

Changes in genomic inbreeding and diversity over half a century in Swedish Red and Swedish Holstein dairy cattle

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Abstract

Swedish Red (SR) and Swedish Holstein (SH) are the dominating commercial dairy cattle breeds in Sweden. Both breeds have undergone substantial changes during the last half century due to intensive selection for breeding goal traits, but also resulting from increased international exchange of breeding animals and genetic drift. The aim of this study was to learn more about changes in genomic diversity and inbreeding in these two breeds over time. Therefore, semen samples from old bulls were genotyped using the 150K Genomic Profiler SNP array and combined with 50K SNP array genotype data, obtained for more recent bulls from the Nordic Cattle Genetic Evaluation. Different measures of level of homozygosity, genomic inbreeding, relatedness and changes in allele frequency were estimated for bulls born during different time periods from the 1950s until 2020. In total, more than 33,000 SNPs for 9737 SR and 5041 SH bulls were included in the analysis using PLINK v1.9. The results showed higher average homozygosity for SR than for SH bulls up to around 2000, but the difference was very small after that. The average inbreeding coefficients based on deviation from expected homozygosity as well as on runs of homozygosity decreased until the early 1980s in both breeds, whereafter they started to increase again for SH, but stayed more stable for SR. From the 1990s onwards, SH displayed higher average inbreeding coefficients than SR. In the last studied birth year group (2015–2020), the mean inbreeding coefficient based on runs of homozygosity was 5.9% for SH and 3.7% for SR. A principal component analysis showed a pattern of genetic relationships related to the birth year period of the bulls, illustrating the gradual change of the genetic material within each breed. The change in allele frequency over time was generally larger for SH than for SR. The results show that the inbreeding level was higher half a century ago than at present, and the inbreeding levels were lower than in some other studied populations. Still, the increase seen for inbreeding coefficients and homozygosity, especially in SH during recent years, should be considered in future breeding strategies.

KEYWORDS

allele frequency, dairy bulls, inbreeding coefficient, runs of homozygosity

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1 | INTRODUCTION

Commercial dairy cattle breeds are intensively selected to suit current or predicted future market needs. At different time periods, new techniques and breeding regimes have been implemented for Swedish dairy cattle, such as the use of frozen semen for artificial insemination in the 1950s, which enabled cryo-preservation of semen in a national gene bank since the 1960s (Swedish Board of Agriculture, 2006). The Interbull genetic evaluation of bulls was introduced in 1994 (Philipsson, 2005). The exchange of breeding animals between Sweden, Denmark, and Finland intensified with the establishment of the Nordic Cattle Genetic Evaluation in 2002, leading to joint breeding programmes for red dairy cattle breeds (RDC) and Holstein, respectively (Bengtsson, Stålhammar, Strandberg, Eriksson, & Fikse, 2020) and in 2005 the first joint Nordic breeding values also for cows were published. The method best linear unbiased prediction (BLUP) was implemented for genetic evaluation in 1984, and around 2009, genomic selection was implemented as an even more efficient selection tool (Bengtsson et al., 2020). Along with these improvements, the need to monitor genetic diversity has increased (Forutan et al., 2018).

Today, the Swedish Red (SR) is a synthetic breed, largely influenced by Finnish, Norwegian and Danish red breeds, but that also shows genetic similarities to some old native Swedish cattle breeds (Upadhyay et al., 2019). The Swedish Holstein (SH) started as a strain of Friesian cattle (Svensk Låglandsboskap, SLB), but the influence of Holstein increased from the 1970s until an almost complete Holsteinization of the breed (Bett et al., 2010). With the aim to study consequences of such developments, we estimated and compared different measures of genetic diversity and inbreeding in Swedish commercial dairy bulls during different time periods since the 1950s.

In contrast to pedigree-based estimates, genomic measures of diversity and inbreeding are not dependent on the depth and correctness of available pedigrees. This makes them attractive tools for studying genetic changes over time, provided that genotypes of animals from different time periods are available. A variety of different genomic inbreeding measures have been suggested, and different types of measures have different properties (Meuwissen, Sonesson, Gebregiwergis, & Woolliams, 2020). Inbreeding coefficients (F) based on runs of homozygosity (ROH), stretches of genomic regions with identical haplotypes from each parent, have been shown to be efficient to detect the proportion of the whole genome that is identical by descent, regardless of the age of alleles or allele frequency (Alemu et al., 2021). Another example is inbreeding coefficients based on the excess, or deviation, in homozygosity in an

individual from expected homozygosity under random mating. This marker-by-marker inbreeding measure was shown to have similar properties as F_{ROH} in the study by Alemu et al. (2021), but the F_{ROH} was found to be the better performing of the two measures. The general level of homozygosity is another measure often used (Martikainen, Sironen, & Uimari, 2017).

The aim of this study was to learn more about changes in genomic diversity and inbreeding in these two breeds over time. We estimated overall homozygosity and inbreeding coefficients based on deviation from expected homozygosity as well as based on runs of homozygosity for both Swedish Red and Swedish Holstein bulls born from 1950s until 2020. We also used a principal component analysis to study patterns of genetic relationships related to the birth year period of the bulls, and studied the change in allele frequency over time. The changes in genomic inbreeding across different time periods, in which various new technology and/or breeding strategies were applied, is of interest from a scientific as well as practical breeding perspective. Such knowledge in combination with theoretical predictions can improve our ability to predict the outcome of new developments in breeding programs.

2 | MATERIALS AND METHODS

2.1 | Genotype data

In total, genotypes from 9745 SR and 5042 SH bulls born from 1951 to 2020 were available. Most bulls were genotyped outside this study using the 50K Illumina SNP array (v1 or v2) and their genotypes were obtained from the Nordic Cattle Genetic Evaluation. In addition, 90 old SR and 83 old SH bulls were genotyped from old sperm samples provided by the AI-company VikingGenetics, using the 150K Genomic Profiler SNP array from GeneSeek®. These old bulls were selected among active AI-bulls of each time period, avoiding close relatives such as siblings, with the help of a representative from the AI-company VikingGenetics.

In total 39,161 autosomal SNPs overlapping between the different arrays, with a non-zero minor allele frequency (MAF) were found. All 29 autosomes were similarly covered, with one SNP per 63.7 kb (SD 3.8, range from 55.2 to 75) and a covered genome length of 2,510,381 kb. After filtering for a call rate higher than 0.9, 32,858 and 32,979 SNPs were kept for SR and SH, respectively, giving a density of 75.5 kb/SNP. Only individuals with a genotyping rate of above 0.9 were kept, leaving 9737 SR and 5041 SH bulls for further analysis (Table 1). For analysis of both breeds jointly 33,308 SNPs

TABLE 1 Number of genotyped bulls born in different years for Swedish Red (SR) and Swedish Holstein (SH)

Breed	Birth year									
	<1965	1965–1979	1980–1984	1985–1989	1990–1994	1995–1999	2000–2004	2005–2009	2010–2014	2015–2020
SR	33	54	41	261	424	382	351	452	3,611	4,128
SH	25	33	19	60	90	146	177	591	1,965	1,935

were used. No pruning for low MAF, deviation from Hardy–Weinberg equilibrium (HWE) or strong linkage disequilibrium (LD) was done. Because of the long time span studied and the known changes of both breeds due to extensive use of foreign genetic material, we did not trust that imputation of missing genotypes in the oldest bulls would work well for our research purpose, and thus chose not to apply it.

2.2 | Homozygosity, runs of homozygosity and inbreeding

Calculation of homozygosity, runs of homozygosity (ROH), ROH-based inbreeding coefficient F_{ROH} , and inbreeding coefficient based on deviation of observed from expected homozygosity (based on allele frequencies of bulls born before 1980; F_{dev}) was done using PLINK v1.9 (Purcell et al., 2007). Observed homozygosity (Hom_{obs}) was defined as the proportion of homozygous SNPs and the deviation from expected homozygosity was estimated using the `--het` command, using the allele frequencies of bulls born before 1980 as reference. F_{dev} was calculated for each individual using the `--het` command, as:

$$F_{dev} = \frac{nHOM_{obs} - nHOM_{exp}}{nSNP - nHOM_{exp}}$$

where $nHOM_{obs}$ is the number of observed homozygous loci for individual i , $nHOM_{exp}$ is the Hardy–Weinberg expected mean number of homozygous loci in the studied sample of individuals, i.e.

$$nHOM_{exp} = \sum_i 1 - 2p_i(1 - p_i)$$

where the sum is over all SNPs (Keller, Visscher, & Goddard, 2011).

For the ROH definition, the following settings were used: a ROH length of at least 40 SNPs and 1,000 kb, minimum SNP density of 75 (kb/SNP), up to 500 kb allowed gap between SNPs, 0.08 as proportion overlapping windows required to be homozygous, 1 missing and 0 heterozygous SNPs allowed per window. F_{ROH} for each individual was calculated as the aggregate length of ROH segments in kb divided by the total length of the genome covered by SNPs, and the resulting value was adjusted by dividing with the F_{ROH} that a simulated completely inbred individual received using the above settings (0.9197). The used settings for plink were based on recommendations in Meyermans, Gorssen, Buys, and Janssens (2020).

2.3 | Principal component analysis and change in allele frequency

Principal component analysis (PCA) was done using PLINK v1.9 (Purcell et al., 2007), and the first and second principal components were plotted to illustrate genomic relatedness between bulls within and between the two breeds, as well as within and between birth year groups for each breed. To avoid undue influence of the large number of genotyped individuals born in later years, a random subset of bulls was used for the PCA. For SR, all bulls were used up to the birth year 1989 ($n = 389$), but for the birth year periods 1990–1999, 2000–2009, and 2010–2020, 389 bulls were used for each period (in total 1,556 bulls). For SH, all bulls were used up to birth year 1999, but for 2000–2009 and 2010–2020, 236 bulls (the number of bulls born in the 1990s) were used for each birth year period (in total 845 bulls).

The change in allele frequency from old bulls born up through 1979 to more recent bulls born 2010 and later was calculated for each locus and summarized to illustrate the distribution of the changes within each breed. A positive

value is an increase of the frequency of the allele designated as minor allele in old bulls.

3 | RESULTS

3.1 | Homozygosity, runs of homozygosity and inbreeding

Higher average homozygosity was estimated for SR than SH bulls up to around 2000, but the level was similar in later years (Figure 1). The inbreeding coefficient based on deviation from expected homozygosity (F_{dev}) was positive in the earliest years in both breeds, then negative after 1980, but increasing towards and above 0 from 1990s in SH. For SR F_{dev} stayed negative and more less constant (Figure 1).

The F_{ROH} was similarly showing a higher level of inbreeding in the early years and decreased for both breeds until the 1980s (Figure 1). F_{ROH} then stayed rather stable for SR from 1980s onward. For SH, however, it started to increase again to higher levels than before and also higher

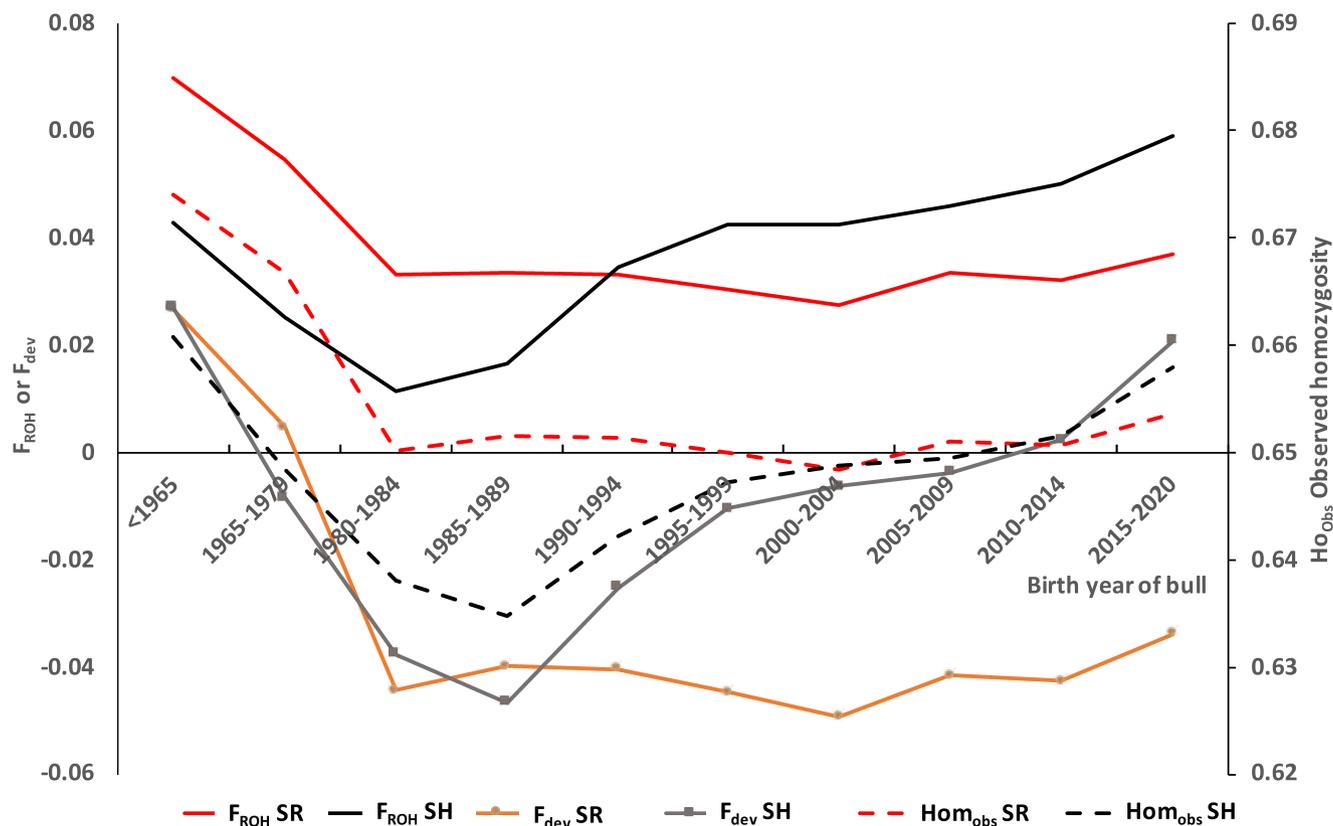


FIGURE 1 Average inbreeding coefficient based on runs of homozygosity (F_{ROH}) and on deviation from expected homozygosity (F_{dev}), and average observed homozygosity (Hom_{obs}) for Swedish Red (SR) and Swedish Holstein (SH) bulls born in different time periods

than for SR. In summary, all three measures follow the same general pattern, with a drop from the early years to a stable (SR) or increasing level (SH) from then onward.

3.2 | Principal component analysis and change in allele frequency

The PCA-plot for each breed showed a gradual but distinct pattern related to the birth time periods of the bulls, from the mid-1960s to 2020 (Figure 2). This pattern in relatedness within breed was more marked for the SH than for the SR bulls. The first (PC1) and second (PC2) principal component explained 2.1% and 1.3% of the variation for SR, and 3.0% and 1.1% for SH, respectively. In the joint PCA-plot, the two breeds were clearly separated (Figure 3). Whereas the breed separation was explained by both PC1 and PC2 for the older birth-year groups, mainly PC1 distinguished the breeds in the latest birth-year group.

In general, larger changes in allele frequency over time was seen for the SH compared with SR bulls, as illustrated by the wider distribution for SH in Figure 4 (SD 0.118 and 0.176 for SR and SH, respectively). The average change was 0.032 for SR and 0.045 for SH between bulls in the most recent birth year group (2010–2020) and bulls born before 1980.

4 | DISCUSSION

A sufficiently large genetic variation is fundamental for genetic selection to improve livestock. Loss of genetic

diversity can reduce the adaptability to new situations and societal demands, the importance of which becomes more pronounced in view of increasing climate change. In addition, increased homozygosity as a consequence of inbreeding increases the risk of expression of harmful alleles and inbreeding depression. Negative impact of increased genomic inbreeding on fertility was for example shown in Finnish Ayrshire cattle (Martikainen et al., 2017). In this study we applied genomic methods to study genetic diversity in old, as well as recent, dairy bulls in Sweden.

4.1 | Historical changes visible in the genome

We found that the general shape of development of genetic diversity was very similar regardless of which measure was used (F_{ROH} , F_{dev} or Hom_{obs}). This was also the case for inbreeding trends in Holstein and Jersey based on ROH compared with excess of homozygosity presented by Scott, Haile-Mariam, Cocks, and Pryce (2021). Furthermore, both SR and SH in our study showed high levels of inbreeding for the oldest bulls followed by a decrease until the 1980s. The trend during this period could be a result of going from local breeding within the country, or even within regions of the country, with only a few breeding herds, to more exchange of bulls across the whole country as well as imports from other countries when the use of AI increased.

Selection on pedigree-based BLUP breeding values would be expected to give a higher inbreeding rate per generation than mass selection, because the use of family

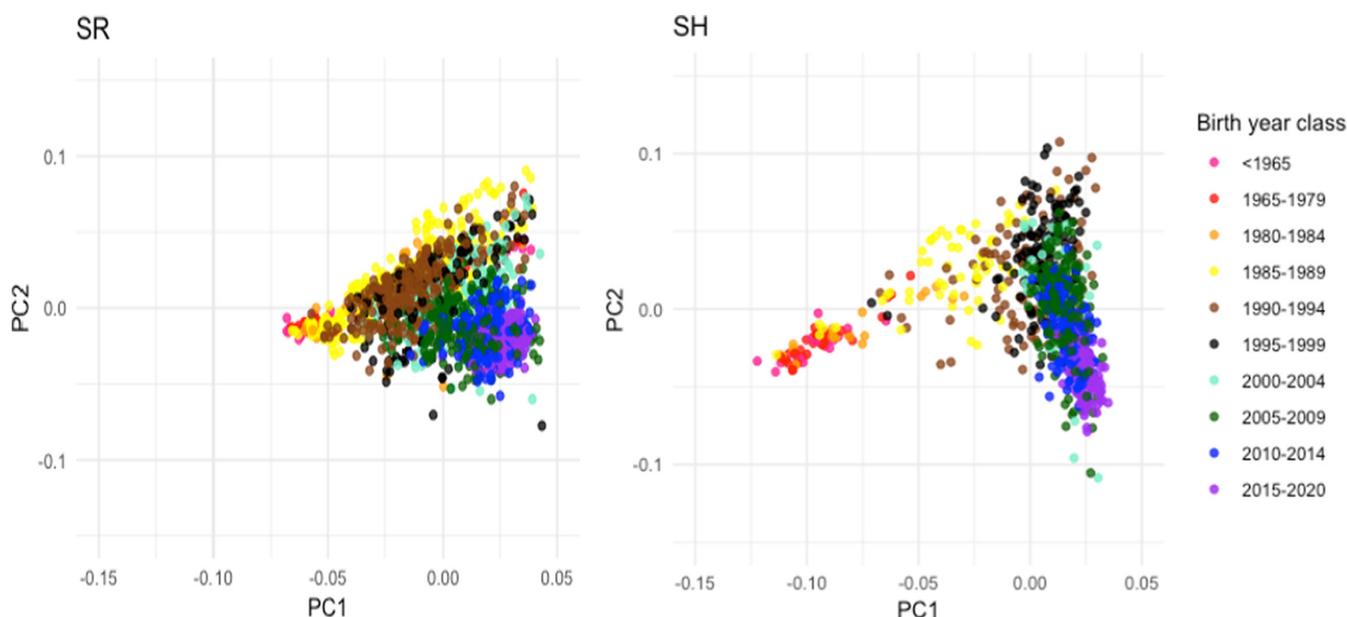


FIGURE 2 Principal component (PC) analysis of genetic relatedness between bulls born in different years, for Swedish Red (SR) and Swedish Holstein (SH) analysed separately. The first (PC1) and second (PC2) principal component explained 2.1% and 1.3% of the variation for SR, and 3.0% and 1.1% for SH, respectively

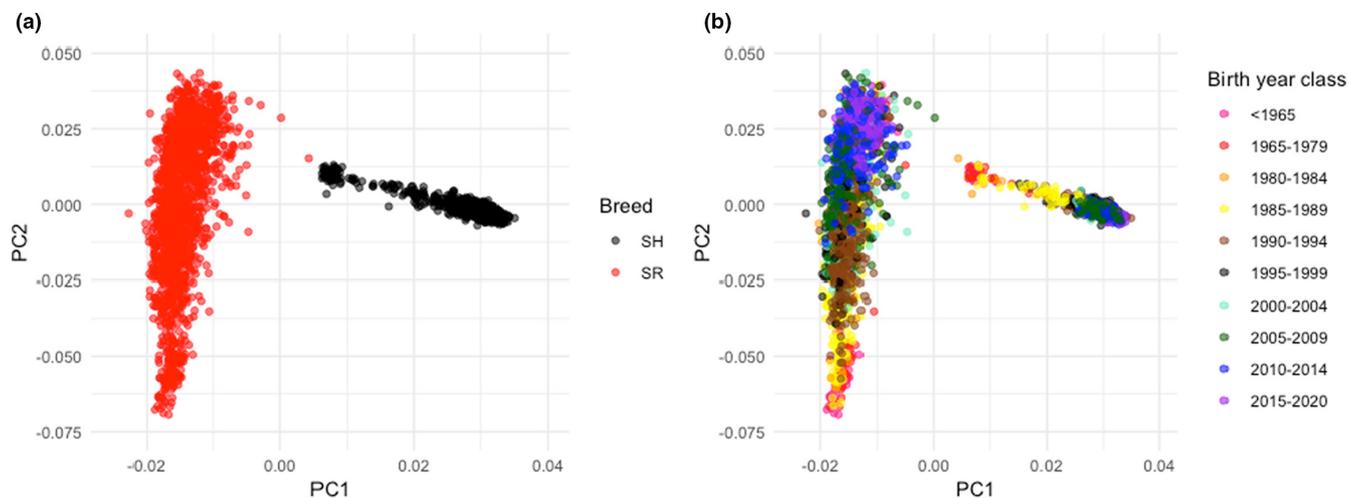


FIGURE 3 Principal component (PC) analysis of genetic relatedness between bulls for both breeds (Swedish Red (SR) and Swedish Holstein (SH)) analysed together. In (a) breeds are separated by colour, in (b) bulls are coloured according to birth year class across breeds. First and second PC explained 7.8% and 1.3% of the variation, respectively

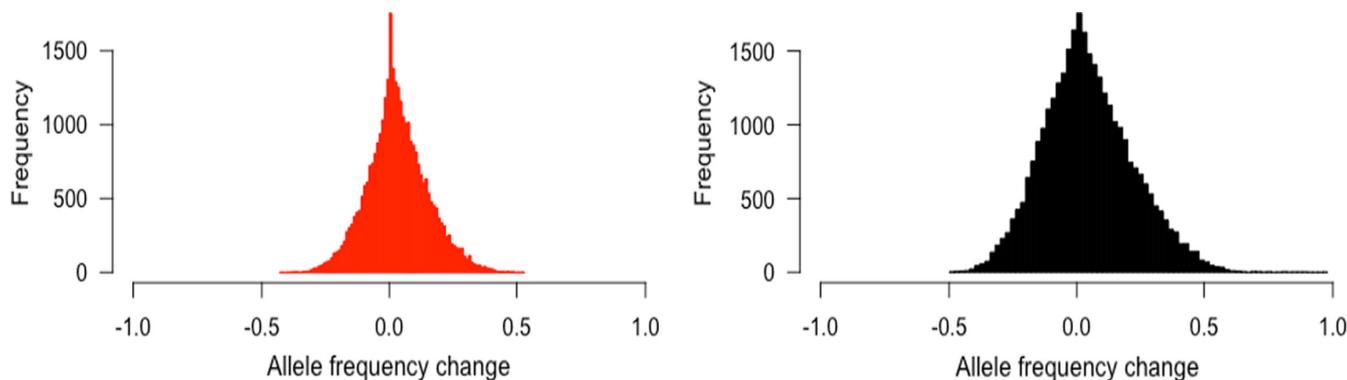


FIGURE 4 Allele frequency change from old bulls (born before 1980) to recent bulls (born 2010–2020), Swedish Red in the left panel, Swedish Holstein in the right panel (a positive value is an increase of the frequency of the alleles designated as minor allele in old bulls)

information increases the chance of co-selection of relatives (Forutan et al., 2018). BLUP breeding values for dairy cattle was introduced in Sweden in 1984. From the 1980s onwards, the trajectory differed between the breeds: SR had a stable level, whereas for SH there was an increase, mainly during the 1980s and 1990s. The stable period for SR could be owing to the continuous importation of mainly Finnish Ayrshire bulls and semen, thus counteracting any increase in inbreeding from BLUP selection. The beginning of this period coincides with the rather fast transformation of the old Swedish Friesian cattle (SLB) into Holstein. The proportion of Holstein genes increased from around 20% in the beginning of 1980s to around 90% in the mid-1990s (Bett et al., 2010). Apparently, the introduced US bulls were genomically more inbred than the Swedish bulls of that time.

The Holsteinization probably contributed to the larger change in allele frequency over time seen in SH compared with in SR (Figure 4). The continued divergence between birth-year groups within breed also in later years after the

Holsteinization process was more or less completed for SH, shown mainly in the second principal component in the PCA-plot (Figure 2), would thus likely be due to selection for favourable genotypes and drift. Genetic drift was shown to be of great importance for the loss of genetic diversity in Canadian Holsteins (Stachowicz, Sargolzaei, Miglior, & Schenkel, 2011).

Changes in breeding strategies and technology over time created differences in selection of AI-bulls, and also influenced the availability of genomic information for the present study. For the oldest time period in our study, we genotyped stored semen samples for bulls known to be influential in the population, but tried to avoid close relatives and select bulls from different families and locations of AI-stations in Sweden to capture more of the genetic variation at that time. When preparing for the introduction of genomic selection, old AI-bulls from the 1980s and onwards, representing different families, were genotyped to complement the information. For SR, from around 1990 to 2009, the number of bulls genotyped indicate that almost

all young bulls that were progeny tested were genotyped, however, for SH it is a smaller sample because genotypes were also available from other countries (Pers. comm. Hans Stålhammar, VikingGenetics). In recent years, a larger number of young bulls have been genotyped each year and most bulls selected for breeding are used for a shorter time period. We could not completely adjust for such differences across time in our study, but we believe that the included bulls were reasonably representative for the different time periods.

4.2 | Post genomic selection situation

The reduction in generation interval as a consequence of the introduction of genomic selection has been suggested to be the main cause of increased inbreeding rates per year in dairy cattle in recent years (Forutan et al., 2018; Scott et al., 2021), and this has increased the awareness of breeding companies and organizations to manage genetic diversity. Scott et al. (2021) found a severalfold increase in pedigree-based inbreeding rates in Australian Holstein AI-bulls born 2013–2017, after introduction of genomic selection, compared to those born 2000–2012. They also reported an increased genomic inbreeding rate for Holstein males and females born 2013–2017. Doekes, Veerkamp, Bijma, Hiemstra, and Windig (2018) studied genomic inbreeding in Dutch-Flemish Holstein-Friesian AI-bulls born from 1986 to 2015 and reported a steep increase in ROH-based inbreeding from 2010, after a temporary decrease around 2000 when optimum contribution selection was applied. Doublet et al. (2019) also detected a significantly higher rate of inbreeding (F_{ROH}) for Holstein bulls born 2012–2015 compared with those born 2005–2010. This was not the case for bulls of the French breeds Montbéliarde and Normande, however.

In the present study, the last birth year group (2015–2020) tended to have a higher level of all three measures of inbreeding than the previous birth year group. This could be an effect of the greater use of genomic selection.

4.3 | Choice and definition of measures

Most studies of inbreeding trends that go far back in time are based on pedigree information. The low pedigree completeness in historical data, such as illustrated by Makanjuola et al. (2020), may cause underestimation of inbreeding levels in the oldest animals, which can be avoided by use of genomic information. Due to recombination, old inbreeding is seen as shorter ROH than recent inbreeding, and genomic measures such as F_{ROH} do not accumulate inbreeding over time to the extent that homozygosity and

pedigree-based measures do (Meuwissen et al., 2020). In our study we had access to genotypes for animals born in different time periods, representing snapshots of the inbreeding situation at those points in time. We chose not to include pedigree-based inbreeding measures due to poor pedigree completeness for the oldest animals. However, Bengtsson et al. (2022) estimated high correlations (≥ 0.83) between genomic and pedigree-based relationship measures in Nordic RDC born 2011–2020.

The current level of F_{ROH} in both SR and SH appears to be considerably lower than that in the Canadian Holstein population studied by Makanjuola et al. (2020), where it increased from around 0.1 in 1990 to around 0.17–0.19 in 2018. In Australian Holstein (Pryce, Haile-Mariam, Goddard, & Hayes, 2014) found a similar level of homozygosity (0.65) as for SH born 2000 and later, in our study. Martikainen et al. (2017) found F_{ROH} ranging from 0.04 to 0.09 in Finnish Red cows born 2002–2014, which is more comparable to our results. However, their estimate of Hom_{obs} was 0.63, which was lower than our values. Doekes et al. (2018) found levels of F_{ROH} and Hom_{obs} of 0.067 and 0.64 in Dutch-Flemish Holstein-Friesian bulls born 1986–2015. Bjelland, Weigel, Vukasinovic, and Nkrumah (2013) found lower values of 0.038 and 0.605, respectively, among US Holstein cows born in the early 2000s. They did, however, prune for low MAF and deviation from HWE.

Meyermans et al. (2020) showed that the choice of settings in PLINK, such as minimal density requirements, can have substantial impact on the detection of ROH. We cannot rule out that some differences in settings may have contributed to differences in F_{ROH} between, say, the Swedish and Finnish red populations, however, for comparison over time within the same population, all measures seem to give a similar trajectory.

The choice of quality control settings can also influence the estimates of genomic inbreeding. Meyermans et al. (2020) pointed out that there is no consensus regarding the value of pruning data for MAF or LD before ROH analysis. They showed that even mild pruning for MAF could result in large homozygous regions being overlooked. The same authors found that LD pruning can also affect detection of long ROH, but that the effect was highly population dependent. Criteria for deviations from HWE are also widely used in quality control of genomic data to remove genotyping errors. However, such deviations can be due to various causes, including inbreeding and selection (Chen, Cole, & Grond-Ginsbach, 2017). In our data we expected both selection and inbreeding and differences in allele frequency in the older, compared to more recent bulls and wanted to include rare variants. We chose not to prune for MAF, LD or departure from HWE, but instead followed the recommendations for ROH settings

by Meyermans et al. (2020). Similarly to effects of ROH definitions, differences in data pruning can also hamper direct comparisons between levels of genomic inbreeding between studies.

The actual inbreeding level notwithstanding, our results show that, except for the F_{ROH} in Holstein, the average inbreeding as well as homozygosity level was higher more than half a century ago than at present. However, the inbreeding level in SH is currently increasing, which should be considered in breeding strategies.

5 | CONCLUSIONS

The changes in genomic inbreeding and homozygosity levels over half a century in Swedish commercial cattle breeds seen in this study, reflects increased introgression of foreign genetic material, as well as ongoing selection for desired traits. Average inbreeding coefficients and homozygosity levels decreased with birth year for bulls of both breeds until the 1980s, whereafter they remained stable for Swedish Red but increased for Swedish Holstein. Gradual changes of the populations were also seen in the pattern of genetic relationships within and between birth-year groups of bulls, and in allele frequency changes. The current average levels of inbreeding based on runs of homozygosity are not high compared to publications for other populations, but attention should be paid to the increase seen in recent years, especially in the Swedish Holstein.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from VikingGenetics and/or the Nordic Cattle Genetic Evaluation. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the author(s) with the permission of VikingGenetics and the Nordic Cattle Genetic Evaluation.

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