UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
FACULDADE DE AGRONOMIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOTECNIA

KARINE APARECIDA RODRIGUES DE SOUZA

ABORDAGENS GENÔMICAS PARA CARACTERIZAÇÃO DA ESTRUTURA GENÉTICA POPULACIONAL E HOMOZIGOSIDADE EM PORCOS DAS RAÇAS MOURA, CRIOULA DA ARGENTINA E COMERCIAIS

Porto Alegre

2023

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Tese apresentada como um dos requisitos à obtenção do grau de Doutor em Zootecnia

Área de concentração Melhoramento Genético Animal

Porto Alegre (RS), Brasil
Junho, 2023

CIP - Catalogação na Publicação

Souza, Karine Aparecida Rodrigues de
ABORDAGENS GENÔMICAS PARA CARACTERIZAÇÃO DA ESTRUTURA GENÉTICA POPULACIONAL E HOMOZIGOSIDADE EM PORCOS DAS RAÇAS MOURA, CRIOULA DA ARGENTINA E COMERCIAIS / Karine Aparecida Rodrigues de Souza. -- 2023.
167 f.
Orientador: José Braccini Neto.

Coorientador: Marson Bruck Warpechowski.

Tese (Doutorado) -- Universidade Federal do Rio Grande do Sul, Faculdade de Agronomia, Programa de Pós-Graduação em Zootecnia, Porto Alegre, BR-RS, 2023.

1. Assinaturas de seleção . 2. Corrida de Homozigose . 3. Suínos . 4. Ancestralidade . 5. Raças localmente adaptadas . I. Neto, José Braccini, orient. II. Warpechowski, Marson Bruck, coorient. III. Título.

Elaborada pelo Sistema de Geração Automática de Ficha Catalográfica da UFRGS com os dados fornecidos pelo(a) autor(a).

Karine Aparecida Rodrigues de Souza
Mestre em Zootecnia

TESE

Submetida como parte dos requisitos

para obtenção do Grau de

DOUTORA EM ZOOTECNIA

Programa de Pós-Graduação em Zootecnia

Faculdade de Agronomia

Universidade Federal do Rio Grande do Sul

Porto Alegre (RS), Brasil

Aprovada em: 02.06.2023
Pela Banca Examinadora

Homologado em: 22/03/2024
Por

gov.br Documento assinado digitalmente
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DEDICATÓRIA

À minha avó Maria, a quem chamo de mãe Carminha, e ao meu avô Silvino;
À minha avó Laurentina (*in memoriam*), a minha saudade diária.

Dedico.

AGRADECIMENTOS

Obrigada, Deus, por permanecer ao meu lado.

Vó Lôra, que a senhora esteja aí de cima vendo mais essa etapa concluída, que foi de muito sofrimento nesses meses por sua perda. Meu muito obrigada por todas as orações, apoio, incentivo, preocupação, conselhos e confiança

À minha Mãe Carminha e ao meu avô Silvino, obrigada por todas as ligações e mensagens ao longo desses anos longe da minha terra natal. Conseguiram se fazer presente em meio à distância física.

Ao meu sobrinho Victor Emanuel, você é a minha alegria.

Ao Hamilton, pelo apoio, força e companheirismo sempre. Te amo.

Meus sinceros agradecimentos a todos os meus amigos (as) e companheiros (as) nesta caminhada: Ariadna, Aline, Samira, Clarissa, Larissa, Raphaela, Annayara, Raquel, Dayane, Débora, Jussara, Fernando e Idael, pela grande amizade e pela ajuda de sempre.

À Universidade Federal do Rio Grande do Sul, pela oportunidade nessa formação.

À CAPES, pela concessão da bolsa de estudo.

Ao Professor Dr. Braccini, pelo acolhimento, ensinamentos, orientação e amizade; ao Professor Dr. Marson, pela coorientação e ensino sobre a raça Moura, pela qual ele tem tanta admiração e muito conhecimento.

Ao professor Dr. Jaime Araújo Cobuci e a todos os docentes do PPGZ, pelos ensinamentos e esclarecimentos prestados.

À Dr. Darilene, pela amizade, disponibilidade e colaboração ao longo desse projeto. Você foi essencial para a execução desse trabalho.

Ao grupo de pesquisa Megagen, em especial aos meus colegas, Alexandra, Giovani, Maíza e Maiara, pelos ensinamentos e amizade.

Aos amigos mineiros que a UFRGS me presentou, Wanderson e Victor, obrigada por fazerem essa caminhada mais leve, pelas boas risadas e pelos bons passeios.

Aos amigos que Porto Alegre me presenteou: Cris, Nathalia, Muanca e Fatyma, já estou com saudades.

OBRIGADA!

“Você é o único representante
do seu sonho na face da terra,
se isso não fizer você correr,
eu não sei o que vai..

Somos maior, nos basta só
sonha e seguir”

(Emicida)

“Foi embora um fruto, mas a
árvore ficou. E suas raízes são
muito fundas para tentarem
arrancar”

(Itamar Vieira Junior)

ABORDAGENS GENÔMICAS PARA CARACTERIZAÇÃO DA ESTRUTURA GENÉTICA POPULACIONAL E HOMOZIGOSIDADE EM PORCOS DAS RAÇAS MOURA, CRIOULA DA ARGENTINA E COMERCIAIS

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Orientador: Professor Dr. José Braccini Neto

RESUMO

O porco, *Sus scrofa*, é uma espécie exótica no continente americano, introduzida pelos colonizadores portugueses e espanhóis. Devido à grande diversidade de ambientes no continente, que varia desde climas tropicais e subtropicais quentes até climas de altitude, como o altiplano, surgiram raças localmente adaptadas, que são particularmente tolerantes ou resistentes a doenças locais e ambientes extremos distintos. No entanto, a partir do início do século XX, devido à substituição por raças comerciais, cruzamentos indiscriminados e endogamia, houve diminuição no plantel das raças localmente adaptadas ou crioulas, e algumas raças chegaram a correr risco de extinção. Portanto, o objetivo geral deste estudo foi (i) identificar e caracterizar os segmentos homozigotos presentes no genoma dos porcos das raças localmente adaptadas (Moura e Crioula Argentina da região das Misiones) e das raças comerciais (Duroc, Landrace, Large White e Pietrain); (ii) estimar e correlacionar os coeficientes de endogamia genômico por execuções de homozigose (F_{ROH}) e da matriz genômica de parentesco (F_{GRM}); (iii) associar as regiões homozigotas mais frequentes nessas populações a genes envolvidos na expressão de características econômicas; (iv) identificar no Moura assinaturas de seleção e atribuir a ancestralidade dessas marcas. No capítulo II foram utilizados dados de 84 animais Moura, 87 Duroc, 138 Landrace, 84 Large White e 66 Pietrain com 40.662 SNPs. Através do software PLINK foram identificados um total de 25.538 ROHs (n=2.730 Moura, n=6.846 Duroc, n=7.599 Landrace, n=4.922 Large White e n=3.441 Pietrain). As ilhas de ROH (corridas de homozigose – *"runs of homozygosity"*) foram evidentes em regiões genômicas associadas a importantes características econômicas. Foram identificadas ilhas de ROH sobrepostas na raça Moura e Duroc, os genes presentes nos termos enriquecidos (p>0,05) foram associados a qualidade da carne. Os coeficientes de endogamia foram maiores na raça Duroc (F_{GRM} = 0,384 e $F_{ROH\ total}$ = 0,265), e menores nas raças Pietrain (F_{GRM} = 0,318 e $F_{ROH\ total}$ = 0,177) e Moura (F_{GRM} = 0,329 e $F_{ROH\ total}$ = 0,142). A maior correlação entre os coeficientes de endogamia foi entre $F_{ROH\text{-}total}$ com $F_{ROH\ >16\ Mb}$ para todas as raças. O capítulo III visou explorar a ancestralidade dos porcos Moura (n = 84), avaliando o compartilhamento das pegadas genômicas da raça localmente adaptada com raças comerciais (Duroc n = 87, Landrace n = 138, Large White n= 84 e Pietrain n = 66) e uma raça crioula Argentina da região das Misiones (n = 9). Após o controle de qualidade, o banco de dados resultou em 40.555 SNPs. O software PLINK v1.90 foi empregado para calcular as ROHs, onde 1% dos SNPs mais frequentes foram usados para determinar as regiões de assinaturas de seleção. O software ADMIXTURE foi utilizado para calcular a probabilidade de ancestralidade para cada ilha de homozigose identificada e sobreposta entre os porcos Moura e as demais raças analisadas. Diversas regiões genômicas compartilhadas entre o Moura e Duroc foram identificadas, provavelmente relacionadas às raças fundadoras em comum. Além disso, cinco ilhas de homozigose foram observadas, sobrepostas entre

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[1]Tese de Doutorado em Zootecnia – Faculdade de Agronomia, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brasil. (167 p.), Junho de 2023.

os animais da raça Moura, Crioula Argentina das Misiones, Duroc e Landrace, contendo genes candidatos associados a características economicamente importantes. Nossos resultados podem ser valiosos para futuros programas de conservação e melhoramento que visam conservar e utilizar de forma sustentável esses importantes recursos.

Palavras-chave: assinaturas de seleção, recursos genéticos, SNP, *Sus scrofa*

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GENOMIC APPROACHES FOR CHARACTERIZING POPULATION GENETIC STRUCTURE AND HOMOZYGOSITY IN MOURA, ARGENTINA CREOLE, AND COMMERCIAL PIG BREEDS

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ABSTRACT:

The pig, *Sus scrofa*, is an exotic species in the American continent, introduced by Portuguese and Spanish colonizers. Due to the great diversity of environments on the continent, ranging from hot tropical and subtropical climates to high-altitude climates, such as the highlands, locally adapted breeds have emerged, which are particularly tolerant or resistant to local diseases and distinct extreme environments. However, since the early 20th century, due to the substitution by commercial breeds, indiscriminate crossbreeding, and inbreeding, there has been a decrease in the population of locally adapted or creole breeds, and some breeds have even been at risk of extinction. Therefore, the general objective of this study was (i) to identify and characterize the homozygous segments present in the genome of pigs from locally adapted breeds (Moura and Crioula Argentina from the Misiones region) and commercial breeds (Duroc, Landrace, Large White, and Pietrain); (ii) to estimate and correlate the genomic inbreeding coefficients through runs of homozygosity (FROH) and the genomic relationship matrix (FGRM); (iii) to associate the most frequent homozygous regions in these populations with genes involved in the expression of economic traits; (iv) to identify selection signatures in Moura and assign ancestry to these marks. In Chapter II, data from 84 Moura, 87 Duroc, 138 Landrace, 84 Large White, and 66 Pietrain animals with 40,662 SNPs were used. Using PLINK software, a total of 25,538 ROHs were identified (n=2,730 Moura, n=6,846 Duroc, n=7,599 Landrace, n=4,922 Large White, and n=3,441 Pietrain). Runs of homozygosity islands were evident in genomic regions associated with important economic traits. ROH islands were identified overlapping in the Moura and Duroc breeds, and genes present in enriched terms (p>0.05) were associated with meat quality. Inbreeding coefficients were higher in the Duroc breed (FGRM = 0.384 and total FROH = 0.265), and lower in the Pietrain (FGRM = 0.318 and total FROH = 0.177) and Moura breeds (FGRM = 0.329 and total FROH = 0.142). The highest correlation between inbreeding coefficients was found between total FROH and FROH >16 Mb for all breeds. Chapter III aimed to explore the ancestry of Moura pigs (n = 84), evaluating the sharing of genomic footprints of the locally adapted breed with commercial breeds (Duroc n = 87, Landrace n = 138, Large White n = 84, and Pietrain n = 66) and a Crioula Argentina breed from the Misiones region (n = 9). After quality control, the database resulted in 40,555 SNPs. PLINK v1.90 software was employed to calculate ROHs, where 1% of the most frequent SNPs were used to determine the regions of selection signatures. ADMIXTURE software was used to calculate the probability of ancestry for each homozygosity island identified and overlapped between Moura pigs and the other analyzed breeds. Several shared genomic regions between Moura and Duroc were identified, likely related to common founder breeds. Additionally, five ROH islands were observed, overlapped among Moura, Crioula Argentina from Misiones, Duroc, and Landrace animals, containing candidate genes associated with economically important

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traits. Our results may be valuable for future conservation and improvement programs aimed at conserving and sustainably utilizing these important resources.

Keywords: genetic resources, selection signature, SNP, *Sus scrofa*

[1]Doctoral Thesis in Animal Science – Faculdade de Agronomia, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil. (167 p.), June, 2023.

SUMÁRIO

LISTA DE FIGURAS

CAPÍTULO I

LISTA DE TABELAS

CAPÍTULO II

LISTA DE FIGURAS

CAPÍTULO II

LISTA DE TABELAS

CAPÍTULO III

LISTA DE FIGURAS

CAPÍTULO III

LISTA DE ABREVIATURAS E SIGLAS

Bp = Par de base

cM = Centimorgan

DNA= Ácido Desoxirribonucleico

F_{GRM} = Inbreeding derived from a genomic relationship matrix

F_{ROH} = Inbreeding coefficient based on runs of homozygosity

IBD = Identical by descent

IBS = Identical by state

Kb= kilobase

LD = Linkage disequilibrium

MAF = Minor allele frequency

Mb = Mega pair of bases

Ne = Effective population size

QTL = Quantitative trait loci

ROH = Runs of homozygosity

SNP = Single nucleotide polymorphism

CAPÍTULO I

1. Introdução

Na segunda viagem de Colombo em 1493, o primeiro suíno doméstico chegou ao continente americano, vindo das Ilhas Canárias (Rodero; Delgado; Rodero, 1992). Ao longo do período de expansão e adaptação às condições locais, os porcos oriundos da Península Ibérica reproduziram-se rapidamente por todo o continente (Crosby, 2003; Linares; Linares; Mendoza, 2011). Os descendentes de porcos de ascendência ibérica apresentam uma grande variedade de populações com diferentes características fenotípicas e adaptadas a uma enorme variedade de ambientes e sistemas de produção, estendendo-se dos Estados Unidos à Argentina, e de condições quase desérticas ao clima tropical (Bernitez; Sanchez, 2001).

Na segunda metade do século XX, houve intensificação da produção de suínos em todo o mundo, acarretando em ameaças às populações locais, e os porcos crioulos ou localmente adaptados foram levados à quase extinção (Mariante; Egito, 2002). As poucas populações remanescentes, atualmente, estão amplamente espalhadas, muitas vezes com pequeno número de animais. A conservação das raças locais está sobretudo condicionada pela sua relevância econômica, mas também depende do valor sociocultural da adaptação às condições agroclimáticas locais, da contribuição para o desenvolvimento das comunidades locais, das zonas marginais e da importância científica (Revidatti, 2009).

A caracterização genética desses recursos é uma etapa preliminar para o desenvolvimento de programas de conservação e para impulsionar a promoção da raça local e o seu uso sustentável (Saura *et al.*, 2015). O aumento da taxa de endogamia é um assunto importante e de muita preocupação, pois tem como consequência direta a redução da heterozigosidade e, consequentemente, o aumento da homozigosidade e da frequência de alelos recessivos deletérios que podem reduzir o desempenho fenotípico e a viabilidade dos indivíduos (Zhang *et al.*, 2015). Como resultado da endogamia, ocorre a herança de haplótipos idênticos por descendência (*IBD – Identical By Descent*), que originam às corridas de homozigose (ROH) – definida como vários alelos de marcadores SNP em homozigose em sequência no genoma dos seus sucessores (Howrigan; Simonson; Keller, 2011; Ku *et al.*, 2011).

As ROHs têm permitido identificar relações genéticas entre indivíduos, além de fornecer informações da autozigosidade dos genomas individuais e populacionais, permitindo distinguir entre a endogamia recente e antiga, de acordo com os tamanhos

das regiões autozigóticas (Mcquillan *et al.*, 2008). As ROHs também podem ser utilizadas para a identificação de marcas de seleção, uma vez que essas regiões podem abrigar genes relacionados a seleção, que são comuns entre diferentes indivíduos e tem alta frequência na população (Peripolli *et al.*, 2018). A caracterização das ROHs tem sido empregada em animais domésticos, mas possui uma importância particular em raças localmente adaptadas, em que a identificação de genes relacionados a adaptação é de suma importância para o futuro da suinocultura, frente as questões de mudanças climáticas eminentes.

2. Revisão Bibliográfica

2.1. Raça Moura

A raça Moura, de acordo com suas características fenotípicas, pertence ao tronco ibérico, porém o histórico desta raça não menciona ao certo a sua procedência genética (Fávero *et al.*, 2007). Essa raça foi bastante difundida nos estados do Rio Grande do Sul, Paraná e Santa Catarina, nas primeiras décadas do século passado, apresentando como características marcantes prolificidade e rusticidade (Silva, 1987). Trabalhos recentes apontam qualidade da carne e alto marmoreio como características que a tornam útil em cruzamentos industriais (Bertol *et al.*, 2010, 2013; Figueiredo *et al.*, 2023).

O fenótipo do porco Moura apresenta perfil cefálico do tipo subcôncavo ou retilíneo, orelhas intermediárias entre os tipos célticas e ibéricas, a pelagem preta entremeada de pelos brancos lisos (tordilha), é a característica mais marcante da raça (Silva, 1987). Além disso, possui uma leve papada, pescoço curto, peito medianamente largo, dorso e lombo largo, e pouca massa muscular. É capaz de sobreviver às condições mais adversas e geralmente é criado solto (Sollero, 2006). De acordo com Machado (1967), apresenta uma boa progênie quando cruzado com suínos da raça Landrace.

2.2. Raça Crioula Argentina da região das Misiones

A raça Crioula Argentina das Misiones, foi difundida no Nordeste da Argentina (NEA), na região das Misiones. Essa raça apresenta baixo rendimento em relação às raças importadas, as suas condições de exploração e manejo impossibilitaram sua caracterização (Revidatti *et al.*, 2005). É utilizada na suinocultura de subsistência, que geralmente é realizada em conjunto com outas espécies (caprinos, ovinos e aves). A suinocultura de subsistência tem interferência direta na vida das populações que dela sobrevivem, mas quando se trata dessa atividade, uma análise profunda não é fácil de ser realizada, devido à falta de dados e informações (Revidatti, 2009).

Os recursos genéticos crioulos podem se tornar uma via de sustentabilidade para a produção da região. Além de representarem um reservatório de variabilidade genética que pode enriquecer e atualizar em um futuro o germoplasma suíno, principalmente devido a sua capacidade de aproveitar os recursos naturais disponíveis e diversos subprodutos agrícolas (Revidatti *et al.*, 2004).

2.3. Raças comerciais

Os suínos Duroc são o resultado de cruzamento entre as raças Red Jersey e Old Duroc no Estados Unidos, no século XIX. Estas duas raças fundadoras provêm de suínos de origens muito diferentes. Há indícios de suínos europeus, como a Berkshire, suínos africanos com influência ibérica, como o suíno vermelho da Guiné e, muito possivelmente porcos ibéricos de pelagem vermelha (Banker, 1923). Os animais foram desenvolvidos com o objetivo de obter carne com maiores níveis de gordura intramuscular (Barton-Gade,1988) e, consequentemente, melhorar a qualidade sensorial (Cameron *et al*., 1990).

A raça Landrace original foi desenvolvida na Dinamarca por volta de 1830 e 1840, através do cruzamento de suínos exógenos (alemães, chineses, portugueses e espanhóis) com a raça Large White, com o objetivo de produzir um bacon mais consistente para exportação. O Landrace dinamarquês ganhou tal reputação na produção de bacon devido ao seu comprimento corporal, rendimento e magreza (Porter, 1993). Devido à sua prolificidade e precocidade, pode ser utilizado tanto na linha fêmea quanto na linha macho, mas devido às suas habilidades maternas, a raça preferencialmente é utilizada na linha fêmea (Irgang, 2014).

Os animais Large White são conhecidos por terem se originado no norte da Inglaterra, predominantemente em Yorkshire. No entanto, a ascendência inicial é difícil de rastrear, mas acredita-se que a raça se desenvolveu a partir das raças brancas locais do Old English durante o século XIX (Case, 2009). Apresenta alta prolificidade, ótima taxa reprodutiva, crescimento diário e eficiência alimentar, sendo utilizada principalmente como linha materna, mas seu alto ganho de peso também a direciona para linhas paternas (Irgang, 2014).

A raça Pietrain foi desenvolvida na Bélgica em 1920 (Jones, 1998), e até 1950 era praticamente desconhecida na Europa. Os animais e as linhas desenvolvidas com

base nesta raça apresentam baixa gordura intramuscular e baixa retenção de água (Chesnais, 2002). É frequente a perda de seus reprodutores em acasalamentos nas horas mais quentes do dia, sendo muito comuns problemas cardíacos nessa raça (Cavalcanti, 2000).

2.4. Importância da conservação genética das raças localmente adaptadas

As raças localmente adaptadas são compatíveis e eficientes com seus ambientes ecológicos, sendo, consequentemente, elemento chave na manutenção dos ecossistemas locais (Ramos; Mariante, 2011). Diante disso, a utilização, manutenção e o desenvolvimento das raças localmente adaptadas já adaptadas a ambientes tropicas, de baixa tecnificação e desafiadores, são de extrema importância para manter a produção de alimento nesses ecossistemas (Ribeiro; Arandas, 2018). Espera-se que animais geneticamente adaptados a essas condições sejam mais produtivas sem a necessidade de grandes investimentos, sendo fundamentais para comunidades locais (Revidatti *et al.*, 2004).

Estudos realizados nessas raças permitiram a identificação de estratégias otimizadas de utilização desses animais em sistemas de produção localizados em regiões de maior estresse calórico, regiões de alimentação com qualidade reduzida e exposição às doenças e parasitas (Ribeiro; Arandas, 2018). Deste modo, pode-se minimizar o uso de insumos químicos como medicamentos carrapaticidas, o que promove o emprego da raça em sistemas de produção naturais, graças à manutenção das informações contidas em seu genoma, que favorecem a adaptação e sua maior resistência. Além disso, os recursos genéticos locais possibilitam identificar genes que poderão ser utilizados para introgredir essas características produtivas e de manutenção da saúde nas demais raças (Silva *et al.*, 2005).

Para evitar a extinção desse recurso genético é necessário realizar ações de conservação, e dentre as metodologias existentes para conservar a diversidade genética animal, incluem-se as conservações *ex situ* e *in situ*. A conservação considerada *ex situ* pode ser *in vitro*, quando o material genético (sêmen, ovócitos ou embriões) é mantido em botijões de nitrogênio líquido, ou Bancos de Germoplasma,

ou *in vivo*, quando os animais são mantidos fora do local onde foram naturalmente selecionados (como preservação em zoológicos) (Revidatti, 2009).

Neste contexto, desde 1983, a Empresa Brasileira de Pesquisa e Agropecuária (EMBRAPA) abrange em seu Programa de Conservação de Recursos Genético, até então exclusivo para o germoplasma de planta, a conservação de recursos genéticos animais. Este programa compreende a conservação destes recursos em universidades, propriedades particulares, empresas estaduais de pesquisa e centros de pesquisa da própria EMBRAPA, sob a coordenação da Embrapa Recursos Genéticos e Biotecnologias (Brasília – DF) (Sollero, 2006).

A modelagem revelou a possibilidade de utilizar a edição gênica para inserir alelos benéficos em raças de suínos, o que pode manter ou até mesmo acelerar a taxa de melhoria genética alcançada por meio de programas tradicionais de melhoramento (Ceasar *et al*., 2016). Essa abordagem se mostra mais vantajosa em relação ao longo processo de transferência desses alelos de raças distantes, conhecido como introgressão (Heiser, 1973). Através da edição genômica, é viável introduzir de forma precisa alelos úteis, tais como aqueles relacionados à tolerância ao calor e a resistência a doenças, em raças de suínos localmente adaptadas que já estão adaptadas aos ambientes locais, contribuindo para o aprimoramento de sua produtividade. Entretanto, a incorporação da edição genômica em programas de melhoramento genético de suínos dependerá significativamente das decisões globais que envolvem a regulamentação e a governança dessa tecnologia para animais destinados à alimentação.

A perda de recursos genéticos representa risco para a segurança alimentar e o desenvolvimento sustentável. Além disso, a perda dessas raças localmente adaptadas pode acarretar consequências significativas, como a erosão cultural, a redução das oportunidades de desenvolvimento das economias rurais e a limitação de opções futuras de desenvolvimento baseadas em produtos e serviços de origem animal procedentes de raças específicas. Os impactos ambientais negativos também podem ocorrer, assim como a perda de características únicas associadas a essas raças (FAO, 2007).

As etapas envolvidas no processo de conservação de espécies abrangem a identificação das populações em diluição genética ou risco de extinção; a caracterização fenotípica e genética; e a avaliação do potencial produtivo da

população (Egito; Mariante; Albuquerque, 2002). Um dos fatores mais relevantes a ser levando em consideração é o grau de desaparecimento a que está raça está submetida. No entanto, é difícil de ser avaliado, pois há outros tantos fatores envolvidos na sobrevivência de uma raça, além de influenciar a variação genética contida dentro dela. Por estes motivos, muitas vezes esta identificação encontra-se fora do controle (Gandini *et al.*, 2004).

Em seu estudo, Ruane (1999) determinou um painel de critérios a serem levados em consideração ao se determinar se uma raça é merecedora de participar de um programa de conservação. As características únicas da raça e o grau de desaparecimento são um dos critérios principais discutido. Do ponto de vista econômico, as diversidades funcionais e genéticas também devem ser usadas na determinação das diferenças entre raças, bem como na decisão de quais devem ser prioritariamente preservadas.

Na situação em que tantas raças ainda se encontram em perigo de extinção, é necessário que os recursos limitados (financeiro e pessoal) disponíveis sejam melhor utilizados, visando garantir que o máximo possível de diversidade genética sobreviva ao futuro. Uma vez que muitas das raças ameaçadas, principalmente nos países em desenvolvimento, ainda não foram devidamente caracterizadas, a estratégia deve ser documentar de forma rápida e econômica esses recursos genéticos com o intuito de evitar a sua extinção (Ruane, 1999).

2.5. Corridas de homozigose

A proporção do genoma que contém SNPs homozigotos (Mcquillan *et al.*, 2008) e os elementos da diagonal da matriz genômica de parentesco (Vanraden, 2008) são exemplos de medidas genômicas que podem ser utilizadas para determinar o nível de endogamia ao longo do genoma. No entanto, possuem a limitação de não distinguir entre identidade por descendência (IBD) e identidade por estado (IBS). Uma possibilidade para contornar esse problema é utilizar as corridas de homozigose (Pryce *et al.*, 2014). De acordo com Gibson *et al.* (2006) as ROHs são segmentos contínuos e ininterruptos de sequências de DNA sem heterozigose em organismos diploides. Elas ocorrem quando pais com um ancestral comum passam segmentos cromossômicos compartilhados idênticos por descendência (IBD) para a sua progênie

(Wright, 1922). Esse fenômeno resulta em segmentos homozigotos contínuos herdados no genoma da prole, caracterizados como ROH (Figura 1) (Broman; Weber, 1999).

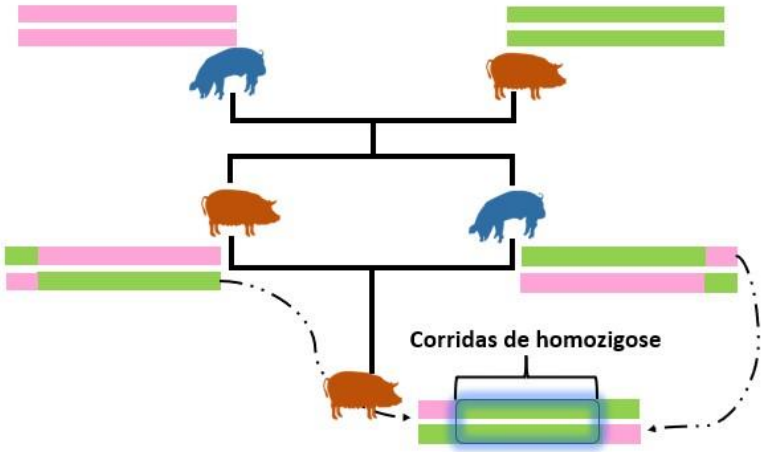

Figura 1. Ilustração de uma corrida de homozigose (Adaptado de: https://theg-cat.com/2022/06/02/runaway-inbreeding-how-runs-of-homozygosity-impact-conservation-management/)

Quando comparados à diagonal da matriz genômica ou à proporção de SNPs homozigotos, segmentos longos de ROH apresentam pouca probabilidade de terem surgido ao acaso, e provavelmente são fragmentos de cromossomos homólogos em um mesmo indivíduo que são IBD (Keller *et al.*, 2012). Os segmentos longos do cromossomo ao longo do tempo são interrompidos por eventos de recombinação, portanto ROHs mais longas tendem a ser segmentos autozigóticos originados de ancestrais recentes em comum. Em contrapartida, ROHs mais curtas provavelmente são originárias de ancestrais mais remotos, contudo, também podem incluir alguns segmentos que não são IBD. Deste modo, os comprimentos de ROH podem ser esclarecedores quanto à ancestralidade da endogamia (Figura 2) (Ferenčaković *et al.*, 2013).

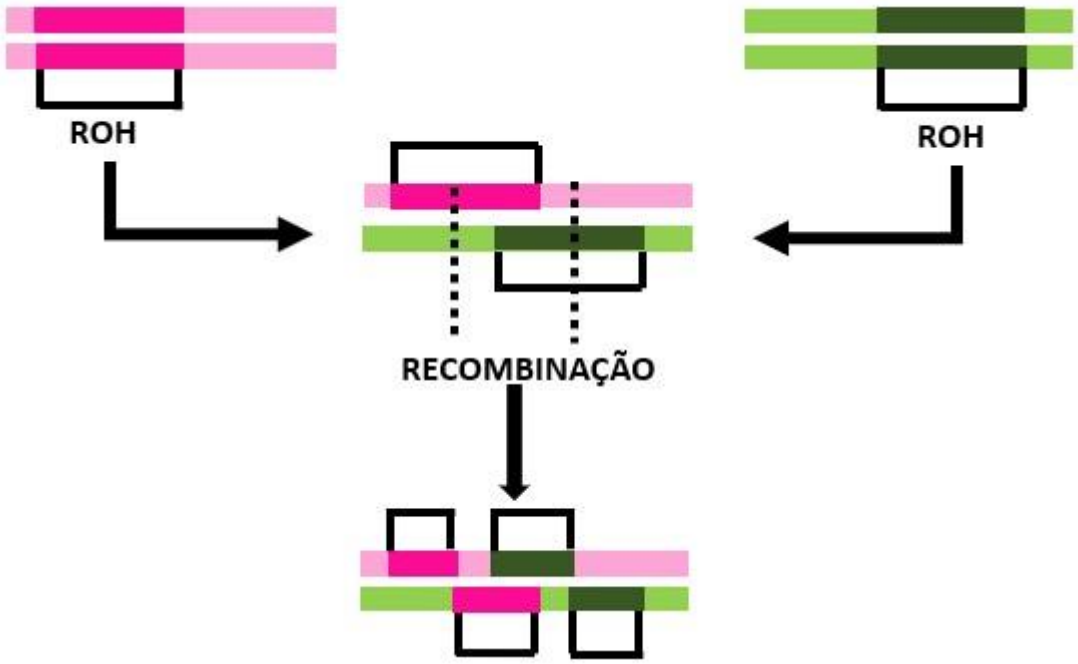

Figura 2. Como a recombinação desmonta a ROH longa. Apesar de ambos os ancestrais possuírem algumas ROHs muito longas, um evento de recombinação na seção intermediária desta seção divides essas ROHs nos dois cromossomos, reduzindo seu comprimento total, respectivamente. (Adaptado de: https://theg-cat.com/2022/06/02/runaway-inbreeding-how-runs-of-homozygosity-impact-conservation-management/)

A frequência e extensão das ROHs podem informar a respeito dos níveis de endogamia de uma população ou indivíduo, no entanto, é possível o surgimento de ROHs através de diferentes mecanismos, como deriva genética, seleção natural ou artificial, gargalos populacionais e acasalamento entre indivíduos aparentados (Zavarez *et al.*, 2015). Em compensação, algumas vezes as ROHs podem aparecer em indivíduos não-endogâmicos, talvez devido ao desequilíbrio de ligação (LD) ou recombinações em certas regiões genômicas e mutações (Gibson *et al.*, 2006). Nesse sentido, a partir das ROHs os coeficientes de endogamia genômicos (F_{ROH}) podem ser identificadas por meio do comprimento das ROHs (Purfield *et al.*, 2012).

2.6. Corridas de homozigose em suínos

As ROHs foram analisadas pela primeira vez em populações humanas (Gibson; Morton; Collins, 2006; Kirin *et al.*, 2010; Mcquillan *et al.*, 2008) e estudos em populações pecuárias seguiram-se, incluindo bovinos (Bjelland *et al.*, 2013; Ferencakovic *et al.*, 2011; Purfield *et al.*, 2012) e suínos (Ai; Huang; Ren, 2013; Bosse *et al.*, 2012). Sempre buscando identificar e caracterizar os segmentos homozigotos em relação a história das populações em relação à endogamia.

As ROHs têm sido utilizadas para identificar assinaturas de seleção em algumas raças de suínos em conservação em todo o mundo. Lukić *et al.* (2020), Schiavo *et al.* (2020), Szmatoła *et al.* (2020) e Yang *et al.* (2017) utilizaram ROHs para identificar assinaturas de seleção em populações indígenas de suínos na Croácia, Itália, Polônia e Ásia, Europa e América, respectivamente. Os estudos demonstraram que os suínos nativos dessas regiões tiverem que se adaptar aos estressores enfrentados em seus ambientes, como estresse por calor, disponibilidade de alimentos abaixo do ideal ou desafios a seus sistemas imunológicos por patógenos devido à falta de protocolos de vacinação. Todos os estudos usaram chips SNP de 60 K marcadores, mas diferiram nos softwares e parâmetros usados para detectar as ROHs. Contudo, em todos os estudos, a detecção das ROHs permitiu a identificação de assinaturas de seleção e genes que estiveram sob seleção nessas populações. Genes identificados nas regiões ROH confirmaram a presença de pressão seletiva natural para comportamento animal, desenvolvimento muscular e corporal, funcionamento do sistema imunológico e características de carcaça. As informações dos estudos citados auxiliam no entendimento das regiões do genoma que controlam as características biológicas que permitem a adaptação ambiental e relacionados a qualidade da carne. Os autores Schiavo *et al.*(2021) investigaram ROHs em um total de 1.131 porcos de 20 raças suínas locais europeias e em três raças cosmopolitas. Eles identificaram várias ilhas de ROH em regiões que englobavam genes conhecidos por afetar características morfológicas, contribuindo para a compreensão da história genética das raças e fornecendo informações para gerenciar esses recursos genéticos.

Fang *et al.* (2021) e Wang *et al.* (2021) analisaram a raça indígena chinesa Laiwu, conhecida pelo seu alto teor de gordura intramuscular, sendo um excelente

recurso para o melhoramento genético da qualidade da carne em suínos comerciais. Eles utilizaram a ROH para detectar assinaturas de seleção para mapear os genes candidatos associados a características economicamente importantes. No estudo de Fang *et al.* (2021), utilizaram as ROHs para estimar o coeficiente de endogamia, detectando segmentos de ROH com mais de 1 Mb, cujo o comprimento médio foi de 3,76 Mb, onde os segmentos curtos (1-5 Mb) dominaram. Ambos os estudos identificaram genes relacionados a qualidade da carne e reprodução. Esses resultados ajudam a entender as características dos porcos Laiwu e fornecem informações para futuras estratégias promissoras com o intuito de aprimorar os programas de seleção genômica, manejo da endogamia e a conservação genética, visando otimizar o potencial genético e a sustentabilidade da raça.

2.7. Coeficiente de endogamia genômico (F_{ROH})

O coeficiente de endogamia é tradicionalmente estimado a partir de informações derivadas de dados de pedigree (Wright, 1922). O desenvolvimento de painéis de SNP de alta densidade levou a um interesse crescente no cálculo de coeficientes de endogamia com informação molecular em animais (Jiang *et al.*, 2022; Krupa *et al.*, 2021; Zorc *et al.*, 2022). Dados moleculares são mais eficazes para estimar a autozigosidade e detectar os efeitos endogamia que dados de pedigree devido à sua capacidade de fornecer informações diretas sobre o genoma de um indivíduo, em vez de depender apenas da informação genealógica disponível no pedigree (Keller; Visscher; Goddard, 2011). Com a informação molecular, os coeficientes de endogamia podem ser estimados a partir de genótipos homozigotos ROH (F_{ROH}) (Peripolli *et al.*, 2017). As estimativas da F_{ROH} podem identificar a história da endogamia com base no comprimento da ROH, mesmo na ausência de informações genealógicas (Peripolli *et al.*, 2017). Portanto, os dados moleculares oferecem uma abordagem mais abrangente e precisa para avaliar a endogamia e seus efeitos nos programas de melhoramento genético.

2.8. Assinaturas de seleção detectadas por execuções de homozigose

As assinaturas de seleção delimitam regiões do genoma que são, ou foram funcionalmente importantes e, portanto, estiveram sob seleção natural ou artificial (Gurgul *et al.*, 2018). Se um alelo confere vantagem adaptativa ou de produção, é mais provável que seu portador prospere e deixe mais descendentes do que o não portador e, como consequência, o haplótipo contendo esse alelo benéfico tende a se espalhar rapidamente e aumenta a frequência na população (Schaffner; Sabeti, 2008). Variantes vizinhas a essa mutação benéfica também tendem a aumentar a frequência em um processo conhecido como efeito “carona” (Figura 3) (Fay; Wu, 2000; Smith; Haigh, 1974), e os padrões de desequilíbrio de ligação estendido entre a mutação favorável e os SNPs vizinhos podem ser observados (Schaffner; Sabeti, 2008; Voight *et al.*, 2006).

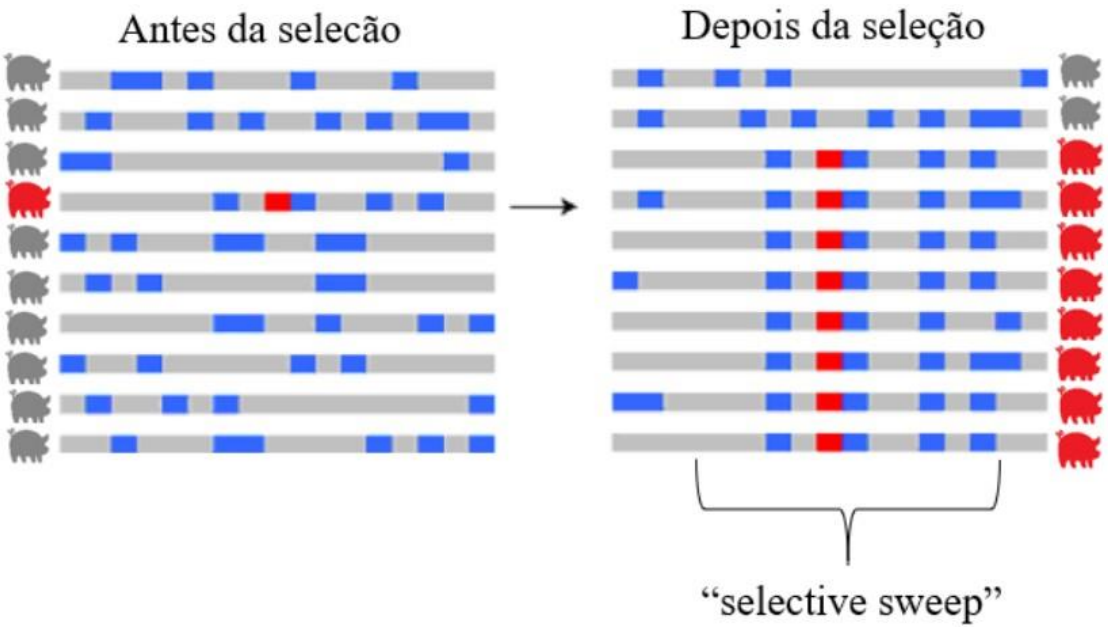

Figura 3. Esquema demonstrando a criação da “selective sweep”, ou arrasto seletivo. Observem-se os alelos ao longo do cromossomo de diferentes indivíduos, incluindo o alelo selecionado (em vermelho), antes e após a seleção. Os alelos ancestrais (originados de ancestral comum) estão em cinza e os derivados (originados por mutação ou fluxo gênico) em azul. Após a seleção, o alelo favorável (vermelho) alcança alta frequência, os alelos nas proximidades, ligados a ele, também aumentam sua frequência (efeito carona – “hitchhike”), devido ao desequilíbrio de ligação entre eles, conservando uma região do genoma (“selective sweep”) e criando uma assinatura de seleção. (Adaptado de Schaffner; Sabeti (2008)).

Conforme descrito acima, se uma população sofre eventos de pressão de seleção, ela deixa padrões tratáveis distintos de variação genética que se desviam estatisticamente do esperado puramente ao acaso (Kim; Stephan, 2002; Oleksyk; Smith; O'brien, 2010). Para detectar essas regiões de seleção, é possível identificar a sobreposição de regiões homozigotas compartilhadas por uma porcentagem maior de indivíduos em uma população (ilhas ROH), comumente consideradas como o resultado da seleção em torno de um locus alvo ou indicam baixa taxa de recombinação em regiões genômicas específicas (Pemberton *et al.*, 2012; Peripolli *et al.*, 2017, 2018).

Uma investigação mais profunda nessas regiões identificadas como assinaturas, pode revelar genes candidatos que controlam características economicamente importantes (Fang *et al.*, 2021; Wang *et al.*, 2022; Wu *et al.*, 2021). Essas informações podem ajudar a entender melhor os mecanismos de seleção em populações de animais de produção. Por outro lado, as ROHs também podem ser usadas para identificar haplótipos associados ao desempenho reduzido (Howard *et al.*, 2017). A meta-análise de Doekes; Bijma; Windig (2021) aborda a identificação de ROHs em diversas espécies, como bovinos, suínos, frangos, ovinos, caprinos, equinos e coelhos, que apresentam efeitos desfavoráveis em características de interesse. Identificar ROHs específicas associadas a características desfavoráveis permite aos pesquisadores entender melhor as implicações biológicas da homozigose em loci específicos (Baes *et al.*, 2019) e o melhor gerenciamento de haplótipos ou mutações desfavoráveis em programas de melhoramento (Cole, 2015; Kinghorn, 2011). Além disso, essas informações auxiliam na compreensão de como e por que a ROH pode afetar características de interesse, fornecendo *insights* valiosos sobre os processo genéticos e biológicos envolvidos e auxiliando no desenvolvimento de estratégias mais eficazes para o melhoramento génetico.

De acordo com Zhao *et al.* (2021) o comprimento total da ROH nos cromossomos autossomos para os bovinos de corte da raça Simental utilizados no estudo está fracamente correlacionado com as características de produção, porém não são estatisticamente significativos. Doekes *et al.* (2019) relataram aumento de 0,03 kg para a endogamia antiga (ROH curta) em gado leiteiro Holandês-Frísio. Esses estudos demonstram que os comprimentos das ROHs não necessariamente têm o mesmo efeito sobre as características. O efeito das ROHs nas características pode

variar dependendo de diversos fatores, incluindo o tamanho da ROH, a posição no genoma, a presença de genes ou variantes associadas à caracterísiticas em questão, e interações genéticas e ambientais.

2.9. Estrutura genética e populacional

Devido à grande resolução alcançada pelas plataformas de genotipagem, é possível utilizar ferramentas de computação capazes de traçar a estrutura da população, fornecendo informações sobre padrões de dispersão e eventos históricos recentes e antigos da população de interesse (Lawson *et al.*, 2012). No entanto, é importante ressaltar que, embora essas plataformas tenham alcançado uma grande resolução, um painel desenvolvido para raças de suínos domésticos comerciais pode deixar de identificar uma variação encontrada em raças localmente adaptadas, devido às variações genéticas únicas dessas populações (Berry & Spangler *et al.*,2023). Estudos a respeito da estrutura genética de populações de diversas espécies de animais domésticos, especialmente de raças nativas, são essenciais na manutenção da sua variabilidade genética, estabelecimento de políticas de conservação e contribuição para a sua sustentabilidade (Muñoz *et al.*, 2019).

Estudos dessa natureza possibilitam que se avalie a composição genética de populações de interesse, tornando possível avaliar questões como características de interesse do ponto de vista zootécnico, susceptibilidade a doenças, origem e parentesco. Essas abordagens vem se tornando cada vez mais frequentes, possibilitando por análises paralelas de centenas de milhares de SNPs que se encontram distribuídos ao longo do genoma dos indivíduos (Fedorova *et al.*, 2022, com aves; Kukučková *et al.*, 2017, com bovinos; Criscione *et al.*, 2022; Islam *et al.*, 2019; Signer-Hasler *et al.*, 2022, com caprinos; Mchugo *et al.*, 2019; Purfield *et al.*, 2017; Shi *et al.*, 2023, com ovinos; Bâlteanu *et al.*, 2019; Burgos-Paz *et al.*, 2013; Yang *et al.*, 2017, com suínos). Estimar e conhecer os níveis de endogamia torna imprescindível o papel da diversidade genética dentro de uma população na redução de efeitos negativos da mesma (Pekkala *et al.*, 2014; Pemberton *et al.*, 2017).

Os SNPs geram uma grande quantidade de informações genotípicas em pouco tempo e com alta taxa de confiabilidade e repetibilidade, o que auxiliam na inferência populacional e elucidação de possíveis locos que foram objetos de pressões seletivas

(Lawson *et al.*, 2012). Os dados gerados a partir de genotipagem de milhares de marcadores SNPs podem ser usados em análises multivariadas, como a análise de componentes principais (PCA – principal componente analysis), que é eficiente no auxílio de estudos que visam avaliar a variação entre grupos genéticos e seus indivíduos (Jombart, 2008; Price *et al.*, 2006). A PCA é capaz de elucidar informações a respeito não somente da variabilidade genética randômica (variação intrapopulacional), mas também sobre a variabilidade entre os indivíduos (Jombart; Devillard; Balloux, 2010). Para realizar a PCA, é necessário conhecer previamente a estrutura populacional dos indivíduos analisados, não sendo possível extrair essa informação somente a partir dos dados (Nogueira, 2021). Essa ferramenta apresenta grande potencial e utilidade na conservação das informações originais dos alelos dos componentes principais (PC), representados por cada eixo da projeção gráfica construída a partir dos dados gerados na análise. Isso reduz drasticamente a dimensão das variáveis envolvidas.

O software ADMIXTURE pode ser utilizado em análises de raças localmente adaptadas. Ele estima o coeficiente de ancestralidade como parâmetros de modelo estatístico, adotando o modelo de verossimilhança. Estima simultaneamente as frequências alélicas juntamente com as proporções de ascendência. Além disso, é capaz de executar testes de clusters supervisionados para avaliar a ancestralidade de híbridos reais e simulados (Alexander; Novembre; Lange, 2009).

Em suínos, estudos sobre estrutura da população foram aplicados em programas de conservação em animais da Península Ibérica (Cortés *et al.,* 2016; Gama *et al.,* 2013), considerando a estratificação da população entre suínos domesticados e selvagens de populações nativas da região, a partir de análises de componentes principais (Herrero-Medrano *et al.*, 2013). Esse tipo de análise também pode ser realizada em estudos de diversidade genética, como no estudo realizado por Ai; Huang; Ren, (2013). Além disso, estudos de estratificação da população foram aplicados utilizando o ADMIXTURE em trabalhos com raças crioulas americanas, como o de Revidatti *et al.* (2021), que buscou investigar a diversidade genética, estrutura e relações raciais dessas populações.

3. Hipóteses

Os animais da raça Moura são mais endogâmicos em relação às raças comerciais, devido ao fato de ter estado em vias de extinção, enquanto as raças comerciais passaram por processos seletivos intensivos ao longo do tempo. No entanto, é importante reconhecer que as raças comerciais também podem ter experimentado endogamia significativa como resultado desses processos seletivos. As ilhas de ROH e as regiões genômicas homozigotas compartilhadas possuem genes relacionados à qualidade da carne, o que nos permite entender melhor os mecanismos de seleção na produção de carne de qualidade superior na raça Moura.

As raças Moura, Crioula Argentina e comerciais apresentam estruturação populacional e ancestrais em comum. Quanto à ancestralidade das assinaturas d análise de estruturação populacional identificou regiões compartilhadas entre o Moura e o Duroc por apresentarem a mesma raça ancestral em comum. Quanto à ancestralidade das assinaturas, existe uma aproximação genética entre o Moura e a raça Crioula da Argentina.

4. Objetivos

Caracterizar regiões genômicas através de corridas de homozigose em animais da raça Moura, em comparação com as raças comerciais e a raça crioula da Argentina, visando identificar níveis de endogamia, genes e QTLs relevantes, assinaturas de seleção e ancestralidade genética no genoma dessa população.

Objetivos específicos:

I. Avaliar e caracterizar os níveis de endogamia genômico nas raças de suínos estudadas;

II. Identificar ilhas de ROH e anotar genes e QTLs relevantes para características de interesse econômico para a raça Moura;

III. Identificar assinaturas de seleção através das corridas de homozigose;

IV. Avaliar a estrutura populacional e ancestralidade das assinaturas presentes no genoma dos animais Moura;

CAPÍTULO II – Genomic inbreeding estimated through runs of homozygosity in Moura pigs and four commercial swine breeds[1]

[1] Artigo aceito para publicação na revista Livestock Science 08 de Fevereiro de 2024.

Genomic inbreeding estimated through runs of homozygosity in Moura pigs and four commercial swine breeds

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Abstract

The transmission of identical haplotypes from a common ancestor creates long stretches of homozygous genotypes, known as runs of homozygosity (ROHs). Longer haplotypes are inherited from recent common ancestors, and shorter haplotypes, from distant ancestors. In this study, we performed a comparative analysis of the genomic data of the Moura pig breed, a locally adapted breed from Brazil, that typically grows in extensive or semi-intensive systems, in comparison to the commercial breeds Duroc, Landrace, Large White, and Pietrain. We investigated ROH patterns and different inbreeding coefficients in order to guide long-term breeding programs, rescue efforts, and breed evaluation programs. To understand these patterns, we performed a detailed genome characterization of 459 animals, of which 84 were Moura, 87 Duroc, 138 Landrace, 84 Large White and 66 Pietrain swine, performed using Illumina Porcine v2 BeadChip markers.

Inbreeding coefficients based on the genomic relationship matrix and ROH were calculated, indicating that Moura pigs displayed the highest ROH frequency (greater than 8 Mb) compared to the other swine breeds. This demonstrates that Moura pigs exhibit greater inbreeding in recent generations, probably due to severe reductions in the number of animals. Furthermore, genes related to meat quality were detected on the ROH islands superimposed on the Moura and Duroc breeds, comprising one of the main characteristics of both breeds. Kinship analysis revealed notable genetic diversity among Moura pigs, with the majority of comparisons indicating the absence of direct parentage. Our findings contribute to a better understanding of the genomic profile of the locally adapted Moura breed. Additionally, they underscore the importance of monitoring inbreeding as a starting point for genetic improvement programs and genomic studies of this breed.

Keywords: inbreeding coefficient; single nucleotide polymorphism; locally adapted Brazilian breed; *Sus scrofa*

1. Introduction

Brazilian swine farming was established mainly by carrying out absorption crosses between locally adapted breeds and exotic breeds with high genetic potential selected throughout temperate climate regions (Egito et al., 2002). Swine comprised an important source of food in Brazil up to the beginning of the 20th century, However, due to market transformations and industry and consumer preferences, locally adapted breeds began being replaced by more productive exotic breeds with less carcass fat (Leite et al., 2021). From this point on, Brazilian pig breeds have been facing decreasing numbers and diversity, with some even facing extinction risks (Macêdo et al., 2020).

The Moura breed emerged in southern Brazil (Machado, 1967) during the first decades of the last century, although the precise period is unknown (Fávero et al., 2007). These animals are noteworthy for their hardiness, prolificacy, marbling and good meat aptitude (Bertol et al., 2010; Machado, 1967; Silva, 1987; Torres, 1968). However, from the 1970s onwards, locally adapted pig breeds experienced demographic declines due to the beginning of genetic improvements in Brazil and the arrival of pigs from Europe and North America (Maciel, 2019). The search for information about Moura pigs goes back to the first in situ conservation herd, in 1985, financed by Banco do Brazil and run by the Federal University of Paraná (UFPR). The project entitled “Performance, Management, Reproduction and Feeding Alternative in Pigs of the Moura Breed” aimed to recover, evaluate, fix and multiply pigs of the Moura breed (Juliatto, 2016).

To date, some farms in the states of Rio Grande do Sul, Santa Catarina and Paraná, in addition to public institutions such as the Federal University of

Paraná (UFPR, Curitiba/PR), EMBRAPA – Swine and Poultry (CNPSA, Concórdia/SC); the “Júlio de Mesquita Filho” Paulista State University (UNESP, Ilha Solteira/SP) and the Santa Catarina State University (UDESC, Lages/SC) have established conservation programs comprising small herds with the purpose of preserving genetic Moura variability (Juliatto, 2016). The demographic decline of this breed is expected to reduce genetic variation that may, in turn, lead to less genetic gain opportunities in the future and increase inbreeding levels, threatening the conservation of this breed.

Few studies have been carried out employing molecular markers reflecting genetic variations and inbreeding on locally adapted Brazilian swine breeds compared to commercial pig breeds (Burgos-Paz et al., 2013; Cesconeto et al., 2017; Silva et al., 2011; Sollero et al., 2009). Genomic tools allow the simultaneous genotyping of thousands of polymorphisms throughout the genome, enabling the identification of stretches of homozygous genotypes. Runs of homozygosity (ROH) are continuous homozygous genome segments with identical haplotypes inherited from both parents. The extent and frequency of ROHs can inform about the ancestry of an individual animal and that of the entire population. Inbreeding can also be estimated by ROH, where the longer the ROH, the greater the likelihood of recent lineage inbreeding, due to limited recombination opportunities for disrupting these haplotype segments (McQuillan et al., 2008).

Furthermore, ROH analyses allows for the calculation of inbreeding coefficients (F_{ROH}) for populations with no or poor-quality pedigree records. Another way to obtain inbreeding coefficients is to use the identity by state (IBS) method, which summarizes single nucleotide polymorphisms (SNP) per SNP

using a genomic relationship matrix. (F_{GRM}; VanRaden et al., 2011). Previous studies have described that the genome-wide ROH distribution is not random, and some *loci* have been identified as containing the highest ROH frequencies (Bosse et al., 2012). These loci are called “ROH islands” and are possibly created as a result of the presence of alleles that have undergone selection and are close to fixation (Zhang et al., 2015). Therefore, ROH island analyses can identify the location of variants under selection and reveal selected traits in different populations (Bosse et al., 2012).

In this context, the aim of the present study was to characterize ROH Moura pig genome patterns compared to the commercial swine breeds Duroc, Landrace, Large White and Pietrain, estimate genomic inbreeding coefficients through the genomic relationship matrix (F_{GRM}) and through the continuous homozygous segments (F_{ROH}), identify genomic regions characterized by ROH islands influenced by inbreeding, and determine the main genes present in these shared islands. Furthermore, we aimed to expand our investigation by analyzing kinship relationships among Moura breed animals, allowing for a deeper understanding of the genetic structure of this population.

2. Material and Methods

2.1 Ethics Declaration

Approval from an Animal Care and Use Committee was not required in this study, as the information was obtained from a pre-existing database provided by several Brazilian public institutions: EMBRAPA – Swine and Poultry (CNPSA), EMBRAPA – Genetic Resources and Biotechnology (CENARGEN), Federal University of Rio Grande do Sul (UFRGS), the Federal University of Paraná

(UFPR), the Passo Fundo University (UPF), in addition to the publically available Dryad Digital Repository Yang et al. (2017).

2.2 Genotyping, Quality Control and Principal Component Analysis

The genotype data from Brazilian public institutions and the DRYAD digital repository were merged with PLINK V1.9 (Chang et al., 2015) using only SNPs with unique IDs and chromosomal positions as identified by the SNPchiMp v.3 software (Nicolazzi et al., 2015). Genotype data were merged using the --merge command. To ensure proper merging, we allowed samples without sex information using the (`--allow-no-sex`) option. We restricted the analysis to the first 18 chromosomes using (`--chr 1-18`). Additionally, we chose to recode the data through the (`--recode`) option. After merging the data, we had 459 animals and 40,662 SNPs for further Quality Control (QC) (supplementary Figure S1).

The genotype bank of Brazilian public institutions contained the sequences of 75 Moura pigs from three institutional herds descended from the *ex-situ* conservation herd created at UFPR in 1985 from eight breeding farms in the Southern Region (UFPR, n=25) (Botan et al., 2019). In addition to thirteen other private and two institutional squads, considered in-situ remnants, located in the regions of Concórdia-SC (n=04), Bodocó-PE (n=01), Ouricuri-PE (n=01), Exu-PE (n=01), Araripina-PE (n=01), Granito-PE (n=02), Parnamirim-PE (n=01), São José do Egypt-PE (n=01), Distrito Federal-DF (n=01), Carlos Barbosa-RS (n=05), Candelária-RS (n=10), Ponte Alta-SC (n=6), UDESC-SC (n=4), Santa Cecília-SC (n=2) and São Mateus do Sul-PR (n=10). Moreover, eight animals from each of the commercial breeds Duroc, Landrace, Large White and Pietrain

were included, all genotyped using the Illumina Porcine v2 marker chip (Ramos et al., 2009) and containing 61,565 SNPs. Additionally, SNP array data from an additional 352 animals [Moura (n=9), Duroc (n=79), Landrace (n=130), Large White (n=76) and Pietrain (n=58)] were obtained from the Repository Digital Dryad, containing 61,772 SNPs.

To compare our data with worldwide datasets, the commercial breeds were represented by more than three different populations to provide additional controls. This dataset was then merged with the Brazilian samples to produce a consensus dataset. Quality control (QC) was performed via the PLINK version 1.9 software (Chang et al., 2015). Animals with a call rate of less than 90% (correctly genotyped genome percentage) were discarded (`--mind 0.90`).

Only autosomal SNPs with a call rate of over 95% (percentage of each SNP genotyping in all samples) (`--geno 0.95`) were analyzed, assisting in increasing data accuracy. (Oliphant et al., 2002). The file format conversion to BED format (`--make-bed`), exclusion of founders (`--nonfounders`), and execution without the web interface (`--noweb`) optimized the data processing. No filterings for minor allele frequency (MAF) and the Hardy-Weinberg balance (HWE) were performed, as the purpose was to detect homozygous stretches and this pruning could affect the results (Ferenčaković et al., 2013). After merging the genotypes and quality control, the final dataset comprised with comprised 459 animals belonging to the five analyzed breeds (supplementary Table S1) with 40,662 SNPs distributed throughout autosomal chromosomes (supplementary Table S2).

A Principal Component Analysis (PCA) was performed using the PLINK version 1.9 software to visualize genetic distances between the studied

populations (Chang et al., 2015). The “ggplot2” R package was used to represent the animals in two-dimensional scales (Wickham, 2010) and the “scatterplot3D” package was employed for three-dimensional scales (Ligges and Mächler, 2003).

2.3 Detection of runs of homozygosity (ROH)

The PLINK v1.9 software (Chang et al., 2015) was used to identify ROH (supplementary Figure S2). No pruning was performed based on linkage disequilibrium to avoid biases introduced by this practice (Marras et al., 2015), but a minimum length of 1 Mbp for ROH detection was defined to exclude short and common ROHs arising from frequent porcine genome linkage disequilibrium. The ROH detection parameters were similar to those applied by Ferenčaković et al. (2013), Marras et al. (2015) and Schiavo et al., (2020a), as follows: (i) minimum number of consecutive homozygous SNPs included in the ROH of 15 (`--homozyg-snp 15`); (ii) missing genotypes were not allowed (`--no-pheno`); (iii) minimum length of the region of 1 Mbp ROH (`--homozyg-kb 1000`); (iv) number of heterozygous SNPs allowed in the ROH of 0 (`--homozyg-window-het 0`); (v) minimum SNP density in a genome window of 1 SNP every 100 Kbp (`--homozyg-density 100`); (vi) maximum allowable distance between consecutive SNPs of 1000 Kbp (`--homozyg-gap 1000`); (vii) homozygous SNP clustering (`--homozyg group`). Fisher (1954) observed that the expected length of a DNA segment identical by descent follows the exponential distribution with a mean equal to g x cM, where g is the number of generations from the common ancestor and cM is the centimorgan unit. Assuming 1 cM = 1 Mbp, ROH with lengths of 1, 2, 4, 8, and 16 Mbp are expected to originate from a common ancestor occurring approximately 50, 25, 12, 6, and 3 generations ago,

respectively. Therefore, ROHs were categorized into five classes according to Ferenčaković et al. (2013), Kirin et al. (2010) and Schiavo et al., (2020b), as <2, 2 to 4, 4 to 8, 8 to 16 and > 16 Mb, identified as ROH $_{1\text{-}2\ Mb}$, ROH $_{2\text{-}4\ Mb}$, ROH $_{4\text{-}8\ Mb}$, ROH $_{8\text{-}16\ MB}$ and ROH $_{>\ 16\ Mb}$, respectively.

2.4 Inbreeding coefficients

Two types of genomic inbreeding coefficients (F) were considered, F_{ROH}, estimated through continuous homozygous segments and F_{GRM}, estimated based on the diagonal elements of the genomic relationship matrix.

The ROH genomic inbreeding coefficient F_{ROH} was calculated for each animal as the ratio between continuous homozygous segments in relation to the autosomal genome (McQuillan et al., 2008):

$$F_{ROH} = \frac{\sum_{j=1}^{n} L_{ROHj}}{L_{total}}$$

Where L_{ROH} is the total ROH length in an individual j and L_{total} is the total length of the autosomal genome covered by markers as depicted in supplementary Table S2. The ROH segments were detected using the PLINK v1.90 software (Chang et al., 2015). The F_{ROH} for each animal was calculated including all ROH classes (< 2 Mbp; $F_{ROH1\text{-}2}$) or including ROH 2 to 4 Mbp ($F_{ROH2\text{-}4}$), ROH 4 to 8 Mbp ($F_{ROH4\text{-}8}$), ROH 8 to 16 Mbp ($F_{ROH8\text{-}16}$) and ROH > 16 Mbp ($F_{ROH>16}$), following the mentioned length classification criteria.

To determine the F_{GRM}, the matrix G was built using the PreGSf90 package from BLUPF90 (Misztal et al., 2014), according to VanRaden et al. (2011), employing the following equation:

$$G = \frac{ZZ'}{2\sum_{i=1}^{n} pi(1-pi)}$$

Where G is the genomic matrix, Z is a matrix of genotypes that can be obtained through *Z=M-P*, where the matrix *M* specifies which alleles each individual inherited (markers coded as 0, 1, or 2 for homozygous alternative, heterozygous, and reference homozygous allele, respectively), and the matrix *P*, whose elements in column l are equal to 2 *(pi)* where *pi* is the frequency of the reference allele at the locus, assumed as fixed pi =0.5, as proposed by VanRaden et al. (2011) . The inbreeding coefficient of animals i is equal to G_{ii} – 1. The diagonal elements of the matrix G represent the relationship of the animal with itself, employed to evaluate the genomic inbreeding coefficient (F_{GRM}).

The Kruskal-Wallis test for dependent samples was used to compare the genomic inbreeding coefficient calculation methods and the different ROH size classes (Kruskal and Wallis, 1952). Furthermore, correlation analyses between different inbreeding coefficient classes were performed to assess the strength of the associations between the different estimates.

2.5 Parentage analysis

Genomic identity by descent (IBD) between pairs of samples was estimated with the PI-HAT coefficient, which describes the probability of sharing 0, 1, or 2 IBD alleles by pairs of individuals from the same homogeneous random mating population (Purcell et al., 2007). The PI-HAT coefficient is calculated based on the sharing probabilities of IBD alleles, including 0 IBD alleles identical by descent (Z0), 1 IBD allele (Z1), and 2 IBD alleles (Z2), using the formula PI-HAT = P (IBD = 2) + 0.5 x P (IBD = 1).

In parent-child (PO) relationships, Z0 and Z2 are expected to equal 0, and Z1 is expected to equal 1. In quadratic pairs, Z0 and Z1 are expected to equal 0.5, while Z2 must equal 0. Therefore, PI-HAT values around 0.5 indicate first-degree or closer relationships.

To evaluate these relationships, we established a cutoff criterion of 0.2 for the results obtained in PLINK (Chang et al., 2015). PI-HAT values above this threshold were used to create a heat map in the R software, with the help of the ggplot2 package (Wickham, 2010). This cutoff criterion was applied to improve the graphical visualization of relationships between genotypes.

2.6 Identification of ROH Islands and Gene Annotation

The ROH regions shared between individuals are commonly associated as a reflection of population selection pressure (Pemberton et al., 2012). To detect the ROH islands, we used the output files generated by the PLINK v1.90 software (Chang et al., 2015) after applying the command-line settings presented in supplementary Figure S2. This analysis was conducted separately for each swine breed included in our study, and we subsequently calculated the number of times that a single SNP appeared within an ROH using the data produced by the software.

We selected the 1% most frequent SNPs, following the approach recommended by both Pemberton et al. (2012) and Mészáros et al. (2015). These studies defined "ROH islands" as areas where the SNPs demonstrated extreme frequencies of ROH, identified as outliers (representing the upper 99% of the distribution, according to the BOXPLOT) (supplementary Figure S3). The ROH islands were then formed by consecutive SNPs with ROH occurrences above or

equal to the determined limits and located at a distance ≤ 1 Mb from each other, following the definition established by (Schiavo et al., 2020b).

The gene contents of the determined ROH islands were annotated using the porcine reference genome obtained at the ENSEMBL BIOMART database (http://www.ensembl.org/biomart/martview/) and the NCBI file SSCROFA11.1 GFF. Genes obtained from ENSEMBL were stored for subsequent use in the functional annotation analysis employing the ShinyGo v0.741 (Ge et al., 2020) with a p-value cutoff of 0.05, and the top 30 pathways were displayed.

To illustrate the population structure of ROH islands shared between Moura pigs and commercial breeds, we conducted a PCA analysis. This analysis aimed to understand how breeds group based on SNPs located in that specific region. The main components were calculated using the PLINK v1.9 software (Chang et al., 2015), and the PCA visualization was generated in the R environment with the help of the 'ggplot2' package (Wickham, 2010).

3. Results

3.1 Population structure of commercial and Moura swine breeds

Principal Component Analysis (PCA) groups individuals based on their genetic proximity, allowing for the spatial visualization of genomic variation among these populations. In PCA (Figure 1 A, B), we can observe four distinct major clusters, with the Duroc breed being the most homogeneous among them, and the Moura breed exhibiting greater heterogeneity.

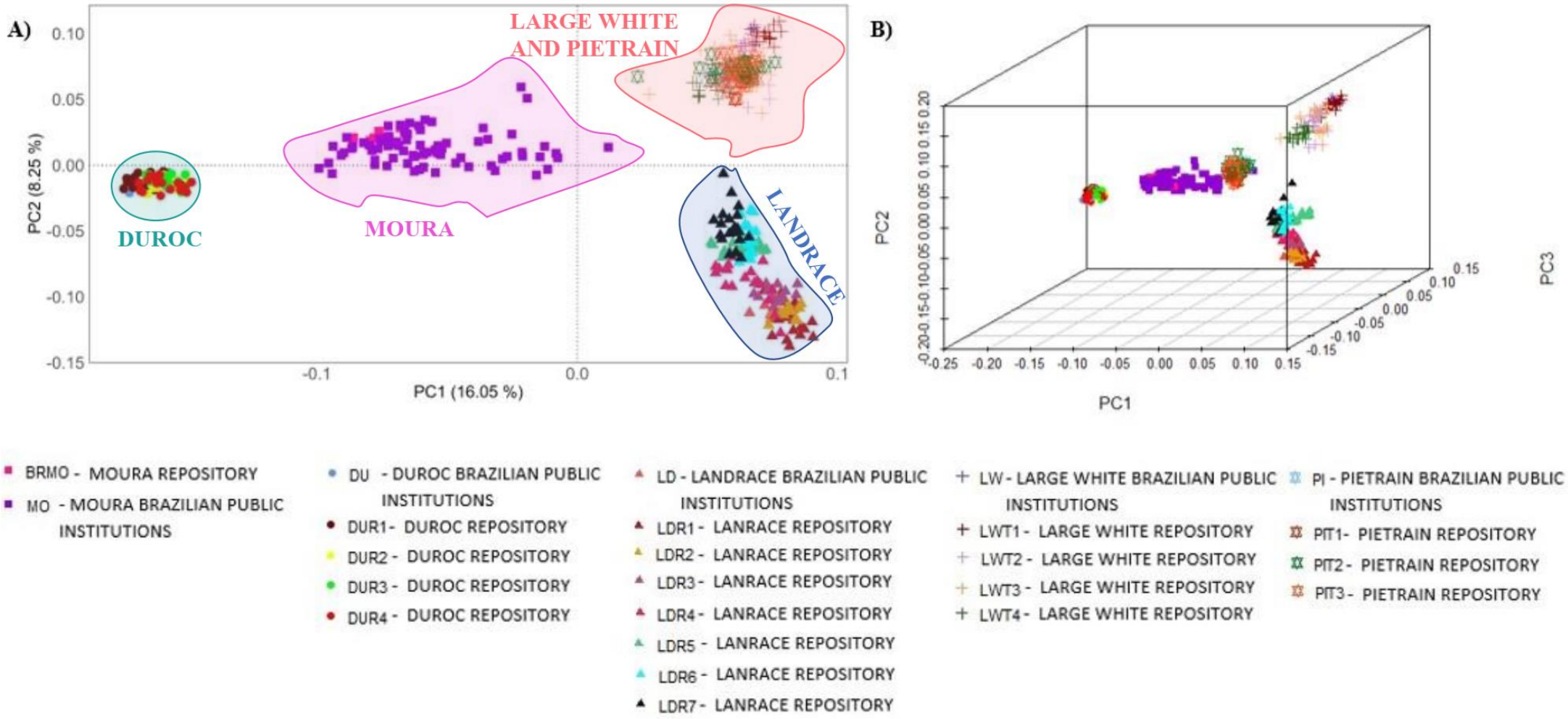

Figure 1 Major components of the five swine populations studied herein. A) Two-dimensional plot, B) three-dimensional plot.

3.2 Runs of homozygosity (ROH) characterization

Runs of homozygosity were identified in almost all individuals belonging to the five swine breeds, except for one Moura sample, which was excluded because it presented errors in more than 10% of the markers. A total of 25,538 homozygous segments were found, ranging from 7,599 in Landrace to 2,730 in Moura swine, while the highest average length was detected in Moura pigs (56.103 Mb) and the lowest, in Landrace (49.341 Mb) pigs. Among all the ROH, 798 were less than 2 Mb in length, while 8,833 ROHs ranged from 2-4 Mb, 8,543 ROHs from 4-8 Mb, 4,470 ROHs from 8-16, and 2,894 ROHs > 16 Mb (Table 1). The relative frequencies of the detected ROH are depicted in Figure 2.

Table 1. Descriptive statistics concerning the number of runs of homozygosity (nROH) and average length (Av. length) categorized into five classes for the five swine breends analyzed in the present study.

Breed	**Class**	***n*ROH**	**Percentage (%)**	**Av. length ± SD**
DU	ROH $_{1\text{-}2\ Mb}$	215	3.14	1.776 ± 0.212
	ROH $_{2\text{-}4\ Mb}$	2,350	34.33	3.033 ± 0.548
	ROH $_{4\text{-}8\ Mb}$	2,319	33.87	5.585 ± 1.140
	ROH $_{8\text{-}16\ Mb}$	1,183	17.28	11.021 ± 2.239
	ROH $_{>16\ Mb}$	779	11.38	29.392 ± 15.419
	TOTAL	6,846	100	8.238 ± 9.679
LD	ROH $_{1\text{-}2\ Mb}$	258	3.39	1.779 ± 0.176
	ROH $_{2\text{-}4\ Mb}$	2,711	35.68	2.977 ± 0.544
	ROH $_{4\text{-}8\ Mb}$	2,501	32.91	5.598 ± 1.122
	ROH $_{8\text{-}16\ Mb}$	1,320	17.37	11.049 ± 2.224
	ROH $_{>16\ Mb}$	809	10.65	27.938 ± 13.159

	TOTAL	7,599	100	7.858 ± 8.714
LW	ROH $_{1\text{-}2\ Mb}$	160	3.25	1.776 ± 0.206
	ROH $_{2\text{-}4\ Mb}$	1,767	35.90	3.001 ± 0.549
	ROH $_{4\text{-}8\ Mb}$	1,716	34.86	5.554 ± 1.101
	ROH $_{8\text{-}16\ Mb}$	818	16.62	10.986 ± 2.235
	ROH $_{>16\ Mb}$	461	9.37	29.588 ± 18.014
	TOTAL	4,922	100	7.669 ± 9.317
MO	ROH $_{1\text{-}2\ Mb}$	76	2.78	1.678 ± 0.282
	ROH $_{2\text{-}4\ Mb}$	841	30.81	3.005 ± 0.545
	ROH $_{4\text{-}8\ Mb}$	836	30.62	5.602 ± 1.112
	ROH $_{8\text{-}16\ Mb}$	526	19.27	11.277 ± 2.215
	ROH $_{>16\ Mb}$	451	16.52	34.541 ± 19.556
	TOTAL	2,730	100	10.567 ± 13.672
PI	ROH $_{1\text{-}2\ Mb}$	89	2.59	1.735 ± 0.208
	ROH $_{2\text{-}4\ Mb}$	1,164	33.83	3.025 ± 0.533
	ROH $_{4\text{-}8\ Mb}$	1,171	34.03	5.652 ± 1.142
	ROH $_{8\text{-}16\ Mb}$	623	18.10	11.159 ± 2.257
	ROH $_{>16\ Mb}$	394	11.45	29.002 ± 13.836
	TOTAL	3,441	100	8.332 ± 9.317

DU = Duroc; LD = Landrace; LW =Large White; MO = Moura; PI = Pietrain; SD = Standard deviation.

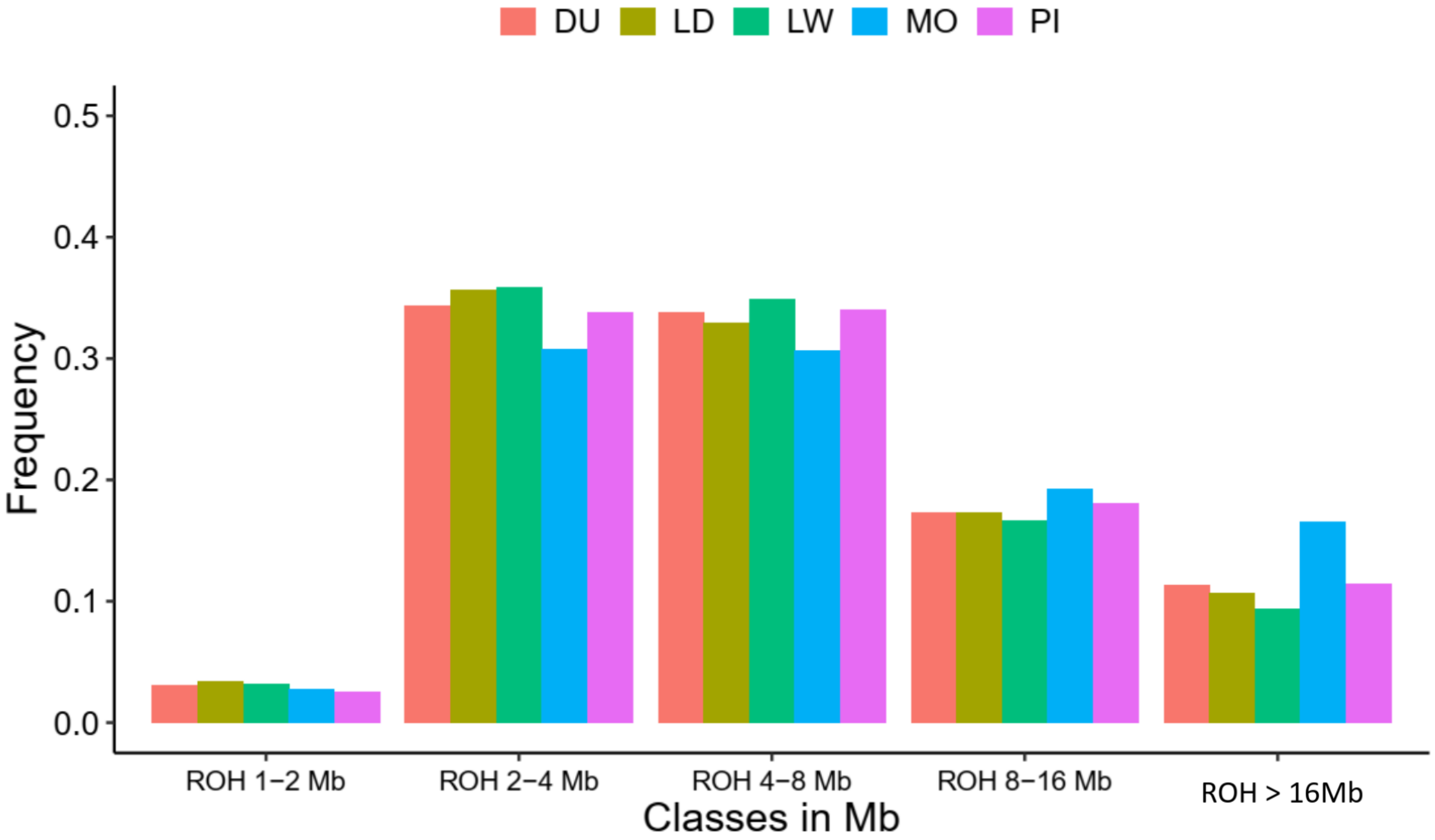

Figure 2 Relative frequencies of five different length runs of homozygosity (ROH) categories for each studied breed. DU = Duroc; LD = Landrace, LW = Large White; MO = Moura; PI = Pietrain.

The Moura breed presented the highest percentage of long ROHs (over 8 Mb), of about 35.8%, indicating recent inbreeding up to five generations ago. The commercial swine breeds exhibited higher frequencies of short ROH (less than 4 Mb). Runs of homozygosity of 2-4 Mb and 4-8 Mb were the most frequent in all breeds, at 68.9% in commercial breeds and 61.4% in Moura breeds. Compared to the commercial breeds, Moura pigs exhibited the lowest number of total ROHs.

The number of ROHs on the chromosomes varied across all five breeds (Figure 3). The lowest number of ROHs per chromosome in all breeds were noted in SSC10 (*Sus scrofa* chromosome 10), SSC11, SSC12, SSC16, SSC17 and SSC18, all less than 100 Mb in length (supplementary Table S2), while the highest number of ROHs were observed in SSC1, SSC7 and SSC13, of which SSC1 and SSC13 are larger than 200 Mb. It is noteworthy that SSC1 in the Landrace breed presented the highest number of ROH (994), with 31.7% of homozygous of 4-8 Mb fragment stretches and 2.52% 1-2 Mb fragment stretches.

Animals with the same cumulative ROH lengths presents different numbers of ROH of different lengths (Figure 4). Duroc animals exhibited 102 ROH, the highest value among breeds. The Duroc and Moura breeds presented some extreme individuals, with ROH lengths greater than 1,000 Mb, of 1,231,060 Mb and 1,151,820 Mb, respectively, while one Moura animal exhibited extremely short ROHs, with a total length of less than 20 Mb (18.582 Mb).

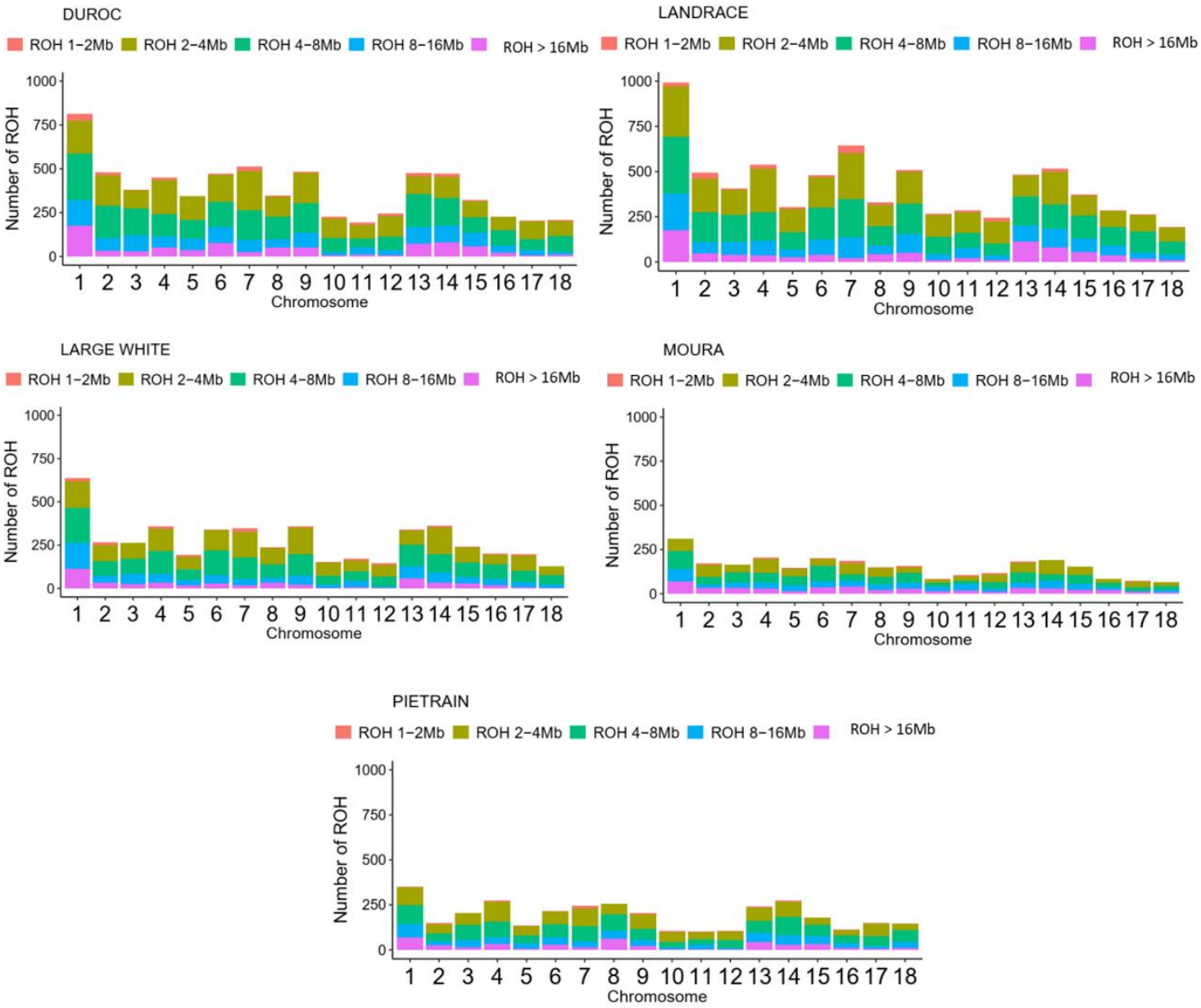

Figure 3 Distribution of the number of runs of homozygosity (ROH) categorized into five size classes per chromosome for each studied swine breed.

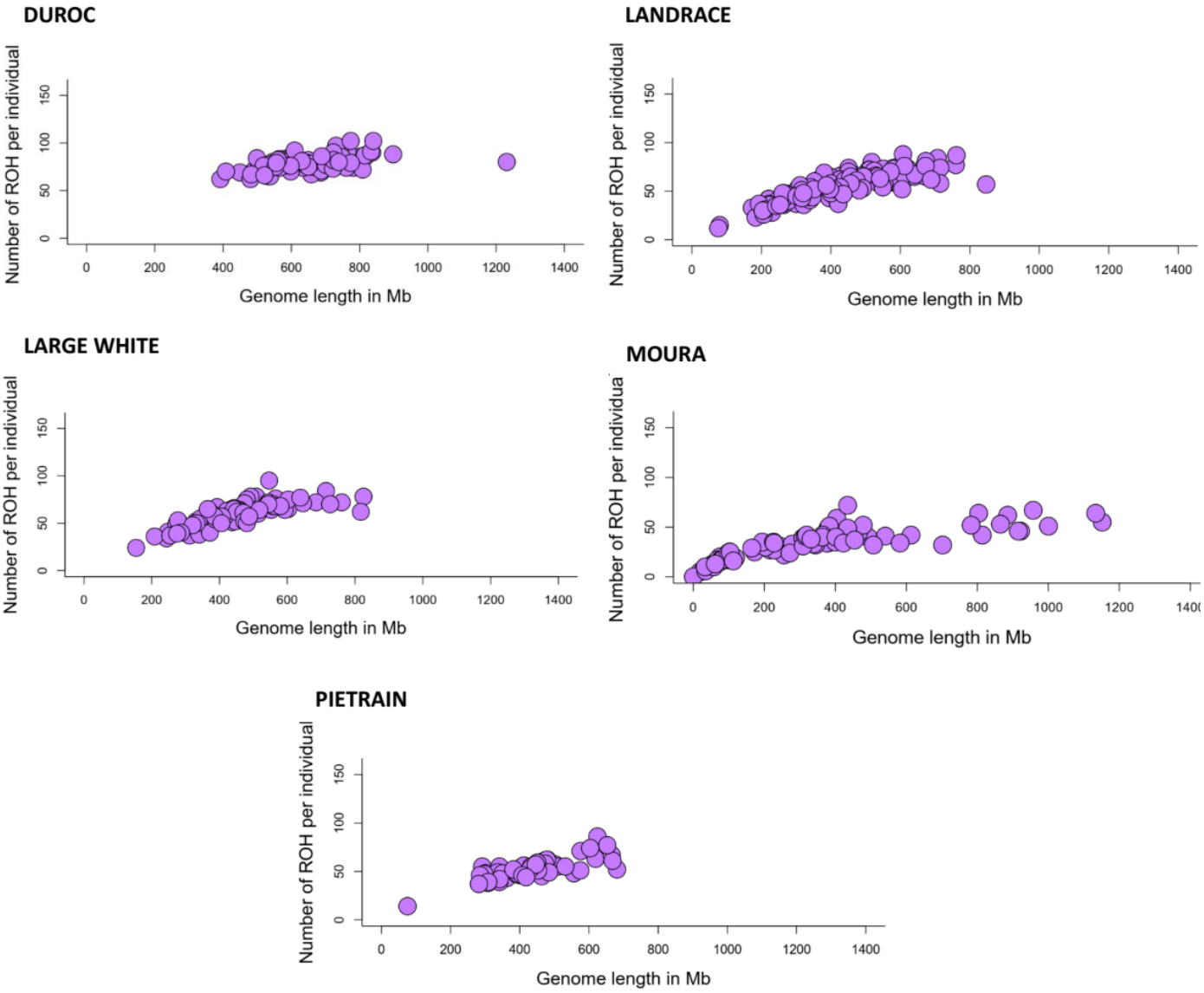

Figure 4 Total number of runs of homozygosity (ROHs) greater than 1 Mb and total genome length (Mb) covered by ROH segments by Duroc, Landrace, Large White, Moura and Pietrain swine breed individuals.

3.3 Genomic inbreeding coefficient estimates

Descriptive statistics for the F_{GRM} and F_{ROH} coefficients based on the five ROH classes are displayed in Table 2 and depicted in supplementary Figure S4. The mean coefficients were low for all studied breeds. The inbreeding coefficients F_{GRM} and total F_{ROH} were higher in the Duroc breed, and lower in the Pietrain and Moura breeds respectively (supplementary Figure S4 A, B). $F_{ROH\ >16\ Mb}$ estimates were significantly higher (p-value <0.05) than $F_{ROH\ 1\text{-}2\ Mb}$, $F_{ROH\ 2\text{-}4\ Mb}$, $F_{ROH\ 4\text{-}8\ Mb}$ and $F_{ROH\ 8\text{-}16\ Mb}$ estimates for the Duroc, Landrace, Large White and Pietrain swine breed, while Moura $F_{ROH\ 4\text{-}8\ Mb}$, $F_{ROH\ 8\text{-}16}$ and $F_{ROH\ >16\ Mb}$ did not differ for the Moura population.

Table 2. Descriptive statistics for the genomic inbreeding coefficients F_{ROH} and F_{GRM} in each studied swine breed.

Breed	Coefficients	Min	Mean	Max	SD	CV (%)	*n*
DU	F_{GRM}	0.292	0.384^{e}	0.587	0.044	11.393	87
	$F_{ROH\ total}$	0.160	0.265^{a}	0.503	0.051	19.436	87
	$FROH_{\ 1\text{-}2\ Mb}$	0.000	0.001^{f}	0.004	0.001	58.023	81
	$FROH_{\ 2\text{-}4\ Mb}$	0.018	0.033^{d}	0.055	0.006	19.392	87
	$FROH_{\ 4\text{-}8\ Mb}$	0.035	0.060^{c}	0.091	0.012	20.113	87
	$FROH_{\ 8\text{-}16\ Mb}$	0.020	0.061^{c}	0.096	0.018	30.709	87
	$FROH_{\ >16\ Mb}$	0.031	0.107^{b}	0.335	0.046	43.251	87
LD	F_{GRM}	0.000	0.351^{e}	0.466	0.059	16.981	137
	$F_{ROH\ total}$	0.030	0.176^{a}	0.346	0.063	35.764	138
	$FROH_{\ 1\text{-}2\ Mb}$	0.000	0.001^{f}	0.006	0.001	83.104	111
	$FROH_{\ 2\text{-}4\ Mb}$	0.003	0.023^{d}	0.041	0.007	30.183	138

	$FROH_{4\text{-}8\ Mb}$	0.006	0.041[c]	0.075	0.013	32.664	138
	$FROH_{8\text{-}16\ Mb}$	0.003	0.043[c]	0.090	0.017	40.291	138
	$FROH_{>16\ Mb}$	0.000	0.066[b]	0.250	0.043	64.962	134
LW	F_{GRM}	0.228	0.350[e]	0.471	0.049	14.275	84
	$F_{ROH\ total}$	0.063	0.183[a]	0.337	0.056	30.722	84
	$FROH_{1\text{-}2\ Mb}$	0.000	0.001[f]	0.003	0.001	72.707	68
	$FROH_{2\text{-}4\ Mb}$	0.007	0.025[d]	0.050	0.006	25.932	84
	$FROH_{4\text{-}8\ Mb}$	0.012	0.046[b]	0.071	0.012	26.751	84
	$FROH_{8\text{-}16\ Mb}$	0.004	0.043[c]	0.097	0.017	39.670	84
	$FROH_{>16\ Mb}$	0.000	0.066[b]	0.233	0.044	67.352	83
MO	F_{GRM}	0.000	0.329[d]	0.573	0.106	32.329	81
	$F_{ROH\ total}$	0.007	0.142[a]	0.470	0.115	81.322	83
	$FROH_{1\text{-}2\ Mb}$	0.000	0.000[d]	0.003	0.000	104.403	53
	$FROH_{2\text{-}4\ Mb}$	0.000	0.012[c]	0.036	0.006	48.893	82
	$FROH_{4\text{-}8\ Mb}$	0.002	0.023[b]	0.067	0.012	54.166	83
	$FROH_{8\text{-}16\ Mb}$	0.000	0.029[b]	0.071	0.021	72.085	77
	$FROH_{>16\ Mb}$	0.000	0.076[b]	0.374	0.093	121.454	61
PI	F_{GRM}	0.164	0.318[e]	0.420	0.042	13.297	66
	$F_{ROH\ total}$	0.030	0.177[a]	0.278	0.045	25.462	66
	$FROH_{1\text{-}2\ Mb}$	0.000	0.000[f]	0.002	0.000	90.395	47
	$FROH_{2\text{-}4\ Mb}$	0.006	0.021[d]	0.039	0.006	28.225	66
	$FROH_{4\text{-}8\ Mb}$	0.017	0.040[c]	0.083	0.011	27.814	66
	$FROH_{8\text{-}16\ Mb}$	0.006	0.043[c]	0.088	0.016	37.403	66
	$FROH_{>16\ Mb}$	0.000	0.070[b]	0.179	0.033	47.686	65

Min= minimum, Max= maximum, SD= standard deviation, n= number of animals, different letters in the column are significantly different ($p<0.05$) by the Kruskal-Wallis test.

Low negative correlations were observed between F_{GRM} and F_{ROH} (Table 3). The correlations between F_{GRM} and $F_{ROH\ >16\ Mb}$ were the lowest within the Duroc and Landrace breeds, as follows: F_{GRM}-$F_{ROH\ 1\text{-}2\ Mb}$ for Large White, FROH total-$F_{ROH\ 1\text{-}2\ Mb}$ for Moura and for $F_{ROH\ 1\text{-}2\ Mb}$-$F_{ROH\ 4\text{-}8\ Mb}$ Pietrain. The highest correlations were detected between total $F_{ROH\ total}$-$F_{ROH\ >16\ Mb}$ for all breeds.

Table 3. Pearson correlation coefficients between genomic inbreeding parameters in all studied swine breeds.

Breed	Parameters	$F_{ROH\ total}$	$F_{ROH\ 1\text{-}2\ Mb}$	$F_{ROH\ 2\text{-}4\ Mb}$	$F_{ROH\ 4\text{-}8\ Mb}$	$F_{ROH\ 8\text{-}16\ Mb}$	$F_{ROH\ >16\ Mb}$	F_{GRM}
DU	$F_{ROH\ TOTAL}$	1.000	0.011	-0.110	0.130	0.440***	0.910***	0.094
	$F_{ROH\ 1\text{-}2\ Mb}$		1.000	-0.120	0.072	0.000	-0.012	0.045
	$F_{ROH\ 2\text{-}4\ Mb}$			1.000	0.015	-0.290**	-0150	0.082
	$F_{ROH\ 4\text{-}8\ Mb}$				1.000	-0.048	-0.100	0.078
	$F_{ROH\ 8\text{-}16\ Mb}$					1.000	0.140	0.150
	$F_{ROH\ >16\ Mb}$						1.000	0.009
	F_{GRM}							1.000
LD	$F_{ROH\ TOTAL}$	1.000	0.270**	0.460***	0.660***	0.680***	0.890***	-0.048
	$F_{ROH\ 1\text{-}2\ Mb}$		1.000	0.390***	0.200*	0.280***	0.120	-0.078
	$F_{ROH\ 2\text{-}4\ Mb}$			1.000	0.380***	0.410***	0.210*	-0.220**
	$F_{ROH\ 4\text{-}8\ Mb}$				1.000	0.530***	0.380***	-0.062
	$F_{ROH\ 8\text{-}16\ Mb}$					1.000	0.360***	0.021
	$F_{ROH\ >16\ Mb}$						1.000	-0.019
	F_{GRM}							1.000
LW	$F_{ROH\ TOTAL}$	1.000	0.130	0.520***	0.520***	0.450***	0.860***	-0.055
	$F_{ROH\ 1\text{-}2\ Mb}$		1.000	0.200	0.160	0.036	0.059	0.007
	$F_{ROH\ 2\text{-}4\ Mb}$			1.000	0.460***	0.410***	0.210	0.082

	$F_{ROH\ 4\text{-}8\ Mb}$				1.000	0.350**	0.180	0.084
	$F_{ROH\ 8\text{-}16\ Mb}$					1.000	0.020	0.070
	$F_{ROH\ >16\ Mb}$						1.000	-0.130
	F_{GRM}							1.000
MO	$F_{ROH\ TOTAL}$	1.000	-0.020	0.230*	0.590***	0.790***	0.970***	-0.270*
	$F_{ROH\ 1\text{-}2\ Mb}$		1.000	0.250*	0.059	0.140	-0.088	0.051
	$F_{ROH\ 2\text{-}4\ Mb}$			1.000	0.470***	0.370***	0.067	-0.300**
	$F_{ROH\ 4\text{-}8\ Mb}$				1.000	0.660***	0.410***	-0.400***
	$F_{ROH\ 8\text{-}16\ Mb}$					1.000	0.630***	-0.250*
	$F_{ROH\ >16\ Mb}$						1.000	-0.210*
	F_{GRM}							1.000
PI	$F_{ROH\ TOTAL}$	1.000	0.140	0.380**	0.490***	0.500***	0.860***	-0.056
	$F_{ROH\ 1\text{-}2\ Mb}$		1.000	0.049	-0.007	0.270*	0.022	-0.140
	$F_{ROH\ 2\text{-}4\ Mb}$			1.000	0.350**	0.032	0.190	-0.310*
	$F_{ROH\ 4\text{-}8\ Mb}$				1.000	0.160	0.180	-0.120
	$F_{ROH\ 8\text{-}16\ Mb}$					1.000	0.130	0.004
	$F_{ROH\ >16\ Mb}$						1.000	0.022
	F_{GRM}							1.000

F_{ROH} = inbreeding coefficient based on runs of homozygosity subdivided into six classes and F_{GRM} = inbreeding coefficient based on genomic relationship matrix. *P<0.05, **P<0.01, ***P<0.001.

3.4 Parentage analysis

The probability of Moura animals sharing IBD alleles was investigated by assigning the appropriate relationship category. The most informative relationships, with PI-HAT values above 0.2, are depicted in the heat map (Figure 5). Out of a total of 3846 comparisons, 63.91% showed values equal to zero,

suggesting the absence of relatedness. Remarkably, 1.20% of the comparisons revealed values above 0.5, indicating a high genetic similarity among the individuals. Additionally, a comparison among animals from the state of Pernambuco revealed an exceptionally high value of 0.99, highlighting a notable genetic similarity among these animals.

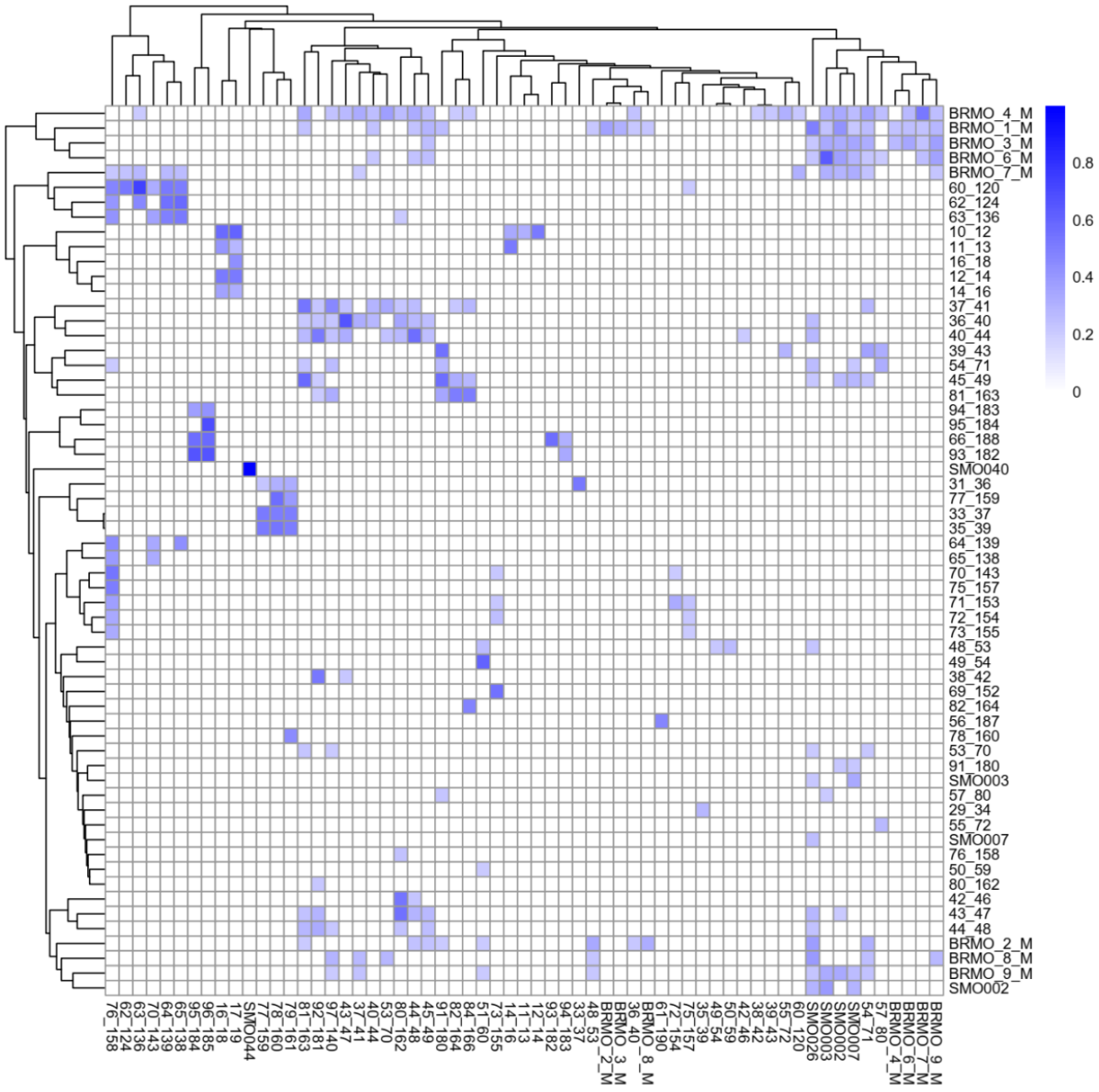

Figure 5 Heatmaps representing genome-wide identity by descent (IBD) between pairs of Moura animals estimated with the PI-HAT coefficient.

3.5 Genomic Regions with High ROH Frequency: functional annotation and PCA analysis of shared ROH islands

An analysis of the frequency of SNPs within ROHs in the studied populations allowed for the determination of the genomic ROH distribution (Figure 6) and identification of genome regions termed ROH islands, containing the most frequent SNPs. Seven ROH islands were detected in the Duroc breed, in SSC1, SSC2, SSC3, SSC7, SSC9 and SSC14, with the highest number of islands found in SC14 (Table 4), covering 39.80 Mb of the genomic sequence. The Landrace breed presented eleven ROH islands in SSC1, SSC2, SSC3, SSC7, SSC13, SSC14 and SSC17, the highest compared to the other studied breeds, with five located in SSC1, with the total length of these regions covering 50.43 Mb. With regard to the Large White breed, eight ROH islands were observed in SSC1, SSC4, SSC6, SSC7, SSC13 and SSC16, with the largest number of islands located in SSC1 (three islands), and total length of these regions comprising 51.65 Mb. Eight ROH islands were detected in the Moura breed, in SSC1, SSC2, SSC6, SSC7 and SSC14, with the largest number of islands found in SSC7, and a total length of covering 41.51 Mb. Three of the four ROH islands observed in the Pietrain breed were found in SSC8, covering a total of 39.20 Mb of the genomic sequence, similar in length to Duroc pigs.

The ROH island present in the SSC2 of the Moura animals overlapped the island located in the SSC2 of the Duroc animals in the 87,210846-91,358399 region. The same was noted for Moura, Duroc, and Landrace animals concerning the ROH island present in SSC7 (55,840723-59,713204). Landrace and Large White animals also presented an overlapping island in SSC1, in the region 237,820401-243,4839. The genetic content of the ROH islands shared among

the studied animals was analyzed through functional enrichment analysis of the genes contained within them to estimate the significant functional potential of the detected ROH islands (supplementary Table S3).

When analyzing the PCA plot on SSC2, where the Moura breed shares an ROH island with Duroc animals, we observed that nineteen Moura animals show a greater genetic proximity to this breed (supplementary Figure S5). However, on SSC7, which is shared by Moura, Duroc, and Landrace, we did not observe any genetic overlap between these breeds (supplementary Figure S6).

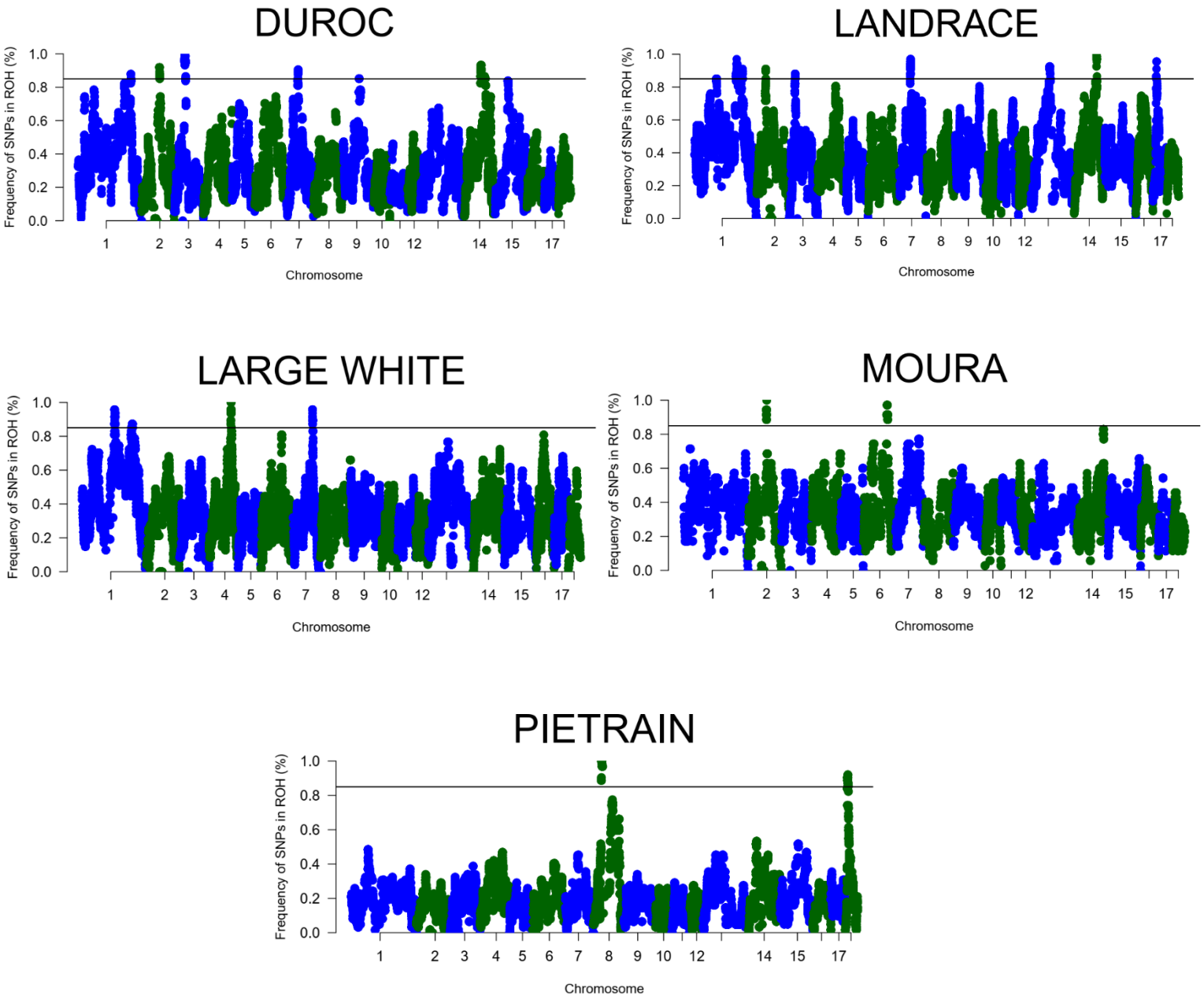

Figure 6 Manhattan plot of the ROH frequency distribution in the genomes of the studied swine breeds. The line parallel to the X-axis represents the top 1% of the frequency of SNPs in a run of homozygosity (ROH). SNPs above that line correspond to ROH islands.

Table 4. Runs of homozygosity islands detected in the swine breeds assessed herein.

Breed	SSC	Start, bp	Final, bp	Size (Mb)	Number of SNPs
	1	260.759.054	263.967.147	3,21	17
	2	87.090.537	91.444.137	4,35	59
	3	48.285.128	58.093.104	9,81	124
DU	7	55.626.692	59.726.993	4,10	50
	9	76.876.687	80.550.062	3,67	28
	14	79.336.087	87.594.130	8,26	124
	14	99.235.332	105.637.815	6,40	70
	1	207.516.673	209.871.496	2,35	8
LD	1	210.244.812	220.647.186	10,40	98
	1	225.408.018	228.449.281	3,04	17
	1	229.467.068	234.021.161	4,55	21
	1	239.900.933	244.293.703	4,39	39
	2	43.185.842	45.677.782	2,49	21
	3	29.733.237	32.517.116	2,78	17
	7	53.871.000	59.806.078	5,93	111
	13	92.356.864	98.460.496	6,10	42
	14	111.926.269	116.466.785	4,54	50
	17	15.767.555	19.631.250	3,86	17
	1	156.545.956	167.046.787	10,50	99
	1	237.848.505	248.156.920	10,31	104
LW	1	255.837.213	258.935.934	3,10	18
	4	105.209.988	112.993.928	7,78	110
	6	100.526.958	104.690.530	4,16	31

	7	94.404.221	99.580.101	5,17	56
	13	92.356.864	98.460.496	6,10	42
	16	34.614.082	39.144.170	4,53	31
MO	1	30.382.948	34.095.690	3,71	54
	2	87.090.537	91.444.137	4,35	59
	6	46.573.330	53.262.806	6,69	53
	6	112.151.461	120.403.051	8,25	96
	7	55.936.530	61.161.734	5,23	43
	7	65.372.154	68.917.223	3,55	18
	7	110.800.323	115.184.239	4,38	54
	14	127.085.070	132.434.467	5,35	58
PI	8	37.893.637	46.395.598	8,50	79
	8	86.618.553	106.991.646	20,37	219
	8	123.661.932	126.296.864	2,63	13
	18	9.378.849	17.079.412	7,70	116

DU = Duroc; LD = Landrace, LW = Large White; MO = Moura; PI = Pietrain.

4. Discussion

4.1 Population structure of commercial and Moura swine

The results of the PCA analysis revealed intra-breed genetic variability among animals of the Moura breed, whose samples were collected in the states of Pernambuco (PE), Distrito Federal (DF), and the city of Candelária (RS). These animals presented a genetic composition distinct from the main group, which consists of descendants of the original UFPR conservation herd, distributed in Apucarana, EMBRAPA, and UNESP, as well as in the Lages region. Some animals from the São Mateus do Sul herd and others from UFPR showed greater

proximity to Candelária, while others got closer to Carlos Barbosa, a result similar to that found by Botan et al. (2019). This demonstrates that all groups share common genetic components, but genetic diversity *in situ* remnants is greater and includes genetic components not yet present in *ex-situ* conservation herds. In addition, the greater genetic similarity detected between Large White and Pietrain swine is related to the development of the Pietrain breed, which was founded by crossing local pigs (Indigenous White Pig) with Berkshire, Large White and Bayeux swine (Departement Landbouw en Visserij et al., 2016).

4.2 Characterization of runs of homozygosity

The findings reported herein indicate significant differences in the number and length of ROH in the five studied swine breeds. Long ROHs can indicate the relatedness of recent generations, with the shorter the generations, the less likely that a ROH fragment will be interrupted by recombination, while longer ROHs indicate a greater inbreeding probability (Kirin et al., 2010; McQuillan et al., 2008). The Moura breed presented a higher number of ROH lengths than the commercial breeds in the > 8 Mb class, indicating greater recent Moura inbreeding. Duroc, Landrace, Large White and Pietrain pigs are commercial breeds with a long husbandry history. Moura pigs, on the other hand, belong to locally adapted Brazilian breeds, and mating between related animals is frequent due to a common practice in small pig farms (Silva, 2014), favoring loss of genetic diversity and increased inbreeding (Silva et al., 2011; Sollero et al., 2009).

The ROH 2-4 Mb and 4-8 Mb classes were the most frequent in all breeds. However, our results should be interpreted with caution, as according to Ferencakovic et al. (2013) and Peripolli et al. (2017), low-density chips may lead

to an overestimation of the number of short-length ROHs (< 4 Mb), while high-density chips lead to an overestimation of the number of long ROHs (> 8 Mb), probably due to heterozygous genotypes present in these ROHs, increasing marker density. However, our results are in line with those observed by Schiavo et al. (2020a) and Szmatoła et al. (2020) when comparing commercial and locally adapted breeds. Compared to the Moura breed, the studied commercial breeds presented a higher total number of ROHs, suggesting that the population has been small for a long time, but that the source population is substantial in size (Bosse et al., 2012). By examining different European and Asian pig populations Bosse et al. (2012) found that the European wild pig genome contained the highest number of ROH, indicating a decreased genetic diversity in European populations compared to Asian populations.

The number of ROH differs from chromosome to chromosome being proportional to chromosome length (Fang et al., 2021). Furthermore, previous work by Bosse et al. (2012) and Pemberton et al. (2012) demonstrated that ROH distributions are not uniform, presenting distinct continental patterns. This heterogeneity in ROH distributions has been partially attributed to variation in recombination events and genome-wide guanine-cytosine (GC) content rather than selection alone. For example, Bosse et al. (2012) carried out a study in pigs and observed that longer ROH were predominantly located in regions of low recombination in the central part of the chromosomes, while shorter ROH had a relatively greater distribution in telomeric regions. These findings highlight the complexity of ROH variation and its relationship to recombination events and genomic structure.

In the present study, all breeds presented the highest number of ROH on SSC1, SSC7 and SSC13, with SSC1 and SSC13 having the largest chromosomes (supplementary Table S2). This result is similar to that reported by Joaquim et al. (2019 and Wang et al. (2022), who also described the highest number of ROH in SSC1 in the Landrace and Duroc breeds, respectively. The lowest numbers of ROH were found in SSC10, SSC11, SSC12, SSC16, SSC17 and SSC18, corroborating Shi et al. (2020), who detected the lowest number of ROH in SSC12 in the Large White breed and Wang et al. (2022), who detected the lowest number of ROH in SSC10 in the Duroc breed.

Animals with the same cumulative ROH length may present different numbers of ROHs with different lengths due to different distances from the last common ancestor (Mészáros et al., 2015) . Some Moura animals presented cumulative lengths greater than 1,000 Mb and less than 20 Mb, reflecting a lack of effective inbreeding management. The animals over 1,000 Mb in length come from the UDESC and Ponte Alta herds and originate from the herd of producer Antoninho Camargo, from Fazenda Canoas. During the study of the phenotypic characterization of the remaining pigs of the Moura breed, conducted by Juliatto (2016), a significant difference was observed only in the UDESC and Ponte Alta herds. This is due to the fact that the animals in these herds were selected based on other selection characteristics. These results highlight the importance of considering genetic diversity and the adequate implementation of inbreeding management in the preservation and improvement of the Moura breed.

4.3 Genomic inbreeding coefficient estimates

The inbreeding coefficients based on long ROHs (F_{ROH} > 8Mb) presented the highest averages in all breeds, similar to the results reported by Saura et al. (2015) when studying Iberian pigs. The Moura breed presented the lowest F_{ROH} values considering minimum ROH lengths (ranging from F_{ROH} = 0.000 to 0.029 to $F_{ROH\ 1\text{-}2\ Mb}$ to $F_{ROH\ 8\text{-}16\ Mb}$). The low F_{ROH} values detected here are in line with the results reported by Botan et al. (2019), which ranged from zero to 0.19 in the Moura breed. Few scientific studies are available on locally adapted Brazilian breeds, although low values were observed in a locally adapted Chinese breed by Wu et al. (2020), similar to those reported herein. The Duroc breed presented the highest F_{ROH} values (from 0.107 to 0.001, considering the different ROH classes), similar to the results reported by Schiavo et al. (2020a).

The inbreeding coefficient estimates differed according to the calculation method (F_{GRM} and F_{ROH}), and mean F_{GRM} values were considerably higher than F_{ROH} values, indicating considerable variations between breeds. Similarly, Schiavo et al., (2020a), also found higher F_{GRM} values in comparison to F_{ROH} and classes, in addition to commercial pig breeds, exhibited the highest inbreeding values for most coefficients compared to locally adapted breeds. These results may indicate that the F_{GRM} method tends to overestimate inbreeding values, due to the presence of IBS and IBD alleles, and assumptions for basic allele frequencies, as noted by Forutan et al. (2018) in a simulation study in cattle. This may explain why the F_{GRM} was higher than the F_{ROH} in the present study. Therefore, the inbreeding level estimated from F_{ROH} may be closer to the true inbreeding level, as ROH comprises a direct autozygosity measure. Recent inbreeding (*i.e.,* $F_{ROH\ >16}$) presented the highest correlation with $F_{ROH\ total}$ in all

breeds, while the most distant inbreeding (*i.e.,* $F_{ROH\ 1\text{-}2\ Mb}$) displayed the lowest correlation with Moura pigs (-0.020). The high correlation between $F_{ROH\ >16}$ and $F_{ROH\ total}$ corroborates studies in Holstein cattle (Doekes et al., 2019; Ghoreishifar et al., 2023; Makanjuola et al., 2020) and swine (Saura et al., 2015). According to Figure 2, ROH $_{2\text{-}4\ Mb}$ (short length ROH presented the highest frequency in relation to the other classes. However, only a small number of F_{ROH} is explained by $F_{ROH\ 1\text{-}2\ Mb}$ and $F_{ROH\ 2\text{-}4\ Mb}$ (supplementary Figure S7). Therefore, longer ROHs created from more recent inbreeding covered a greater amount of the genome compared to shorter ROHs, contributing more to total inbreeding. According to Ghoreishifar et al (2023), this could, to some extent, explain the greater correlation between total and recent inbreeding. Negative correlations should be interpreted with caution, as although short ROHs may have originated from remote common ancestors, they may also be masked or included in some of the longer ROHs (Saura et al., 2015).

4.4 Parentage analysis

The PI-HAT values calculated in pairwise comparisons were significantly higher among the animals from the cities of Exu and Granito in the state of Pernambuco. According to most studies, PI-HAT values equal to or greater than 0.99 are often considered duplicate samples (Gilles et al., 2017; Oussalah et al., 2017). The high genetic similarity among the animals from these cities suggests the presence of close relatedness or possibly duplicate samples. The second highest PI-HAT value (0.79) was found between a sample from the city of Ponte Alta and UDESC; these animals have origins in the Camargo lineage. This high genetic similarity emphasizes the importance of investigating the genetic history

and population diversity of these animals for a deeper understanding of their ancestry and evolution. When compared, the animals from the city of Carlos Barbosa presented PI-HAT values ranging from 0.65 to 0.73, suggesting moderate genetic diversity. The animals in the Carlos Barbosa region are remnants of a single family. This herd is considered a 'new lineage' because there were no records of animals collected from this city or region to make up the initial UFPR herd in 1985. These results reinforce the hypothesis of recent inbreeding since the high genetic similarity measured by PI-HAT values suggests close kinship, which is in agreement with the presence of long ROHs in Moura animals.

4.5 Genomic Regions with High ROH Frequency: functional annotation and PCA analysis of shared ROH islands

The Moura and Duroc breeds presented overlapping ROH islands in a 4 Mb region between 87 and 91 Mb in SSC2. In this region, sixteen genes were identified, including the *JMY* gene, which is associated with pig embryo development (Lin et al., 2015). Furthermore, the genes *VCAN*, *CMYA5*, and *BHMT* were found linked to muscle development, fat deposition, carcass traits, and meat quality (Card et al., 2019; Piórkowska et al., 2018; Xu et al., 2011).

The Moura, Duroc, and Landrace breeds exhibited an overlap in a region of 3 Mb on SSC7, located between 55 and 69 Mb, in which sixteen genes were common to all three breeds. One of these genes is *SEMA7A*, which, according to Körner et al. (2021), is crucial for the resolution of severe inflammation observed in children and mice. The *CYP11A1* gene, as demonstrated by Robic et al. (2011), influences the levels of androsterone in pig fat. Furthermore, HMG domain protein 20A (*HMG20A*), as indicated by Li et al. (2022), presents a high

expression in the initial phase of adipogenic differentiation of porcine intramuscular fat, suggesting its involvement in the regulation of adipogenesis.

We identified overlap on SSC1 between the Landrace and Large White breeds, in a region spanning 5 Mb from 237 Mb to 243 Mb, which encompasses thirteen common genes. The gene *TGFBR1* is associated with growth-related traits, including average daily gains, as reported by Chen et al. (2012). Furthermore, according to Wu et al. (2020), the gene *COL15A1* is considered a relevant candidate gene for meat quality.

The Pietrain breed did not present any overlapping ROH islands with the other studied breeds, although the highest number of islands was detected in SSC8, similar to that reported by Gorssen et al. (2020) and Ganteil et al. (2020), in which all Pietrain populations displayed numerous overlapping islands on chromosome 8, suggesting the presence of a selection signature in this region.

The PCA analysis in SSC2 indicated that the Moura populations are genetically divergent, likely due to their different origins. Most of the animals overlapping with the Duroc breed are from UDESC and UFPR, originating from the herd of producer Antoninho Camargo, which was the most populous among the remaining Moura herds. In SSC7, we did not identify genetic overlap between the Moura, Duroc, and Landrace breeds. Notably, an animal of the Moura breed, originating from the Ouricuri-PE region, exhibited a significant genetic similarity with animals of the Large White and Pietrain breeds. Furthermore, seven other animals demonstrated genetic proximity to this population, the majority of which come from the regions of Pernambuco, Candelária, and the UFPR herd. Maintaining the diversity of the Moura breed depends on the conservation and multiplication of the remaining *in-situ* breeding stock.

5. Conclusion

The locally adapted Moura breed exhibits a higher frequency and average length of long ROHs (greater than 8 Mb) than the other breeds evaluated herein, indicating recent inbreeding. Commercial breeds exhibit a wide variety of ROH in their genomes, resulting from higher F_{ROH} values. Furthermore, overlapping ROH islands were observed between the Moura and Duroc swine populations, and the genes found in these islands are significantly associated to meat quality traits, whose high quality is recognized in both breeds. The kinship analysis among Moura animals revealed the absence of direct kinship in most comparisons. However, the significant genetic similarity between animals from the Camargo herd highlights the importance of investigating the genetic history and population diversity of these populations, which contributes to a deeper understanding of their ancestry and evolution. The highest number of ROH islands was identified in SSC8 in the Pietrain population, suggesting a possible selection signature in this region, which may be related to inbreeding and coat color selection during breed development. These results indicate that special attention is required in Moura mating schemes, as this breed presented the highest percentage of long ROHs, in order to avoid possible inbreeding depression and minimize potential economic risks affected by the inbreeding, also revealing genomic regions under selection in the Moura breed, which harbor potentially interesting genes for targeted selection in commercial lineages.

Acknowledgements

The authors would like to thank the National Center for Genetic Resources and Biotechnology for providing DNA samples from Moura pigs, as well as Elizabete C. Silva and Gleison R. de Biazio for their support in preparing and sending the material for genotyping. Thanks are also due to the Coordination for the Improvement of Higher Education Personnel (CAPES) and the National Council for Scientific and Technological Development (CNPq, 303263/2021-0) for partial funding and scholarships, as well as to Dr. Mônica Corrêa Ledur – EMBRAPA poultry and swine, Ricardo Zanella – University of Passo Fundo (UPF), Dr. Marson Bruck Warpechowski – Federal University of Paraná (UPF) and Dr. José Braccini Neto (UFRGS). Finally, we would also like to thank Moura pig breeders.

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COMPLEMENTARY MATERIAL

Table S1 Sample description for four different breeds of pigs used in the study.

Abbreviation	Country	Population	Origin of the genotype database	Number of animals
BRMO	Brasil	Moura	Repository	9
MO	Brasil	Moura	Brazilian public institutions	75
DU	Brasil	Duroc	Brazilian public institutions	8
DUR1	Dinamarca	Duroc	Repository	19
DUR2	USA	Duroc	Repository	20
DUR3	Holanda	Duroc	Repository	20
DUR4	China	Duroc	Repository	20
LD	Brasil	Landrace	Brazilian public institutions	8
LDR1	Dinamarca	Landrace	Repository	20
LDR2	Noruega	Landrace	Repository	15
LDR3	Finlândia	Landrace	Repository	15
LDR4	China	Landrace	Repository	20
LDR5	USA	Landrace	Repository	20
LDR6	Espanha	Landrace	Repository	20
LDR7	Holanda	Landrace	Repository	20
LW	Brasil	Large White	Brazilian public institutions	8
LWT1	Dinamarca	Large White	Repository	16
LWT2	China	Large White	Repository	20
LWT3	USA	Large White	Repository	20
LWT4	Holanda	Large White	Repository	20
PI	Brasil	Pietrain	Brazilian public institutions	8
PIT1	USA	Pietrain	Repository	20
PIT2	Holanda	Pietrain	Repository	20
PIT3	Alemanha	Pietrain	Repository	18
TOTAL				**459**

Table S2 Marker distribution along the genome of pigs (*Sus scrofa*) per chromosome.

SSC[1]	Size[2]	No. SNP[3]	% SNP[4]
1	315.214	4,933	12.13
2	162.298	2,564	6.31
3	144.353	2,251	5.54
4	143.462	2,811	6.91
5	111.370	1,786	4.39
6	157.758	2,546	6.26
7	137.683	2,654	6.53
8	148.081	2,156	5.30
9	153.454	2,563	6.30
10	78.137	1,386	3.41
11	87657	1,452	3.57
12	63.499	1,267	3.12
13	218.211	3,144	7.73
14	153.786	3,097	7.62
15	157.342	2,181	5.36
16	86.875	1,473	3.62
17	69.326	1,336	3.29
18	60.911	1,062	2.61
Total	2,449.417	40,662	100

[1]*Sus scrofa* autosome; [2] Chromosome size, in Megabase; [3]Number of SNPs per chromosome; [4]Porcentage of SNPs per chromosome.

Table S3 Runs of homozygosity (ROH) islands in the analyzed population showing (*p<0.05*). The table reports for each breed, the chromosome (SSC), physical position (in Mb), length (Mb), and annotated genes associated with each ROH island.

Breed	SSC[1]	Physical Position (Mb)	Length (Mb)	Genes
DU	2	87,210846:91,358399	4,147553	*SCAMP1, BHMT, JMY, TENT2, CMYA5, THBS4, SPZ1, ZFYV16, FAM151B, MSH3, RASGRF2, CKMT2, ZCCHC9, ATG10, ATP6AP1L, VCAN*
	7	55,482387:59,713204	4,230817	*ZNF710, SEMA4B, NGRN, VPS33B, PRC1, FBXO22, TMEM266, ISL2, RCN2, PSTPIP1, HMG20A, CSPG4, IMP3, SNUPN, PTPN9, SIN3A, MAN2C1, LOC106504438, RPP25, COX5A, FAM219B, SCAMP2, ULK3, CYP1A1, EDC3, UBL7, SEMA7A, CYP11A1, STRA6, STOML1, INSYN1, NPTN*
LD	1	207,504016:243,48399	35,979974	*FREM1, CER1, ZDHHC21, NFIB, MPDZ, PTPRD, DMAC1, GLDC, RANBP6, KIAA2026, ERMP1, PLGRKT, RLN2, INSL6, AK3, SPATA6L, GLIS3, RFX3, LOC106509183, PUM3, GCNT1, FOXB2, VPS13A, CEP78, PSAT1, TLE4, NANS, GALNT12, COL15A1, TGFBR1, SEC61B, NR4A3,*

				STX17, INVS, MSANTD3-TMEFF1, CAVIN4, PLPPR1, ZNF189, RNF20
	7	53,909425:59,713204	5,803779	*CFAP100, ACAN, ABHD2, FANCI, TICRR, WDR93, MESP2, ZNF710, SEMA4B, NGRN, VPS33B, PRC1, FBXO22, TMEM266, ISL2, RCN2, PSTPIP1, HMG20A, CSPG4, IMP3, SNUPN, PTPN9, SIN3A, MAN2C1, LOC106504438, RPP25, COX5A, FAM219B, SCAMP2, ULK3, CYP1A1, EDC3, UBL7, SEMA7A, CYP11A1, STRA6, STOML1, INSYN1, NPTN*
LW				
	1	156,741987:258,04461	101,302623	*LOC110261637, VPS4B, KDSR, PIGN, RNF152, MC4R, CCBE1, LMAN1, CPLX4, RAX, ALPK2, ATP8B1, SLC51B, KBTBD13, HACD3, SLC24A1, RAB11A, DIS3L, MAP2K1, ZWILCH, SMAD6, SMAD3, IQCH, C1H15orf61, MAP2K5, SKOR1, PIAS1, FEM1B, CORO2B, SPESP1, NOX5, GLCE, ZCCHC7, GRHPR, POLR1E, FRMPD1, TRMT10B, DCAF10, ALDH1B1, LOC102168060, NCBP1, FOXE1, NANS, GALNT12, COL15A1, TGFBR1, SEC61B, NR4A3, STX17, INVS, MSANTD3-TMEFF1, CAVIN4, PLPPR1,*

				ZNF189, RNF20, SMC2, LOC100518052, OR13C8, LOC100520168, LOC100739563, LOC100739528, LOC100739365, SLC44A1, FSD1L, TAL2, TMEM38B, ZNF462, PAPPA, TRIM32, TLR4
	7	94,445001:99,514168	5,069167	*PCNX1, SIPA1L1, RGS6, DCAF4, RBM25, PSEN1, PAPLN, RIOX1, ACOT4, ACOT6, DNAL1, PTGR2, ZNF410, COQ6, BBOF1, LIN52, VSX2, VRTN, ISCA2, FCF1, YLPM1, DLST, EIF2B2, ZC2HC1C, FOS, JDP2, FLVCR2, TTLL5, IFT43, GPATCH2L, ESRRB*
MO				
	2	87,210846:91,358399	4,147553	*SCAMP1, BHMT, JMY, TENT2, CMYA5, THBS4, SPZ1, ZFYVE16, FAM151B, MSH3, RASGRF2, CKMT2, ZCCHC9, ATG10, ATP6AP1L, VCAN*
	7	55,840723:114,76613	58,925407	*PRC1, FBXO22, TMEM266, ISL2, RCN2, PSTPIP1, HMG20A, FAM219B, SCAMP2, ULK3, CYP1A1, EDC3, UBL7, SEMA7A, CYP11A1, STRA6, STOML1, INSYN1, NPTN, HCN4, ADPGK, HEXA, CELF6, PKM, GRAMD2A, SEC23A, EGLN3, GRP33, DTD2,*

		HEATR5A, HECTD1, STRN3, TDP1, KCNK13, PSMC1, CALM2, CPSF2, SLC24A4, RIN3, GOLGA5, CHGA, TMEM251, UBR7, LOC100157935, UNC79

[1] SSC: *Sus scrofa*. DU = Duroc; LD = Landrace, LW = Large White; MO = Moura.

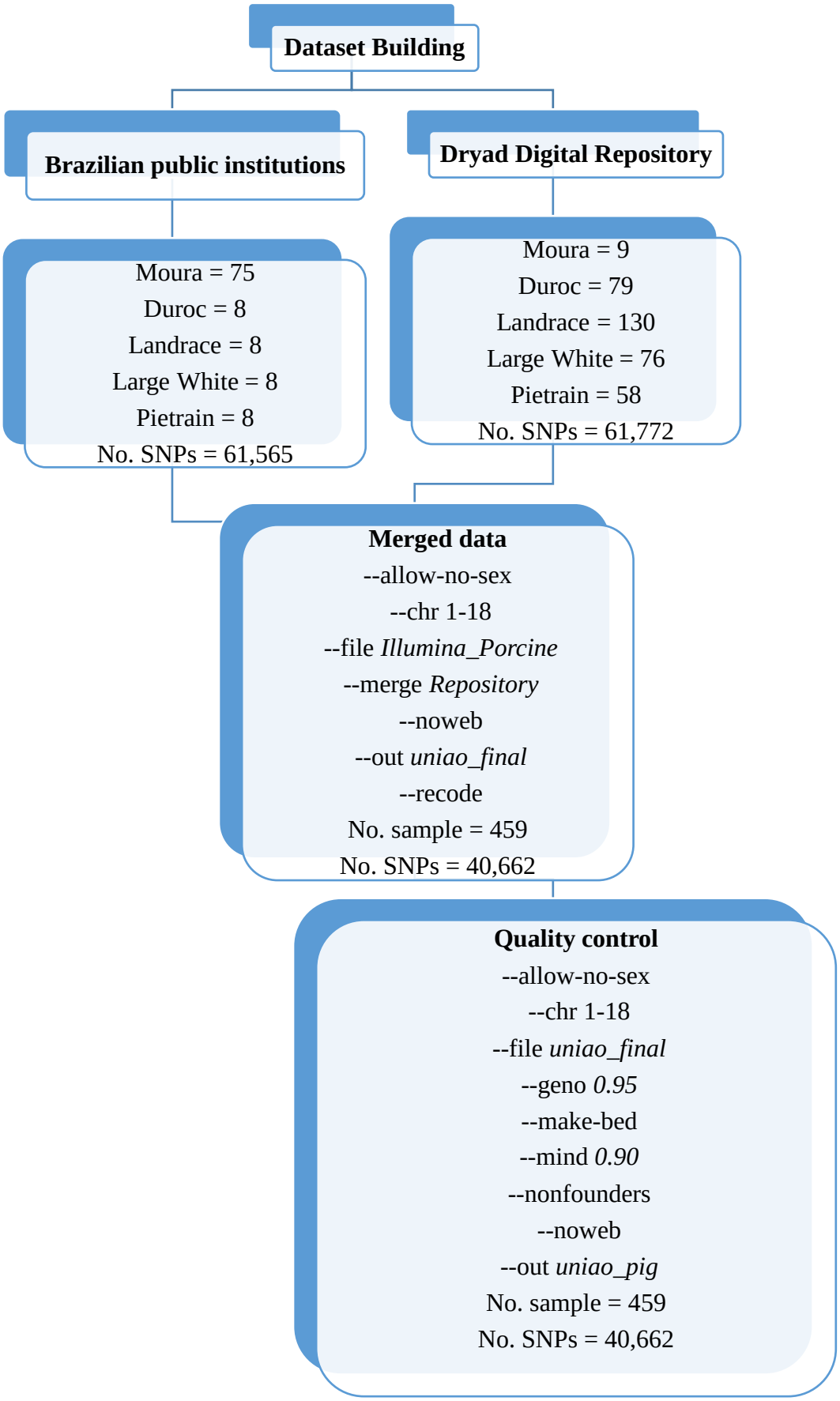

Fig. S1. Flowchart detailing the database merging and quality control processes using the PLINK software.

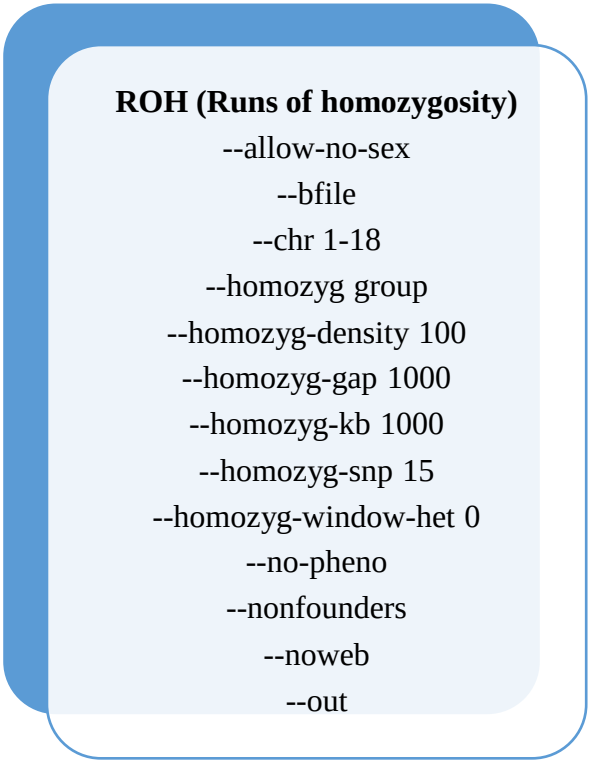

Fig. S2. Description of the parameters used for the detection of Runs of Homozygosity (ROH) in the PLINK software.

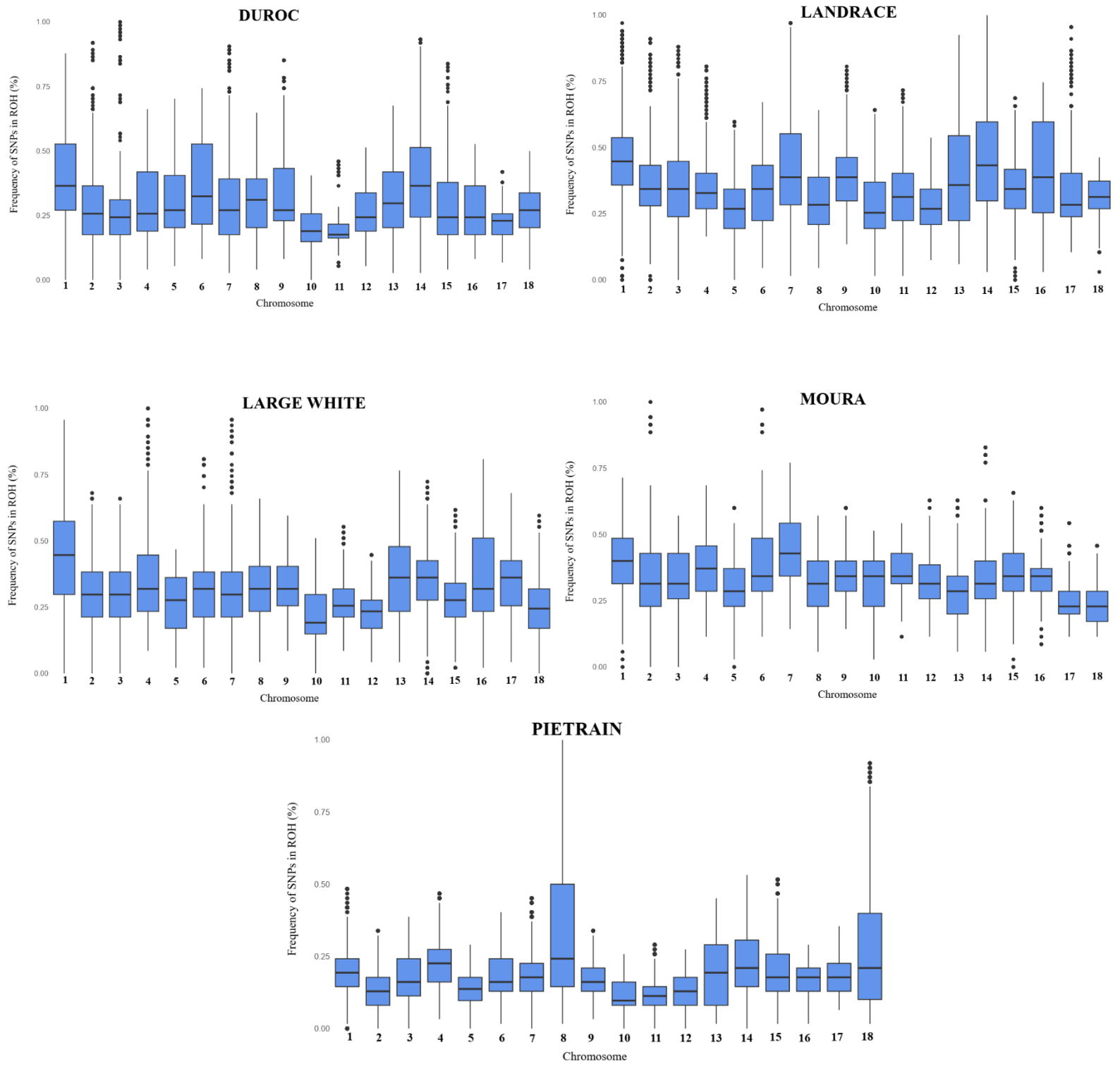

Fig. S3. Frequency of SNPs in ROH for the autosomal chromosomes of the five genotyped swine breeds, presented using a Boxplot distribution. The black line represents the average SNP frequencies on each chromosome, while black dots highlight outliers.

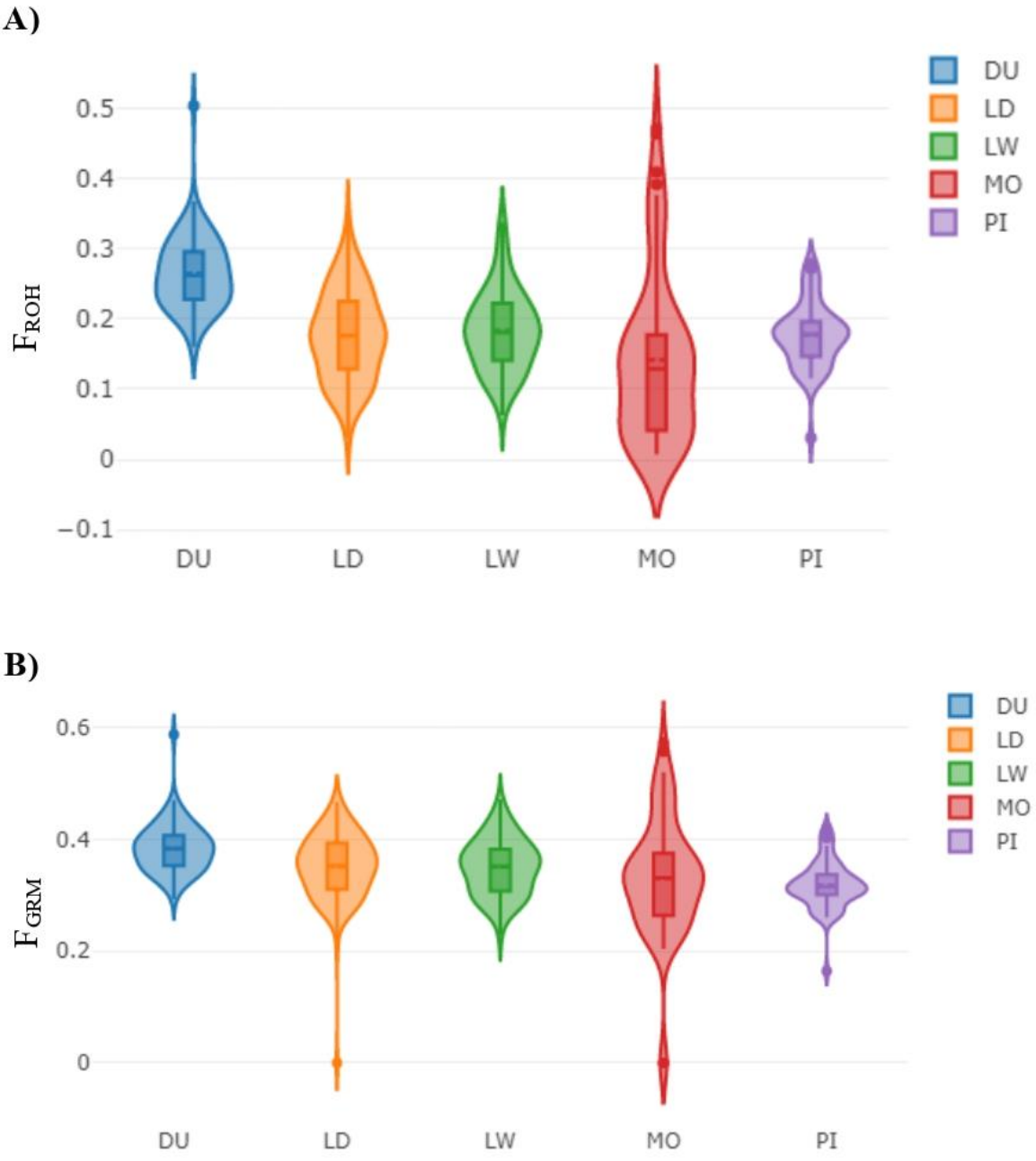

Fig. S4. Runs of homozygosity (ROH) inbreeding coefficient (F_{ROH}) based on genomic relatedness matrix (F_{GRM}) in the five studied swine breeds. (A) F_{ROH} distribution in the five studied swine breeds. B F_{GRM} distribution in the five studied swine breeds. DU = Duroc; LD = Landrace; LW = Large White; MO = Moura; PI = Pietrain.

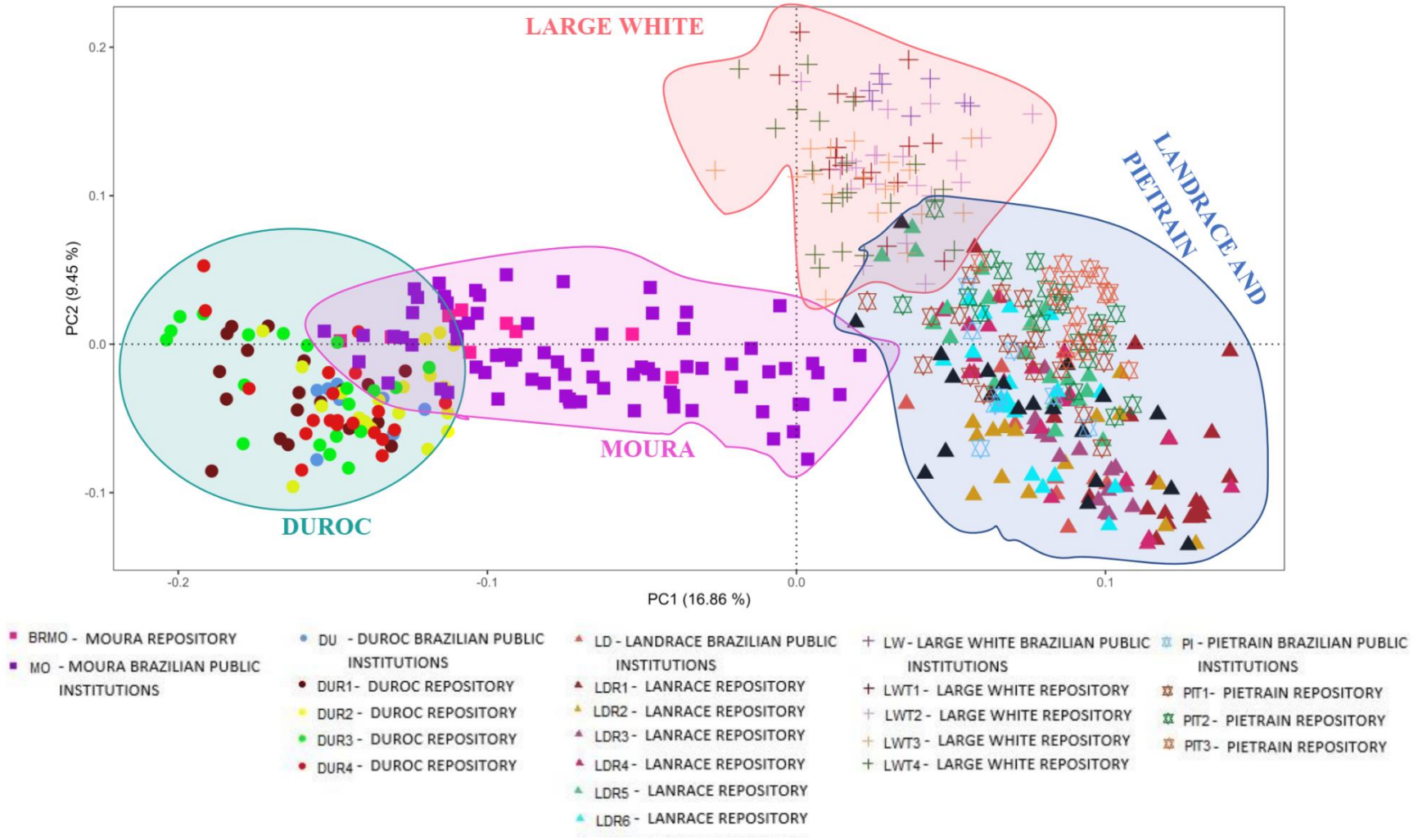

Fig. S5. PCA plot for Duroc (DU, DUR1, DUR2, DUR3, and DUR4), Landrace (LD, LDR1, LDR2, LDR3, LDR4, LDR5, LDR6, and LDR7), Large White (LW, LWT1, LWT2, LWT3, and LWT4), Pietrain (PI, PIT1, PIT2, and PIT3), and Moura (BRMO and MO) swine breeds using genotypes from the ROH island on chromosome 2. The numbers in parentheses on each axis represent the proportion of variance explained by each principal component.

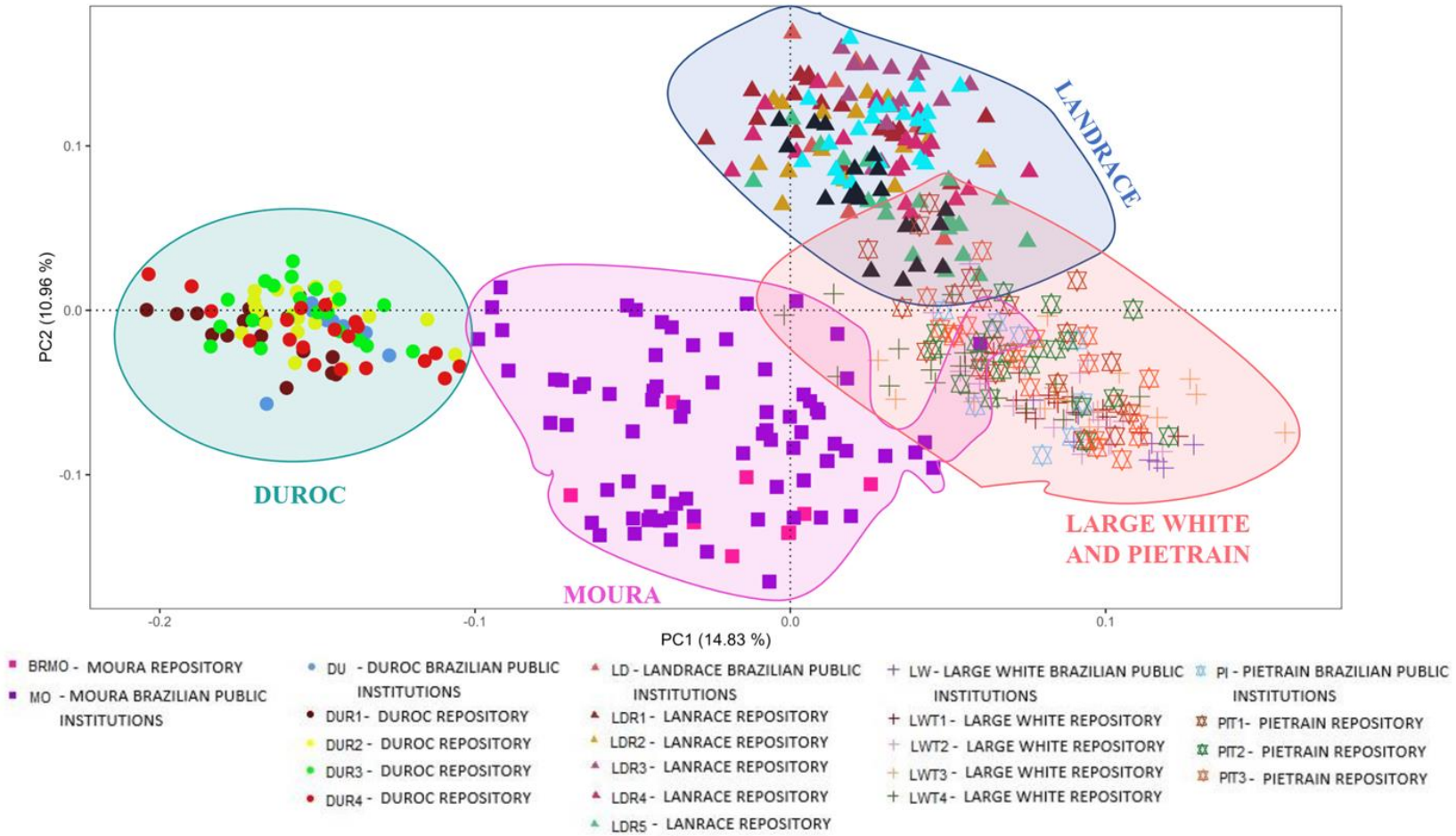

Fig. S6. PCA plot for Duroc (DU, DUR1, DUR2, DUR3, and DUR4), Landrace (LD, LDR1, LDR2, LDR3, LDR4, LDR5, LDR6, and LDR7), Large White (LW, LWT1, LWT2, LWT3, and LWT4), Pietrain (PI, PIT1, PIT2, and PIT3), and Moura (BRMO and MO) swine breeds using genotypes from the ROH island on chromosome 7. The numbers in parentheses on each axis represent the proportion of variance explained by each principal component.

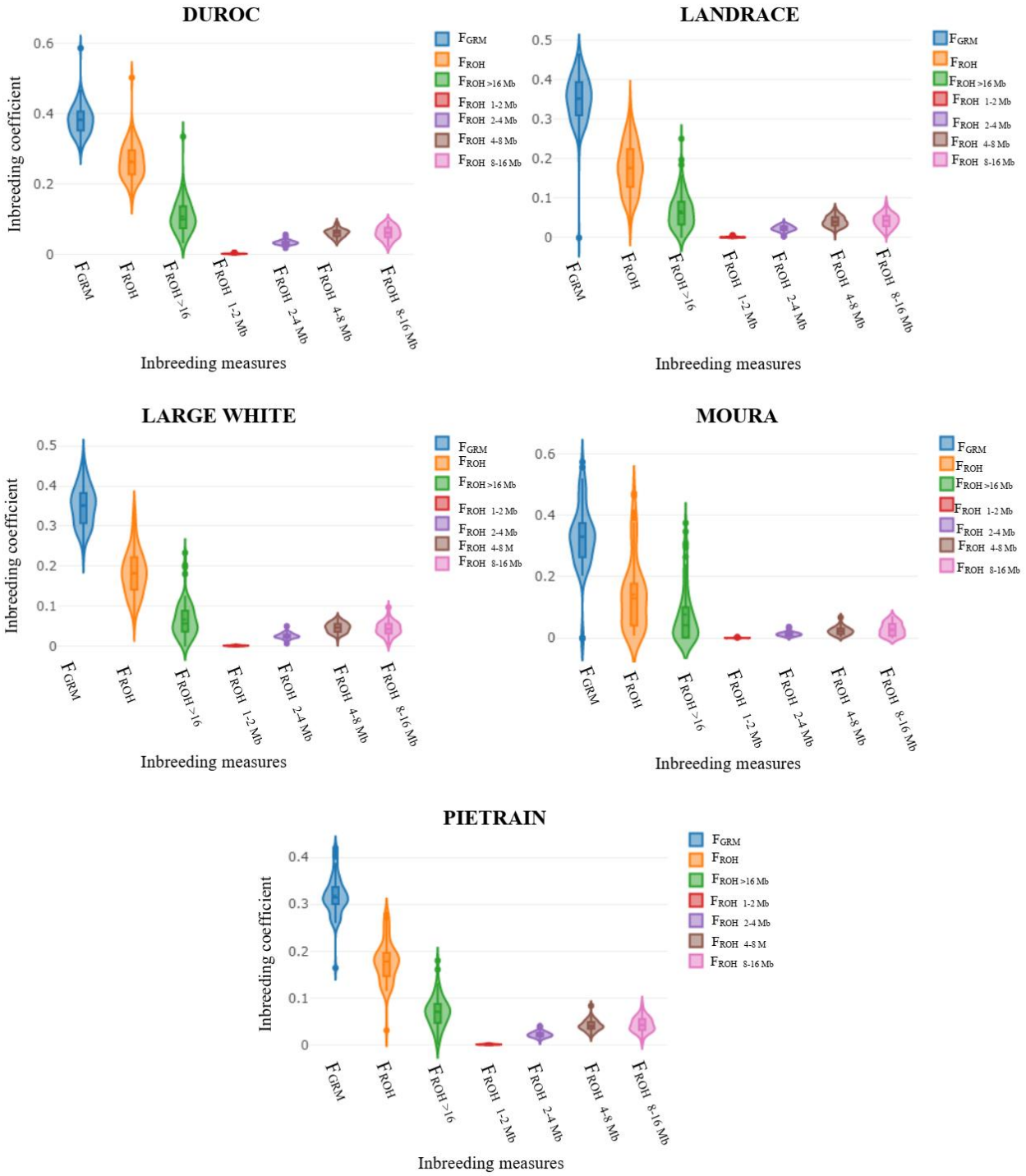

Fig. S7. Violin Plots of Estimated Inbreeding Coefficients for Duroc, Landrace, Large White, Moura, and Pietrain swine breeds using various methods across datasets. Included are the inbreeding from the genomic relationship matrix (F_{GRM}) and inbreeding coefficients derived from runs of homozygosity (F_{ROH}) in different configurations, such as F_{ROH}, $F_{ROH\ 1\text{-}2\ Mb}$, $F_{ROH\ 2\text{-}4\ Mb}$, $F_{ROH\ 4\text{-}8\ Mb}$, $F_{ROH\ 8\text{-}16\ Mb}$, and $F_{ROH\ >16}$.

CAPÍTULO III- Population structure and selection signatures in Moura pigs compared to commercial breeds and a Creole breed from Argentina

Population structure and selection signatures in Moura pigs compared to commercial breeds and a Creole breed from Argentina

Abstract

Runs of Homozygosity (ROH) are continuous segments of the genome that arise due to inbreeding, resulting in the inheritance of identical haplotypes from both parents who shared a common ancestor. The population genetic structure of animals belonging to six pig breeds, two Creoles breeds from the Americas (Moura and Creole Argentina das Misiones) and four commercial breeds (Duroc, Landrace, Large White, and Pietrain) were systematically evaluated. The occurrence and distribution of ROHs were verified, using the ROHs to estimate the inbreeding coefficients. Finally, genomic regions with a high frequency of ROHs and candidate genes associated with these regions were identified. In the PCA analysis, the animals of the Moura and Argentine Crioula das Misiones breeds were grouped, a result consistent with other studies, as revealed by the population structure and principal component analysis. The ROHs identified for the Creole Argentina das Misiones and Landrace were short (<4 Mb), while the Moura animals had a higher number of long ROHs (>8 Mb in length). The F_{ROH} values for the Moura breed and the commercial breeds were higher in the long segments (ROH>16 Mb), indicating recent inbreeding, around three generations ago. A total of five overlapping regions revealed a high frequency of ROHs among Moura, Creole Argentina das Misiones, Duroc and Landrace breeds, with seven candidate genes associated with economically important traits in pigs, mainly related to lipid metabolism and fat content (*BHMT2 and BHMT*) in Moura and Duroc pigs.

Keywords: admixture, genetic structure, runs of homozygosity, ROH island

1. Introduction

In the 16th century, there was the arrival of the genus Suis to the American continent, brought by European colonizers (Cavalcanti, 1985; Crosby, 2003). The rapid adaptability of these animals and the importance of pigs as a protein source for human consumption allowed the breeding and dispersion of animals with productive characteristics favorable to the environment (Cesconeto, 2016). After

changes in the market from the early 20th century in Latin America, some exotic breeds were imported due to their higher productivity, despite being selected for temperate regions and not possessing the adaptability characteristics of locally adapted or creole breeds (Mariante; Egito, 2002).

Currently, many of the breeds brought by immigrants make up several genetic groups of locally adapted pigs, being created with virtually no selection other than that carried out by nature (Sollero *et al*., 2009). These animals are important to local communities, with pork and lard being the basis of protein and energy in these communities. In general, village pigs behave as commensal animals, and feralization is also common, either because some areas were deliberately repopulated or because the animals escape, carrying out this process of transition from domesticated animals to wild animals (Burgos-Paz *et al*., 2013).

Within this context, the study of phylogeny and phylogeography are very complex, because, although the original pigs introduced in the Americas should have been related to Iberian pigs and, in particular, those from the Canary Islands, the study of existing villages and locally adapted pigs, which now populate the continent, are likely to be very complex (Burgos-Paz *et al*., 2013).

In Brazil, there are about thirteen locally adapted breeds and/or identified ecotypes, but only two were registered with the Brazilian Association of Pig Breeders (ABCS): the Piau breed and the Moura breed, which is considered one of the oldest (Vianna, 1975). The Moura animals multiplied and were distributed in the southern states of the country, where fattening took place in the field so that the animals consumed the pine nuts, between the months of April and

September, similar to the system adopted in Spain and Portugal for the production of matured hams (Sollero, 2006).

Similar to locally adapted breeds in Brazil, the production of Creoles pigs in the provinces of the Argentine Northeast (Corrientes, Chaco, Formosa, and Misiones), although not described as active in terms of the market, is known to play an important role in the economy and survival of small farmers, for whom these native animals have become adapted to the environments they inhabit (Revidatti, 2009).

Comparing exotic breeds (Duroc, Landrace, Large White, and Pietrain), the Moura breed and the Creole pig breed from Argentina, have lower production rates, being unattractive for production on an industrial scale (Čandek-Potokar *et al.,* 2019). However, they present lower losses due to thermal stress, in addition to the greater deposition of fat and marbling, mainly Moura animals.

Efficient conservation of the Moura breed is crucial to preserve its unique genetic material and adaptive characteristics in the face of increasing pressure from crossbreeding with commercial breeds. To achieve this goal, it is essential to understand the population structure of Moura pigs through the analysis of runs of homozygosity (ROHs). This study aims to identify selection signatures and shared regions with commercial breeds (Duroc, Landrace, Large White, and Pietrain) and the native Argentine breed (Creole Misiones), with the objective of pinpointing genetic loci and QTLs associated with traits of interest in the Moura breed. Furthermore, it seeks to compare ROH patterns among different swine populations, thus stimulating the efficient conservation of the Moura pig as a genetic resource reserve.

2. MATERIAL AND METHODS

2.1. Ethics Declaration

Approval from an Animal Care and Use Committee was not required in this study, as the information was obtained from a pre-existing database provided by EMBRAPA – Swine and Poultry (CNPSA), EMBRAPA – Genetic Resources and Biotechnology (CENARGEN), Federal University of Rio Grande do Sul (UFRGS), the Federal University of Paraná (UFPR), the Passo Fundo University (UPF) and the publically available Dryad Digital Repository (Yang *et al.*, 2017).

2.2. Animals, genotyping and quality control

The Brazilian genotype bank contained 8 animals/each of the commercial breeds (Duroc, Landrace, Large White, and Pietrain) raised in the South region. The 75 Moura pigs (South = 60, Southeast = 2, Northeast = 8 and Midwest = 5), samples from the southern region were collected from four institutional herds. A particular herd is descended from the *ex-situ* conservation herd created in 1985 at UFPR, in addition to other private and institutional herds considered in-situ (Botan *et al*., 2019). The animals were genotyped with the Illumina Porcine v2 BeadChip markers (Ramos *et al*., 2009) with 61,565 SNPs. Were incorporated into the genotype bank 361 animals from other countries, of the breeds: Moura (n= 9), Creole Argentina das Misiones (n= 9), Duroc (n= 79), Landrace (n= 130), Large White (n= 76) and Pietrain (n= 58), were obtained from the Dryad Digital

Repository genotyped with the Illumina 60K SNP (Ramos *et al*., 2009) with 61,772 SNPs (Supplementary Table S1).

The commercial breeds from the digital repository were represented by more than three different populations to provide additional controls, in addition to allowing extrapolation of the results more efficiently. Merging these banks was made possible by updating the reference map using SNPchiMp v.3 (Nicolazzi *et al*., 2015), ensuring that the names and locations of the SNPs were consistent across the merged populations.

Subsequently, PLINK software version 1.9 (Purcell *et al*., 2007) was used for data quality control. Animals with a call rate < 0.90 were discarded (`--mind 0.1`). Only autosomal SNPs with a call rate above 0.95 (`--geno 0.05`) were analyzed, excluding low-quality results, which contributes to increasing data accuracy (Oliphant *et al*., 2002). No filtering for minor allele frequency (MAF) and Hardy-Weinberg balance (HWE) was performed, as this exclusion could underestimate ROH coverage (Meyermans *et al.*, 2020). After merging the genotypes and quality control, the final data set consisted of 468 animals of the six breeds with 40,555 SNPs distributed on autosomal chromosomes.

2.3. Population structure and effective population size

To visualize the genetic proximities between the six Brazilian and foreign pig breeds, through principal component analysis (PCA), the PLINK software version 1.9 was used (Chang *et al*., 2015). A scatter plot was generated to visualize the first and second principal components based on a standardized

variance relationship matrix created using the R package "ggplot2" (Wickham, 2010), and the "scatterplot3D" package in three-dimensional scale (Ligges; Mächler, 2003).

The ADMIXTURE software (Alexander; Novembre; Lange, 2009) was used to infer the most likely number of ancestral populations (K = 2-6) based on population genotype data. All SNPs present in the chromosomes identified as islands of ROH shared among Moura animals and the other breeds in the study were considered. The ideal number of clusters (K value) was determined as the one with the lowest cross-validation error. The results of the ADMIXTURE analysis were visualized using the CLUMPAK online platform (Kopelman et al., 2015).

The effective population size (Ne) in recent and remote generations was estimated using SNP data with the SNeP software (Barbato *et al*., 2015). The effective historical population size is estimated by considering the level of binding at intervals of different widths and the rate of recombination; The calculation is based on the basic formula:

$$E(r^2) = (1 - 4N_e\boldsymbol{c})^{-\mathbf{1}}$$

Wherein, the estimate of $E(r^2)$ depends on the distance between the SNPs in the windows and $\boldsymbol{c}$ is the recombination rate, held at 1 x 10^{-8} by default. The SNeP software calculates Ne in past and recent generations, correcting the equation by including the number of samples and phasing information. Default parameters were used, except for the maximum distance in base pairs (bp) between the analyzed SNPs, which was similar to those used by (Schiavo *et al*.,

2021), set at 10 Mb, and the bandwidth for LD calculation, which was set at 100 kb.

2.4. Identification of ROHs

To identify the homozygous runs in each individual, PLINK v1.9 software was used, which uses the sliding window technique to scan each individual's genotype at each marker position to detect homozygous segments (Howrigan; Simonson; Keller, 2011). The ROHs were defined through the following parameters: (1) minimum length of 1 Mbp *(-homozyg-kb 1000*) to detect ROH; (2) the minimum number of 50 consecutive SNPs *(-homozyg-snp 50*), included in a ROH, was obtained by the equation proposed by (Lencz *et al*., 2007):

$$l = \frac{log_e \frac{\propto}{n_s \times n_i}}{log_e(1 - het)}$$

Where $\propto$ is the percentage of false-positive ROH (defined as 0.05 in the present study), n_s is the number of SNPs per individual, n_i is the number of individuals, het is the heterozygosity at all SNPs and log_e is the neperian logarithm operator; (3) no heterozygotes and absent genotypes were allowed; (4) minimum SNP density in a genome window of 1 SNP every 100 kbp (*-homozyg-density 100*); (5) the maximum allowable distance between consecutive SNPs of 1000 kbp (*-homozyg-gap 1000*). The ROHs were classified into five categories of different sizes: 1-2 Mb, 2-4 Mb, 4-8 Mb, 8-16 Mb and > 16 Mb (Ferenčaković *et al*., 2013; Kirin *et al*., 2010; Schiavo *et al*., 2021; Schiavo *et al*., 2020a).

2.5. Inbreeding coefficient

The coefficient of inbreeding based on ROH (F_{ROH}) was calculated for each animal using the following formula (Mcquillan *et al*., 2008):

$$F_{ROH} = \frac{\sum_{j=1}^{n} L_{ROHj}}{L_{total}}$$

On what, L_{ROH} is the total length of ROH of an individual j and L_{total} is the total length of the autosomal genome covered by SNPs, which was 2.44 Gb in our study. Five ROH length categories were determined so that the analysis of inbreeding coefficients based on ROH length would provide information on inbreeding during five different time intervals ($F_{ROH1\text{-}2\ Mb}$, $F_{ROH2\text{-}4\ Mb}$, $F_{ROH4\ \text{-}8\ Mb}$, $F_{ROH8\text{-}\ 16\ Mb}$ and $F_{ROH\ >\ 16\ Mb}$). According to Fisher (1954), the physical length of an ROH is expected to follow an exponential distribution with a mean equal to 100/2g x cM, where g represents the number of generations of interest since the common ancestor. Assuming that 1 cM = 1 Mbp, an ROH with lengths of 1, 2, 4, 8, and 16 Mbp is expected to come from a common ancestor occurring 50, 25, 12, 6, and 3 generations ago, respectively.

2.6. Detection of common ROHs and gene annotation

To identify genomic regions with a high frequency of ROHs, we used the file generated by the PLINK v1.90 software (CHANG et al., 2015), to estimate the number of times that a SNP appeared in a ROH among individuals. “ROH islands” were identified as a region of adjacent SNPs with an ROH frequency per SNP above the 1% threshold. The genes annotated in the genome version of the

SSCROFA11.1 pigs mapped on the identified ROH islands were considered as candidate selection signatures and were retrieved using the ENSEMBL BIOMART tool (http://www.ensembl.org/biomart/martview/). The functional enrichment analysis of GO terms (Genetic Ontology) and KEGG pathways (Kyoto Encyclopedia of Genes and Genomes) was performed using the DAVID tool (Huang; Sherman; Lempicki, 2009). Only GO terms and KEGG pathways with significant enrichment ($p<0.05$) based on Fisher's exact test were included in the analysis. The biological function of each gene annotated in the ROH islands was determined through an extensive literature search. Furthermore, with the help of the Pig QTL, a search was carried out for known QTLs present in the ROH islands in the swine Moura.

3. Results

3.1. Analysis of population structure between breeds and effective population size

The results of the PCA analysis allowed visualizing the genomic relationship between the sampled animals (Figure 1A, B). Principal component 1 (PC1) explained 15.78% of the genomic variation, while principal component 2 (PC2) explained 8.1%. These values indicate the relative contribution of each component to the total variation observed in the genomic data. The two-dimensional graph distinguished the Landrace and Duroc breeds, while two clouds were formed by the Large White/Pietrain and Moura/Creoles Argentina Misiones breeds (Figure 1A). The abscissa axis revealed a clear segregation between the commercial genetic groups Large White/Pietrain and Landrace in

relation to the Duroc breed, widely recognized for its commercial use in the industry. The Moura breed and Argentine Creole Misiones were plotted in the center of the PCA, well-separated and distant from the commercial groups. In the three-dimensional figure, the third component explained less variation, however, it was able to separate the Large White and Pietrain pigs, but not the Moura and Argentinian Creole animals. The other races remained distinct (Figure 1B).

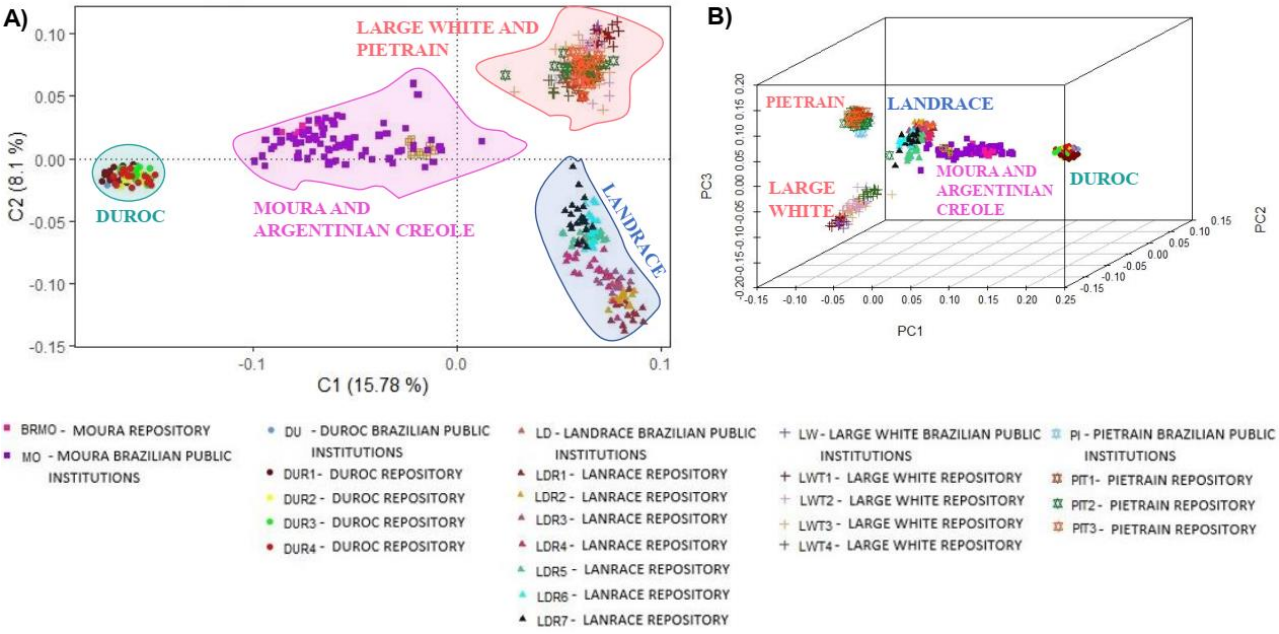

Figure 1. Principal component analysis graph for the six pig breeds. A) Two-dimensional; B) three-dimensional.

The admixture of the six swine breeds (K = 2-6 clusters) for chromosome 2 is illustrated in Figure 2, while Figure 3 represents the mixture for chromosome 7. At K = 2, the clustering algorithm separated the DU breed from LD, LW, PI, and ARCR on both chromosomes. For chromosome 2, the clustering levels of K=2, K=3, and K=4 reveal a higher degree of ancestry between the Duroc and Moura breeds, which share an ROH island on this chromosome, while the Moura breed shows mixing signatures with the commercial breeds Landrace, Large

White, and Pietrain. On chromosome 7, the clustering levels of K=2 and K=3 reflect a higher degree of sharing between the ARCR, LW, and PI breeds. For both chromosomes at K=6, we can observe a certain relationship between the Moura animals and the Argentine Creole breed from Misiones, although they do not belong to a homogeneous group.

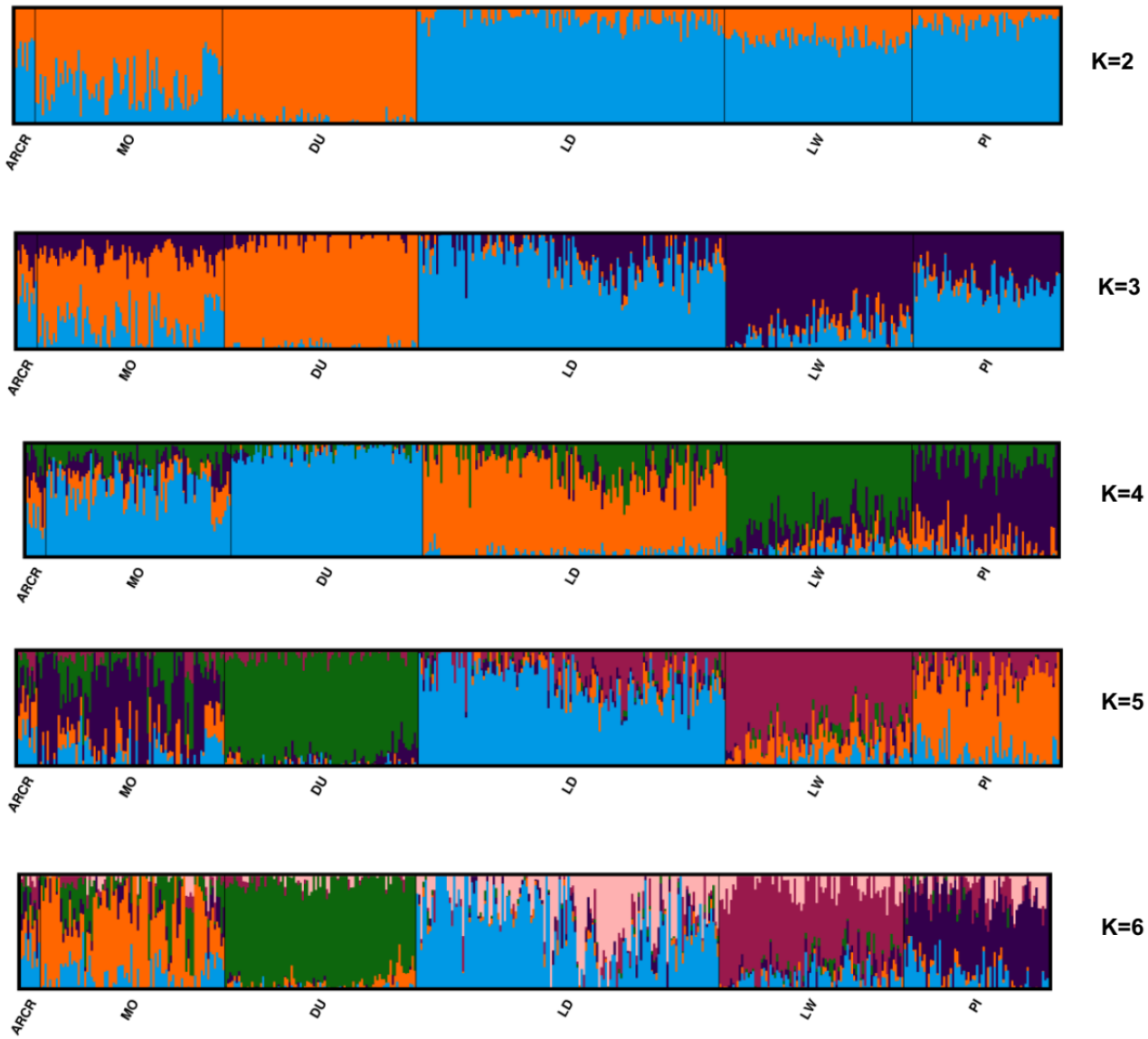

Figure 2. ADMIXTURE results (K= 2-6) for the genetic structure of six pig breeds on chromosome 2. ARCR= Creole Argentina das Misiones; MO= Moura; DU= Duroc; LD= Landrace; LW= Large White; PI= Pietrain.

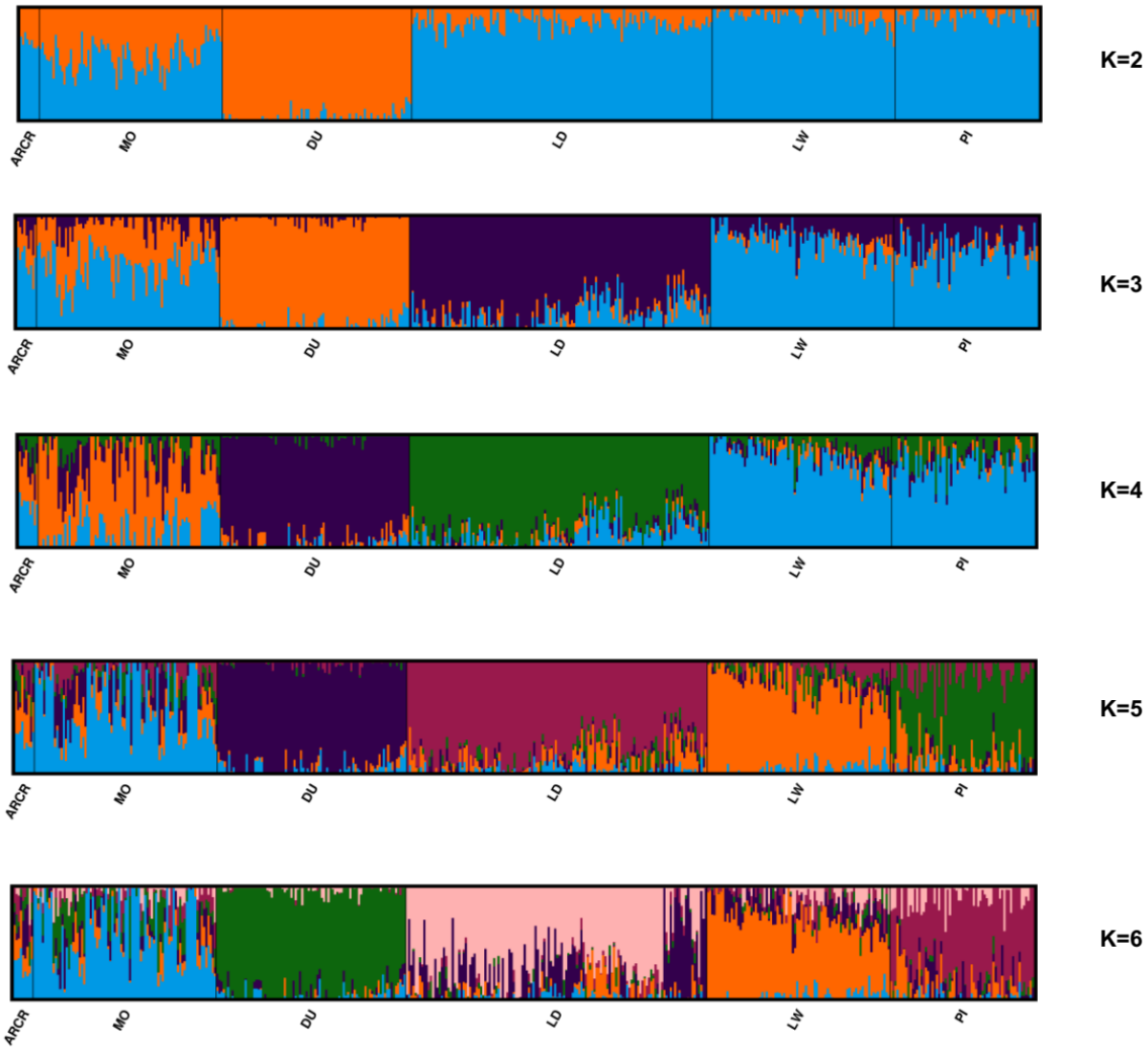

Figure 3. ADMIXTURE results (K= 2-6) for the genetic structure of six pig breeds on chromosome 7. ARCR= Creole Argentina das Misiones; MO= Moura; DU= Duroc; LD= Landrace; LW= Large White; PI= Pietrain.

All studied swine populations showed a declining trend in effective population size (Supplementary Table S2 and Figure 4). The Ne varied among the breeds, ranging from 183 (DU) to 343 (MO) 108 generations ago, and more recently from 17 (ARC) to 79 (LW) (five generations ago). The commercial breeds

(LW, LD, PI, and DU) showed the smaller declines in Ne, while the Creole breeds (MO and ARC) had the greatest declines.

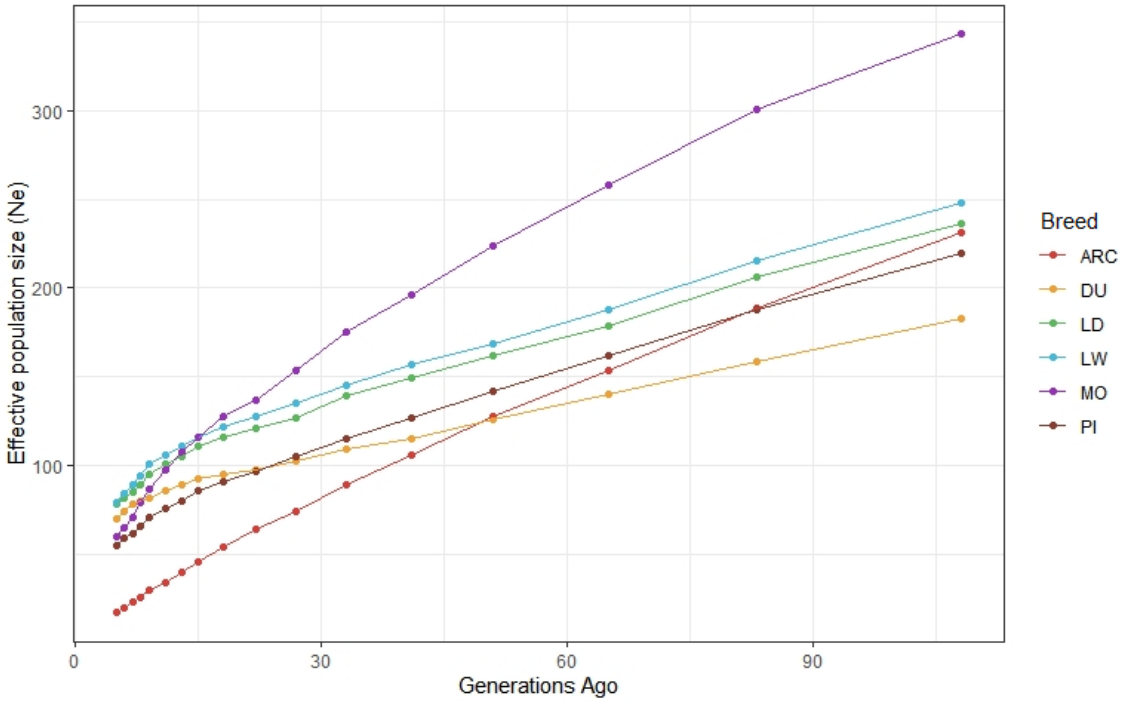

Figure 4. Estimates of effective population size (Ne) for pig populations ARCR = Creole Argentina das Misiones; MO = Moura; DU = Duroc; LD = Landrace; LW =Large White; PI = Pietrain.

3.2. Runs of homozygosity, inbreeding coefficients, and selective sweeps based on ROH

The ROH length classes and estimated mean inbreeding coefficients based on ROH length are presented in Table 1. A total of 7,163, 6,544, 4,663, 3,299, 2,560, and 120 ROHs were observed in Landrace, Duroc, Large White, Pietrain, Moura, and Argentine Creole from Misiones pigs, respectively. The

average ROH length was smaller in the $R_{OH\ 1\text{-}2\ Mb}$ class and larger in the $R_{OH\ >16\ Mb}$ class for all breeds.

Argentine Creole from Misiones and Landrace exhibited the highest percentage of ROH numbers in the shorter classes (<4 Mb), while Moura had the highest percentage for longer classes (>8 Mb), Moura animals had the highest percentage of ROH numbers in the middle classes (4-8 Mb). Commercial breeds concentrated the highest percentage of ROH in the 2-4Mb and 4-8Mb classes.

The inbreeding of individuals belonging to the Moura breed is strongly concentrated in segments larger than 16 Mb, evidencing recent inbreeding in these populations and in other evaluated commercial breeds. Except in the Argentine Creole animals from Misiones that uniformly distributed inbreeding coefficients ranging from 2-4 Mb to > 16 Mb, where they exhibited the lowest levels of inbreeding $F_{ROH\text{-}TOTAL}$ compared to other breeds (Figure 5).

Table 1. Descriptive statistics of the number of homozygosity runs (nROH), average length and standard deviation, and inbreeding coefficient (F_{ROH}) divided into five classes for the six swine breeds.

Breed[1]	**Class**	***n*ROH (%)**	**Av. lenght ± SD**	**F_{ROH}**
ARC	ROH $_{1\text{-}2\ Mb}$	4 (3.33)	1.794 ± 0.136	0.0003
	ROH $_{2\text{-}4\ Mb}$	54 (45)	2.932 ± 0.508	0.0071
	ROH $_{4\text{-}8\ Mb}$	40 (33.33)	5.427 ± 0.964	0.0098
	ROH $_{8\text{-}16\ Mb}$	15 (12.5)	10.260 ± 1.315	0.0069
	ROH $_{>16\ Mb}$	7 (5.84)	28.116 ± 9.058	0.0089
	TOTAL	120 (100)	6.111 ± 6.387	0.0333
MO	ROH $_{1\text{-}2\ Mb}$	34 (1.33)	1.852 ± 0.150	0.0003
	ROH $_{2\text{-}4\ Mb}$	725 (28.32)	3.048 ± 0.539	0.0108
	ROH $_{4\text{-}8\ Mb}$	822 (32.11)	5.628 ± 1.110	0.0227
	ROH $_{8\text{-}16\ Mb}$	524 (20.47)	11.282 ± 2.229	0.0291
	ROH $_{>16\ Mb}$	455 (17.77)	33.993 ± 18.124	0.0761
	TOTAL	2.560 (100)	11.046 ± 13.493	0.1392
DU	ROH $_{1\text{-}2\ Mb}$	128 (1.96)	1.837 ± 0.139	0.0011

	ROH 2-4 Mb	2,154 (32.92)	3.055 ± 0.546	0.0309
	ROH 4-8 Mb	2,318 (35.42)	5.621 ± 1.149	0.0612
	ROH 8-16 Mb	1,180 (18.03)	11.027 ± 2.228	0.0611
	ROH >16 Mb	764 (11.67)	29.059 ± 15.041	0.1043
	TOTAL	6,544 (100)	8.414 ± 9.586	0.2587
LD	ROH 1-2 Mb	148 (2.07)	1.816 ± 0.141	0.0007
	ROH 2-4 Mb	2,409 (33.63)	3.012 ± 0.541	0.0214
	ROH 4-8 Mb	2,483 (34.66)	5.606 ± 1.121	0.0412
	ROH 8-16 Mb	1,319 (18.42)	11.055 ± 2.223	0.0431
	ROH >16 Mb	804 (11.22)	27.780 ± 13.067	0.0661
	TOTAL	7,163 (100)	8.148 ± 8.795	0.1728
LW	ROH 1-2 Mb	83 (1.78)	1.828 ± 0.130	0.0007
	ROH 2-4 Mb	1,600 (34.31)	3.034 ± 0.546	0.0236
	ROH 4-8 Mb	1,704 (36.54)	5.563 ± 1.100	0.0461
	ROH 8-16 Mb	815 (17.48)	11.021 ± 2.241	0.0437
	ROH >16 Mb	461 (9.89)	29.390 ± 17.565	0.0659
	TOTAL	4,663 (100)	7.938 ± 9.487	0.1801
PI	ROH 1-2 Mb	50 (1.51)	1.823 ± 0.149	0.0005
	ROH 2-4 Mb	1,063 (32.22)	3.043 ± 0.532	0.0200
	ROH 4-8 Mb	1,171 (35.50)	5.656 ± 1.141	0.0410
	ROH 8-16 Mb	626 (18.98)	11.173 ± 2.263	0.0433
	ROH >16 Mb	389 (11.79)	28.751 ± 13.712	0.0692
	TOTAL	3,299 (100)	8.526 ± 9.301	0.1742

[1]DU = Duroc; LD = Landrace; LW =Large White; MO = Moura; PI = Pietrain; SD = Standard deviation.

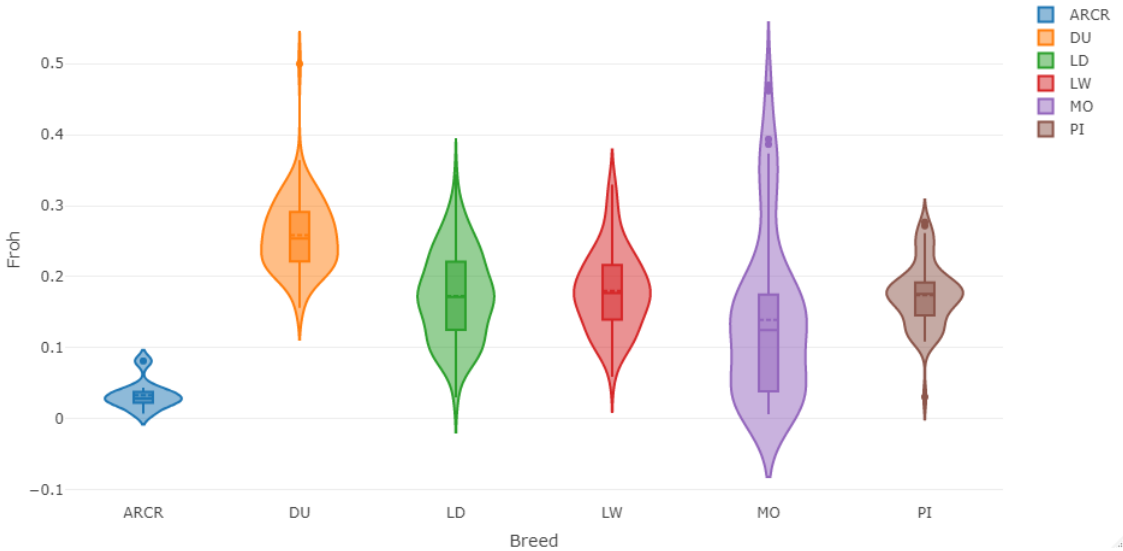

Figure 5 Distribution of the ROH inbreeding coefficient (FROH) in the six pig breeds. ARCR = Creola Argentina das Misiones; DU = Duroc; LD = Landrace; LW =Large White; MO = Moura; PI = Pietrain.

In the Moura breed, seven genomic regions showed the upper limit of 1% of the SNPs most shared by the population and were considered as selection marks. Out of these seven regions, five were also observed in the Duroc breed, one was shared with Pietrain, and the last one was shared with Duroc and Argentine Creole from Misiones (Figure 6).

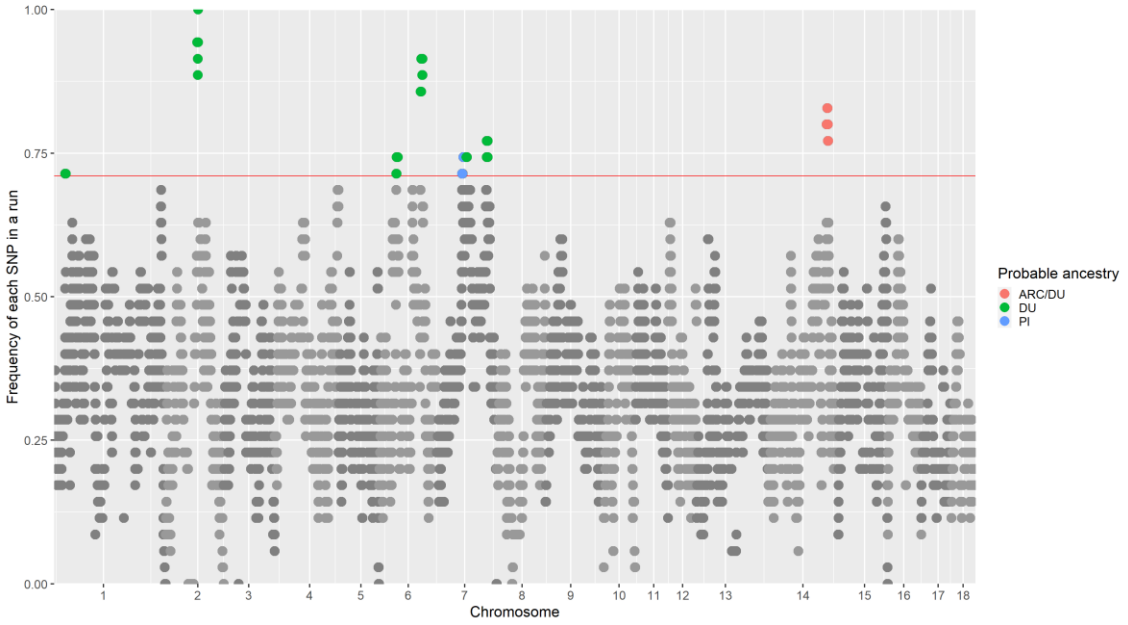

Figure 6 Frequency of each SNP in a homozygous run (ROH) in the Moura population shown according to chromosome and position. The horizontal line indicates the 1% threshold to classify the SNP as an ROH island. Segments highlighted according to probable descent. ARCR = Creole Argentina das Misiones; DU = Duroc; PI = Pietrain.

3.3. Gene Ontology (GO) enrichment analysis of candidate genes in regions of putative selection signatures

The Gene Ontology (GO) enrichment analysis was performed separately for each breed, and Table 2 presents overlapping terms between breeds. The

process enriched in Moura, Creola Argentina das Misiones, Duroc and Landrace breeds had the the Mpp 10 complex (GO:0034457) in common on chromosome 7. Another process was significant on chromosome SSC 7 for the Duroc and Landrace breeds (GO:0045499). The Moura and Duroc breeds showed significant genes in the complex biosynthetic process of Methionine (GO:0009086) on chromosome SSC 2, in addition to the activity of Betaine-homocysteine S-methyltransferase (GO:0047150). Binding to the calcitonin receptor (GO:0031716) was significant for Argentine Creole Misiones and Landrace breeds. The chemorepellent activity process was involved in Duroc and Landrace breeds, and the calcitonin receptor binding in Argentine Creole from Misiones and Landrace breeds. The development of the nervous system (GO:0007399), the platelet-derived growth factor receptor signaling pathway (GO:0048008), and the negative regulation of axon extension involved in axon guidance (GO:0048843) were associated with the Landrace breed, and the positive regulation of oligodendrocyte differentiation (GO:0048714) and transmembrane transporter activity (GO:0022857) was associated with the Pietrain breed (Supplementary Table S3).

Seven candidate genes present in the significant terms (IMP3, SNUPN, BHMT2, BHMT, SEMA4B, SEMA7A and CRSP3) are related to prostate cancer, reproduction, lipid metabolism, fat deposition, cell metastasis inhibition, inflammation, and metastasis suppressor. The results of the search for QTLs in these regions revealed an association with economically important characteristics, such as meat and fat quality (Table 3) for the Moura breed.

The Gene Ontology (GO) enrichment analysis was performed separately for each breed (Supplementary Table S3), and Table 2 presents overlapping terms between breeds. Genes enriched in Moura, Creola Argentina das Misiones, Duroc, and Landrace breeds were involved in the Mpp 10 complex, while Moura and Duroc breeds were involved in the biosynthetic process of methionine and betaine-homocysteine S-methyltransferase activity. The chemorepellent activity process was involved in Duroc and Landrace breeds, and the calcitonin receptor binding in Argentine Creole from Misiones and Landrace breeds. The development of the nervous system, the platelet-derived growth factor receptor signaling pathway, and the negative regulation of axon extension involved in axon guidance were associated with the Landrace breed, and the positive regulation of oligodendrocyte differentiation and transmembrane transporter activity was associated with the Pietrain breed. Table 2 presents the overlapping terms among the breeds, with seven candidate genes (*IMP3, SNUPN, BHMT2, BHMT, SEMA4B, SEMA7A, and CRSP3*) related to prostate cancer, reproduction, lipid metabolism, fat deposition, inhibition of cell metastasis, inflammation, and metastasis suppressor. The QTL enrichment results for the Moura breed revealed that ROH islands were associated with QTLs of economically important traits such as meat quality and fat (Table 3).

Table 2. Genes Ontology (GO) annotation analysis of terms overlapping the selection of signatures detected by ROH.

Breed[1]	Terms	SSC[2]	Chromosome position (kb)	Candidates genes
MO, ARC, DU and LD	Mpp 10 complex (GO:0034457)	7	58,038-58,065	*IMP3, SNUPN*
DU and LD	Chemorepellent activity (GO:0045499)	7	55,753-59,119	*SEMA4B, SEMA7A*
MO and DU	Methionine biosynthetic process (GO:0009086)	2	87,090-91,444	*BHMT2, BHMT*
MO and DU	Betaine-homocysteine S-methyltransferase activity (GO:0047150)	2	87,090-91,444	*BHMT2, BHMT*
ARC and LD	Calcitonin receptor binding (GO:0031716)	2	43,185-46,133	*CRSP3*

[1]MO = MOURA; ARCR = CREOLA ARGENTINA DAS MISIONES; DU = DUROC; LD = LANDRACE; [2]*Sus scrofa* autossomo

Table 3. Homozygous regions observed in Moura pigs and identification of underlying QTL genes in each region.

1. SSC[1]	Gene Symbol	QTL[2]	Trait name	Authors
2	BHMT	QTL:2800	Number of muscle fibers per unit area	(Wimmers *et al.*, 2006)
		QTL:2799	Total muscle fiber number	(Wimmers *et al.*, 2006)
6	DSG3	QTL:194724	Fat androstenone level	(Drag *et al.*, 2019)
6	AXL	QTL:211773	Teat number	(Zhuang *et al.*, 2020)
6	APOC2	QTL:37823	Mean platelet volume	(Wang *et al.*, 2012)
6	APOE	QTL:126045	Backfat at tenth rib	(Fan *et al.*, 2009)
		QTL:126046	Gait score (overall)	(Fan *et al.*, 2009)
		QTL:65400	Average backfat thickness	(Wang *et al.*, 2013)
6	GSK3A	QTL:65398	Backfat at last rib	(Wang *et al.*, 2013)
		QTL:65399	Backfat at rump	(Wang *et al.*, 2013)
		QTL:65397	Loin muscle area	(Wang *et al.*, 2013)
		QTL:37835; QTL:37819; QTL:37831	Mean platelet volume	(Wang *et al.*, 2012)

6	DSG3	QTL:194724	Fat androstenone level	(Drag *et al.*, 2019)
6	DLL3	QTL:37837	Mean platelet volume	(Wang *et al.*, 2012)
6	ACTN4	QTL:37830	Mean platelet volume	(Wang *et al.*, 2012)
		QTL:7671	Average backfat thickness	(Kadarmideen, 2008)
		QTL:7669	Average daily gain	(Kadarmideen, 2008)
6	RYR1	QTL:258454	Backfat at tenth rib	(Ding *et al.*, 2022)
		QTL:213564	Intramuscular fat content	(Wang *et al.*, 2019)
		QTL:7670	Loin	(Kadarmideen, 2008)
		QTL:7672; QTL:7673	Muscle pH	(Kadarmideen, 2008)
		QTL:7674; QTL:7675	Osteochondrosis score	(Kadarmideen, 2008)
		QTL:17699; QTL:17698	Spinal curvature	(Lindholm-Perry *et al.*, 2010)
		QTL:13461; QTL:13468	ATP breakdown rate	(Sieczkowska *et al.*, 2010)
		QTL:13467	Average glycogen	(Sieczkowska *et al.*, 2010)

		QTL:13466; QTL:13459	Average glycolytic potential	(Sieczkowska *et al.*, 2010)
		QTL:13460; QTL:13473	Average lactate	(Sieczkowska *et al.*, 2010)
7	PKM	QTL:13472; QTL:13464; QTL:13465	Drip loss	(Sieczkowska *et al.*, 2010)
		QTL:13471	Meat color L*	(Sieczkowska *et al.*, 2010)
		QTL:13463; QTL:13469; QTL:13470; QTL:13462	Muscle pH	(Sieczkowska *et al.*, 2010)
		QTL:55770	Obesity index	(Kogelman *et al.*, 2014)

[1]*Sus scrofa* autossomo; [2] QTLs identified in Pig QTL database

4. Discussion

4.1. Analysis of population structure between breeds and effective population size

The PCA graphs (Fig. 1A, B) and the ADMIXTURE results (Fig. 2 and Fig. 3) indicated the existence of genetic proximity between Moura and Creole Argentina pigs from Misiones. A similar result was found by Burgos-Paz *et al*. (2013), where they observed a separation between Brazilian Creole breeds and American breeds, while the Moura breed remained close to Paraguayan wild boars and Creole Argentina das Misiones. Commercial breeds (Duroc, Landrace, Large White, and Pietrain) are associated with modern selection and are clearly separated, but with three divergent clusters: Duroc vs. Large White/Pietrain vs. Landrace. The Moura and Creole Argentina das Misiones pigs are situated in the middle and appear relatively uniform when compared to the variation across the entire species, similar to the findings of Souza *et al*. (2010).

Using the ADMIXTURE software, it was observed that for K= 2, on chromosome 2, the first hierarchical division was evident between Duroc and the LD, LW, PI, and ARCR breeds, which is consistent with the results obtained by MUJIBI et al. (2018) when analyzing the genetic diversity of Kenyan local pig breeds compared to Duroc, Landrace, Large White, Yorkshire, and Wild Boar breeds. Remarkably, a significant sharing of ancestry between Moura and Duroc on chromosome 2 (> 61%) was observed at K= 2, K= 3, and K= 4 levels. Additionally, the Moura breed showed strong evidence of admixture with the Landrace, Large White, and Pietrain breeds on chromosome 7, supporting the

conclusions of Souza *et al*. (2010), who provided a comprehensive view of the genome of Creole pig populations throughout the Americas. These results clearly demonstrate the importance of ancestral sharing in characterizing the genetic relationships among different pig breeds

It is believed that the Duroc breed was imported to America by Christopher Columbus from Spain or Portugal and underwent further breed development in the late 1800s in the USA (Mujibi *et al*., 2018). The Duroc breed is considered a relatively recent breed (Duroc-Jersey) developed in the USA (Porter, 1993), derived from pig populations of various lineages (including Iberian and African pigs). The higher ancestry sharing between Moura and Duroc may be related to the fact that they originate from the same group of pigs raised by Spanish Jesuits.

The Creole Argentina from Misiones breed showed a higher degree of genetic similarity with the Landrace and Large White breeds. All clustering levels clearly indicate the mixed nature of the Moura and Creole Argentina from Misiones populations, which reflects the history of locally adapted breeds due to population fragmentation followed by genetic drift in the past, as well as the consequences of possible mixing with imported pig breeds (Revidatti *et al*., 2021).

In conservation programs for local animal genetic resources, maintaining genetic variability and controlling inbreeding are crucial (Saura *et al*., 2013). The Moura breed exhibited a Ne (effective population size) greater than 50 for all generations, which is a higher result compared to the findings of Carneiro *et al*. (2014) using pedigree data (Ne= 30). The decline in estimated Ne

over time indicates that the ancestral population, based on 108 generations ago, had a much larger Ne (n= 343) compared to more recent generations.

In general, the Ne of commercial pig breeds experienced a smaller decline compared to creole breeds, a result similar to the findings of Zhang *et al*. (2018) when studying commercial and Chinese pig breeds. According to Amaral *et al*. (2008), this occurs due to the greater linkage disequilibrium in commercial pig breeds.

The population of Creole Argentina das Misiones pigs, among the pig breeds evaluated in this study, showed the lowest effective population size for all generations (Supplementary Table S2), which may be related to the small number of animals. Despite this potential bias, the SNP-based estimation from the sixth generation onwards was above 20, a result similar to the findings of Revidatti *et al*. (2021) using microsatellite markers, where the Creole breeds from the humid and dry regions of Northeast Argentina had Ne above 20. According to FAO (2013), the effective population size should be above 50, which is the minimum target for maintaining genetic resources. Regarding the commercial breeds, the Large White breed had the highest Ne in all generations, a result similar to that found by Schiavo *et al*. (2020a); Schiavo *et al*. (2020b).

4.2. Runs of homozygosity, coefficient, and selective sweeps based on ROH

The average length of ROH in all breeds increased with the increase in length classes. Short ROHs evolved in the past as a result of ancestral recombination processes (Ceballos *et al*., 2018). The results showed that the

percentage of long ROHs (>8 Mb) in the Moura breed was the highest among the studied pig breed populations, indicating a recent occurrence of inbreeding.

The highest percentage of short ROHs was observed in the Creole Argentina das Misiones and Landrace breeds, while the average percentage was found in the Duroc, Large White, and Pietrain breeds. Small and medium ROHs (<8 Mb) tend to reflect ancient inbreeding as these segments have been broken up by repeated meiotic events (Kirin *et al*., 2010). Additionally, the total number of ROHs in the ARC breed was the lowest among all breeds, which is likely related to the small number of animals. Similar results were observed by Wu *et al*. (2020) when studying a native pig breed from China, where the animals located in the Spsongpanna region had the lowest total number of ROHs due to the smaller population size.

The coefficient of inbreeding derived from ROH (F_{ROH}) can provide more accurate measures of inbreeding levels compared to those based on pedigree records (Peripolli *et al*., 2017). Generally, the F_{ROH} of locally adapted breeds tends to be lower than that of commercial breeds, which was observed in the present study (Fig. 5). The Duroc breed obtained the highest FROH values (ranging from 0.0011 to 0.1043 considering different minimum lengths of ROH) among the commercial breeds. Similar results were observed by SCHIAVO, G. et al. (2020a) when comparing the Italian Duroc with the Italian Large White and Italian Landrace breeds. The commercial breeds and Moura breed showed the highest values of the inbreeding coefficient for FROH >16 Mb, indicating a recent reduction in genetic diversity and an increase in homozygosity within the past three generations. This result supports the historical background of the Moura

breed, as an initial survey on the breed revealed only three remaining *in situ* nuclei that still possessed pure Moura herds in Candelária-RS, Carlos Barbosa-RS, and the region of Lages-SC. This justifies the recent inbreeding in these animals.

Although its origin is uncertain, the Moura pig breed, according to its genotypic characteristics, belongs to the Iberian lineage (Fávero*, et al*., 2007). It exhibits specific phenotypic traits and possesses its own genetic composition, originating from natural or artificial selection processes that have transmitted and preserved certain regions from the founding breeds. Of the 7 homozygous regions identified, five originated from Duroc, while the other regions originated from Pietrain, with one region showing a mixed origin between the Creole Argentina das Misiones breed and Duroc (Fig. 6). Throughout our study, we observed significant contributions of Duroc pigs to the Moura breed, which aligns with the findings of Burgos-Paz *et al*. (2013) and Souza *et al*. (2010). These findings reinforce the idea that the Moura breed shares genomic regions with Duroc due to their common ancestry. This is further supported by the mixed homozygous region between Duroc and Creole Argentina from Misiones, highlighting the genetic proximity of Moura to pig breeds originating from Spanish colonies in the Americas.

4.3. Analysis of Gene Ontology Enrichment of Candidate Genes in Regions of Putative Selection Signatures

The ROH islands harbor several candidate genes that control economically important traits in pigs. We identified five overlapping genomic

regions among the MO, ARC, DU, and LD breeds with a high frequency of ROHs, housing seven candidate genes. Among these, three genes (*IMP3, SEMA4B, and CRSP3*) are involved in cancer, one (*SNUPN*) is associated with reproduction, two (*BHMT2, BHMT*) are involved in fat deposition, and one (*SEMA7A*) is related to the immune system. The *SEMA4B* gene inhibits the invasion of non-small cell lung cancer and significantly reduces its growth (Jian *et al*., 2015). IMP3 is overexpressed in prostate cancer, accelerating cancer progression through the activation of the PI3K/AKT/mTOR signaling pathway (Zhang *et al*., 2020). *SNUPN* plays an important role in embryo development and is involved in human muscle atrophy (Narayanan *et al*., 2002). The gene *SEMA7A* is crucial for the resolution of severe inflammation observed in mice and children (Körner *et al*., 2021). *BHMT* is related to body weight, fat deposition, and energy metabolism (Card *et al*., 2019). *BHMT2* is a regulator in lipid metabolism (Ma *et al*., 2021).

The *BHMT2* and *BHMT* genes are promising genes as both the quantity and quality of fatty acid composition in pork are dependent on the entire lipid metabolism that develops throughout the animal's life. The presence of these genes in two islands shared between Moura and Duroc animals corroborates the information from Cameron *et al*. (1990) in which the meat of Duroc animals is more succulent, probably due to the higher content of intramuscular fat present and Luz, (2019) in which the greater slaughter weight of Moura pigs resulted in greater fat cover and larger pieces for the production of cured products, without altering the quality of the meat after slaughter. Further exploration of the genetic mechanisms and their impact on phenotypes is worthwhile.

The Large White breed, despite not having any overlapping ROH regions with other breeds, possesses the *NEURL1* gene associated with the development of the nervous system (GO:0007399) and the *NR4A3* gene associated with platelet-derived growth factor receptor signaling pathway (GO:0048008) and negative regulation of axon extension involved in axon guidance (GO:0048843). According to Mo *et al*. (2022), the *NEURL1* gene is a candidate gene related to reproductive traits. The *NR4A3* gene is involved in the process of fatty acid oxidation (Pearen *et al*., 2013). The Pietrain breed did not show any overlapping ROH island, was identified the *NR4A3* gene associated with the upregulation of oligodendrocyte differentiation (GO:0048714) and the *SLC13A4* gene associated with transmembrane transporter activity (GO:0022857). According to Barnes *et al*. (2017), the co-localization of *SLC13A4* on the same chromosome in pigs, humans, and mice suggests that this gene related to *SLC12A1* may be derived from a gene duplication event through evolution.

Through sequence alignment in Pig QTL, we noticed that most of the segments harbored genes that could regulate important biologic functions of Moura and most of them may have an impact on economic traits. In this analysis, those regions were mostly linked with meat and carcass traits in Pig QTLdb, for example, QTL:65400 and QTL:7671 were related to backfat thickness. In addition, a great part of them was relevant to fat, like QTL:126045, QTL:65398, QTL:65399, QTL:258454, and QTL:213564. Our results indicate that the Moura breed possesses economically important characteristics, highlighting the need for its maintenance, conservation, and promotion.

5. Conclusion

Compared to the other breeds, the Moura breed exhibited higher genetic diversity, with a lower degree of inbreeding compared to commercial breeds and a larger effective population size. The common ancestry of Moura and Duroc breeds probably relates to their common founding breeds. The Creole Argentina das Misiones breed showed overlap and genetic sharing with the Moura breed, indicating genetic proximity between Moura and the swine breeds present in regions of Spanish colonization. Several genes were identified in the ROH islands of Moura pigs, associated with fat deposition and backfat thickness. These results highlight a new direction of research regarding the genetic structure of the Moura population, which can effectively contribute to the conservation and use of this valuable local variety. The integration of this genetic information into breeding programs can promote the development of more efficient strains adapted to local conditions, thus contributing to the long-term sustainability and options for the Moura breed.

Acknowledgment

The authors would like to thank the National Center for Genetic Resources and Biotechnology for providing DNA samples from Moura pigs, as well as Elizabete C. Silva and Gleison R. de Biazio for their support in preparing and sending the material for genotyping. Thanks are also due to the Coordination for the Improvement of Higher Education Personnel (CAPES) and the National Council for Scientific and Technological Development (CNPq, 303263/2021-0) for partial funding and scholarships, as well as to Dr. Mônica Corrêa Ledur – EMBRAPA poultry and swine, Ricardo Zanella – University of Passo Fundo (UPF), Dr. Marson Bruck Warpechowski – Federal University of Paraná (UPF) and Dr. José Braccini Neto (UFRGS). Finally, we would also like to thank Moura pig breeders.

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COMPLEMENTARY MATERIAL

Supplementary Table 1. Pigs genotyped in this study

Abbreviation	Country	Population	Number of animals
BRMO	Brasil	Moura	9
MO	Brasil	Moura	75
ARC	Argentina	Creole	9
DU	Brasil	Duroc	8
DUR1	Dinamarca	Duroc	19
DUR2	USA	Duroc	20
DUR3	Holanda	Duroc	20
DUR4	China	Duroc	20
LD	Brasil	Landrace	8
LDR1	Dinamarca	Landrace	20
LDR2	Noruega	Landrace	15
LDR3	Finlândia	Landrace	15
LDR4	China	Landrace	20
LDR5	USA	Landrace	20
LDR6	Espanha	Landrace	20
LDR7	Holanda	Landrace	20
LW	Brasil	Large White	8
LWT1	Dinamarca	Large White	16
LWT2	China	Large White	20
LWT3	USA	Large White	20
LWT4	Holanda	Large White	20
PI	Brasil	Pietrain	8
PIT1	USA	Pietrain	20
PIT2	Holanda	Pietrain	20
PIT3	Alemanha	Pietrain	18
TOTAL			**468**

ARCR = Creola Argentina from Misiones; DU = Duroc; LD = Landrace; LW =Large White; MO = Moura; PI = Pietran

Table S2. Effective population size (*Ne*) calculated for each breed. Breeds are indicated with their acronyms.

Gen. ago[1]	ARC	MO	DU	LD	LW	PI
5	17	60	70	78	79	55
6	20	65	74	82	84	59
7	23	71	78	85	89	62
8	26	79	80	89	94	66
9	30	87	82	95	101	71
11	34	98	86	101	106	76
13	40	108	89	105	111	80
15	46	116	93	111	116	86
18	54	128	95	116	122	91
22	64	137	98	121	128	97
27	74	154	103	127	135	105
33	89	175	109	139	145	115
41	106	196	115	149	157	127
51	128	224	126	162	169	142
65	154	258	140	179	188	162
83	189	301	159	206	215	188
108	231	343	183	236	248	220

[1]Number of generation ago; ARCR = Creole Argentina from Misiones; MO = Moura; DU = Duroc; LD = Landrace; LW =Large White; PI = Pietrain

Supplementary file 3 – Genes Ontology (GO) annotation analysis of terms and pathways enriched in KEGG (*p <0.05*) with the analyzed breeds with the analyzed breeds by Fisher's test

Breed	Terms	Genes (SSC)	Nº of genes	*p-value*
ARCR	**GO Biological Process**			
	Negative regulation of gene expression. (GO:0010629)	*ZFP36L2 (3)* *PTH (2)* *PRKN (1)* *PPARG (13)* *XDH (3)*	5	0,0045
	Negative regulation of inflammatory response to antigenic stimulus (GO:0002862)	*MKRN2 (13)* *PSMA1 (2)*	2	0,00085
	GO Cellular component			
	Mpp 10 complex (GO:0034457)	*IMP3 (7)* *SNUPN (7)*	2	0,00018
	Nucleoplasm (GO:0005654)	*BTBD10 (2)* *IMP3 (7)* *NEK1 (14)* *TBXT (1)* *CSPG4 (7)* *MAN2C1 (7)* *PM20D2 (1)* *PPARG (13)* *PSMA1 (2)* *PSMB1 (1)* *PRKD3 (3)* *RPP25 (7)* *RPS6KA2 (1)* *SRSF7 (3)* *SNUPN (7)* *SLC8A1 (3)* *TSEN2 (13)*	17	0,027
	GO Molecular function			
	Iron ion binding (GO:0005506)	*CYP1A1 (1)* *CYP1B1 (3)* *CYP11A1 (7)* *CYP2R1 (2)* *XDH (3)*	5	0,0021
	RNA binding (GO:0003723)	*LOC100739087 (1)* *DHX57 (3)* *A0A287B0N5 PIG* *THUMPD2 (3)* *HNRNPLL (3)* *RPP25 (7)* *RNASET2 (1)* *SRSF7 (3)* *SNUPN (7)*	9	0,0062

Gamma-aminobutyric acid:sodium:chloride symporter activity (GO:0005332)	*SLC6A1 (13)* *SLC6A11 (13)*	2	0,00019
Calcitonin receptor binding (GO:0031716)	*F1S983 PIG* *CRSP3 (2)*	2	0,00046
KEEG Pathway			
Tryptophan metabolismo	*HAAO (3)* *AADAT (14)* *CYP1A1 (7)* *CYP1B1 (3)*	4	0,0001
Steroid hormone biosynthesis	*CYP1A1 (7)* *CYP1B1 (3)* *CYP11A1 (7)* *SRD5A2 (3)*	4	0,00033
Chemical carcinogenesis – reactive oxygen species	*SOS1 (3)* *CYP1A1 (7)* *CYP1B1 (3)* *COX5A (7)* *COX7A2L (3)* *PRKD3 (3)*	6	0,0012
Chemical carcinogenesis – receptor activation	*SOS1 (3)* *CYP1A1 (7)* *CYP1B1 (3)* *DLL1 (1)* *RPS6KA2 (1)*	5	0,0041
Huntington disease	*SIN3A (7)* *COX5A (7)* *COX7A2L (3)* *PPARG (13)* *PSMA1 (2)* *PSMB1 (1)*	6	0,0054
Thermogenesis	*SOS1 (3)* *COX5A (7)* *COX7A2L (3)* *PPARG (13)* *RPS6KA2 (1)*	5	0,0073
Ovarian steroidogenesis	*CYP1A1 (1)* *CYP1B1 (3)* *CYP11A1 (7)*	3	0,0032
Amyotrophiclateral sclerosis	*COX5A (7)* *COX7A2L (3)* *PRKN (1)* *PSMA1 (2)* *PSMB1 (1)* *SRSF7 (3)*	6	0,012
Parkison disease	*COX5A (7)* *COX7A2L (3)*	5	0,013

		PRKN (1) *PSMA1 (2)* *PSMB1 (1)*		
DU	**GO Biological Process**			
	Methionine biosynthetic process (GO:0009086)	*BHMT2 (2)* *BHMT (2)*	2	0,000038
	Cellular response to type I interferon (GO:0071357)	*IFIT3 (14)* *IFIT1 (14)*	2	0,00037
	Glycerol-3-phosphate metabolic process (GO:0006072)	*F1SU50 PIG* *GPD2 (15)*	2	0,00078
	Regulation of defense response to virus (GO:0050688)	*IFIT3 (14)* *IFIT1 (14)*	2	0,00037
	GO Cellular component			
	CORVET complex (GO:0033263)	*VPS33B (7)* *TGFBRAP1 (3)*	2	0,0007
	Mpp10 complex (GO:0034457)	*IMP3 (7)* *SNUPN (7)*	2	0,0002
	Midbody (GO:0030496)	*ANXA11 (14)* *MITD1 (3)* *PKP4 (15)* *TXNDC9 (3)*	4	0,0059
	GO Molecular function			
	Nucleotidyltransferase activity (GO:0016779)	*GDPGP1 (7)* *REV1 (3)* *TENT2 (2)*	3	0,00025
	Carbohydrate binding (GO:0030246)	*XRCC4 (2)* *MAN2C1 (7)* *GALNT13 (15)* *GALNT5 (15)* *SFTPD (14)* *VCAN (2)*	6	0,00015
	Chemorepellent activity (GO:0045499)	*NRG3 (14)* *SEMA4B (7)* *SEMA7A (7)*	3	0,00025
	Betaine-homocysteine S-methyltransferase activity (GO:0047150)	*BHMT2 (2)* *BHMT (2)*	2	0,000035
	Phosphatidylinositol-3,4,5-trisphosphate 3-phosphatase activity (GO:0016314)	*A0A5G2QK45 PIG* *F2Z5H1 PIG*	2	0,00035
LD	**GO Biological Process**			
	Nervous system development (GO:0007399)	*CER1 (1)* *INA (14)*	8	0,0000044

	NEURL1 (14) *PLPPR1 (1)* *SEMA4B (7)* *SEMA7A (7)* *TGFBR1 (1)* *VPS13A (1)*		
Platelet-derived growth factor receptor signaling pathway (GO:0048008)	*TIPARP (13)* *CSPG4 (7)* *NR4A3 (1)*	3	0,00056
L-ascorbic acid metabolic process (GO:0019852)	*F1S5N8 PIG* *GSTO1 (14)* *GSTO2 (14)*	3	0,00000064
Semaphorin-plexin signaling pathway (GO:0071526)	*SEMA4B (7)* *SEMA4G (14)* *SEMA7A (7)*	3	0,0004
Negative regulation of axon extension involved in axon guidance (GO:0048843)	*TIPARP (13)* *CSPG4 (7)* *NR4A3 (1)*	3	0,00056
Negative chemotaxis (GO:0050919)	*SEMA4B (7)* *SEMA4G (14)* *SEMA7A (7)*	3	0,00099
Neural crest cell migration (GO:0001755)	*SEMA4B (7)* *SEMA4G (14)* *SEMA7A (7)*	3	0,0031
GO Cellular component			
Lysosomal membrane (GO:0005765)	*VPS33B (7)* *LITAF (3)* *LAMP5 (17)* *PRC1 (7)* *VPS13A (1)*	5	0,0053
Mpp10 complex (GO:0034457)	*IMP3 (7)* *SNUPN (7)*	2	0,004
Recycling endosome membrane (GO:0055038)	*RAP2B (13)* *LAMP5 (17)* *SCAMP2 (7)*	3	0,0047
GO Molecular function			
Glutathione dehydrogenase (ascorbate) activity (GO:0045174)	*F1S5N8 PIG* *GSTO1 (14)* *GSTO2 (14)*	3	0,00000041
Methylarsonate reductase activity (GO:0050610)	*F1S5N8 PIG* *GSTO1 (14)* *GSTO2 (14)*	3	0,00000041

	Semaphorin receptor binding (GO:0030215)	*SEMA4B (7)* *SEMA4G (14)* *SEMA7A (7)*	3	0,00043
	Chemorepellent activity (GO:0045499)	*SEMA4B (7)* *SEMA4G (14)* *SEMA7A (7)*	3	0,0005
	Glutathione transferase activity (GO:0004364)	*F1S5N8 PIG* *GSTO1 (14)* *GSTO2 (14)*	3	0,0029
	Hormone activity (GO:0005179)	*F1S983 PIG* *INSL6 (1)* *CRSP3 (2)* *RLN2 (2)*	4	0,0047
	Serine transmembrane transporter activity (GO:0022889)	*SFXN2 (14)* *SFXN3 (14)*	2	0,00033
	Calcitonin receptor binding (GO:0031716)	*F1S983 PIG* *CRSP3 (2)*	2	0,00082
	KEEG Pathway			
	Wnt signaling pathway	*TLE4 (1)* *BTRC (14)* *CER1 (1)* *INVS (1)* *PLCB1 (17)* *PLCB4 (17)*	6	0,0013
LW	**GO Biological Process**			
	Thymus development (GO:0048538)	*FOXE1 (1)* *MAP2K1 (1)* *PSEN1 (7)*	3	0,0036
	Negative regulation of osteoblast differentiation (GO:0045668)	*SMAD3 (1)* *SMAD6 (1)* *RIOX1 (7)*	3	0,0042
	Acyl-CoA metabolic development (GO:0006637)	*ACOT6 (7)* *LOC100158115 (7)* *LOC110255332 (7)*	3	0,00081
	Positive regulation of DNA-templated transcription (GO:0045893)	*GPBP1 (16)* *FOXE1 (1)* *MAP2K1 (1)* *PSEN1 (7)* *PSRC1 (4)* *TGFBR1 (1)* *TRIM33 (4)*	7	0,0051
	Thyroid gland development (GO:0030878)	*SMAD3 (1)* *FOXE1 (1)* *MAP2K1 (1)*	3	0,0012

Transforming growth factor beta receptor signaling pathway (GO:0007179)	*FOS (7)* *SMAD3 (1)* *SMAD6 (1)* *TGFBR1 (1)*	4	0,0028
Multivesicular body assembly (GO:0036258)	*RAB11A (1)* *VPS4B (1)*	2	0,00023
Mitotic metaphase plate congression (GO:0007080)	*RAB11A (1)* *PSRC1 (4)* *VPS4B (1)*	3	0,0023
GO Cellular component			
Voltage-gated potassium channel complex (GO:0008076)	*KCNA10 (4)* *KCNA2 (4)* *KCNA3 (4)* *KCND3 (4)*	4	0,002
Cytosol (GO:0005829)	*ATP8B1 (1)* *BCL2L15 (4)* *DENND2D (4)* *DIS3L (1)* *FOS (7)* *GPBP1 (16)* *RAB11A (1)* *SMAD3 (1)* *SMAD6 (1)* *WDR77 (4)* *YLPM1 (7)* *AP4B1 (4)* *AMPD1 (4)* *ALDH1B1 (1)* *DLST (7)* *FEM1B (1)* *GSTM3 (4)* *GRHPR (1)* *LAMTOR5 (4)* *METTL4 (6)* *MAP2K1 (1)* *NCBP1 (1)* *PIGN (1)* *PSRC1 (4)* *PSMA5 (4)* *RGS6 (7)* *SLC44A1 (1)* *TRMT10B (1)* *TTLL5 (7)* *VPS4B (1)* *ZCCHC7 (1)* *ZBTB14 (6)*	32	0,022
GO Molecular function			
R-SMAD binding (GO:0070412)	*FOS (7)* *SMAD3 (1)* *SMAD6 (1)* *TRIM33 (4)*	4	0,000022

co-SMAD binding (GO:0070410)	*SMAD3 (1)* *SMAD6 (1)* *TRIM33 (4)*	3	0,000081
Thiolester hydrolase activity (GO:0016790)	*ACOT6 (7)* *LOC110255332 (7)* *LOC100158115 (7)*	3	0,00015
G protein-coupled adenosine receptor activity (GO:0001609)	*ADORA3 (4)* *TMIGD3 (4)*	2	0,00079
Monocarboxylic acid transmembrane transporter activity (GO:0008028)	*LOC100156854 (4)* *SLC16A1 (4)* *SLC16A4 (4)*	3	0,00011
Voltage-gated potassium channel activity (GO:0005249)	*KCNA10 (4)* *KCNA2 (4)* *KCNA3 (4)* *KCND3 (4)*	4	0,0021
KEEG Pathway			
Neurotrophin signaling pathway	*BCL2 (1)* *NRAS (4)* *MAP2K1 (1)* *MAP2K5 (1)* *MAP3K1 (16)* *NGF (4)* *PSEN1 (7)* *SORT1 (4)*	8	0,0000077
Hepatitis B	*BCL2 (1)* *FOS (7)* *NRAS (4)* *SMAD3 (1)* *MAP2K1 (1)* *MAP3K1 (16)* *TLR4 (1)* *TGFBR1 (1)*	8	0,000084
Colorectal cancer	*BCL2 (1)* *FOS (7)* *NRAS (4)* *SMAD3 (1)* *MAP2K1 (1)* *TGFBR1 (1)*	6	0,00011
Fatty acid stretching	*HACD3 (1)* *LOC110255331 (7)* *LOC100158115 (7)* *LOC110255332 (7)*	4	0,000064
Chronic myeloid leukemia	*NRAS (4)* *SMAD3 (1)* *MAP2K1 (1)* *TGFBR1 (1)*	4	0,0038

Biosynthesis of unsaturated fatty acids	*HACD3 (1)* *LOC110255331 (7)* *LOC100158115 (7)* *LOC110255332 (7)*	4	0,0001
Apoptosis	*BCL2 (1)* *FOS (7)* *NRAS (4)* *MAP2K1 (1)* *NGF (4)*	5	0,0061
MAPK signaling pathway	*FOS (7)* *NRAS (4)* *MAP2K1 (1)* *MAP2K5 (1)* *MAP3K1 (16)* *NGF (4)* *TGFBR1 (1)*	7	0,012
mTOR signaling pathway	*NRAS (4)* *LAMTOR5 (4)* *LPIN2 (6)* *MAP2K1 (1)* *RNF152 (1)*	5	0,0098
Human T-cell leukemia virus infection 1	*FOS (7)* *NRAS (4)* *SMAD3 (1)* *MAP2K1 (1)* *MAP3K1 (16)* *TGFBR1 (1)*	6	0,012
Cellular senescence	*NRAS (4)* *SMAD3 (1)* *LIN52 (7)* *MAP2K1 (1)* *TGFBR1 (1)*	5	0,01
Endocrine resistance	*BCL2 (1)* *FOS (7)* *NRAS (4)* *MAP2K1 (1)*	4	0,0081
PD-L1 expression and PD-1 checkpoint pathway in cancer	*FOS (7)* *NRAS (4)* *BATF (7)* *MAP2K1 (1)* *TLR4 (1)*	5	0,0013
Choline metabolism in cancer	*FOS (7)* *NRAS (4)* *MAP2K1 (1)* *SLC44A1 (1)*	4	0,0091

	Hepatocellular carcinoma	*NRAS (4)* *SMAD3 (1)* *GSTM3 (4)* *MAP2K1 (1)* *TGFBR1 (1)*	5	0,013
	Gastric cancer	*BCL2 (1)* *NRAS (4)* *SMAD3 (1)* *MAP2K1 (1)* *TGFBR1 (1)*	5	0,0088
MO	**GO Biological process**			
	Pantothenate metabolic process (GO:0015939)	*VNN1 (1)* *VNN2 (1)* *VNN3 (1)*	3	0,000002
	Single fertilization (GO:0007338)	*AQN-1 (14)* *BSP1 (6)* *PSP-I (14)* *PSP-II (14)* *AWN (14)*	5	0,00019
	Homophilic cell adhesion via plasma membrane adhesion molecules (GO:0007156)	*DSG1 (6)* *DSG2 (6)* *DSG3 (6)* *DSG4 (6)* *NECTINA2 (6)* *NPTN (7)*	6	0,0028
	Miotic spindle organization (GO:0007052)	*A0A287ALE3 PIG* *A0A287BPN3 PIG* *I3L8P8 PIG* *I3LM30 PIG*	4	0,0015
	Negative regulation of calcium ion export across plasma membrane (GO:1905913)	*CALM1 (7)* *CALM3 (6)*	2	0,00016
	Complement receptor mediated signaling pathway (GO:0002430)	*GPR33 (7)* *C5AR1 (6)*	2	0,00093
	Forebrain cell migration (GO:0021885)	*AXL (6)* *EMX2 (14)*	2	0,00047
	Positive regulation of ryanodine-sensitive calcium-release channel activity (GO:0060316)	*CALM1 (7)* *CALM3 (6)*	2	0,00093
	Retinol metabolic process (GO:0042572)	*CYP1A1 (7)* *LIPE (6)* *TTR (6)*	3	0,0019

Chylomicron remnant clearance (GO:0034382)	*APOC2 (6)* *APOE (6)*	2	0,00047
Regulation of cardiac muscle cell action potential (GO:0098901)	*CALM1 (7)* *CALM3 (6)*	2	0,00016
Positive regulation of cyclic-nucleotide phosphodiesterase activity (GO:0051343)	*CALM1 (7)* *CALM3 (6)*	2	0,00047
Methionine biosynthetic process (GO:0009086)	*BHMT2 (2)* *BHMT (2)*	2	0,00016
GO Cellular component			
Desmosome (GO:0030057)	*DSG1 (6)* *DSG2 (6)* *DSG3 (6)* *DSG4 (6)*	4	0,000049
High-density lipoprotein particle (GO:0034364)	*APOC2 (6)* *APOC4 (6)* *APOE (6)* *NECTINA2 (6)*	4	0,000049
Low-density lipoprotein particle (GO:003462)	*APOC2 (6)* *APOC4 (6)* *APOE (6)*	3	0,000085
Chylomicron (GO:0042627)	*APOC2 (6)* *APOC4 (6)* *APOE (6)*	3	0,00024
Calcium channel complex (GO:0034704)	*CALM1 (7)* *CALM3 (6)* *RYR1 (6)*	3	0,00032
Very-low-density lipoprotein particle (GO:0034361)	*APOC2 (6)* *APOC4 (6)* *APOE (6)*	3	0,00052
Obsolete anchored component of plasma membrane (GO:0046658)	*CD177 (6)* *LYPD4 (6)* *TEX101 (6)*	3	0,0016
Cytoplasmic vesicle membrane (GO:0030659)	*A0A287BCX1 PIG* *RAB4B (6)* *RYR1 (6)* *SLC18A2 (14)*	4	0,0037
Mpp10 complex (GO:0034457)	*IMP3 (7)* *SNUPN (7)*	2	0,00081
Intermediate-density lipoprotein particle (GO:0034363)	*APOC2 (6)* *APOE (6)*	2	0,00081

Plasma membrane raft (GO:0044853)	*CD177 (6)* *LYPD4 (6)* *TEX101 (6)*	3	0,0011
GO Molecular function			
Trace-amine receptor activity (GO:0001594)	*A0A287AG14 PIG* *A0A287B625 PIG* *TAAR2 (1)* *TAAR3 (1)* *LOC100156866 (1)*	5	0,00000001
Pantetheine hydrolase activity (GO:0017159)	*VNN1 (1)* *VNN2 (1)* *VNN3 (1)*	3	0,0000015
Complement receptor activity (GO:0004875)	*GPR33 (7)* *C5AR1 (6)*	2	0,0004
Heparin binding (GO:0008201)	*AQN-1 (14)* *APOE (6)* *BSP1 (6)* *CCN2 (1)* *AWN (14)* *THBS4 (2)*	6	0,002
Betaine-homocysteine S-methyltransferase activity (GO:0047150)	*BHMT2 (2)* *BHMT (2)*	2	0,00013
Complement component C5a receptor activity (GO:0004878)	*C5AR1 (6)* *C5AR2 (6)*	2	0,00013
DNA-binding transcription factor activity, RNA polymerase II-specific (GO:0000981)	*ERFL (6)* *ERF (6)* *FOSB (6)* *ISL2 (7)* *POU2F2 (6)* *RELB (6)* *DEDD2 (6)* *EMX2 (14)* *FOXA3 (6)* *HIF3A (6)* *NPAS1 (6)* *LOC100627091 (6)* *ZNF283 (6)* *ZNF397 (6)* *ZNF546 (6)* *ZNF575 (6)* *ZNF576 (6)*	17	0,013
Kinase activity (GO:0016301)	*ADPGK (7)* *AXL (6)* *CKMT2 (2)* *GSK3A (6)* *ITPKC (6)* *PKM (7)*	6	0,0066
Calcium ion binding (GO:0005509)	*CBLC (6)*	15	0,0057

		XRCC4 (2) *ACTN4 (6)* *CALM1 (7)* *CALM3 (6)* *DLL3 (6)* *DSG1 (6)* *DSG2 (6)* *DSG3 (6)* *DSG4 (6)* *LTBP4 (6)* *RCN2 (7)* *RYR1 (6)* *THBS4 (2)* *VCAN (2)*		
	Obsolete N-terminal myristoylation domain binding (GO:0031997)	*CALM1 (7)* *CALM3 (6)*	2	0,00013
	Adenylate cyclase activator activity (GO:0010856)	*CALM1 (7)* *CALM3 (6)*	2	0,0004
	Diacylglycerol diphosphate phosphatase activity (GO:0000810)	*WDR11 (14)* *PLPP4 (14)*	2	0,00079
	KEEG Pathway			
	Aldosterone synthesis and secretion	*ATP1A3 (6)* *CALM1 (7)* *CALM3 (6)* *CYPA1 (7)* *LIPE (6)*	5	1,0
	Pantothenate and CoA biosynthesis	*VNN1 (1)* *VNN2 (1)* *VNN3 (1)*	3	1,0
	Parkinson disease	*CALM1 (7)* *CALM3 (6)* *LOC100157935 (7)* *KLC3 (6)* *PSMC1 (7)* *PSMC4 (6)* *PSMD8 (6)* *SLC18A2 (14)*	8	1,0
	Amphetamine addiction	*FOSB (6)* *CALM1 (7)* *CALM3 (6)* *SLC18A2 (14)*	4	1,0
PI	**GO Biological process**			
	Positive regulation of tyrosine phosphorylation of STAT protein (GO:0042531)	*KIT (8)* *IL2 (8)* *IL21 (8)*	3	0,000067
	Tyrosine phosphorylation of STAT protein (GO:0007260)	*IL2 (8)* *IL21 (8)*	2	0,000067

Positive regulation of oligodendrocyte differentiation (GO:0048714)	*TCDD (3)* *CSPG4 (7)* *NR4A3 (1)*	2	0,0012
GO Cellular component			
Guanylate cyclase complex, soluble (GO:0008074)	*GUCY1A1 (8)* *GUCY1B1 (8)*	2	0,074
GO Molecular function			
Transmembrane transporter activity (GO:0022857)	*SVOPL (18)* *MFSD8 (8)* *SLC13A4 (18)* *SLC35B4 (18)* *SLC37A3 (18)* *SLC7A11 (8)*	6	0,000075
Guanylate cyclase activity (GO:0004383)	*GUCY1A1 (8)* *GUCY1B1 (8)*	2	0,00047
Interleukin-2 receptor binding (GO:0005134)	*IL2 (8)* *IL21 (8)*	2	0,00061
KEEG Pathway			
Long term depression	*GRIA2 (8)* *GUCY1A1 (8)* *GUCY1B1 (8)*	3	0,0013
cGMP-PKG signaling pathway	*CREB3L2 (18)* *GUCY1A1 (8)* *GUCY1B1 (8)* *PDE5A (8)*	4	0,0032
Gap junction	*GUCY1A1 (8)* *GUCY1B1 (8)* *PDGFRA (8)*	3	0,0037
Human T-cell leucemia vírus 1 infection	*CREB3L2 (18)* *CCNA2 (8)* *IL2 (8)* *MAD2L1 (8)*	4	0,0092
Circadian entrainment	*GRIA2 (8)* *GUCY1A1 (8)* *GUCY1B1 (8)*	3	0,0057

ARCR = Creola Argentina from Misiones; DU = Duroc; LD = Landrace; LW =Large White; MO = Moura; PI = Pietran

6. Considerações finais

A inclusão de dados genômicos oferece novas perspectivas para estudos das raças localmente adaptadas, como a Moura e a Crioula Argentina das Misiones. Os dados genômicos possibilitam uma análise mais abrangente da diversidade genética, fornecendo insights valiosos para a conservação e utilização sustentável dessas variedades locais. Os resultados apresentados neste trabalho indicam que os parâmetros utilizados para determinar ROH podem afetar as análises; ao aumentar o número mínimo de SNPs consecutivos, observou-se uma diminuição correspondente no número de ROHs. Embora seja um resultado comum em estudos de análise genômica, sua importância reside na necessidade de cuidadosa seleção dos parâmetros em estudos futuros, o que contribui para a robustez e intepretação precisa dos resultados obtidos em estudos de ROH.

A distribuição de ROH para a raça Moura sugere uma maior contribuição da endogamia recente, uma vez que houve prevalência de ROHs longas no genoma. A análise da frequência de ROHs comuns por SNP levou à identificação de assinaturas de seleção nos cromossomos SSC2 e SSC7 na raça Moura, permitindo anotar genes candidatos associados à qualidade da carne, sistema imunológico e reprodução entre o Moura, a raça Crioula da Argentina das Misiones, Duroc e Landrace. Adicionalmente, identificamos QTLs na raça Moura relacionados a gordura, fibras musculares, espessura do toucinho, área muscular do lombo e ganho médio diário, confirmando a expectativa de que os porcos Moura apresentam melhor qualidade da carne.

Ao caracterizar a estrutura genética populacional, constatamos que a raça Moura e Duroc possuem origens genéticas consideravelmente parecidas, devido à provável raça ancestral de ambas. No geral, nossas descobertas são importantes para programas de acasalamento em suínos e seleção dos animais, servindo com uma referência útil.

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Vita

Karine Aparecida Rodrigues de Souza nasceu em 17 de março de 1990, no município de Pirapora, no estado de Minas Gerais, filha de Newilton Alves de Souza e Celia Rodrigues Ferreira.

Ingressou no primeiro semestre de 2008 no Curso de Zootecnia do antigo CEFET – Bambuí, atual Instituto Federal de Minas Gerais (IFMG). No primeiro semestre de 2009, transferiu o curso para a Universidade Federal de Minas Gerais – UFMG, localizada no município de Montes Claros. Em março de 2013, graduou-se Zootecnia.

Ingressou no primeiro semestre de 2015 no Programa de Pós-Graduação em Zootecnia da Universidade Federal dos Vales do Jequitinhonha e Mucuri, mestrado sob a orientação do Professor Dr. Martinho de Almeida e Silva, e em abril de 2015, defendeu a dissertação intitulada ‘Sensibilidade dos valores genéticos para características de desempenho, carcaça e qualidade da carne de codornas de corte às mudanças da relação treonina: lisina da dieta’, obtendo o título de Mestre em Zootecnia na área de concentração em Produção Animal.

Ingressou no primeiro semestre de 2019 no Programa de Pós-Graduação em Zootecnia da Universidade Federal do Rio Grande do Sul, na Faculdade de Agronomia, para realizar o doutorado sob orientação do Professor Dr. José Braccini Neto, desenvolvendo pesquisa na área de Melhoramento genético animal, com foco em dados genômicos em raças de suínos.