Estimating the effective population size of Swedish native cattle

- understanding the demographic trajectories of indigenous Swedish cattle breeds

Den effektiva populationsstorleken hos svenska koraser. Uppskattningar av demografisk historia.

Dolapo Adepoju

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Swedish University of Agricultural Sciences, SLU
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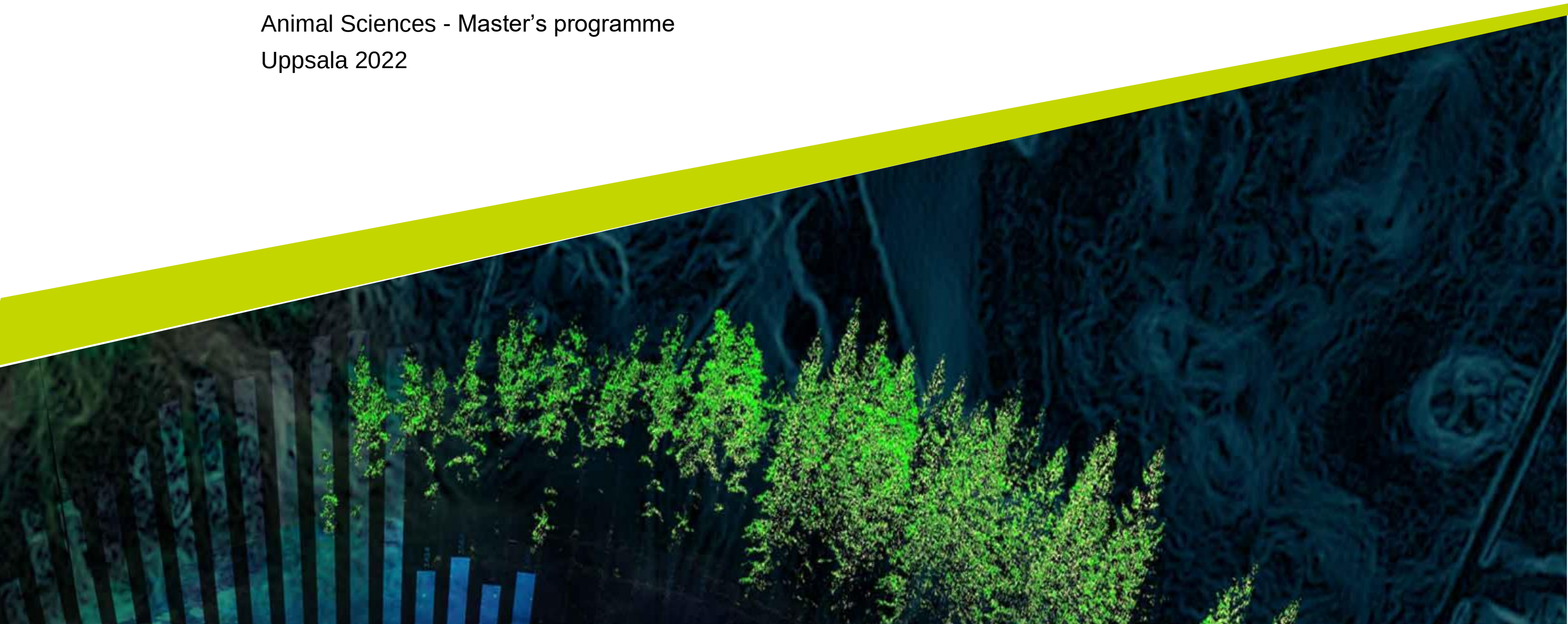

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Abstract

The indigenous cattle populations are on the decline globally with the continuous improvement of genetic gains in commercial breeds. Due to their unique adaptive features to the local ecosystem, traditional cattle breeds are pools of valuable genetic resources that could help combat the impact of climate change in the near future. However, besides the census population sizes, it is crucial to assess the impacts of genetic drift to design strategic breeding programmes to improve genetic diversity and safeguard the breeds against genetic erosion.

This study estimated the effective population sizes (Ne) of nine Swedish native cattle breeds from 147 individuals genotyped with GenSeek GGP Bovine 150K and 33 samples from whole-genome sequence data using the observed linkage disequilibrium spectrum. Demographic trajectories of up to 200 generations ago were also inferred to match the decline observed to a series of events that have shaped the breeds' current status.

The estimated result showed that two breeds (Bohuskulla and Väne) have Ne values within Ne ≤ 50, indicating critical status. Also, four are in the endangered zone (Ringamålako, Fjällnara, Swedish Polled, and Swedish Red Polled) with Ne ≤ 100, and only three breeds (Holstein Friesian, Swedish Red Cattle, and Swedish Mountain Cattle) are considered stable to limit total fitness loss up to 10% with Ne ≥ 100. Also, a general dramatic decline was observed between the 12th to 15th generations across all breeds, which suggests that the reduction in the population of Swedish native cattle breeds began with breed formation.

While maintaining high Ne is critical for the conservation of indigenous cattle, using the pedigree method or demographic might not provide accurate estimates due to several limitations. These include overlapping generations and a lack of pedigree information. Therefore, besides preventing inbreeding, Ne estimates from genomic data should be adopted in the breeding and conservation strategies of Swedish native cattle breeds. They are non-dependent on pedigree information and demographic data.

Keywords: Swedish native cattle, effective population size, genetic drift, cattle demographic trajectories, native cattle conservation

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Abbreviations

BHP	Bohus Polled Cattle
FNC	Fjallnära Cattle
SHF	Swedish Holstein Friesian
RMC	Ringamålako Cattle
SMC	Swedish Mountain Cattle
SPC	Swedish Polled Cattle
SRC	Swedish Red Cattle
VAC	Väne Cattle
LD	Linkage Disequilibrium
GONE	The Genetic Optimisation for Ne Estimation

1. INTRODUCTION

Climate change, selection, migration, and other geological events have significant impacts on shaping the ancestral history of livestock species. The change in recently inferred demography history in population genetics and conservation biology can help decipher the timeframe of population decline. Thus, studying the evolutionary history of animals facilitates separating anthropogenic (human-induced activities) from natural factors such as genetic drift, migration, mutation, and recombination (Quéméré *et al.*, 2012)

Indigenous animal breeds are often overlooked and under-prioritised in many production systems due to the low quality and quantity of products such as meat and milk (Tapio *et al.*, 2006).

Specifically, the native cattle breeds have been increasingly endangered, primarily due to the demand and preference for high-producing exotic breeds. The continuous negligence of these breeds has resulted in the loss of their genetic diversity. This lack of genetic variation poses a significant threat to the sustainability of these cattle breeds, for example, in the case of disease outbreaks (Bett *et al.*, 2013).

Although Sweden focuses on conserving indigenous breeds as a vital genetic resource and source of cultural heritage, using exotic breeds for commercial production have reduced the number of native Swedish cattle breeds (Upadhyay *et al.*, 2019).

While commercial cattle breeds usually outperform native Swedish cattle populations in milk yield and meat quality, native breeds have several advantages over their exotic counterparts (Hiemstra, 2010). For example, traditional cattle have a long history of adaptation to the local environment and varying climatic conditions (Gao *et al*., 2017). Also, some indigenous cattle possess superior functional and production traits. For instance, Swedish Fjäll cattle produce milk with a better protein composition that is more suitable for cheese-making than the Holstein-Friesian breed (Upadhyay *et al*., 2019).

Furthermore, research shows that local cattle have superior grazing patterns to exotic breeds. Thus, they are more valuable for managing grassland with diverse vegetation (Lien *et al*., 1999). Besides, native breeds may offer the resilience required for global food security (Hoffmann, 2010).

Conscious efforts have been made to conserve Swedish animal genetic resources, including the Swedish traditional cattle breeds (Swedish Board of Agriculture, 2009). Also, Upadhyay *et al*. (2019) had previously revealed the genetic diversity and relatedness of Swedish native cattle populations compared to other European cattle breeds. Johansson *et al*. (2020) also build on these data to explore the genetic differences between the two subpopulations of Swedish mountain cattle breeds – Fjäll and Fjällnära. However, there has been no study on estimating the effective population sizes of Swedish native cattle until now.

The adequate population size (N_e) is one of the critical genetic parameters that uncover the evolutional history of animals. It has a wide range of applications in measuring genetic drift, population structure, selection, mutation, migration, and other essential factors that contribute to the changes observed in the genetic architecture of animals (Wang *et al*., 2016).

Many definitions have been employed to explain effective population size. J.F Crow, in 1970, defined effective population size as the size of an idealised population that will produce a similar effect of random sampling on gene frequency as in the actual population (Crow, 2017). Similarly, Jiménez-Mena *et al.* (2016) defined N_e as the size of an idealized population going through an equal rate of genetic drift as the population being studied. However, the definition usually depends on the aspect of genetic drift of interest. This can be the variance of allele frequency or the rate of inbreeding (Husemann *et al.*, 2016). The idealised population has many assumptions, including constant size, random mating, and reproduction with any species member. Also, there are no overlapping generations, and there is a new set of parents for every new generation.

Contrariwise, there are deviations from the Wright-Fisher idealised populations. For instance, non-random variation occurs in mating and reproduction, generations often overlap, many species have two sexes, population size usually varies with time, and species can have subpopulations and distinct phenotypes (Charlesworth, 2009).

A more simplified view of the effective population size is the number of individuals contributing offspring to the production of the next generation or the number of the breeding population (Sbordoni *et al*., 2012). The census population indicates the total number of living animals in some cases. However, due to various factors such as age, unequal male: female ratio, non-random mating, and sexual dominance, not all living animals can contribute to breeding (Kliman *et al*., 2008).

These factors contribute to genetic drift (or loss of genetic variation) and lower N_e. The effective population size is usually lower than the census population size but not in all cases. Therefore, N_e measures the percentage increase of inbreeding per generation and the decrease of heterozygosity (Braude and Templeton, 2009). Also, estimating N_e and inferring demography history serve crucial roles in assessing the risk of extinction of specific breeds and evaluating the effectiveness and sustainability of the genetic management, conservation, or breeding programmes, especially for animals with low census population size (Wang *et al*., 2016; Saura *et al*., 2021).

Several studies have shown that estimated N_e values are more reliable in predicting the demography trajectory and detecting stable, increasing, or declining populations than using the census size, as a high census sizes do not automatically translate to high N_e (Flury *et al*., 2010; Pelletier *et al*., 2019; Makanjuola *et al*., 2020).

Thus, it is crucial to study N_e as it plays an essential role in molecular evolution and variation, which help in breeding and conservation strategy for both plant and animal populations, particularly the native breeds with a high risk of genetic erosion. Ne values differ across the genome, and recent advances in genomic techniques provide better insight into estimating N_e.

There are three broad categories of methods for estimating effective population sizes. These include demographic-based, pedigree-based, and marker-based (Barbato *et al*., 2015). Each of these methods has its unique strength and limitations. For instance, the pedigree-based method requires the full knowledge and complete pedigree history monitored across many generations and assumes no relationship among the sampled population. These conditions are only feasible in a few selected intensively managed breeds (Wang *et al*., 2016). However, with the abundance and reduced cost of high throughput sequence data, attention has been shifted to the marker-based approach with preferences for the Linkage Disequilibrium (LD) technique (Santiago *et al.,* 2020).

Linkage disequilibrium is defined as the non-random association of alleles at different loci in different physical positions across the genome (Barbato *et al*., 2015). The LD-based approach has been deployed in several population genetics studies, including estimating Ne. Several studies suggested that the LD approach is reliable and robust for livestock (Li and Kim, 2015; Martinez *et al*., 2022; Novo *et al*., 2022) and human population genetic studies (Tenesa *et al*., 2007). The LD method uses high-density markers, including single nucleotide polymorphism (SNP) or sequence data. Consequently, several bioinformatics tools built on complex mathematical and statistical algorithms have been developed to extract demographic information from genomic data utilising the LD approach. However, for this study, we have limited our software to two of the most recent implementations that use different LD-based methods; SNeP and GONE.

The SNeP software was developed by Barbato *et al*. (2015). With the availability of enough SNPs and the knowledge of their physical positions in the genome, using SNeP to predict N_e trends can improve understanding of current population demography (Corbin *et al.,* 2012). The recent demography history shows the pattern of changes in the census population and the variation in the effective population size of different breeds.

The genetic optimisation for N_e estimation ("GONE") software was developed by Santiago *et al*. (2020). GONE has been used by several studies to infer the demography history and estimate N_e for different livestock species (Martinez *et al*., 2022; Novo *et al*., 2022). According to the developers, the software is relatively stable against factors such as population temporal sample heterogeneity, population admixture, genotyping errors, and structural division into subpopulations when used on simulated data (Santiago *et al*., 2020).

Estimating effective population size is critical for conservation purposes. Scherf et al. (2015) reported that a 15 to 17 per cent increase in the risk of extinction of animal genetic resources had been documented between 2005 and 2014. Therefore, monitoring population trajectories and the pattern of changes in effective population sizes is fundamental to maintaining genetic diversity for conservation purposes.

Currently, the Swedish Board of Agriculture predicts the status of Swedish cattle breeds based on the number of registered females in the population. Studies have shown that the census population (N) is not an accurate estimate of the animal's extinction status as a breed can go into extinction even before the last animal, gamete, and embryo is lost (Bett *et al*., 2010). This study on estimating the effective population size of Swedish native cattle will estimate values of N_e across different generations, show the demography trend, and attempt to match these with real-life events in different breeds.

Therefore, this study will provide more precise, effective population sizes of Swedish native cattle and probe the trajectories of their demography history, giving insight into improving the effectiveness of breeding programmes and conservation strategies.

1.1 Project Aims

- To estimate the effective population sizes of nine breeds of the Swedish native cattle using the linkage disequilibrium approach.
- To infer the recent demography history of these cattle breeds and relate the changes to various events in Swedish native cattle, including migration, selection, admixture, and other genetic forces.
- To compare SNPs Chip and whole-genome sequence data results.

2. LITERATURE REVIEW

2.1 Indigenous Cattle Breeds

Cattle domestication was reported to have occurred over 10,000 years ago, with many studies citing two to three separate events; from indicine (*Bos indicus)* and taurine (*Bos taurus* having a shared ancestor in aurochs (*Bos primigenius*) with Indus Valley, Fertile Crescent, and the Western Desert of Egypt as possible centres of domestications (Pitt *et al*., 2018).

With a meteoric rise in global population comes the need to increase cattle production to serve human needs, primarily as milk and meat sources. This has culminated in applying genetic methodologies such as quantitative genetics, artificial selection, estimates of breeding values and crossbreeding. Also, improvements in production systems and reproductive techniques have been accelerated, including artificial insemination, embryo transfer, and multiple ovulations (Medugorac *et al*., 2009). However, while these laudable developments have helped increase production, it has equally resulted in a preference for a few certain commercial breeds with superior productivity (Hiemstra, 2010). The intensification of specialisation (milk or beef), and enhanced profitability has driven many local cattle farmers to switch from dual-purpose local breeds to high-performing commercial ones (Malevi, 2002; Kukučková *et al*., 2017).

2.1.1 Decline in indigenous cattle populations and genetic diversity

The global native cattle breeds have experienced a rapid decline in the census population size, often accompanied by a loss of genetic diversity. For instance, the Pinzgau cattle breed is endangered despite its many unique attributes (Kukučková et al., 2017). A study conducted on Greece, Tunisia, and Algeria cattle showed a decline in the population of local breeds, majorly due to economic reasons (Mohamed-Brahmi *et al*., 2022). The report estimated a reduction in native cattle across the Mediterranean from 82% in 1986 to 48% in 2016. Also, González-Cano *et al*. (2022) analysed the genetic diversity of two of the endangered Berrenda breeds of Spanish indigenous cattle. They identified a continuous loss of genetic variation that could worsen over time without an effective measure. The decline in native cattle genetic diversity and population sizes could escalate the disappearance of indigenous cattle breeds due to genetic erosion.

African indigenous cattle breeds are arguably at the top of the list regarding loss of genetic diversity. Mwai *et al*. (2015) reported that African cattle's unique genetic resources are in danger of disappearing due to several factors, such as uncontrolled crossbreeding, importation, and poorly planned breed replacement strategy. All these pointers indicate that the global native cattle populations, effective population sizes and genetic diversity are rapidly declining leading to severe consequences in countering potential climate change effects as indigenous cattle are more suited to local ecosystems (Marsoner *et al*., 2018).

2.1.2 Crossbreeding as a conservation strategy

There have been several attempts to conserve indigenous cattle breeds. Many researchers have proposed crossbreeding to conserve and improve the productivity of native cattle breeds (Scholtz and Theunissen, 2010). However, this conservation strategy poses a severe threat to the existence of original breeds through genetic introgression, as observed in a Svensk Låglandsboskap that has nearly lost all its original traits but retains its original name (Bett *et al*., 2013). Another instance is the case of the infiltration of Danish Red genes in the genome of Flemish Red cows until the proportion of Flemish cattle breeds with zero Danish Red genes became zero in the early 2000s (Lauvie *et al*., 2008). It is almost impossible to retain purebreds in most crossbreeding techniques besides a few, like terminal crossbreeding proposed by Clasen *et al*. (2021). This indicates that crossbreeding, despite all its benefits, is a threat to the existence of indigenous cattle genetic diversity and herd populations.

2.2 Swedish Native Cattle Breeds, History and Historical Uses

The Swedish native cattle have a long, rich history of being a valuable source of food production due to their dual nature (milk and milk production), adaptation to the local environment, and cultural heritage. Before introducing exotic breeds and developing high-performing commercial breeds, the native cattle in their thousand heads played significant socioeconomic importance (Korkman, 1988). However, the mid-20th century birthed a rapid decline in the number of Swedish native cattle due to adopting more efficient breeding programmes such as artificial insemination favouring Holstein-Friesian breeds (Kantanen *et al*., 2000).

Consequently, a few breeds with high production capacity became prevalent while others were neglected, and many became extinct (Bett *et al*., 2013). Another contributing factor to the reduced population size of indigenous Swedish cattle genetic resources is the importation of some breeds from the Netherlands, documented as early as the 16th century (Korkman, 1988).

2.2.1 Swedish Mountain Cattle (SMC)

Swedish Mountain Cattle (Fjäll or Fjällras) is an important traditional breed in Sweden, with a significant role in milk production. It is reported to be related to some Finnish and Norwegian breeds with introgression from Northern Finncattle ("Breed description," 2007). Fjäll herd book was established in 1907, and it is managed by Swedish Mountain Cattle breeding Association (Svensk Fjällrasavel), established in 1995 ("Svensk Fjällrasavel," n.d.) The risk status is currently listed as the "Unknown" risk (FAO, DAD-IS). Upadhyay *et al*. (2019), in their report on the Swedish native cattle population, stated that Fjäll was approximated to consist of 400,000 individuals raised in northern and mid-Sweden towards the end of the 19th century. A year before, only 400 Fjäll breeding cows were in use 1996 ("Breed description," 2007). In contrast, the number of breeding females was 2,100 in 1997, a noticeable improvement in conservation strategy. The last report by FAO, DAD-IS (April 2014) estimated the SMC population to be 6,683, with 1,672 males and 5,011 females.

2.2.2 Fjällnära Cattle (FNC)

The Fjällnära Cattle is another Swedish Mountain Cattle, similar to the Fjäll. Johansson *et al*. (2020) stated that Fjällnära is a subpopulation of the Fjäll that was isolated in remote mountains and less selected for milk production. The breed was recognised by the end of the 1980s. Föreningen Äldre Boskap, the association responsible for the preservation of traditional Fjällnära Cattle was formed in 2008 (Johansson *et al*., 2020). According to DAD-IS data, the Fjällnära only had 304 population size (63 males and 241 females) in 2021 and is considered to be "at-risk" (FAO, DAD-IS).

2.2.3 Ringamåla Cattle (RMC)

The Ringamåla (RMC) cattle breed originated from isolated herds in the southern part of Sweden; Skåne and Blekinge. The breed association for Ringamålako was formed in 1993 and is managed by Föreningen Allmogekon, together with Väne and Bohus Polled Cattle. It has a strong resemblance with the Swedish Red and White Breed (SRB) of the 1940s ("Ringamålako," n.d.). Although there have been conservation strategies in place, the breed is still considered at risk, with the latest population size ranking it at 156 in 2021, with the male: female ratio putting it at 38:118 (FAO, DAD-IS).

2.2.4 Bohus Polled Cattle (BHP)

According to information from Föreningen allmogekon, Bohuskulla originated from Kynnefjäll in the Southwestern part of Sweden, the north of Dalslan and Bohuslän. A report suggested that the two herds that have intermittently exchanged bulls for more than 50 years birthed the Bohus Polled cattle ("Koraserna," n.d.). Research showed that a large proportion of Bohuskulla cattle were exported to Norway in the 19th century up to the end of 1930. Due to its low productivity, the breed was considered an "unimproved" version of Swedish Mountain Cattle

(Eriksson and Petitt, 2020). The 2019 report from DAD-IS considered the breed at risk, with a total population of 114, with 90 breeding females and 24 breeding males.

2.2.5 Swedish Holstein-Friesian (SHF)

The traditional Swedish Friesian, “Svensk Låglandsboskap (SLB)” in Swedish, originated from the southern part of Sweden around 1870, followed by its herd-book establishment in 1880 (“Swedish breeds,” 2009). The Swedish Holstein-Friesian resulted from a cross between the dual-purpose old Swedish-Friesian and the imported Holstein cattle from the Netherlands in a breeding system that started in the 1970s all through the 1990s (Ghoreishifar *et al.*, 2020). Analyses from Upadhyay *et al*. (2019) also confirmed that Swedish Holstein-Friesian is historically related to Dutch cattle breeds. The breed is the second-highest milk producer in Sweden after the Swedish Red and White cattle (“Swedish breeds,” 2009). However, the continuous use of bulls from the Holstein breed to increase milk yield has resulted in a decline in the number of purebred Swedish Friesians. Bett *et al*. (2013) reported that the original Swedish Friesian status should be considered extinct. Currently, Swedish Holstein-Friesian has a total population size of 520431 and is classified as “not at risk” in 2021 (FAO, DAD-IS). However, the original Swedish-Friesian (Svensk Låglandsboskap) only has 100 breeding females with no bull alive besides frozen semen.

2.2.6 Swedish Polled Cattle (SPC)

The amalgamation of two traditional Swedish cattle breeds, Swedish Mountain Cattle (Fjäll) and Swedish Red Polled (Rödkulla), gave birth to Swedish Polled

Cattle (Svensk Kullig Boskap) in 1937. However, there was disagreement regarding the new classification, and breeders continued to pursue different breeding activities, and the SPC maintained its identity as a separate breed (Bett *et al*., 2013). 1938 witnessed the merge of these two breeds, followed by separations in 1984 and 1995 due to disagreement from breeders (Upadhyay *et al*., 2019). SPC's conundrum is that the breed is not purebred enough to be Swedish mountain cattle, nor Swedish Red polled. Thus, the breed was not allowed to be considered Swedish mountain cattle nor Swedish Red polled. Conservation efforts have been made toward improving the productive capacity of Swedish Polled Cattle through crossbreeding with modern commercial cattle breeds (Upadhyay *et al*., 2019). Clasen *et al*. (2021) also proposed a terminal crossbreeding strategy involving Swedish Red Cattle, Swedish Polled Cattle, and purebred Swedish Red. In 2020, 575 females (100 purebreds) were registered in the herd book. However, according to the last update, the breed maintained a total population of 2532 (FAO, DAD-IS). Nevertheless, SPC is still considered endangered but with an upward trend in population size.

2.2.7 Swedish Red Cattle (SRC)

The Swedish Red Cattle (SRC), known as Svensk Röd och Vit Boskap, translated to “Swedish Red and White,” is one of the most abundant Swedish native cattle breeds. The breed accounts for 60% of Sweden’s dairy cow population due to its remarkable milk production performance at the global level (“Swedish breeds,” n.d.). It was reported to be a cross between the now-extinct Rödbrokig Svensk Boskap (Red pied Swedish-RSB) and Swedish Ayrshire (Bett *et al*., 2013). Despite its impressive population size, the breed has reportedly declined from

450,000 in 2011 to 241,746 in 2021. However, the breed is considered stable (FAO, DAD-IS).

2.2.8 Swedish Red Polled Cattle (SRP)

Rodkulla, or Swedish Red Polled (SRP) Cattle, is one of Sweden's oldest indigenous cattle breeds. SPC is related to breeds from Norway and Finland. The breed was reported to vary in phenotypes in the 19th century, from horned to hornless, from brown colour to yellowish red (“Swedish breeds,” n.d.). The breed association was established in 1912, and a reported 30,000 heads existed in the 1930s (Upadhyay *et al.*, 2019). Since 1984, the breed has been managed by The Swedish Red Poll Society (Sveriges Rödkulleförening). It has a record of fluctuation in population sizes, with the lowest population ever set at 20 (“Swedish breeds,” 2009). Conservation strategy has helped accomplish a rise in population size with 647 breeding males, and 1978 breeding females in 2014 (FAO, DAD-IS) compared to 1200 purebred cows and 400 bulls in 2009 (“Rödkullan,” n.d.).

2.2.9 Väne Cattle

The endangered Swedish cattle breed derived its name from the village, Väne-Rye, Västergötland, the western part of Sweden. It was first discovered in the early 1990s, a period when all native cattle with horns were assumed to have vanished. Väne cattle has been isolated from other native cattle breeds for a long time (“Swedish breeds,” 2009). Upadhyay *et al*. (2019) confirmed the restriction of gene flow between Väne and other breeds. The breed association (Föreningen allmogekon) was established in 1993 to manage the conservation strategies of Väne with the primary objective of increasing the population size (Swedish breeds,” 2009). (FAO, DAD-IS) 2019 record listed Väne’s population to be 201, with 25 breeding males and 176 breeding females.

2.3 Extinct Swedish native cattle

Like every indigenous livestock population, many native cattle breeds have been subjected to extinction mainly due to the breeding systems, importation, and abandonment of local breeds (Bett *et al*., 2010) briefly described the trajectories of extinction in Swedish native cattle breeds, a further developed study three years later (Bett *et al*., 2013). According to the reports, breeds such as Herrgård, Skåne, and Småland have become extinct. However, many of them have their genes absorbed in other breeds. The breeds above were all absorbed into Rödbrokig Svensk Boskap (Red pied Swedish-RSB) between 1892 and 1928. Unfortunately, RSB has also been declared extinct (FAO, DAD-IS). These indicate that the trend of declining population sizes in Swedish local cattle populations poses a threat to their existence.

2.4 Importance of Swedish Native Cattle Breeds

Understanding the importance of Swedish native cattle breeds and their critical roles in food production, socioeconomic and biodiversity is crucial to communicating their conservation needs better than before. Although the local Swedish population has a lower quantity of milk and carcass yield than the modern commercial counterparts and the exotic breeds, they possess many unique features that make it imperative to conserve and protect them against genetic erosion (Clasen *et al*., 2021).

Upadhyay *et al*. (2019), estimating the expected heterozygosity (H_e), stated that despite low population sizes generally observed in Swedish cattle breeds, most native cattle possess relatively high genetic diversity ranging from 0.3883 in Swedish-Holstein Friesian and 0.3041 in Väne cattle.

This could be attributed to the use of distantly related breeds and influence from other Nordic breeds. Diversity is required to overcome the limited genetic variation observed in exotic breeds. Also, Swedish native cattle have lived in their local environment for several generations and developed distinct adaptive features that could be a source of a unique genetic pool for future breeding goals to counter the adverse effects of climate change (Bett *et al*., 2010).

Another essential benefit of Swedish native cattle is their ability to produce milk high in milk casein. For example, (Gustavsson *et al*., 2014), in their analyses of the protein composition of Danish and Swedish dairy milk, observed that Swedish Red have a higher concentration of kappa casein compared to milk from other European breeds. (Johansson *et al*., 2020) also suggested that Beta-lactoglobulin *B* allele frequency, essential for cheese production, has increased in Fjäll cattle.

Livestock is a valuable resource for managing the cultural landscape. (Hessle *et al*., 2014) showed that Swedish Mountain Cattle covered longer distances than the Holstein and were more dispersed over a larger vegetation area. Väneko heifers could help control pernicious brushwood with a more effective grazing pattern (Hessle *et al*., 2008). These indicate that native Swedish cattle breeds have the potential to aid in managing natural pastureland better.

Swedish native cattle breeds hold high value as a source of cultural heritage. While economic values are the majorly determinant of conservation strategies, it is imperative to consider their socioeconomic significance and cultural heritage (Kjetså *et al*., 2021). For instance, as part of the Nordic breeds, Swedish Mountain Cattle was recently pronounced as human companions, friends, colleagues, and family members (Ovaska et al., 2021). That implies that native cattle breeds contribute beyond their genetic diversity.

2.5 Effective Population Size and Demographic History

The effective population size (N_e) is one of the most important genetic parameters in population genetics, evolution, animal breeding and conservation genetics (Charlesworth, 2009). N_e is also valuable for improving models to map genes responsible for diseases and quantitative traits of interest in animals, plants, and humans (Hayes *et al*., 2003; Li and Kim, 2015). Sewall Wright (1931) conceptualised that effective population size is a means to calculate the rate at which evolutionary changes have occurred through random sampling of the frequency of alleles in a finite population or the rate of inbreeding (Charlesworth, 2009; Wang *et al*., 2016). On the other hand, demographic inference provides insights into historical events that have affected genetic variations and how different breeds have responded to evolutionary forces (Blischak *et al*., 2020). This can contribute to in-depth knowledge of breed evolution through the genomic signature of selection resulting from trends in N_e (Pitt *et al*., 2019).

Effective population size measures patterns of genetic drift, rate of inbreeding and how different genetic forces such as migration, mutation, and bottleneck have influenced the trajectory of populations across different generations (Wang *et al*., 2016). While a decline in livestock population size and loss of genetic diversity has always been linked to anthropogenic activities, estimating N_e from genomic data can unravel the timeframe for reducing population sizes resulting from natural factors (Quéméré *et al*., 2012). The core reason to estimate the effective population size of animals, especially endangered breeds, results from the assumption that population sizes impact N_e (Sbordoni *et al*., 2012), which in turn, reduces adaptive potential due to the loss of genetic variation (Gossmann *et al*., 2012).

Several studies have proposed different genetic parameters and methods to estimate N_e (Leroy *et al*., 2013a). These include increased homozygosity, loss rates of unique alleles, temporal changes in allele frequency and linkage disequilibrium. Wang (2005) and Wang *et al*. (2016) performed a comprehensive review of different methods of estimating N_e from genetic markers data. However, this research focuses on estimating effective population sizes using the Linkage Disequilibrium (LD). It is one of the most recent approaches with supportive computational methods to infer relevant demography information (Hayes *et al*., 2003; Barbato *et al*., 2015; Santiago *et al*., 2020). Also, it is noteworthy to mention that besides genetic data, N_e can equally be estimated using other sources such as demographic and pedigree data (Gutiérrez *et al*., 2008; Leroy *et al*., 2013). However, only a few intensively managed breeds have complete pedigree information (Barbato *et al*., 2015).

Linkage disequilibrium (LD) is one of the most widely used approaches in estimating N_e from genomic data. The concept behind the LD method originated from the knowledge that for neural loci unlinked with selected loci in isolated populations, LD is inversely proportional to the effective population sizes of markers and the genetic distance between marker sites (Hill, 1981). LD results from various genetic factors, including direct or indirect selection (hitchhiking effects), migration, admixture, genetic drift, and bottlenecks in finite populations (Wang, 2005). Although different methods of estimating N_e using the LD approach were developed a long time ago, their accuracy depends on the genetic marker data only achievable through the recent advanced DNA technologies (Barbato *et al.*, 2015).

Understanding the extent of LD in animal populations can help infer the demography history (MacLeod *et al.*, 2013) and estimate the minimum distance required to effectively calculate coverage between markers during genome-wide association studies (Makina *et al.*, 2015). Thus, the relationship between variance in N_e and LD can be used to infer both recent and ancient effective population sizes (Makina *et al.*, 2015). This emanated from the basic concept that LD between SNPs pairs at various genetic distances provides different information about N_e at different generational time intervals (Santiago *et al.*, 2020).

2.6 Estimate of effective population size and inference of cattle population histories

Studies involving estimating the effective population size and inferring the demography history of cattle breeds have gained attention over the years. Although effective population size and demography history are not entirely the same, they are dependent and are often studied together (Boitard *et al.*, 2016; Pitt *et al.*, 2019;

Martinez *et al*., 2022). This is because factors that shape the demographic histories of animals and humans (genetic drift, bottleneck, expansion, and drop) are often reflected in the variation observed in the effective population sizes. For instance, demographic events such as the founder's effect (a situation where a few samples from the census population that do not reflect the total genetic diversity of the entire population isolate and form a new cluster) will lead to a reduced census population and automatically result in a decline in effective population size. Pitt *et al*. (2019), in their quest to examine the demography history and mechanism behind the adaptation of Creole cattle in the tropic, used Approximate Bayesian Computation developed by Sunnåker *et al*. (2013) and the SNeP software (Barbato *et al*., 2015) to estimate N_e. Both methods detected a diminishing trend in N_e, while ABC analysis identified a decrease in gene flow between herds attributed to the commencement of breed formation.

Also, MacLeod *et al*. (2013), using whole-genome sequencing data with multilocus LD and haplotype homozygosity (MacLeod *et al*. 2009), discovered a strong decline in N_e that dated back to around 170,000 years ago in the two Holstein cattle. Their research further identified the N_e reduction (3,500 – 6,000) that coincided with when cattle were first domesticated. The result showed that the Holstein breed has an estimated 100 N_e, indicating that estimating N_e can help unpack useful information about historical events and the genetic forces that have shaped cattle population size and genetic diversity.

Another recent use of whole-genome sequence data to infer cattle demography history was the work of Weldenegodguad *et al*. (2019). Their study genetically characterised and examined the genetic diversity and demography history of three rare native cattle breeds (Yakutian, Eastern and Western Finncattle) using Li and Durbin (2011) pairwise sequentially Markovian coalescent model. They discovered two significant prehistorical declines in the ancestral species of Eurasian taurine cattle (*Bos primigenius*) attributable to climate change. They also linked the decline in population sizes, genetic diversity, and N_e of these breeds to demographic events such as domestication and selection. Through this research, they were able to extract new information from the breed genome and examine the adaptive features of these breeds regarding the conservation of their genetic resources.

Li and Kim (2015) and Sharma *et al*. (2016) inferred the N_e and the pattern of selection signatures in Hanwoo, a Korean native cattle breed using the LD approach (Sved, 1971) with SNP data. Both studies showed a decline in N_e for the Hanwoo breeds, with the estimated effective population size ranging from 59 to 83. While there was a persistent decline in N_e throughout the generations observed, they recorded a masive sharp decline in the 100th generation followed by two sharp drops in the 50th to 25th and 25th to 10th generation.

2.7 Methods of Estimating Ne (GONE and SNeP)

Irrespective of the methods adopted, estimating effective population sizes and knowledge of demography history and genetic forces surrounding historical events in cattle is vital in developing conservation strategies, especially for the threatened breed with low population sizes. However, this study identifies the LD approach as the ideal choice to estimate N_e and infer recent demography history. Previous studies have shown that they work seamlessly with genomic data and also have computational methodologies and bioinformatics tools available (MacLeod *et al*., 2013; Li and Kim, 2015; Pitt *et al*., 2019) to extract information from both SNP chips (Sharma *et al*., 2016) and whole-genome sequence data (Weldenegodguad *et al*., 2019). Two of these software are SNeP (Barbato *et al*., 2015) and GONE (Santiago *et al*., 2020). Others include NeEstimator (Do *et al*., 2014) and an upgrade of LDNE (Waples and Do, 2008).

2.7.1 SNeP software and its applications in estimating N_e

The SNeP software is one of the earlier LD-based methods of estimating effective population sizes from genomic data. It was developed by Barbato *et al*. (2015). SNeP is a command-line multithread tool that estimates N_e from .ped and .map files obtained using PLINK (Purcell *et al*., 2007). However, users can calculate LD from any other software apart from PLINK, as long as it produces the output files in .ped and .map formats. The software is available for free download at https://sourceforge.net/projects/snepnetrends/, and it works only on Windows and Linux environments at the moment.

SNeP selects a method depending on whether the available data is phased or unphased. Phasing involves all the processes required to infer haplotypes from the available genotype data (Blackburn *et al*., 2020). In other words, phasing identifies different alleles on the paternal and maternal chromosomes. Therefore, the squared correlation coefficient (Hill and Robertson, 1968) that calculates LD from haplotype frequencies is used with phased data. However, when using the unphased data, squared Pearson’s product-moment correlation that estimates LD from coefficient between loci pairs is used. Users can manually choose between phased, unphased or unknown. SNeP calculates historical N_e based on the relationship between N_e, r^2 (squared correlation), and the c (recombination rate). SNeP also allows users to choose between Haldane's (1919) and Kosambi's (1943) mapping functions and apply all corrections to the predicted N_e from LD following Corbin *et a*., (2012). A genetic mapping function explains the rate of combination between two markers due to genetic or map distance between them (Liberman and Karlin, 1984).

Several authors have used the SNeP in estimating N_e and inferring the demography history in cattle (Jemaa *et al*., 2019; Fabbri *et al*., 2020; Chhotaray *et al*., 2021), sheep (Pasandideh *et al*., 2020). The three studies recorded a similar pattern (linear) decline in the N_e curve from the most ancient to the most recent. These have shown that SNeP can estimate N_e and infer the demographic trajectories of cattle. However, most of these reports implied that SNeP is more suitable for inferring ancient demography history (> 100 generations ago). Also, SNeP starts its estimation from the 13th generation, which is not so recent, considering that generation interval could be between 6 – 8 years and even more in some cattle breeds. The assumption behind SNeP stopping its estimation in the 13th generation is that recombination occurs slowly, such that it produces little to no effect on the most recent generations. Another important SNeP concern is that it only detects a linear decline in N_e due to the algorithm used in developing it. Thus, it fails to capture factors that cause sudden changes in population sizes, such as genetic drift, migration, bottleneck, the start of breeding programmes, and conservation efforts (Santiago *et al*.2020).

2.7.2 GONE software and its applications in estimating Ne

Bottleneck, migration, expansions, drop – all these are challenges that many LD-based software fail to address. The quest to develop a computational framework built on complex theoretical and mathematical analyses to accurately estimate N_e and infer recent demography history motivated Santiago *et al*. (2020) to develop GONE. However, it should not be confused with another software with an identical name, GONe (Coombs *et al*., 2012). GONE and all its auxiliary programmes are available for download at https://github.com/esrud/GONE. Like SNeP, it is also command-line based and works on MacOSX and Linux. The input files also require .ped and .map formats.

The Genetic Optimisation for N_e Estimation (GONE) is an update on SNeP and similar methods that adopt a rather simplified approach that assumes that LD between loci pairs across a genetic distance 1/(2t) Morgans defines the value of N_e at specific generations back in time (t). These methods can only identify a linear decline in N_e and inferred demography history. In contrast, GONE based its method on the assumption that the value of LD between loci at any specific genetic distance emanates from the cumulative effects of genetic drift and recombination that have been accumulated across past generations. GONE utilises genetic algorithms (Mitchell, 1998) in inferring demography history data and works with a small sample of individuals. Santiago *et al*. (2020) reported that GONE outperforms earlier methods of inferring demography history, such as NeON (Mezzavilla and Ghirotto, 2015), SNeP (Barbato *et al*., 2015), LinkNe (Hollenbeck *et al*., 2016), a claim which is yet to be validated by unaffiliated researchers. GONE also claim to account for corrections for sampling effects involving both DNA sequencing and genotyping SNP data, whether for phased, unphased or psuedohaploid genotypes.

Pseudo-haploid is the presence of a single allele rather than two, encoded by 0 or 2 with a large amount of missing data (Joseph and Pe'er, 2019).

Users can modify the parameters, including the Minimum Allele Frequencies (MAF), phase, the minimum and the maximum number of chromosomes, the maximum value of recombination rate (hc) and the number of replicates. However, a few studies have shown that GONE runs smoothly with the default parameters, especially for about 200 generations back in time (Saura *et al*., 2021; Novo *et al*., 2022). Unfortunately, no study involving estimating N_e using GONE from cattle data is available at the moment.

3. MATERIALS AND METHODS

3.1 Breed, data, and software information

The first data consisted of 150K Illumina SNP chip data previously used in a study by Upadhyay *et al*. (2019), involving nine Swedish native cattle breeds and 147 individuals. All animals were born between 1970 and 2005. Since secondary data was used, no ethical approval was required for this project. The dataset is available for download at:

https://datadryad.org/stash/dataset/doi:10.5061/dryad.wdbrv15j4

The genotype data were obtained from the whole-genome sequence of the same breeds (5 out of 9) but with different sample sizes. The description of the SNP chip data can be found in **Table 1**, and the genotype data in **Table 2**.

Table 1. Description of breed name, number of sample sizes used in different breeds, and the number of SNPs used per breed as analysed by GONE.

Breeds	Abbreviation	Number of SNPs	Sample size
Swedish Mountain Cattle	SMC	106,664	23
Bohus Polled cattle	BHP	109,275	6
Fjällnära Cattle	FNC	105,399	16
Swedish Polled Cattle	SPC	115,075	12
Swedish Red Polled	SRP	111,303	17
Ringamåla Cattle	RMC	109,593	13
Väne Cattle	VAC	114,926	9
Swedish Holstein-Friesian	SHF	111,979	24
Swedish Red Cattle	SRC	94,031	23

3.2 Genotype Data and Quality Control

Table 2. Description of breed name, number of the sample size used in different breeds, and the number of SNPs used per breed in whole genome sequence data estimated from GONE

Breeds	Abbreviation	Number of SNPs	Sample size
Swedish Mountain Cattle	SMC	666,411	7
Fjällnära cattle	FNC	845,608	4
Swedish Red Polled cattle	SRP	1,007,250	9
Väne cattle	VAC	730,251	5
Swedish Red cattle	SRC	859,820	8

Illumina sequence data from 33 Swedish native cattle were processed using Sarek v2.7.1 (Garcia *et al.*, 2020), a workflow for variant calling implemented in

Nextflow and part of the nf-core collection of pipelines. Sarek runs part of the GATK Best Practices workflow to align the reads of each sample to the reference genome, pre-process the alignment, and perform the first step of variant calling using the HaplotypeCaller GVCF method. After Sarek analysis, the output GVCF files were merged with GATK v4.2.6.1 (Mckenna *et al*., 2010) to perform joint variant calling with the Haplotype Caller.

Next, filtering was performed to include only SNPs that passed these parameters:

QD < 2.0

QUAL < 30.0

SOR > 3.0

FS > 60.0

MQ < 40.0

Finally, conversion to PLINK files split up into breeds.

3.3 Estimating the effective population size

Two software developed based on the linkage disequilibrium approach were used for analysing the effective population sizes. The first is GONE (Santiago *et al*., 2020), and the second is SNeP software (Barbato *et al*., 2015).

3.3.1 Filtering setting while estimating Ne with GONE

Table 2 shows the number of SNPs that survived the filtering settings using GONE’s default input parameters. These include using unknown phase, centiMorgans per Megabase with unknown genetic distance between markers, and Haldane correction. Others include 2,000 as the maximum number of generations for which LD is obtained and 400 as the number of bins with 5 generation gaps, besides the first 10 generations that use 2-gen gaps. The minimum allele frequency ranges from 0 to 1, with 0.0 used as the default, indicating no pruning will be applied. The maximum value of c (recombination rate), hc, is set at 0.05. However, in the case of recent population admixture or breed clustering, the estimated will be biased, and lower hc (0.01) is recommended. Only FNC required using hc = 0.01 due to documented admixture or breed clustering (Johansson *et al*., 2020). All SNPs with zero were removed, and the default 40 replications was used.

3.3.2 Filtering setting while estimating Ne with SNeP

The default parameters for SNeP *were used* all through this analysis. However, only the autosome (chromosome 1 - 29) was analysed, while the sex chromosome was discarded using the PLINK command. This is because the software method does not account for sex chromosomes. Subsequently, .map and .ped data were obtained from PLINK. The default 50,000bp minimum distance between SNPs and 4,000,000bp maximum distance was also selected. The MAF was set at 0.05, and loci with allele frequencies below 0.05 were subsequently removed. The maximum number of SNPs per chromosome is set at 100,000 and N_e was estimated using Corbin *et al*. (2012) formula:

$$N_{T(t)} = \frac{1}{(4f(C_t))} \left(\frac{1}{E\left[r^2_{adj} \mid C_t\right]} - \alpha \right)$$

where:

$N_{T(t)}$ = *effective population size t generations ago*

C_t = *recombination rate of specific distance between markers*

α = *correction for mutation occurrence*

r^2_{adj} = *adjusted LD for sample size and gametic phase*

However, unlike GONE, SNeP does not report the total number of SNPs analysed. Since the phase is unknown, SNeP used both the squared correlation coefficient and squared Pearson's product-moment correlation coefficient between a loci pair to calculate LD. Other parameters were set at default.

3.3.3 Data Visualisation and Plotting

R packages were used to visualise and plot the results derived from GONE and SNeP.

4. RESULTS

4.1 Estimates based on high-density SNP Chip data

This study estimated the effective population sizes and inferred the demographic history of 147 samples of Swedish native cattle from nine indigenous Swedish cattle breeds using two methods built on the Linkage Disequilibrium approach through the SNeP and GONE software.

4.1.1 Total Number of SNPs used estimated from GONE

The total number of SNPs used per breed was recorded using the default parameters. SRC had the highest total number of SNPs at 115,075, closely followed by SRC at 114,926. VAC had the lowest value at 94,031 **(Table 4).**

Table 3. Number of SNPs used in each breed as estimated by GONE with the same filtering settings, except in FNC where hc = 0.01 was used instead of 0.05.

Breed	Sample Size	Total Number of SNPs
Bohus Polled Cattle (BHP)	7	106,664
Fjällnära Cattle (FNC)	16	109,275
Ringamåla Cattle (RMC)	13	105,399
Swedish Holstein-Friesian (SHF)	24	115,075
Swedish Mountain Cattle (SMC)	23	111,303
Swedish Polled Cattle (SPC)	12	109,593
Swedish Red Cattle (SRC)	25	114,926
Swedish red polled cattle (SRP)	18	111,979
Väne cattle (VAC)	9	94,031

4.1.2 Estimated recent effective population size using GONE

The inferred demography history was restricted to 200 out of 676 generations observed, as GONE only accurately estimates the recent change in effective population sizes. Using the default maximum recombination rate of 0.05 and 40 replicates, a general non-linear decline was observed in the demography trajectory for all breeds **(Figure 3).**

Also, questionable FNC estimates were observed, with a meteoric rise from 24 N_e four generations ago to 43,090 in the fifth generation **(Table 4)**. This completely deviated from other breeds' plot patterns and demographic history trajectories. The biased result prompted performing a Principal Component Analysis that helped ascertain admixture populations already discovered by Johansson *et al*. (2020) between a sample of FNC and SMC (**Figure 1).**

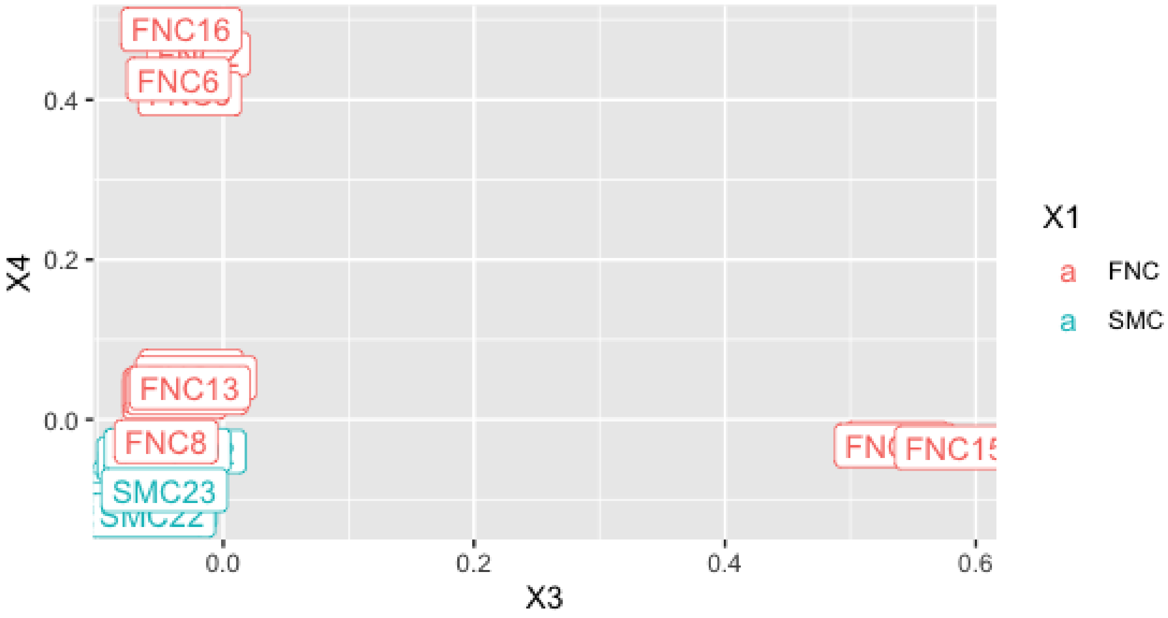

Figure 1. PCA showing clusters between FNC 8 and SMC cattle at the left bottom corner of X4 y-axis between – 0.9 and 0.0 range. The red colour indicates FNC, while the blue colour denotes FNC.

In order to get the actual value for the current estimates, Santiago *et al*. (2020) recommendation was followed by reducing the maximum value of c (hc = 0.01) instead of the default 0.05. The hc parameter controls the level of the recombination rate, that is, the length of pairwise marker distance that GONE will include in the analysis. Therefore, a change in the pattern of N_e estimates were obtained and a change in the rank order **(Figure 2 and Table 7)**. Closer-to-reality estimates were recorded based on breed associations' available information and FAO DAD-IS data. SHF topped the list with 224 *Ne* values, followed by SRC at 168. SMC comes 3rd with 126, followed by its subpopulation, FNC, at 73 N_e. VAC, BHP, and RMC recorded the lowest *Ne* at the most recent generations with 20, 31 and 54 values.

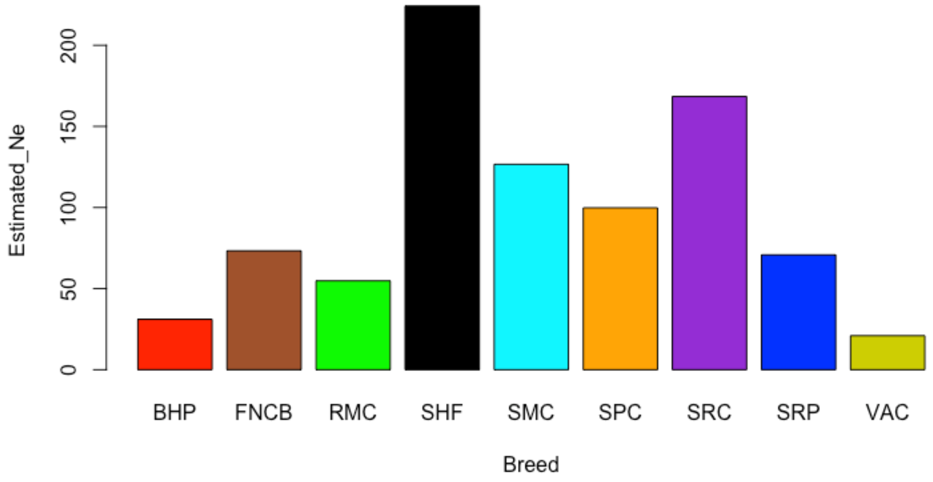

Figure 2. A bar chart showing the estimated Ne for the first generation while using hc =0.01 for FNC and hc = 0.05 for other breeds with GONE software. Each bar on the x-axis represents each breed, while the x-axis shows the estimated N_e *up to 200 generations ago.*

4.1.3 Inferring the demography history from GONE

The demography history shows the trajectory of changes in the breeds. The FNC breed was removed from subsequent analyses to eliminate biases from admixture. All the breeds recorded a non-linear pattern of the curve, with 200 generations having the highest estimates in all breeds.

Estimates of distant historical N_e showed that SRC had the highest value 200 generations ago, with 20,423 (**Figure 3**). The pattern of the curve kept fluctuating, albeit with a decline. However, there was a significant drop between the 28th to 27th from 1775 to 599. SRC retained its position as the top ranked until between the 5th and 4th generation, when there was a drastic drop from 185 to 168. The breed has the second-highest temporal N_e value from 1 to 4 generations ago at 168 (**Table 4)**.

Interestingly, with its current highest N_e (224) from generations one to four, SHF recorded one of the lowest N_e values 200 generations ago, with 4,319. However, the breed has maintained the most stable decline in N_e among all the eight breeds, with no dramatic drop over the past 200 generations.

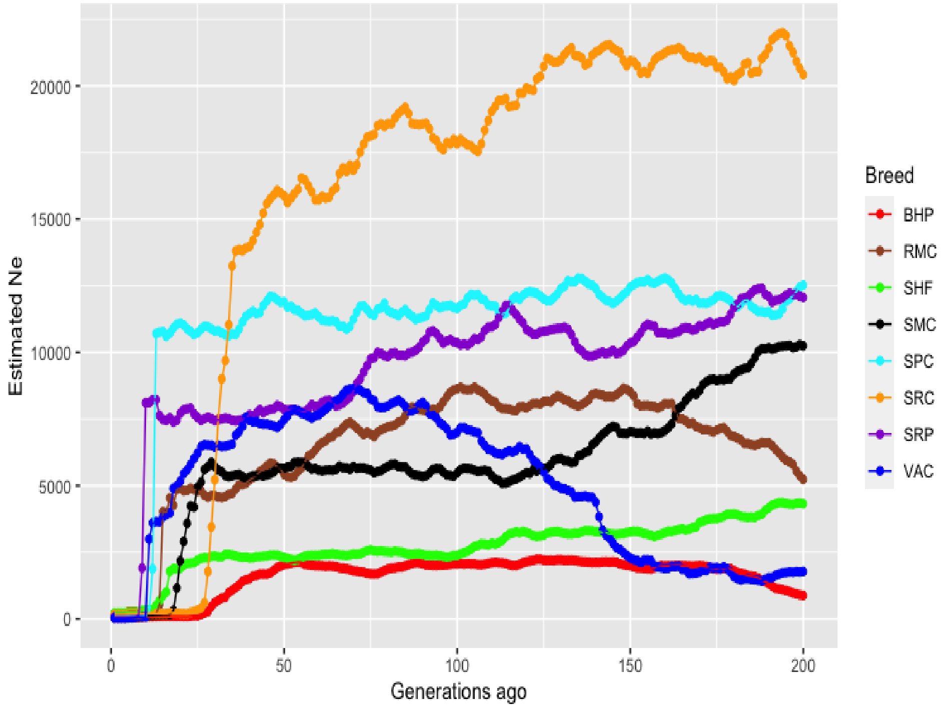

Figure 3. The estimated effective population size of 8 Swedish cattle breeds over time with GONE. The y-axis denotes the estimated Ne while the x-axis represents Generations ago. The colour of the line indicates each breed.

Being one of the most crucial mountain cattle, the SMC also ranked high at 4th 200 generations ago with 10,2045 N_e. A dramatic decline was noted between the 19th and 18th generations when the N_e dropped from 1159 to 306. The breed currently ranks 3rd with 127 N_e.

Although SPC ranks 4th in the most recent N_e, it came second after SRC 200 generations ago. It maintained its consistency with a gradual decline until the 12th generation, when it experienced a dramatic drop, from 10,705 to 1876 in, 11 generations ago (**Table 4**). It further experienced another significant decline between the 11th and 10th generations 1876 to 265. It, however, gained a slight increase in a N_e generation 5 before dropping again in the 4th generation.

SRP was among the highest-ranked N_e 200 generations ago, with 12,050. Like SPC, the SRC pattern of decline was linear until the 10th generation, with a huge drop from 81006 to 1905 and another decline between the ninth and eighth generations ago (1905 to 120). The breed decline has been relatively stable from the 8th generation until the first generation.

RMC has one of the most inconsistent demography trajectories of all eight breeds. The breed recorded 5192 N_e 200 generations ago, before jumping dramatically to 6077 in the 194th generation. This pattern of increase and decrease continued until the 15th generation experienced a sharp drop from 4021 to 533. The lowest N_e value for RMC was recorded at the 8th generation (39) before it gradually increased until the fourth generation (54).

As observed in RMC, BHP also experienced an irregular pattern of N_e trajectory. The N_e value had a steady increase from 200 to the 86th generation. This was followed by a rising and falling pattern before it stabilized in the 34th generation. The decline was gradual until the 8th generation when the N_e shot from 88 to 258th. This was maintained for 3 years before a drastic drop to 31 four generations ago.

VAC also recorded a non-linear pattern of N_e until the 11th generation, when there was a drastic decline (2996 to 76). The breed has consistently declined since ten generations ago and currently has the lowest value (20) of all eight breeds.

Table 4. Estimated Ne obtained from using GONE for generations 1 to 20. The first column indicates the generations, while the remaining column in the first row shows the breed abbreviations.

GEN	BHP	FNC	RMC	SHF	SMC	SPC	SRC	SRP	VAC
1	31	24	55	224	127	100	168	71	21
2	31	24	55	224	127	100	168	71	21
3	31	24	55	224	127	100	168	71	21
4	31	24	55	224	127	100	168	71	21
5	258	43090	48	225	129	106	185	73	29
6	258	43090	43	248	121	104	189	82	35
7	258	43090	40	249	121	102	191	82	56
8	88	43090	39	250	121	103	191	121	80
9	87	46456	60	307	123	118	194	1906	76
10	86	47050	93	321	136	265	196	8107	76
11	86	47258	133	331	137	1876	197	8107	2995

12	86	47312	156	335	139	10705	199	8224	3596
13	90	46726	173	505	146	10757	196	8226	3649
14	95.6	47982	534	681	149	10778	196	7632	3639
15	96	49151	4021	862	164	10603	196	7478	3826
16	96	49348	3995	1008	168	10720	198	7448	3905
17	95	51425	4534	1788	170	10914	224	7544	3972
18	95	52971	4260	1881	306	1052	222	7383	4896
19	94	52350	4857	1875	1160	11052	212	7452	4992
20	94	51736	4902	1899	2176	11095	201	7710	5163

4.1.4 Estimated Ne and demography history from SNeP

SNeP estimates start from the 13th generation as the software does not have the capacity to accurately calculate the most recent N_e and ancient generations due to the limitation of the method used. Therefore, the analyses were limited to 200 generations ago. N_e estimates from SNeP (**Figure 4**) show a smooth decline across all the generations for the nine observed cattle breeds. This indicates the trajectory of how the historical effective population sizes have shrunk over the past < 200 (187) generations. However, despite all breeds displaying a similar pattern in the curve trend, the N_e values differ across different breeds. For instance, SHF has the highest 171 N_e value in the most recent generation (13th), while the SRC came at a distant second with 123 **(Table 5)**. SMC closely follows this with 117 $N_{e.}$ In contrast, BHP has the lowest N_e of just 34 at 13 generations ago, while the Väne Cattle followed closely at 37.

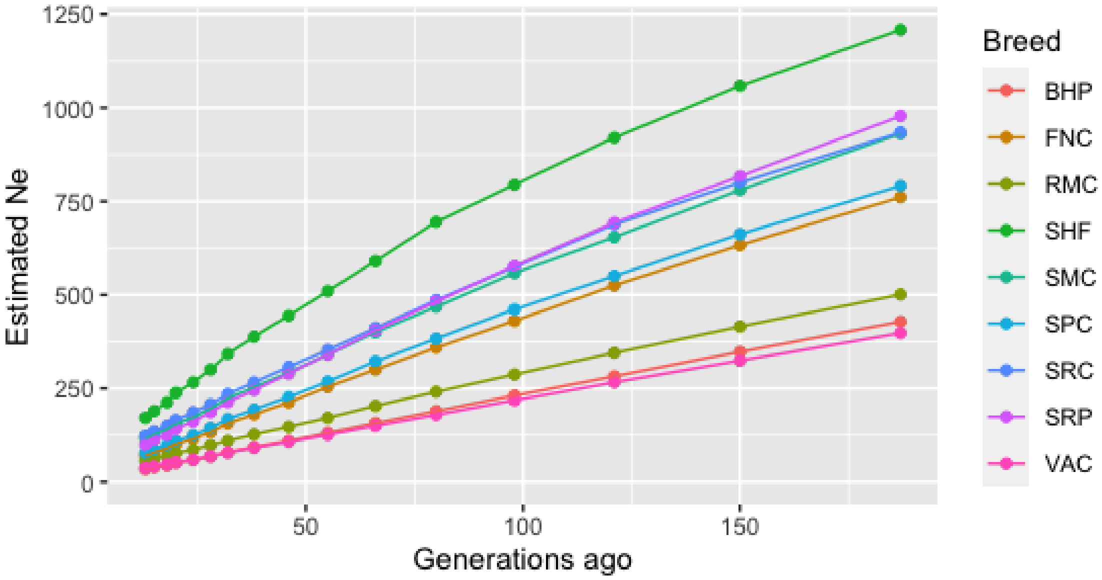

Figure 4. The estimated effective population size of 9 Swedish cattle breeds over time with SNeP. *The y-axis denotes the estimated Ne while the x-axis represents Generations ago. The colour of the line indicates each breed.*

Two mild drops were observed for all breeds between 150 and 121 generations ago and the 46th and 38th generations, as shown in **Table 4**. The decline between the 38th and 13th generations was linear, with no drastic drops.

Table 5. Ne estimates using default parameter in SNeP *showing 13th to 55th generation out of the total 187 generations estimated. The 1st column indicates generations ago (GenAgo), while the other ones are abbreviations for each breed*

GenAgo	**BHP**	**FNC**	**RMC**	**SHF**	**SMC**	**SPC**	**SRC**	**SRP**	**VAC**
13	34	70	56	171	117	77	123	99	37
15	39	78	62	189	128	86	135	112	41
18	44	89	69	212	141	98	150	126	46
20	51	101	77	238	155	110	165	142	52
24	59	116	86	266	173	125	186	161	59
28	68	133	98	300	196	144	207	186	68
32	79	156	110	342	223	168	235	213	78
38	93	180	127	388	253	193	266	245	91
46	110	212	147	444	392	227	307	289	107
55	131	254	171	510	340	268	353	340	126
66	157	300	203	590	400	322	411	405	150
80	189	359	241	695	468	383	486	482	179
98	231	430	287	794	558	461	574	577	218
121	282	525	345	920	654	550	688	693	266
150	348	633	415	108	780	662	800	817	324
187	428	761	501	120	931	791	934	978	398

4.1.5 Comparison between GONE and SNeP Ne Estimates and Demography History

A comparison was made for the effective population sizes obtained from GONE with those derived from *SNeP*. Both methods showed an overall decline in N_e across all breeds. However, the pattern of the curve in *SNeP* was linear and gradual, with no dramatic changes in N_e values ***(Figure 5)***. In contrast, GONE curve patterns were non-linear, with some breeds having up and down trajectories. This could indicate selection programmes, bottlenecks, and conservation strategies.

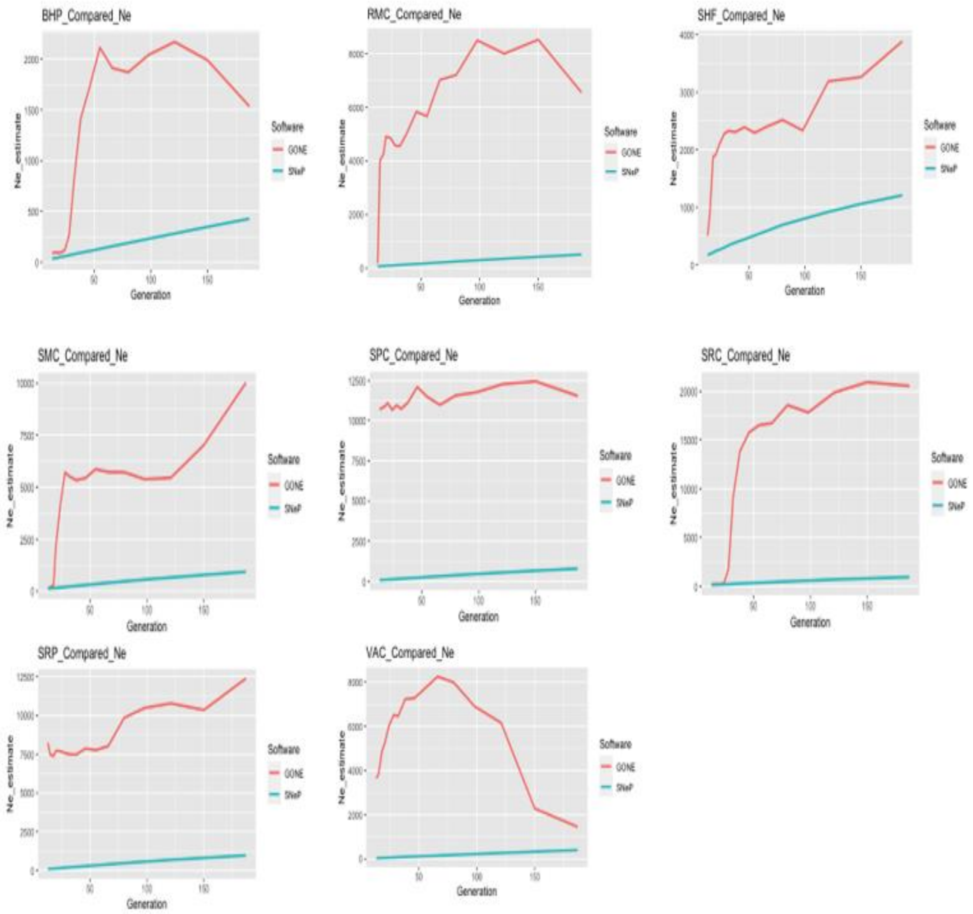

Figure 5. Compared Ne result for GONE and SNeP. The red line represents GONE, while the blue line indicates SNeP. The y-axis denotes the Ne estimate, while the x-axis indicates the generation

Estimates from SNeP, built on (Corbin *et al*., 2012) equation, were lower than GONE estimates with the (Mitchell, 1998) genetic algorithm. Another contrasting point is that GONE provided the most recent estimates (generation one), while

SNeP estimates start from the 13th generation. This indicates that no side-by-side comparison of estimates from GONE and SNeP between 1 and 12 generations ago.

However, even though the results from the GONE and SNeP methods are quantitatively different, they follow a similar curve pattern, and their N_e values have similar rank order using the most recent N_e **(Table 4 & Figure 5).** Both methods ranked SHF, SRC, and SMC as 1st, 2nd, and 3rd, respectively, while RMC, BHP and VAC were the least, with slightly different rank orders (**Table 6**).

*Table 6. Comparison between GONE and SNeP Ne Result for the most recent populations (1st and 13th respectively). ** indicates hc = 0.01.*

Breed	Estimate GONE (rank)	Estimate SNeP (rank)
Bohus Polled Cattle (BHP)	31 (8TH)	34 (9TH)
Fjällnära Cattle (FNC)	73 (5TH)**	70 (6TH)
Ringamålako Cattle (RMC)	54 (7TH)	56 (7TH)
Swedish Holstein-Friesian (SHF)	224 (1ST)	171 (1ST)
Swedish Mountain Cattle (SMC)	126 (3RD)	117 (3RD)
Swedish Red Cattle (SRC)	168 (2ND)	123 (2ND)
Swedish Polled Cattle (SPC)	99 (4TH)	77 (5TH)
Swedish Red Polled (SRP)	70 (6TH)	99 (4TH)
Väne Cattle (VAC)	20.98 (9TH)	37 (8TH)

4.2 Estimates Based on Whole Genome Sequence Data

4.2.1 Estimates from GONE with sequence data

Using the default parameters for GONE, N_e values for five Swedish native cattle breeds were obtained from whole-genome sequencing. Swedish Red Polled Cattle retained the highest Total Number of SNPs with 1,007,250, with the lowest recorded in Swedish Mountain Cattle with 666,411 **(Table 6).**

Table 7. Breeds, sample size and the total number of SNPs used by GONE for whole-genome sequence data.

Breeds	Sample size	Total Number of SNPs
Fjallnära Cattle	4	845,608
Swedish Red Polled	9	1,007,250
Swedish Mountain Cattle	7	666,411
Swedish Red Cattle	8	859,820
Väne Cattle	5	730,251

Surprisingly, SRP recorded the highest N_e 200 generations ago (66,489), a position it maintained before it suffered a drastic decline of almost 50% in the 13th generation (14,407 to 7,213) **(Figure 6).** This was followed by another sharp drop between the 11th and 10th generations (487 to 185). It ranked second in the list for the most recent N_e at 62, with a distant gap between SMC (107) and SRC (126). There is an overlap between SMC, SRP and VAC around 178 generations.

However, as in SNP Chip data, a general decline was experienced across all breeds until recent generations.

Of all the five breeds analysed for whole genome sequence data, SRC has the highest N_e at the most recent generation (126), and the least was observed in VAC (23). It experienced a relatively stable pattern of decline until it suffered a significant drop the 11th generation ago, followed by a slight decline in the 9th and 8th generation **(Table 8)**. The drop continued until the 4th generation before it increased slightly until the most recent generation.

SMC has the most stable pattern of decline across all generations, with no dramatic drops observed.

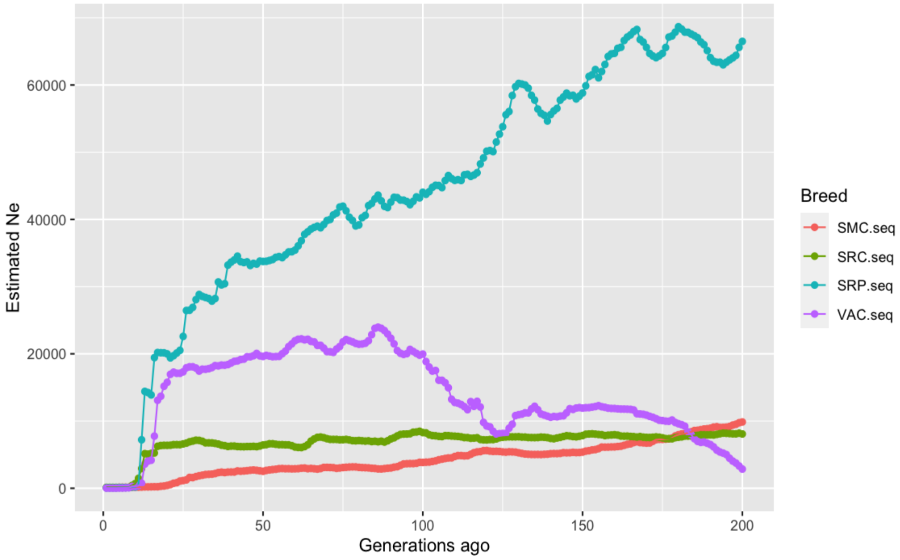

Figure 6. Estimated effective population size for 4 Swedish native cattle across 200 generations ago using GONE. The y-axis denotes the estimated Ne, while the x-axis indicates generations ago. The colour of the line indicates each breed

Table 8. Estimates for 20 generations of five Swedish native cattle breeds derived from sequence data using GONE

Generation	**FNC**	**SMC**	**SRC**	**SRP**	**VAC**
1	41	107	126	62	23
2	41	107	126	62	23
3	41	107	126	62	23
4	41	107	126	62	23
5	12343	148	115	97	34
6	12343	150	113	97	34
7	12343	150	115	96	52
8	12343	149	125	104	73
9	13340	152	414	186	279
10	13674	163	691	185	274
11	13733	164	1464	487	382
12	13742	175	2936	7213	752
13	14180	202	5144	14407	3595
14	14027	201	5067	14236	4043
15	13967	210	5179	13887	4174
16	13864	221	5251	19436	7757
17	13619	220	6243	20195	13090
18	13632	291	6357	20164	13685
19	13687	334	6391	20151	15173
20	13609	424	6386	19994	15757

FNC showed an excessively high decline between the four to five generations (41 to 12,343), a repeat of the SNP data observation **(Table 8).** Also, 5 to 200 generations recorded massive unstable decline and increase, which made the estimate biased and unreliable for this analysis. Therefore, FNC was removed from the plotting. The lowest N_e value was recorded in VAC from the 200th generation (2851) to the most recent generation (23). There were multiple drops across different generations in VAC. However, the two most dramatic declines were observed 13th and 12th generations (3,595 to 751) and the 9th and eighth generations (279 to 73).

4.2.2 Estimates from SNeP with sequence data

SNeP estimate from whole-genome sequence data shows a characteristic linear decline across all generations (**Figure 7**), just like in SNP Chip data **(Figure 4)**. SRC recorded the highest N_e value compared to GONE's result, where SRP was the leading breed 200 generations ago. However, SRC (84) has the highest *Ne* in the most recent generation, as previously observed in GONE's result **(Table 7).** As established in GONE**,** VAC had the lowest N_e value (30) in ancient and recent generations. Interestingly, SMC had the third N_e 200 generations in contrast to recording the second-highest Ne value with GONE at the same time. No dramatic decline was observed in the *SNeP* result for sequence data, as the curve pattern indicates that the demographic trajectories were linear **(Figure 7)**.

Table 8: N_e estimates from SNeP using sequence data of 5 Swedish native cattle breeds for generations 13 to 187. The 1st column indicates generations ago (GenAgo), while the other ones are abbreviations for each breed

GenAgo	FNC	SMC	SRC	SRP	VAC
13	35	54	84	65	30
15	40	62	95	73	34
18	46	68	108	83	39
20	52	77	124	95	45
24	61	89	142	109	51
28	71	100	163	125	59
32	83	118	191	146	69
38	98	132	223	172	82
46	116	157	262	199	96
55	139	181	312	237	114
66	168	217	373	286	137
80	204	263	448	345	165
98	247	319	540	415	202
121	302	395	657	506	248
150	373	478	800	616	306
187	465	584	974	758	378

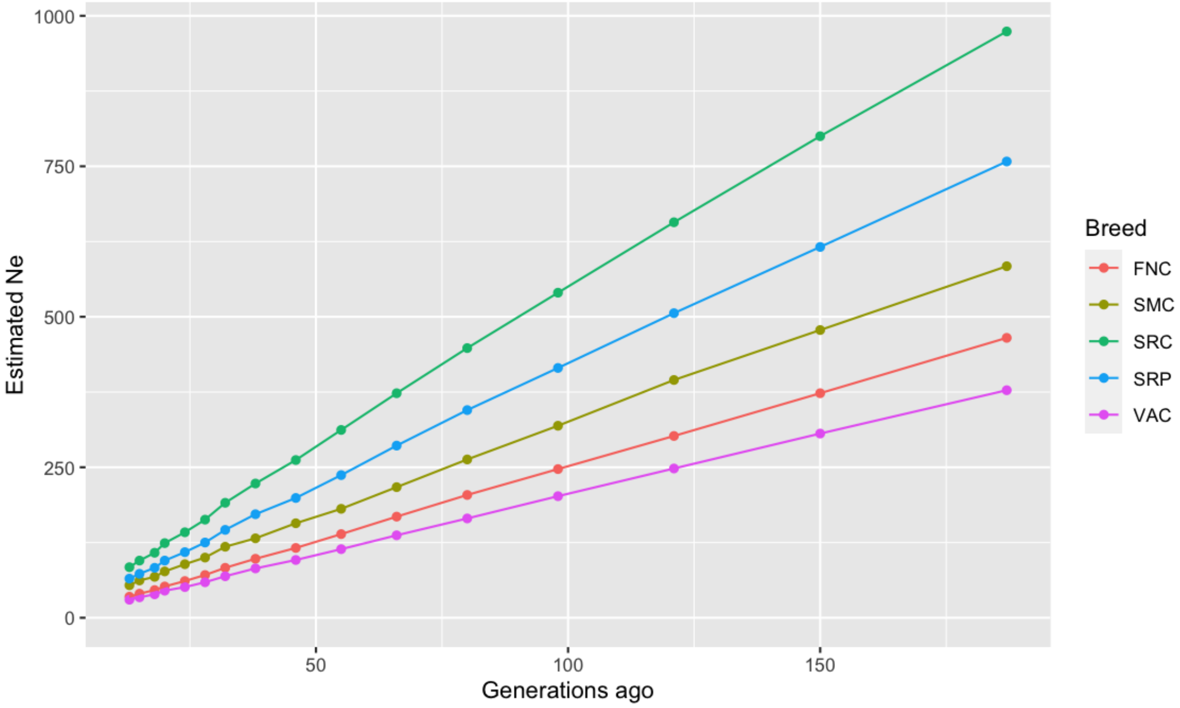

Figure 7. Estimated effective population size for 5 Swedish native cattle across 200 generations ago using SNeP. The y-axis denotes the estimated Ne, while the x-axis indicates generations ago. The colour of the line indicates each breed.

5. DISCUSSION

The effective population size (N_e) and the demography history of the nine Swedish native cattle registered in the Swedish Board of Agriculture were estimated for the first time using the Linkage Disequilibrium approach, using GeneSeek GGP Bovine 150K Illumina SNP chip data. Also, the study complemented the results observed in SNP chip data by comparing it with estimates derived from whole-genome sequence data for five breeds out of the nine Swedish traditional cattle populations using GONE and SNeP software. The study shows varying degrees of effective population size of Swedish native cattle, possibly shaped by different demography events such as breed formation, migration, bottleneck, and founders' effects.

5.1 Demographics trajectory and decline in population size

The non-linear pattern of the N_e curve observed in Swedish native cattle breeds suggests different events culminating in a reduction in census population and effective population sizes due to genetic drift. These fluctuations in the demographic pattern can be attributed to breed formation, importation of animals from different countries leading to admixture, founder events resulting from the isolation of certain breeds (Swedish mountain cattle), merging, and eventual breed separation. Saura *et al*. (2021) obtained a similar pattern of decline between the five to nine generations while estimating the effective population sizes of turbot, seabream and European seabass using GONE, with these drops potentially attributed to artificial selection and founder effect and admixture

All the breeds recorded a decline in effective population sizes from 200 generations ago (circa 1200 years), with an average of 8,824. Comparatively, the most recent observed N_e stands at 874 on average, an almost 90% loss of effective population sizes across breeds. While there are currently no studies that exclusively estimate the effective population size of Swedish cattle breeds, the decline observed in this research corresponds with previous studies that assessed the pattern of changes in N_e values in other traditional cattle breeds (Flury *et al.*, 2010; Li and Kim, 2015; Jemaa *et al.*, 2019). Although the standard value for stable N_e is debatable, there is a consensus that $N_e \leq 50$ is insufficient to avert inbreeding depression and retain fitness within a short period, while $N_e \geq 100$ is considered stable to limit total fitness loss to less than 10% (Frankham *et al.*, 2014). Using 0.05 as the maximum value of the recombination rate, the lowest $N_e < 50$ were recorded in Väne, Fjällnära and Bohuskulla, respectively.

However, when hc = 0.01 was used for FNC due to its admixed origin or breed clustering. The result showed that Bohus Polled, Väne, and Ringåmala recorded the least effective population size with 31, 20 and 54 N_e values, respectively **(Table 3.)** Expectedly, according to FAO DAD-IS, these three breeds have red “at-risk” status and are currently under conservation by Föreningen Allmogekon. Other native breeds are equally endangered (less than 100 N_e) except Swedish Holstein Friesian (224), Swedish Red Cattle (168), and Swedish Mountain Cattle (126). However, only SHF and SRC are considered “Not-at-Risk.” Although this study shows that SMC has recent N_e above 100, the risk status is currently set to “Unknown” according to FAO DAD-IS 2014 population data. Therefore, there should be caution in classifying SMC in the same bracket as SHF and SRC with an already established “Not-at-Risk” status. The relatively high N_e observed in SHF, SRC, and to some extent SMC highlights their considerable census population size (**Table 3)**. However, it should be noted that SMC is comparatively smaller and in probably in a more vulnerable status than SHF and SRC.

Since the total population of animals determines their response to genetic drift, increasing the population of native cattle will ultimately affect their $N_{e.}$ Also, the economic value of breeds determines the attention breeders place on them and subsequently impacts farmers ‘ decisions in keeping them. This was reflected in the census population and the effective population sizes of Swedish Holstein Cattle and Swedish Red Cattle, the two highest milk producers. In contrast, Väne, Bohus Polled, Ringåmala, and Fjällnara, known as poor milk and meat producers, have low census populations and $N_{e.}$

Attempts to match a significant drop in N_e value to real-life events such as breed formation, migration and admixture are subjective and may not reflect the actual occurrences due to differences in the assumed range of generation interval (6 – 8 years) for this study and the sampling points (1970 - 2016). Also, most breed existence predates their discovery, herd book establishment, and breed formation. For instance, there is evidence of a text from 1296 AD that described Fjäll as “small, hornless, white or white greyish, often with dark spots” (Wilson, 1909). Contrariwise, its herd book was established in 1907, while the breeding association was formed in 1995. Furthermore, some original breeds, such as the Swedish

Holstein-Friesian, are considered extinct but introgressed in other breeds and maintain their original names (Bett *et al*., 2013).

Most breeds suffered a massive decline in N_e between 10 and 15 generations ago, which coincides with the start of breed formation. For example, SHF recorded a loss of 176 *Ne* between 14 and 13 generations ago. With an average birth year of 1991, this corresponds to 78 years before sampling (1913), a period when the breed association was formed. However, matching drops in N_e to real-life events in breeds is hypothetical and might not truly represent the occurrences. Although with different N_e values and varying demographic trajectories, both SNP Chip and whole-genome sequence produced similar results and rank order, especially for the most recent generations **(Tables 3 & 6).**

5.2 The special case of FNC

With GONE, the Fjällnära exhibited a deviation from the pattern of the N_e curve for other breeds, while the same linear curve was observed with *SNeP* as in all breeds. The analysis showed a meteoric rise from 24 in four generations ago to 43,090.1 in the 5th generation for SNP data and 41 to 12,343 in sequence data **(Table 3 & 7)**. There was no possible explanation for this massive increment using the breed’s census population size (husdjursstatistik, 2019; DAD-IS). Fjällnära, together with its subpopulation, Fjäll, is managed by Svensk Fjällrasavel and has benefitted from the collaboration between the Swedish Board of Agriculture and Viking Genetics to develop a sustainable breeding plan (“Swedish Mountain Cattle,” n.d.). Therefore, the Fjällnära breed will most likely have a higher census and effective population size than the Väne, Bohuskulla and Ringåmala breeds.

Another partly supporting evidence for the biased result is the census population size of FNC, which is comparatively higher than Väne, Bohus Polled, and Ringåmala. Also, results from Principal Component Analysis showed that one of the samples in the Fjällnära (FNC8) clustered with the Fjäll population **(Figure 1).** This was earlier discovered by Johansson *et al*. (2020) admixture analysis, which showed a recent mixed ancestry between Fjäll and the Fjällnära breeds. Santiago *et al*. (2020) recommended using maximum recombination (hc) value lower than the default 0.05 in an instance where there was a recent admixture (or breed clustering). Therefore, lowering the hc value will exclude marker pairs at a long distance, providing FNC's most recent N_e as 73, a more likely accurate result based on existing knowledge of the breed. However, with hc = 0.01, the current population size and the magnitude of the historically large samples are similar, with an unrealistic N_e at 12 generations ago. Therefore, FNC was eliminated from the analysis to generate unbiased estimates across all breeds.

5.3 Comparison between SNP Chip and Sequence Data

Compared to the Illumina SNP data, whole-genome sequences have a significantly higher total number of SNPs, with an average of 821,861 and 108,693, respectively. This indicates that whole-genome sequence data is more informative with lesser ascertainment bias. Also, it can detect more rare alleles, with a superior ability to discover variants that may be responsible for traits of interest and certain diseases where the sample sizes are large enough. This observation corresponds with Pérez-Enciso *et al*. (2015) experiment that compared the prediction accuracy of whole-genome sequence and chip-assisted data. However, the sample size for this study is not large enough to accurately detect rare alleles.

The estimates obtained from both whole-genome and SNP data, although quantitatively different, have similar N_e outputs, demography trajectories, and curve patterns. However, recent N_e estimates from the whole genome sequence are slightly lower than SNP Chip across all breeds. Nevertheless, the gap is minimal when compared—for instance, 168 versus 125 in SRC and 127 versus 107 in SMC. Likewise, the ranking of the most recent estimates N_e are similar when contrasted **(Table 3 & 7).** Interestingly, both data confirmed the anomalies observed in Fjällnara Cattle, which further suggested that FNC's recent clustering or admixture could be responsible for its biased estimates.

Also, GONE covered 792 generations with whole-genome sequence, compared to 676 in SNP Chip data, while *SNeP* covered 995 and 1000 generations in SNP Chip and sequence data, respectively. This indicates that the whole genome provides more in-depth coverage of the genome region and utilises a higher total number of SNPs than the Illumina SNP Chip data. However, sequencing the whole genome is more expensive and more computationally demanding. Nevertheless, it would be ideal for future studies to utilise whole-genome sequence data due to the merits mentioned above if funding is not a concern.

5.4 Research limitations

Some limitations were encountered during this study. They include sample size, sampling point, missing breeds in sequence data, and lack of algorithm to estimate the most recent generations.

According to Santiago *et al*. (2020), the sample size is one of the factors that could impact the accuracy of the N_e result, particularly in recent generations. This is because a low sample size usually has a weak drift signal. The method requires a large sample size to detect drift signals and correct for sampling errors. While the developers failed to categorise the required minimum sample size per breed, the minimum sample size allowed for this study was four. Therefore, some breeds with smaller sample sizes were discarded from the analysis.

Also, the average birth year for animals used in this study was 1989, with the most recent sampling point being 2016. Although this might not directly impact the result of this analysis, sampling and genotyping younger and live animals could potentially provide a more accurate matching of demographic trajectories with more recent historical events, thereby highlighting the success or otherwise failure of the ongoing conservation strategies for Swedish native cattle.

Furthermore, only five of the nine Swedish native breeds were analysed for the sequence data due to limited financial resources and few cattle for phenotype sampling. Using sequence data for all nine breeds would provide a more accurate basis for comparing the SNP Chip and sequence data results across all breeds.

Lastly, there is a need for algorithms that can accurately estimate N_e for the most recent generations (1 – 3 generations ago). As observed in the *SNeP* result, estimation starts from 13 generations ago (approximately 91 years) when using 7 as the generation interval. This is a huge number of years as this study focuses on estimating the effective population size and inferring the demography history of recent times. However, while GONE provides estimates up to the 4th generation, generations 1 to 4 are exactly the same. The method likely assumes that the recombination rate was too low to affect three generations ago (21 years) significantly. An improved method should accurately account for the first three generations to measure the developments in conservation strategies in the past two decades.

5.5 Relevance of research to conservation programmes, cattle production, and agriculture

Besides contributing to academic knowledge, this research is relevant to agricultural production, cattle farming, breeding, and conservation strategies. Currently, one of the most used methods in estimating N_e has the formula:

$$\mathrm{Ne} = \frac{4NmNf}{(Nm + Nf)}$$

Where;

N_e = *effective population size*

N_m = *number of males*

N_f = *number of females.*

However, this method is limited as it assumes no generation overlap and requires full pedigree knowledge. Also, it can only estimate N_e for a single sampling point. There is no way to go back in time, and thus, it is restricted to having full knowledge of the pedigree to estimate ancient N_e and infer the demography history. In addition, the method cannot identify the historical events such as bottleneck, expansion, and drops that have shaped the breeds over the past years. Therefore, the result obtained in this research could be useful in breeding programmes and conservation strategies for Swedish local cattle breeds.

In order to achieve genetic progress in local breeds, it is imperative to have a full understanding of their demographic histories and how they have responded to different genetic events in time past. This research will facilitate improved conservation as it provides the trajectories of N_e, thereby offering animal breeders the premises to match previous conversation strategies to an improvement in N_e observed.

Studies specifically dedicated to Swedish native cattle breeds are limited. This can communicate a lack of support and incentive to local farmers that have sacrificed economic gains from raising commercial breeds for dedicating their time to protecting indigenous Swedish cattle breeds as a source of cultural heritage, a pool of genetic resources, and a potential solution to future climate challenges. This research can motivate farmers to intensify their efforts in keeping traditional cattle, regardless of the economic values of exotic commercial breeds.

5.6 Conclusion

In summary, the result of this study shows that the current effective population sizes of Swedish native cattle vary across breeds. Two of these breeds have current N_e below the critical value of 50 that research recommends for preventing inbreeding depression and guaranteeing the short-term sustainability of selection programmes. Only three breeds have $N_e \geq 100$, considered stable to limit total fitness loss to less than 10%, while four have N_e below 100. The trajectories of historical N_e unravel crucial declines probably due to the start of breed formation, bottlenecks, migration, and breed clustering. These findings underline the need to increase the genetic architecture of populations used in developing breeding and conservation strategies. This is because prevention of mating between relatives and use of pedigree information as a base for increasing census population might not suffice to increase N_e, particularly in breeds with a small census population size. Therefore, this research suggests the need to adopt genomic data and LD-based methods to estimate N_e before the start of breeding selection to ensure the long-term sustainability of conservation programmes of Swedish native cattle. This emanates from the possibility that estimates from genomic data using the LD method offer more accuracy, are less reliant on pedigree information and can infer the demographic trajectories of cattle breeds across many generations back in time compared to using formulas.

5.7 Recommendations for future research

Future studies should focus on increasing the sample size of SNP Chip and whole-genome sequence data to increase the results' statistical power and accuracy. Also, there should be an effort to develop methods that measure estimates as early as the first five generations. This will potentially provide more accurate estimates of recent estimates that can be placed side-by-side with the ongoing conservation efforts.

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Popular science summary

The traditional native cattle play significant roles as a pool of genetic resources with unique adaptive features to the local ecosystem. Also, indigenous Swedish cattle breeds could be useful in alleviating the effects of climate change that has continuously threatened livestock production across the globe. Besides, they are a source of cultural heritage and foster communal growth and development.

However, native cattle are often neglected and overlooked in commercial production systems despite these impressive features. Moreover, the importation of exotic breeds with more production capacity and poorly planned crossbreeding has led to the extinction of many Swedish native cattle breeds, with the population of existing ones on a rapid decline. In order to develop a sustainable breeding and conservation programme to boost the population of traditional cattle, it is crucial to accurately estimate the effective population size as a result of genetic drift.

Genetic drift explains changes in allele frequency or fluctuation in the number of gene variants due to random chances. Census population (number of live animals) often impacts the effective population size. The higher the number of live animals, the higher the probability of obtaining a high effective population size. However, not all living animals contribute to breeding due to age, imbalance male to female ratio, sexual dominance, and nonrandom mating.

There are several formulas for effective population size based on different assumptions. However, most of them are limited to estimates of a single generation at a time and often require knowledge of pedigree history. Therefore, it is essential to estimate effective population sizes from genomic data, which also allows inferring demographic histories for many generations in time past, without relying on pedigree history.

147 samples from 9 Swedish native cattle breeds were analysed using SNP chip data to estimate the effective population sizes. Additionally, 33 individuals from 5 breeds were assessed using whole-genome sequence data with two methods built on the linkage disequilibrium-based approach. These methods provide estimates of effective population sizes and attempt to show events that have shaped these breeds across many generations.

This analysis showed that two local breeds (Bohuskulla and Väne) have recent effective population sizes below 50. Four breeds (Ringamålako, Fjällnara, Swedish Polled, and Swedish Red Polled) have their estimates below 100, while only three breeds have N_e values above 100 (Holstein Friesian, Swedish Red Cattle, Swedish Mountain Cattle).

Also, most of the declines observed were matched periods where these breeds are formed. At the same time, other genetic events, such as migration, drops, and expansion, also contributes to the pattern of demographic changes.

Discoveries from this research calls for the need to increase the genetic base of Swedish cattle breeds used for breeding purposes. Rather than relying on not mating closely related individuals to avoid inbreeding depression, this research suggests estimating effective population sizes of the cattle breeds using genomic data and the methods used in this study before the start of conservation and breeding programmes for long-term sustainability. With that, there will be less reliant on pedigree information and the generation histories can be traced back in time to observed how these breeds have responded to different genetic events across many generations before. This could also aid in predicting how they will respond in the future.

Future research will benefit from increasing the sample size for both SNP chips and sequence data. Taking samples from younger or living animals will possibly provide more reliable estimates, especially for recent generations.

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