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The genetic composition of the Traditional Irish Horse – towards the development of a DNA-ancestry test for the preservation of traditionally bred Irish Sport Horses

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Abstract: The traditionally bred Irish Sport Horse, known as the Traditional Irish Horse, is an important cultural asset to horse genetic resources in Ireland. We tested the hypothesis that the Irish Sport Horse, which was originally developed from the Irish Hunter, may contain a genetic background distinct from European Warmblood horse populations that would be valuable to preserve. Using genome-wide single nucleotide polymorphism (SNP) data, the results show that Traditional Irish Horses (with confirmed pedigrees) have lower levels of European Warmblood ancestry components than other Irish Sport Horses. These results indicate that measurement of the levels of European Warmblood ancestry components in the Irish Sport Horse may assist in the preservation of traditional Irish lineages.

Keywords: Equine, Genomics, SNP variation, Admixture, Irish Sport Horse, Conservation, Population Genetics

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Introduction

The horse has a long history in Ireland, developing through millennia into several distinct native breeds, from small riding ponies to larger work horses (McCormick, 2007). The earliest archaeological evidence for domesticated horses in Ireland dates to 2,400 BCE in the Early Bronze Age contexts of Newgrange (Bendrey *et al*, 2013). The introduction of the Celtic horse into Ireland can be traced to the 7th century, with images of ridden horses contained within the Book of Kells (Unattributed, 800). The medieval Irish horse was known as the Irish Hobby, resulting from crossing horses from northern Spain with local animals (Hendricks, 1995). The Hobby was noted for speed and agility, and was mentioned in 1296 in documents relating to an Irish contingent of horses brought to Scotland by John de Wogan, Judiciar of Ireland (Lydon, 1954). The Irish Hobby was likely a founder breed for the extant native breeds (McCormick, 2007), the Connemara Pony and Irish Draught, and also likely contributed to the Thoroughbred (Hendricks, 1995).

The Irish Draught was bred as a light, versatile farm, carriage, riding and hunting horse while the Connemara Pony was developed as a multipurpose animal for the harsher conditions of the western Irish seaboard (Hendricks, 1995). The Thoroughbred was developed in the 17th and 18th centuries when stallions from the Middle East were brought to England and crossed with the best racing mares in Britain, many of which were Irish or had been bred from Irish stock (Bower *et al*, 2011).

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Prior to the development of the Thoroughbred, a centuries-old tradition of hunting in Ireland led to the breeding of specialist hunters originating from the Irish Draught horse (Hendricks, 1995). When the Thoroughbred became established in Ireland, it was used extensively for further improvement of the Irish Hunter (Hendricks, 1995). The Irish Hunter was referred to by William Youatt who noted that the Irish bred "a large, long blood-horse of considerable value" (Youatt, 1831). Until 1922 the Irish Hunter was registered in the Hunter Stud Book, but it was later redefined as the Irish Sport Horse and has been registered in the Irish Sport Horse Studbook since 1970. The Irish Sport Horse became the world leader in eventing and has topped the World Breeding Federation for Sport Horses eventing studbook rankings for all but two years since its inception in 1994.

In the 1980s, the crossing of European Warmblood stallions with Irish Sport Horse mares gained popularity (Doyle *et al*, 2022). In 1990, the percentage of foals registered in the Irish Sport Horse Studbook by foreign-bred sires was 1.1% and by 2014 this had increased to 37.5%. This dramatic change in the breed profile of the Irish Sport Horse population has led to a growing concern among breeders that its traditional traits are being displaced by a pan-European sport horse. Demand has developed amongst breeders to identify traditionally bred Irish Sport Horses, referred to as the Traditional Irish Horse, and to establish conservation measures for the lineages descended from the original Irish Hunter.

To date, there is no published study on genetic diversity in the Irish Sport Horse population, and there are only limited published studies on genetic diversity and relatedness among the other Irish horse breeds. Mitochondrial DNA (mtDNA) analyses showed no evidence of clustering of Irish Draught and Connemara Pony mtDNA haplotypes to the exclusion of other breeds, with their distribution among the most common European horse sequences. On the other hand, the Kerry Bog Pony, a rare, recently recharacterized breed, contained an uncommon mtDNA haplotype (McGahern *et al*, 2006). In a study comparing British and Irish native ponies, the Connemara Pony showed no greater divergence among breeds than between British native breeds, which may be due to recent gene flow resulting from historic migration (Reilly *et al*, 1998).

In consideration of the concerns from breeders about the dilution of Irish Sport Horse genetics with European Warmblood genetics, the aim of this study was to establish whether there are genetic differences between the Traditional Irish Horse and European Warmblood breeds by testing the hypothesis that Irish Sport Horses with Warmblood ancestry in their pedigree can be identified using admixture analysis to test for Warmblood introgression. The purpose of a molecular genetics approach is to provide novel information to augment pedigree-based classifications of the Traditional Irish Horse for the long-term preservation of traditional Irish lineages.

Methods

Samples

A total of 133 samples from 8 horse populations (Table 1) were used in the initial analyses, including 2 native Irish breeds (21 Irish Draught and 24 Connemara Pony), 23 Irish Sport Horse (comprised of 8 certified Traditional Irish Horse, 7 Irish Sport Horse with known Warmblood influence in their pedigree, and 8 Irish Sport Horse with some missing pedigree), as well as 3 breeds with known ancestral influence on the Irish Sport Horse (25 Irish Thoroughbred, 14 Hanoverian, and 14 Swiss Warmblood). The results were validated using a set of 12 pedigree-certified Traditional Irish Horses.

Genotyping

SNP genotypes, derived from the equine Illumina SNP50 genotyping array (SNP50), were publicly available for Swiss Warmblood and Hanoverian (Petersen *et al*, 2013). For the other samples, genomic DNA was isolated from blood or hair samples and genotyped on the Affymetrix Axiom Equine genotyping array (SNP670). Quality control (QC) procedures were carried out in PLINK 1.9 (Purcell *et al*, 2007; Chang *et al*, 2015). Only individuals and SNPs with a genotyping rate $>$ 95% were included. A minor allele frequency threshold of $>$ 0.05 was applied. QC criteria were performed separately on the data from the SNP50 and SNP670 genotyping platforms. Only SNPs that passed QC on both platforms were included in the SNP dataset. SNPs were then pruned on the basis of linkage disequilibrium (LD) using the parameter –indep 50 5 2 in PLINK. Pruning of SNPs that are in high LD have been shown to counter the effect of ascertainment bias and to generate meaningful comparisons among breeds (Molomane *et al*, 2018). Following QC and pruning, a set of 9,015 SNPs was used for the analyses.

Population genetics analyses

Pairwise genetic distance (D) between all individuals was calculated using PLINK 1.9 (–distance 1-IBS) and was represented by constructing a neighbour-joining tree. Principal component analysis (PCA) was conducted using PLINK 1.9. PCA plots were generated within the R environment (R Core Team, 2014). The PopGenome package in R was used to calculate the pairwise population differentiation index F_{ST}. Population structure was visualized using an unrooted neighbour-joining tree based on the between-population F_{ST}.

For the analysis of population substructure, model-based clustering was performed using the software package ADMIXTURE (Alexander *et al*, 2009). The model assigns ancestry based on a predefined number of K ancestral populations. Individuals are assigned to K clusters based on allele frequencies and the proportion of ancestry from each population is estimated. The analysis was performed for K ranging from 2 to 8.

Table 1. Breeds, abbreviations, sample sizes (N) and study cohort for horses used in the study.

Population	Abbreviation	N	Cohort
Connemara Pony	CP	24	Ancestral
Hanoverian	HAN	14	Ancestral
Irish Draught	ID	21	Ancestral
Irish Thoroughbred	ITB	25	Ancestral
Irish Sport Horse with Warmblood	ISH WB	8	Test
Irish Sport Horse	ISH	7	Test
Swiss Warmblood	SZW	14	Ancestral
Traditional Irish Horse	TIH	8	Test
Traditional Irish Horse	TIH	12	Validation
Total		**133**	

Results

Genetic distance within and among breeds

The greatest genetic distance between individuals was between a Connemara Pony and a Traditional Irish Horse (D = 0.29) and the closest genetic distance between individuals was between two Irish Thoroughbreds (D = 0.19). The average genetic distances among individuals within breeds ranged from 0.22 (Irish Thoroughbred) to 0.26 (Irish Draught).

The pairwise population differentiation index, $F_{ST,}$ was calculated among breeds (Table 2) and used to create a neighbour-joining tree (Figure 1) to illustrate the topological relationship among breeds. The Traditional Irish Horse was identified as a distinct subset of the Irish Sport Horse population and was more similar to the Irish Sport Horse that did not contain foreign blood (F_{ST} = 0.006) than the Irish Sport Horse with Warmblood (F_{ST} = 0.011). The pairwise genetic difference between the Traditional Irish Horse and Irish Sport Horse with Warmblood (F_{ST} = 0.011) was greater than between Hanoverian and Swiss Warmblood (F_{ST} = 0.008), which are distinct breeds.

To visualize the branching structure among the Irish Sport Horse populations and Warmbloods, genetic distances between individuals were used to create a neighbour-joining tree (Figure 2). Traditional Irish Horse individuals were on branches separate to the two main Warmblood branches with the exception of a single individual that was observed among a predominantly Swiss Warmblood cluster. Five of the eight Irish Sport Horse with Warmblood samples were contained in the two main Hanoverian/Swiss Warmblood branches.

To further visualize the overall population structure, a PCA analysis was performed. In the PCA, PC1 explained 7% of the variance with clear separation of Connemara Pony from the other breeds as well as divergence between Irish Thoroughbred and Irish Draught (Figure 3A). In the plot created from PC2 and PC3 (Figure 3B), there was considerable overlap among the Hanoverian and Swiss Warmblood with a general European Warmblood cluster observed. There was a broad distribution of the Irish Sport Horse population centred among the recorded ancestral breed populations reflecting the varying contributions from the other breeds.

Population substructure

In the admixture analysis, $K = 4$ had the lowest estimate of the standard error of the cross-validation. Based on this result as well as the observations in the PCA plot and knowledge of breed history, $K = 4$ was chosen as the most appropriate number of clusters to use to establish ancestry and quantify admixture within the Irish Sport Horse population (Puechmaille, 2016; Lawson *et al*, 2018).

Unsupervised modelling was used to predict allele frequencies in four ancestral genetic lineages and each individual's genome was partitioned and proportionally assigned to one of the lineages (Figure 4). There was clear evidence of four distinct lineages – Irish Thoroughbred, Connemara Pony, Irish Draught and Warmblood – among the five distinct breed populations. The proportion of Warmblood ancestry in individual Irish Sport Horses ranged from 0.04 to 0.88.

To focus on the Irish Sport Horse alone, the proportion of Warmblood ancestry assigned to each of the 23 Irish Sport Horse samples was used to categorize the samples (Figure 5). Using the proportion of Warmblood admixture as an indicator, the seven Irish Sport Horse samples with the lowest levels of Warmblood lineage were classified as Traditional Irish Horse (Warmblood lineage $\leq$ 0.15 (15%)), the eight with the highest levels were classified as Irish Sport Horse with Warmblood influence and the remainder were assigned as Irish Sport Horse of unknown lineage. Six of the eight Traditional Irish Horse were correctly assigned. Two Traditional Irish Horse were assigned as Irish Sport Horse of unknown lineage, one of which was the Traditional Irish Horse that clustered with the predominantly Swiss Warmblood horses in the neighbour-joining tree. One Irish Sport Horse with missing pedigree was assigned as a Traditional Irish Horse.

All eight Irish Sport Horse with Warmblood were correctly assigned and overall, 20 of the 23 horses were correctly assigned using genotyping data from 9,015 SNPs. These results demonstrate a sensitivity of

Table 2. Pairwise population differentiation index (F_{ST}) among horse breeds: Connemara pony (CP), Hanoverian (HAN), Irish Draught (ID), Irish Sport Horse with Warmblood (ISH WB), Irish Sport Horse (ISH), Swiss Warmblood (SZW), Irish Thoroughbred (ITB), Traditional Irish Horse (TIH).

	CP	HAN	ID	ITB	ISH WB	ISH	SZW	TIH
CP	-							
HAN	0.049	-						
ID	0.041	0.031	-					
ITB	0.096	0.043	0.069	-				
ISH WB	0.049	0.012	0.027	0.040	-			
ISH	0.044	0.014	0.012	0.033	0.012	-		
SZW	0.048	0.008	0.029	0.038	0.011	0.014	-	
TIH	0.052	0.018	0.022	0.020	0.011	0.006	0.014	-

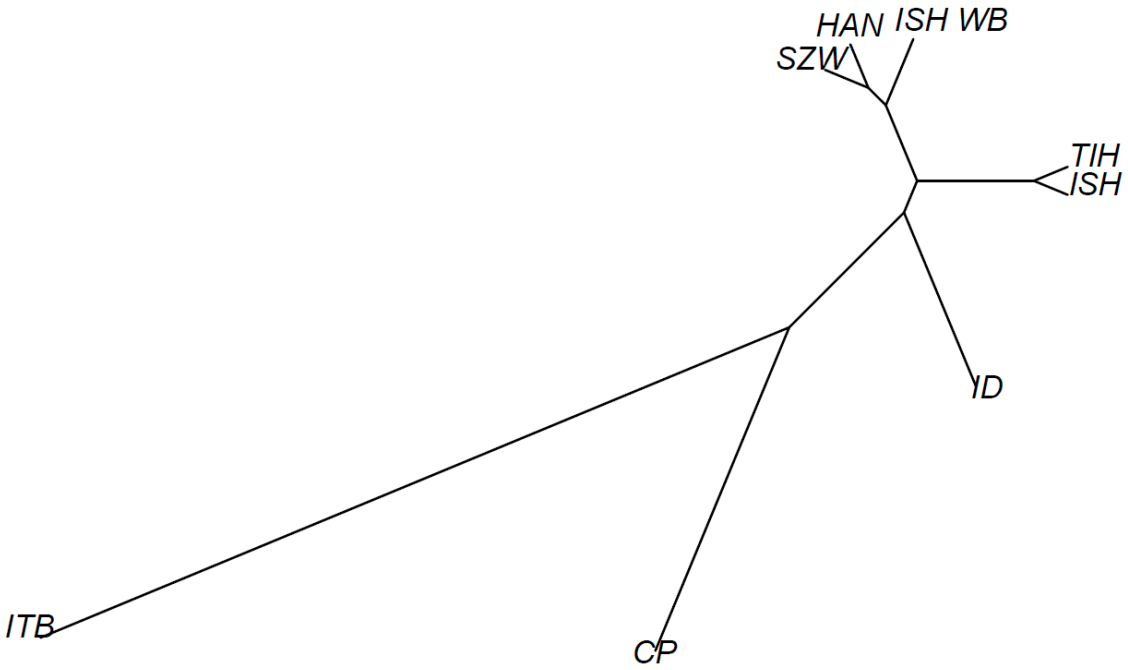

Figure 1. Neighbour-joining tree illustrating the genetic distance between breeds: Connemara pony (CP), Hanoverian (HAN), Irish Draught (ID), Irish Sport Horse with Warmblood (ISH WB), Irish Sport Horse (ISH), Swiss Warmblood (SZW), Irish Thoroughbred (ITB), Traditional Irish Horse (TIH).

75% and specificity of 93% for assigning Irish Sport Horse of unknown ancestry as Traditional Irish Horse, with an accuracy of predicting Traditional Irish Horse from genetic data of 87.5%. Admixture analysis of a validation set of 12 pedigree-certified Traditional Irish Horse revealed similar results with Warmblood lineage contributions in individuals ranging from 0.01 to 0.15.

Discussion

There is a growing trend in equestrian breeding to move away from the traditional approach of selection within breeds, towards developing hybrid sport horses (Gilbert and Gillet, 2011). Originally the Irish Sport Horse was a breed that was established by crossing the Irish Draught with Thoroughbred horses (Reilly *et al*, 1998; Alexander *et al*, 2009). More recently, crossbreeding the Irish Sport Horse with European Warmblood breeds has become popular with the intention of improving the quality of the horses for sport (Doyle *et al*, 2022). This practice threatens the maintenance of genetic variation within the traditional lineages of the Irish Sport Horse that may be beneficial to preserve.

In our phylogenetic analyses, we found that the Irish Sport Horse is genetically distinct from European Warmblood populations. By contrast, there was no clear genetic distinction between the two European Warmblood breeds (Hanoverian and Swiss Warmblood) included in this study. This agrees with a microsatel-

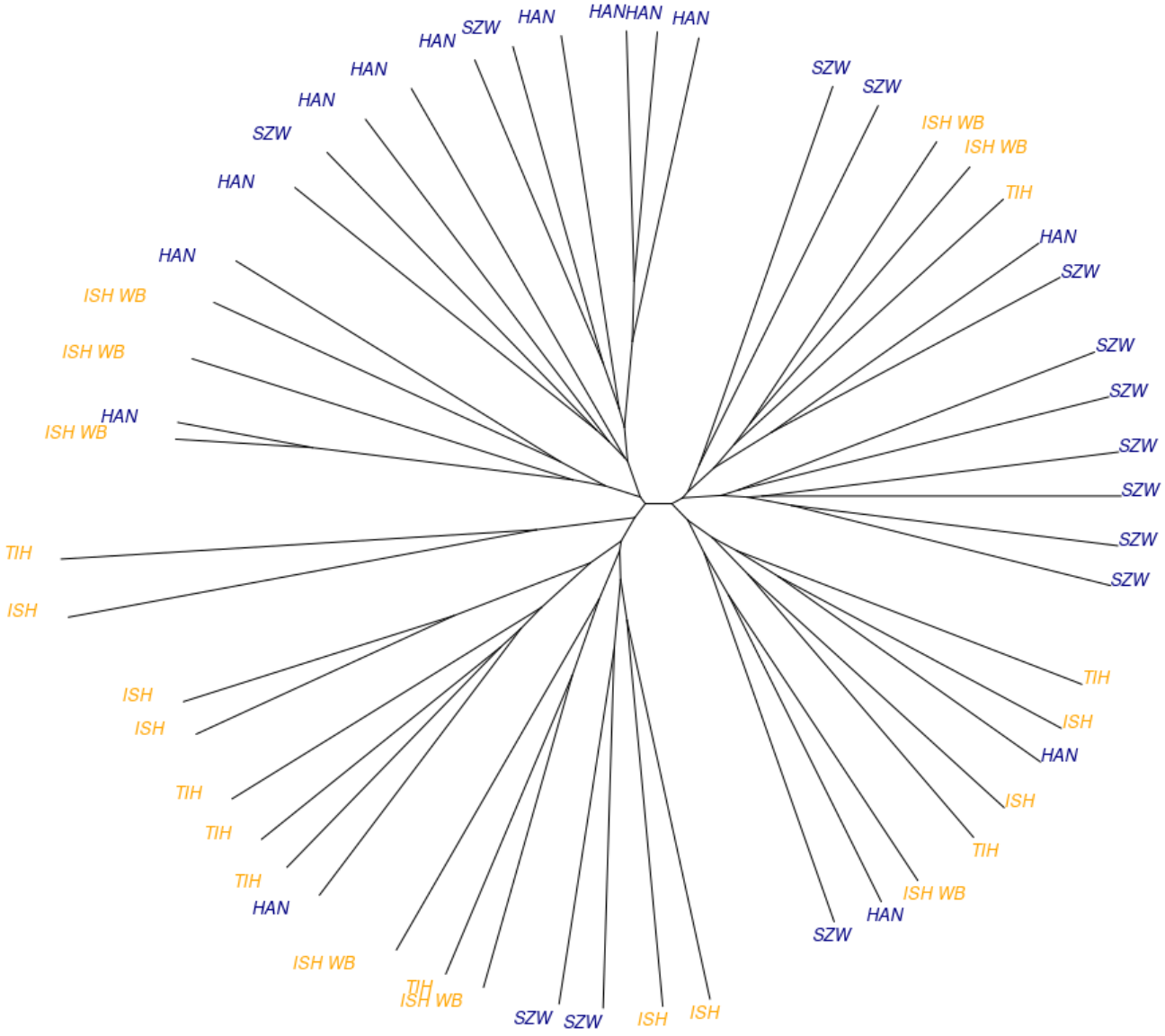

Figure 2. Neighbour-joining tree illustrating individual relationships among Irish Sport Horses (yellow) and Warmbloods (blue; HAN, SZW); including ISH with no foreign blood (ISH), ISH with foreign blood (ISH WB) and Traditional Irish Horse (TIH).

lite genotype-based phylogeny in which Hanoverian clustered closest to other European warmblood breeds (including the Italian Maremmano horse breed) on a branch most distant from other geographically proximal German coldblood breeds (Felicetti *et al*, 2010). The Irish Sport Horse has not previously been included in population genetic diversity studies and there are limited studies including the Irish Draught and Connemara Pony. In a microsatellite, protein and blood group marker study, Hanoverian clustered with Holsteiner, Thoroughbred, Quarter Horse and Irish Draught, suggested to be due to the influence of Thoroughbred in these breeds (Luis *et al*, 2007), and reflected in a more recent genome-wide SNP analysis of genetic diversity in which the European warmbloods (Hanoverian, Swiss Warmblood, Maremmano) clustered with recently admixed Thoroughbred breeds (Petersen *et al*, 2013).

Between breeds, the pairwise genetic difference (F_{ST}) indicated that the Traditional Irish Horse was more different from the Irish Sport Horse with Warmblood than the two European warmblood breeds (Hanoverian, Swiss Warmblood) were from each other. These genetic results indicate that there may be grounds to identify the Traditional Irish Horse as a distinct breed for conservation purposes, should this be desired by breeders. The term 'breed' is generally used to describe a population of animals with common phenotypically distinct traits, and it has been suggested that a breed

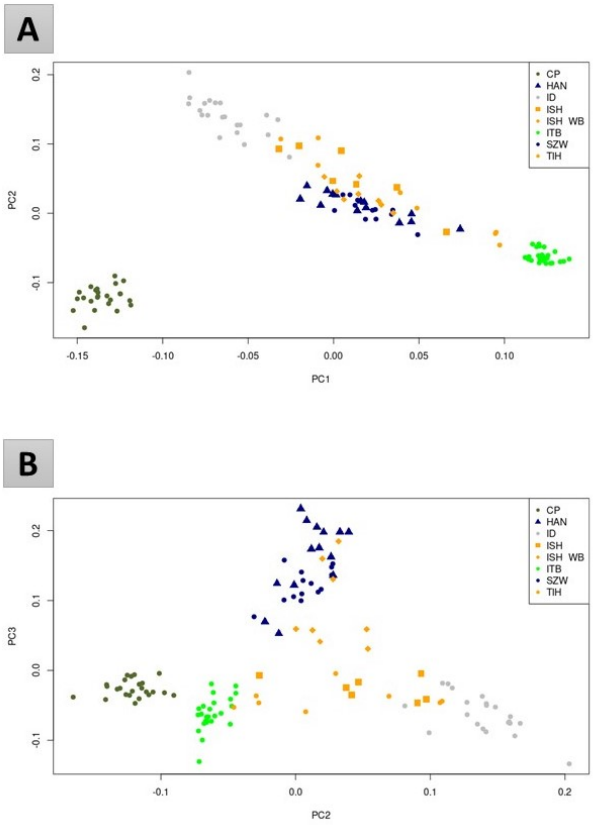

Figure 3. Principal component analysis plots for PC1 and PC2 (A), and PC2 and PC3 (B) for n = 121 individuals coloured according to breed: Connemara Pony (CP), Hanoverian (HAN), Irish Draught (ID), Irish Sport Horse with Warmblood (ISH WB), Irish Sport Horse (ISH), Swiss Warmblood (SZW), Irish Thoroughbred (ITB), Traditional Irish Horse (TIH). PC1, PC2 and PC3 explained 7%, 4% and 3% of the genetic variance, respectively.

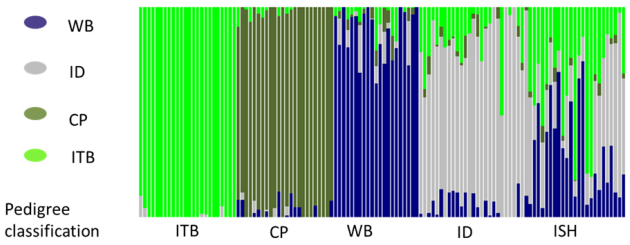

Figure 4. Proportion of genetic ancestry assigned to each breed where a column indicates a single horse and colours represent the four ancestry clusters. The colour of the primary cluster representing each breed ancestral component is depicted in the legend. Breed identifiers are noted at the bottom: Irish Thoroughbred (ITB), Connemara Pony (CP), Warmblood breeds (WB), Irish Draught (ID), Irish Sport Horse (ISH).

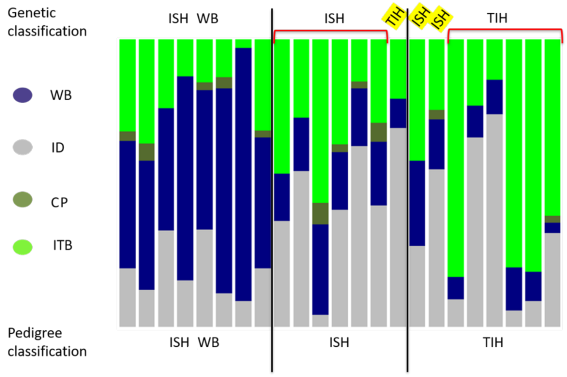

Figure 5. Proportion of genetic ancestry of 23 Irish Sport Horses assigned to each cluster where a column indicates a single horse and colours represent the four clusters. The colour of the primary cluster representing each breed ancestral component is depicted in the legend. The Irish Sport Horses based on genetic classification (top) and pedigree classification (bottom) are indicated as Warmblood (WB), Irish Draught (ID), Connemara Pony (CP), Irish Thoroughbred (ITB), Irish Sport Horse with Warmblood (ISH WB), Irish Sport Horse (ISH), and Traditional Irish Horse (TIH). The vertical black lines separate the horses on the basis of pedigree classification. All except for three horses (yellow highlights) were classified correctly on the basis of genetics; two horses with Traditional Irish Horse pedigrees were genetically assigned as Irish Sport Horse, one horse with Irish Sport Horse pedigree was genetically assigned as Traditional Irish Horse.

may also be a cultural concept defined by breeders (FAO, 2023). However, genetic analyses now enable the examination of distinct and/or common genotypes to provide scientifically informed categorization of breeds (FAO, 2023).

In order to genetically differentiate the Traditional Irish Horse from phenotypically similar Irish Sport Horse with Warmblood, here we evaluated the ancestral genetic contributions to various cohorts of the Irish Sport Horse, defined on the basis of pedigree, to delineate the maximal ancestry component of Warmblood genetics required to determine Traditional Irish Horse status. We observed four of the eight Irish Sport Horse with Warmblood to have comparable Warmblood ancestry to horses in the Hanoverian and Swiss Warmblood cohorts; however, a distinguishing feature of the Irish Sport Horse with Warmblood was a greater Irish Draught influence compared to the Hanoverian and Swiss Warmblood cohorts. In some of the Irish Sport Horse with Warmblood, there was more Warmblood ancestry component than in some of the European Warmblood animals.

Since by 2014 more than 37% of registered Irish Sport Horses had Warmblood ancestry recorded in their pedigrees, our results indicate that concerns regarding European Warmblood introgression and the creation of a homogeneous pan-European sport horse population are valid. Without a dedicated breeding programme for the Traditional Irish Horse, the unique genetic heritage of the Irish Sport Horse may be lost. Current efforts to recognize and assign Traditional Irish Horse

status to traditionally bred horses are hindered by the fact that many Irish Sport Horses may have an unregistered dam or sire in their pedigree. This is a situation where ancestral profiling using genomics-based technologies could provide a basis for identifying the Irish Sport Horse with traditional lineages. The FAO practical guide for genomic characterization of animal genetic resources notes that "Genetic tools now allow for errors in recording of parentage to be identified and remedied; this is especially useful in the case of unknown paternity" (FAO, 2023). This has immediate practical implications, since in this study there was one Irish Sport Horse with missing pedigree that had Warmblood ancestry within the range of the Traditional Irish Horse (10%), indicating that this individual has a traditional genetic heritage. Applying a cut-off of $\leq$ 15%, Warmblood ancestry would have an accuracy of prediction of 87.5% for the Traditional Irish Horse.

Conclusion

Considering the unique position of the Irish Sport Horse within the international sport horse world, with traits for elite eventing abilities and versatility as a valued leisure horse, the Traditional Irish Horse should be conserved and the genetic legacy of the Irish Hunter protected. The FAO practical guide for genomic characterization of animal genetic resources notes that the results of genomic characterization studies "should also be used to improve the management of the AnGR [Animal Genetic Resources] involved" (FAO, 2023). The application of genetic ancestry testing to identify the Traditional Irish Horse, particularly in the absence of complete pedigree information for a horse, would provide a novel route for conservation efforts and the promotion of the Irish horse in equestrian sport.

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Data availability

Data will be publicly available on the European Variation Archive http://www.ebi.ac.uk/eva/

Authors' contribution

BAM contributed to the study design, performed the data analysis and interpretation, drafted the manuscript and approved the submitted manuscript. DH conceived the project, contributed to the study design and sample acquisition. AC conceived the project, contributed to the study design and sample acquisition. EWH conceived the project, contributed to the study design, performed the interpretation, drafted the manuscript, revised the manuscript and produced the final submitted manuscript.

Conflict of interest

BAM is employed by and EWH is a shareholder in Plusvital Ltd. Plusvital Ltd funded the project in-kind with salaries and technical resources.

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