AI by breeders in the past, this kind of gene flow was most likely also visible in the MDS analysis (Fig.1). In summary, in the MDS analysis, close breeder-groups of

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animals shared common ancestors, in the recent or even distant past, due to animal transfers between farms as well as, potentially, AI.

3.4. Principal component analysis of pseudo-phenotypes

The weighted PCA gave information on selection objectives for a total of 16 different owners, including the CIAP and the Belgian Piétrain programme, sending boars for progeny-testing. Moreover, there were 13 Walloon owners that had sent boars for progeny-testing since 2009, illustrating a loss of four owners over ten years of the progeny-testing scheme. As a reminder, owners are considered as the nominator of the boar for progeny-testing and can be the same person as the boar's breeder.

Eigenvalues and percentage of variance for the weighted PCA are presented in Table 2. The first two components were chosen with the criteria of an eigenvalue superior to 1 and a minimum of 70% of the variance explained (Gomes Arandas et al., 2017). The first component explained 49.28% of the variance and the second 34.70% (83.98% in total).

Figure 3 illustrates the relationships between pseudo-phenotypes and components of the PCA. Table 3 presents the correlations of the different pseudo-phenotypes with the first two components and their p-values, while Table 4 presents the contributions of these pseudo-phenotypes to the first two components of the PCA. The first component was related to growth, and the second one to meat traits. Conformation was explained by both components.

While the MDS analysis based on pedigree highlighted gene flows between farms, often linked to geographic distances, PCA illustrated the selection objectives of farms.

Figure 4 depicts the mean positions of owner-groups, represented by a square, on the PCA. To interpret Figure 4, the use of the different directions followed by the different pseudo-phenotypes found in Figure 3 is necessary. Owner-groups of the first quadrant (clockwise) provided boars with high backfat thickness. Owner-groups on the first two quadrants and near

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the X-axis had boars with high carcass weight and ADG, whereas in the third quadrant they had boars showing high meat percentage. Finally, in the last quadrant, they provided boars with high conformation and consumption indexes. By excluding owner-groups 1, 11, 14 and 19, we can see that owners have selected more for meat or conformation traits, the specificities of the Piétrain breed. Owner-group 11 presented very high backfat thickness which is particularly uncommon in Piétrain pigs. However, this owner has since closed his business and the disappearance of his animals may have caused a loss of diversity. Owner-group 6 was an outlier and had distinguishable characteristics that might need to be preserved. However, this owner was closely linked with Flanders and therefore may be less representative of Walloon characteristics. Moreover, owner-group 6 was only responsible for three animals, not coming from the same breeders, which also explained why boars from this owner-group were so far from each other (Fig.5). From Figure 4, we can also conclude that, as owner-group 11 no longer exists, the diversity of close owner-groups 9 and 10 should be preserved, especially for group 9 that is distinct from other owner-groups. Based on our results, the Belgian Piétrain programme (owner-group 21) seemed to choose highly conformed boars. Our results may be useful for helping them to organise the inclusion of more diverse boars to preserve a larger part of the existing genetic variability in the Walloon Piétrain population.

In Figure 5, the distribution of boars, colour-coded per owner-group on the PCA, is provided. The same interpretation as for Figure 4 can be used. Boars of the first quadrant (clockwise) had high backfat thickness. On the first two quadrants and near the X-axis, they had high carcass weight and ADG, whereas in the third quadrant they had high meat percentage. Finally, in the last quadrant they had high conformation and consumption indexes.

Despite the lack of preselection from owner 1, almost all his animals were located in the first two quadrants (Fig.5) which implied a rather homogeneous focus on growth traits of this

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owner. Some owner-groups (6, 9, 10, 11, 14, 20 and 21) presented great dispersion. Owner-groups 20 and 21, representing respectively the CIAP and the Belgian Piétrain programme, nominated more diverse animals, explaining the large dispersion observed in these groups. Owner-group 14 represented different German owners which could not be individually identified, which also potentially explains the observed wider dispersion among animals from this owner-group.

Finally, by looking at the genetic diversity parameter, mean inbreeding coefficient, N_e and PCA of pseudo-phenotypes (Fig.4 and 5), we may infer that the overall diversity of Walloon Piétrain pigs seems to be well preserved so far. However, given the limited size of the population, various threats can shift this precarious balance. Among these, one can cite the excessive use of external boars and the spread of contagious diseases leading to the culling of healthy Walloon Piétrain pigs.

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3.5. Separation power of pseudo-phenotypes

As a great dispersion of individuals was seen in the PCA (Fig.5), separation powers of pseudo-phenotypes were computed in order to determine which pseudo-phenotypes discriminate the most different owners. The different separation powers are presented in Table 5. In general, owners seemed to be the more divergent for deregressed average daily gain and for consumption index (growth traits). That is why the Belgian Piétrain programme should ensure representative samples for these traits. Moreover, animals with superior meat performances should be tested and enter the programme as they seem to be rare. Note that the Piétrain already shows exceptional meat characteristics compared to other breeds. In the owner's point of view, it is totally justified to keep these superior animals for their traditional Piétrain characteristics. However, less good animals for these traits may also be kept since these kinds of animal may carry important genes for other, also important, traits (e.g. growth).

It should be the mission of the Belgian Piétrain programme to conserve both types of animals. Through their characterisation in the progeny-testing scheme, Piétrain breeding could choose preserved genetic material of boars of interest in the future.

3.6. Simultaneous use of pedigree and phenotypes

The use of both pedigree and phenotypes in this study was interesting as groups that were genetically close did not have similar performances based on PCA (Fig.4). For example, groups 3, 6, 11 and 15 were in the core cluster (cluster D) of MDS (Fig.1) but spread out in PCA (Fig.4). The MDS established the genetic relationships of animals whereas PCA reflected breeding goals. This indicates that the selection work of the owners had an important place in studying the diversity of a potentially endangered breed. Our results support other authors that emphasise the importance of using physical traits for preservation purposes, since some of them cannot be captured by genetic distance computations (Fabuel et al., 2004; Ruane, 1999). We therefore suggest the addition of phenotypic measures when studying the genetic diversity of a breed as it adds a certain amount of information to the pedigree. In the Walloon Piétrain population, this approach is limited by the fact that boars nominated for progeny-testing are generally preselected. Nevertheless, these preselected boars should provide a good indication of which alleles will be available for the next generation of Piétrains. A further step will be the use of Walloon genotypes to supplement the overview of genetic diversity and help the design of conservation measures.

4. Conclusions

Our study demonstrated that pedigree information was very important to determine levels of inbreeding and gene flow between groups of boars raised by different breeders, while pseudo-phenotypic measures allowed us to discriminate between the rather heterogeneous progeny-

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tested boar population, with owner-groups having specific types of animals carrying potentially interesting or rare alleles.

The Walloon Piétrain population seems to maintain sufficient diversity so far. However, some adaptations should be made in the management of the genetic diversity without compromising genetic improvement. The Belgian Piétrain programme should use advanced tools (e.g. optimal contribution as proposed by Meuwissen, 1997) and organised transfers of animals between breeders (e.g. through breeding circles proposed by Windig and Kaal, 2008) to maintain diversity even under selection. Moreover, the Belgian Piétrain programme and the progeny-testing scheme could play a more active role in finding equilibrium between preserving all genetic diversity and selecting the best germplasm for genetic progress purposes now and in the future.

In a subsequent study, we will investigate the genomic diversity and differences of our population compared to other Piétrain populations. Under the condition of sufficient genetic specificity, as for other local breeds in Wallonia, Piétrain could be included in agri-environmental measures. These measures provide a framework for financial assistance by the government to breeders to support genetic diversity. They have been found to be very effective and can be rather easily put into practice, pending European Commission acceptation of national strategy plans including support for endangered breeds. Finally, governments in general should also support specific measures to protect rare purebred animals against disease threats. Currently, culling strategies during disease outbreaks are not designed to protect animals with high genetic value. The results of this study were strong indications that many of the still operating Piétrain breeders in Wallonia very often have specific genetic material that also merits in-situ preservation.

Declaration of Interest

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The authors declare that they have no conflicts of interest.

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Hélène Wilmot: Conceptualization, Methodology, Software, Formal Analysis, Writing. ***Rodrigo Reis Mota****:* Reviewing, Software**. Sylvie Vanderick***:* Resources, Reviewing**. Nicolas Gengler:** Supervision, Writing, Reviewing and Editing.

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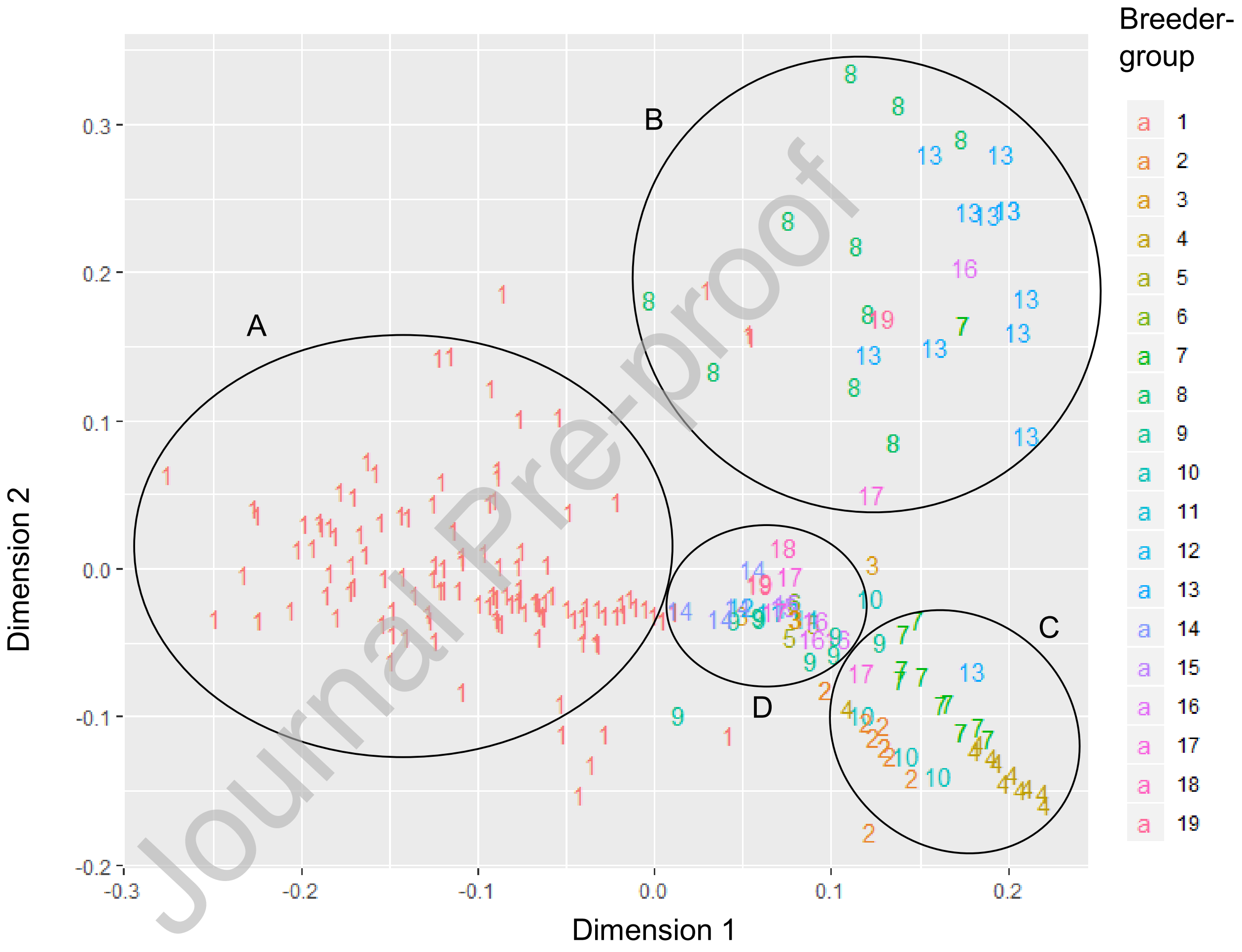

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Figure 1. Multi-dimensional scaling between 219 progeny-tested boars from 19 breeder-groups.

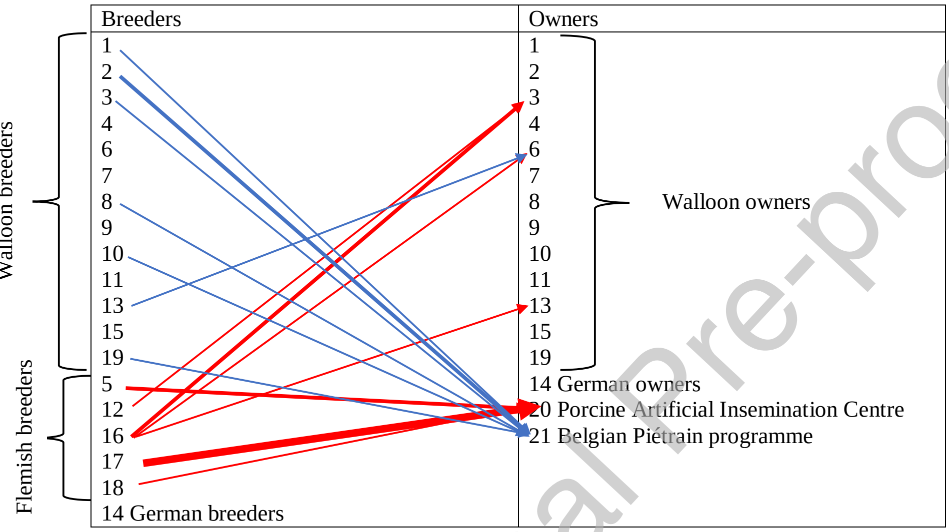

Figure 2. Transfers of boars. Thickness of arrows is proportional to the number of boars transferred. Blue arrows represent transfers from Walloon breeders. Red arrows represent transfers from Flemish breeders.

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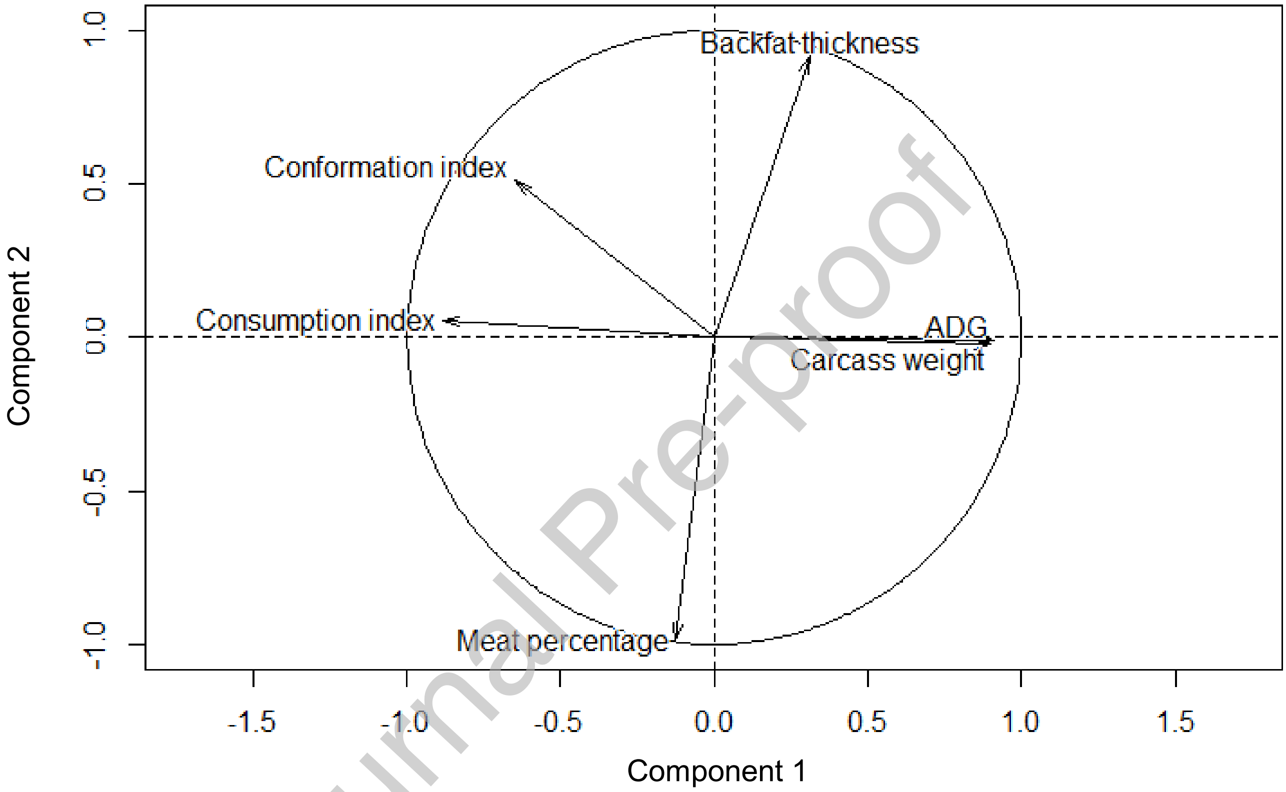

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Figure 3. Trait factor map. ADG: deregressed estimated breeding value (EBV) of average daily gain; Carcass weight: deregressed EBV of carcass weight; Backfat thickness: deregressed EBV of backfat thickness at station; Meat percentage: deregressed EBV of meat percentage at station; Conformation index: deregressed EBV of conformation index; Consumption index: deregressed EBV of consumption index.

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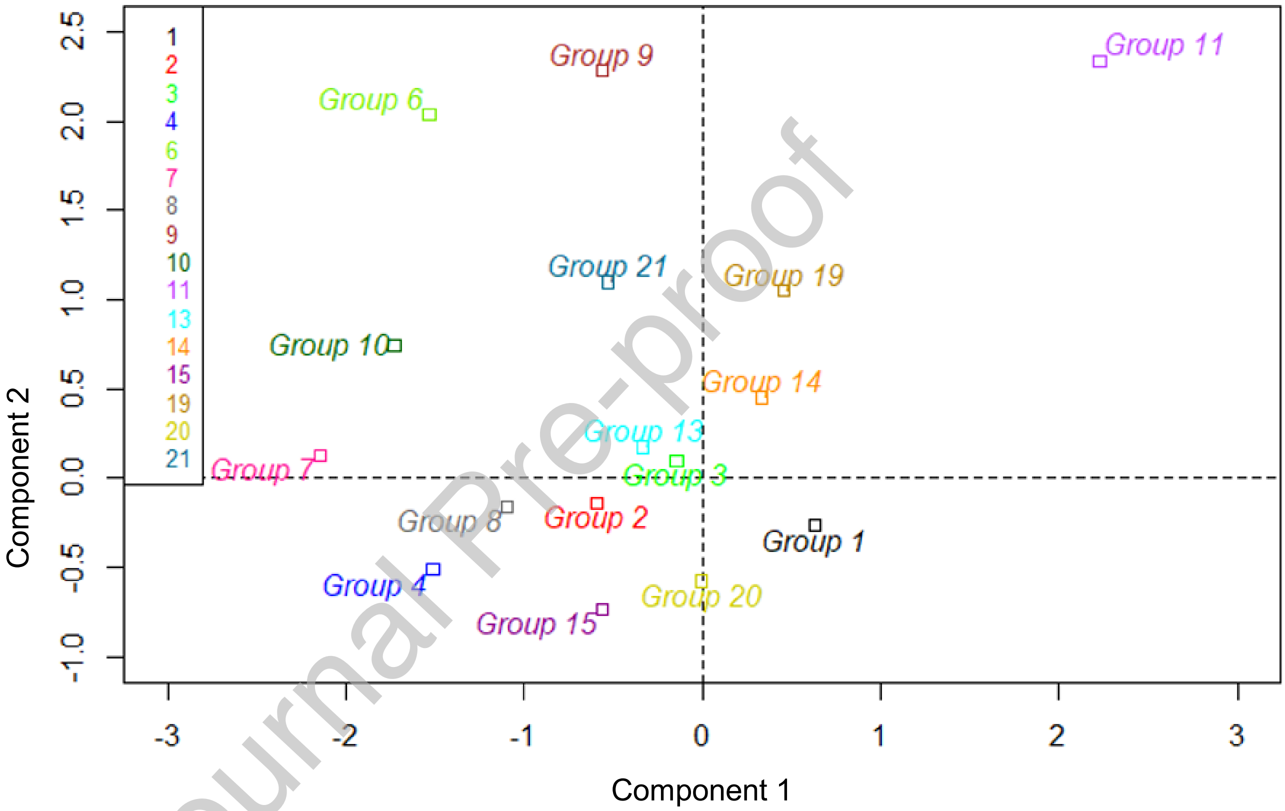

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Figure 4. Principal component analysis of owner-groups. Means of each group are represented by square symbols.

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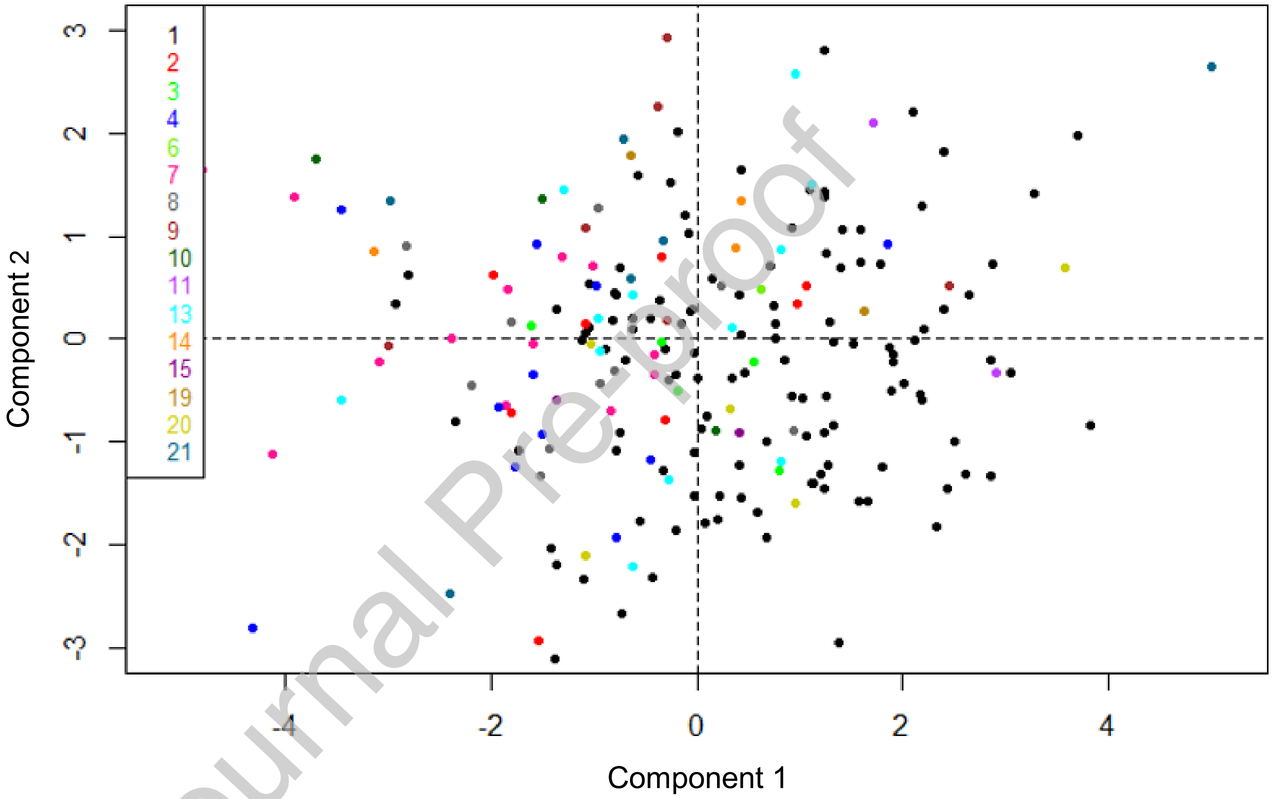

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Figure 5. Individual factor map (principal component analysis) of the 219 boars, colour-coded by owner-group.

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Table 1.

Additional information about breeders/owners concerning their region and country of origin, the number of progeny-tested boars born at the farm, the number of boars provided to progeny-testing and their transfers.

Breeder/ owner	**Region (Country)**	**Progeny-tested boars born at the farm**	**Boars provided to progeny-testing**	**Supplementary information**
1	Wallonia (Belgium)	121	120	*
2	Wallonia (Belgium)	10	8	*
3	Wallonia (Belgium)	4	6	*; **
4	Wallonia (Belgium)	11	11	
5	Flanders (Belgium)	2	0	****
6	Wallonia (Belgium)	1	3	**
7	Wallonia (Belgium)	13	13	
8	Wallonia (Belgium)	11	10	*
9	Wallonia (Belgium)	8	8	
10	Wallonia (Belgium)	4	3	*
11	Wallonia (Belgium)	3	3	
12	Flanders (Belgium)	1	0	***
13	Wallonia (Belgium)	12	12	**; ***
14	(Germany)	4	4	
15	Wallonia (Belgium)	2	2	
16	Flanders (Belgium)	4	0	***
17	Flanders (Belgium)	4	0	****
18	Flanders (Belgium)	1	0	****
19	Wallonia (Belgium)	3	2	*
20	Wallonia (Belgium)	/	7	CIAP; only considered as an owner
21	Wallonia (Belgium)	/	7	Belgian Piétrain programme; only considered as an owner*****

*: provided one or two boars to the Belgian Piétrain programme; **: transfer of one or more boars *from* another farm; ***: transfer of one or more boars *to* another farm; ****: CIAP became the owner of one/several boars; *****: Belgian Piétrain programme responsible for cryopreservation of Walloon boars' semen. CIAP: Porcine Artificial Insemination Centre.

Table 2.

Eigenvalue, percentage of total variance and cumulative variance of the principal components (PC).

PC	**Eigenvalue**	**Variance (%)**	**Cumulative variance (%)**
1	2.96	49.28	49.28
2	2.08	34.70	83.98
3	0.81	13.43	97.41
4	0.11	1.81	99.21
5	0.03	0.58	99.80
6	0.01	0.20	100.00

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Table 3.

Correlations between pseudo-phenotypes and the first two principal components (PC) and their respective p-values.

Pseudo-phenotypes	**PC 1**	**p-value 1**	**PC 2**	**p-value 2**
ADG[a]	0.91	< 0.001	–0.01	0.91
Carcass weight	0.90	< 0.001	–0.02	0.77
Backfat thickness	0.31	< 0.001	0.92	< 0.001
Meat percentage	–0.13	0.12	–0.99	< 0.001
Conformation index	–0.65	< 0.001	0.51	< 0.001
Consumption index[b]	–0.88	< 0.001	0.05	0.50

[a]: average daily gain; [b]: ratio of intake over average daily gain.

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Table 4.

Contributions (in %) of pseudo-phenotypes to the first two principal components (PC).

Pseudo-phenotypes	**PC 1**	**PC 2**
ADG[a]	28.17	< 0.01
Carcass weight	27.36	0.03
Backfat thickness	3.25	40.40
Meat percentage	0.55	46.82
Conformation index	14.21	12.61
Consumption index[b]	16.46	0.14

[a]: average daily gain; [b]: ratio of intake over average daily gain.

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Table 5.

Separation power of pseudo-phenotypes.

Pseudo-phenotypes	**Separation power**
ADG[a]	6.44
Carcass weight	4.16
Backfat thickness	2.79
Meat percentage	3.67
Conformation index	2.63
Consumption index[b]	7.61

[a]: average daily gain; [b]: ratio of intake over average daily gain.

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