



ORIGINAL ARTICLE

Microsatellite diversity of the Nordic type of goats in relation to breed conservation: how relevant is pure ancestry?

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Summary

In the last decades, several endangered breeds of livestock species have been re-established effectively. However, the successful revival of the Dutch and Danish Landrace goats involved crossing with exotic breeds and the ancestry of the current populations is therefore not clear. We have generated genotypes for 27 FAO-recommended microsatellites of these landraces and three phenotypically similar Nordic-type landraces and compared these breeds with central European, Mediterranean and south-west Asian goats. We found decreasing levels of genetic diversity with increasing distance from the south-west Asian domestication site with a south-east-to-north-west cline that is clearly steeper than the Mediterranean east-to-west cline. In terms of genetic diversity, the Dutch Landrace comes next to the isolated Icelandic breed, which has an extremely low diversity. The Norwegian coastal goat and the Finnish and Icelandic landraces are clearly related. It appears that by a combination of mixed origin and a population bottleneck, the Dutch and Danish Landraces are separated from the other breeds. However, the current Dutch and Danish populations with the multicoloured and long-horned appearance effectively substitute for the original breed, illustrating that for conservation of cultural heritage, the phenotype of a breed is more relevant than pure ancestry and the genetic diversity of the original breed. More in general, we propose that for conservation, the retention of genetic diversity of an original breed and of the visual phenotype by which the breed is recognized and defined needs to be considered separately.

Introduction

In comparison with other farm animals in the developed world, goats are not of major economic importance, but nonetheless contribute considerably to the diversity of livestock production. The Saanen and Boer breeds are the major producers of goat milk and meat, respectively, and the Angora and Kashmere goats provide special types of wool (Mason 1984). Many local goat breeds are suitable for marginal, often mountainous areas, in developing countries for small holders and in developed countries for hobby breeding (Porter 1996; Dohner 2001). As horses and cats, goats easily survive if escaped from the domestic habitat and have established more feral populations than any other livestock species (Mason 1984).

The Nordic type of goats is a primitive longhaired and multicoloured type, which are kept as landraces in Finland, Sweden, Norway, Denmark, Iceland, Britain, Ireland and the Netherlands (<http://www.ansi.okstate.edu/breeds/goats/index.html/goats>). The Icelandic goats are believed to descend from Scandinavian animals imported more than 1000 years ago (Baldursdottir *et al.* 2012). In Britain, authentic goats mainly survived as feral populations (Mason 1984; Porter 1996). The original Danish Landrace has in the 19th century been crossed with German Harz and Swiss Saanen goat (<http://naturerhverv.dk/landbrug/genetiske-ressourcer/husdyrgenetiske-ressourcer/husdyrarter/faar-og-geder/#c9129>).

In the beginning of the 20th century, Dutch Landrace goats were influenced by Saanen and Toggenburg goats. Following a serious decline after the World War II, the Dutch Landrace population was revived and remained popular as backyard goat for smallholders. However, after the mid-20th century, the Dutch Landrace goats nearly disappeared by the rationalization of animal husbandry, and in 1958, only a few animals were left (Frankenhuis & Hazenbroek 1984). A second revival started in the Blijdorp Zoo in Rotterdam, possibly with only two animals, and was continued with four males and four females in the village of Leersum. These animals along with six additional unregistered animals of unknown origin became the ancestors of the current population of approximately 2000 animals, which are kept by hobby breeders and are used in nature management systems.

Molecular markers now allow studying breed relationships and geographic patterns of diversity as indicators of migrations, admixture and genetic bottlenecks (Groeneveld *et al.* 2010). A study of south-west Asian, Mediterranean and central

European goats using the FAO-recommended microsatellites (Canon *et al.* 2006) revealed a clear clustering of breeds from the same region and a decrease in the genetic diversity with increasing distance from the domestication site in south-west Asia to Central Europe. However, northern European goats have so far not been investigated on the DNA level.

In an attempt to characterize further the phylogeography of European goats and to trace the ancestry of the Dutch and Danish Landraces, we have compared microsatellite genotypes of these breeds with those of other Nordic and European goat breeds (Canon *et al.* 2006; Glowatzki-Mullis *et al.* 2008). We propose that the complex history of the Danish and Dutch Landraces, which confounds the regional pattern of breed relationships, does not affect their status of heritage breeds.

Materials and methods

Samples from 32 Dutch goats from different breeding lines were collected with a Genotek nasal swab kit. DNA was extracted by standard procedures from blood samples of 35 Danish, 32 Finnish, 32 Norwegian and 16 Icelandic goats from six farms and from tissue samples of five Iranian Bezoars collected in the wild (Table S1). Genotyping with the FAO-recommended microsatellites (FAO, 2011) was performed as described (Canon *et al.* 2006), but markers BM6444, DRBP and SRCRSP7 were excluded from analysis because of departure from HW equilibrium and SRCRSP3 because of a low scoring success in our samples. Harmonization of allele lengths with previous data (Canon *et al.* 2006; Glowatzki-Mullis *et al.* 2008) was achieved by genotyping two samples from the Econogene data set (Canon *et al.* 2006), which allowed a combination with this data set and an overlapping data set panel of Swiss goat breeds as well as the African Boer goats (Glowatzki-Mullis *et al.* 2008). The Dutch Landrace goat was also genotyped for 37 microsatellite markers selected for genotyping ibex goats (*Capra ibex*, Biebach & Keller 2009), 11 of which were shared with the FAO panel (Table S1).

A separate data set of the Turkish Angora, Honamli, Kil, Kilis and Norduz breeds (Ağaoğlu & Ertuğrul 2012) shared with our data set the Angora breed and 13 of the 26 FAO microsatellites. Sharing the Angora breed allowed a tentative harmonization of allele sizes for the 13 common microsatellites (see Supporting Information).

Data were analysed with the Microsatellite Tool Kit (<http://animalgenomics.ucd.ie/sdepark/ms-toolkit/>),

and allelic richness was calculated with the *FSTAT* program using a sample size of 13. Genetic distances were calculated with the *MICROSAT* program (Minch 1997). Reynolds' genetic distance was visualized via NeighbourNet graphs using *SPLITSTREE* version 4.0 (Reynolds *et al.* 1983; Huson 1998). Distances from the domestication site (Naderi *et al.* 2008) in kilometres were calculated as

$$\begin{aligned} & \text{acos}(\sin(\text{lat}1 \cdot \pi/180)\sin(\text{lat}2 \cdot \pi/180) \\ & + \cos(\text{lat}1 \cdot \pi/180)\cos(\text{lat}2 \cdot \pi/180)\cos(\text{lon}2 \cdot \pi/180 \\ & - \text{lon}1 \cdot \pi/180)).(6378.135), \end{aligned}$$

in which *acos* is the arccosine, *lat*1 and *lon*1 latitude and longitude, respectively, of the breed in degrees (www.econogene.eu), and *lat*2 (37.67°) and *lon*2 (43.05°) the coordinates of a central point in the estimated domestication area in east Anatolia. The correlation of genetic and geographic distances was visualized by linear regression. Model-based clustering was carried out as described previously (Canon *et al.* 2006) with 150 000 burnins and 350 000 simulations.

Results

We found a good correlation of the two most common diversity parameter expected heterozygosity (H_E) and allelic richness (Table S1, r^2 0.94). To survey the patterns of genetic diversity, we plotted in Figure 1a H_E against the distance from the domestication site. A decrease in diversity with increasing distance is most evident in the northern European breeds. Clines were

observed from east to west and south-east to north-west, respectively, with a clear difference between the two (broken lines in Figure 1a). Icelandic goats have an extremely low diversity (H_E 0.279, complete homozygosity in six of 26 markers). From the other breeds, the Dutch Nordic goat is the most inbred breed (H_E 0.527, two homozygous markers).

Inbreeding coefficients within breeds (F_{IS}) on the basis of expected and observed heterozygosities are for most breeds in the range of 0.04–0.12 (Figure 1b). Exceptionally, high values are observed for the Icelandic goats (Baldursdottir *et al.* 2012) and for the French Pyrenean breed. In contrast, low values are observed for the Swiss Appenzell, Saanen, St. Gallen Booted and Toggenburg goats.

For model-based clustering (Pritchard *et al.* 2000) the northern European breeds were analyzed together with the German Fawn and Thuringian Wald goats. We also added the Swiss Saanen and Toggenburg, which are reported to have influenced the Danish and Dutch Landraces and the Thuringian Wald goat (Porter 1996). Figure 2 shows a consistent clustering of the Norwegian and Finnish goats, which at $k = 3$ and 4 form a separate cluster with the Icelandic breed, excluding, however, the Dutch and Danish landraces. The patterns reproduce the documented incrossing of Toggenburg in the Thuringian Forest, but not the introgression of Saanen or Toggenburg in the Danish and Dutch breeds. However, these introgressions may very well have been masked by later shifts in allele frequencies as a consequence of the severe population bottlenecks in both breeds.

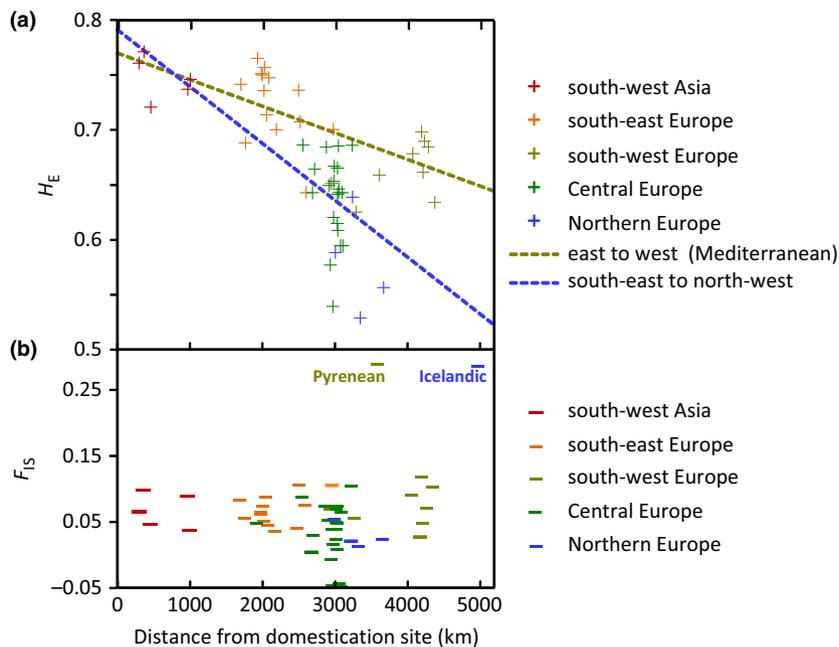


Figure 1 (a) Expected heterozygosity (H_E) plotted against the distance from the domestication site. The trend lines were generated by least-square analysis and show the observed clines in heterozygosity from east to west and south-east to north-west. The low heterozygosity of the Icelandic goat (0.28) is outside the range of the plot. (b) Inbreeding coefficient (F_{IS}), calculated as $(H_E - H_O)/H_E$.

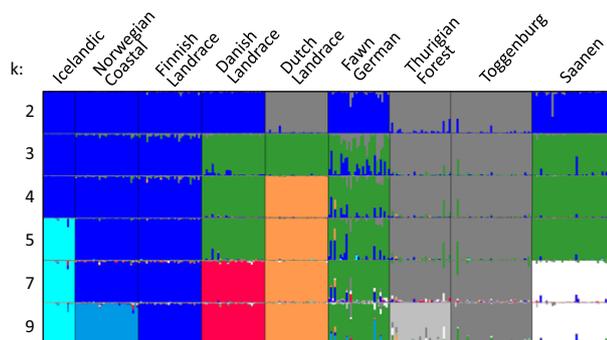


Figure 2 Model-based clustering with indicated number of clusters (k). For each k value, the program was run four times and only patterns are shown that were inferred at least three times. Only at $k = 2$, all four runs generated the same pattern. The clustering of the Norwegian and Finnish breeds and of the Thuringian Forest and Toggenburg was also observed if the north European breeds were analysed together with central European, Mediterranean and south-west Asian breeds shown in Figure S1. According to the Evanno criterion (Evanno *et al.* 2005), $k = 5$ is the most likely number of clusters.

Visualization of the genetic distances (Figure S1, Table S2) reproduces the clustering of south-west Asian, Italian with south-east European, Iberian and central European breeds (Canon *et al.* 2006) as well as the clustering of Finnish, Norwegian and Icelandic Nordic goats. Although the low quality of the bezoar DNA samples may have led to allele dropout and have shifted the estimated allele frequencies, its position in the tree confirms the relatedness of the Turkish breeds to the first domesticates. The separate position of African Boer goats is partly due to low heterozygosity (H_E 0.602), but also illustrates the strong geographic differentiation of goats (Canon *et al.* 2006; Groeneveld *et al.* 2010).

The Finnish, Norwegian and Icelandic Nordic breeds again form a separate cluster with as closest relative the northernmost continental breed represented in our data set, the Fawn German (BDE, *Bunte Deutsche Edelziege*). Remarkably, the extremely low diversity of the Icelandic goats did not obscure their Scandinavian origin (Figure S1). On the other hand, sharing of short branches suggests a spurious affinity of the Danish Landrace with the Nordic cluster and of the Dutch Landrace with the Swiss Saanen, respectively (Figure S1).

As the complex phylogenetic networks as shown in Figure S1 may obscure other phylogenetic relationships and the relationships between the breed clusters (Lenstra *et al.*, 2012), we reduced the complexity of the data set. Figure 3a shows a network of the regional clusters (Table S3) together with breeds that are intermediate between the clusters (Hungarian Native, French Pyrenean, French Rove, Fawn German) or

occupy extreme positions (Bezoar, African Boer). This network clearly visualizes the genetic trends from south-west Asia to northern and south-west Europe. Replacing the Nordic cluster by the four separate Nordic breeds (Figure 3b) again clusters the Finnish, Norwegian and Iceland goats. However, in this network, the Dutch and Danish breeds are clearly separate from the more northern Nordic breeds and are linked to the network close to the central European cluster.

This is confirmed by a network of the north European breeds and Swiss Saanen with the central European cluster indicating the root of the network (Figure 3c). This network also suggests a shared genetic history of Saanen and the Dutch Landrace goat, which is in agreement with Figure S1 and is not observed if Saanen is replaced by any other central European breed. A clustering of the Dutch and Danish landraces is more spurious, but is also observed in Figure 3b.

In general, European breeds have distinct phenotypes and are, as evidenced by the long genetic distances, genetically clearly differentiated, yet are genetically clustered according to their region of origin (Canon *et al.* 2006; this study). Similar observations have been reported for Asian goats (Nomura *et al.* 2012). In contrast, the four Turkish breeds represented in our data set combine phenotypic variation with short genetic distances. We have explored this further by a tentative meta-analysis of our 26-microsatellite data set with an independent data set of five Turkish breeds (Ağaoğlu & Ertuğrul 2012), which shares the Ankara (=Angora) breed and 13 microsatellites with our data set. In the resulting network (Figure S2), the duplicate samplings of the Angora are closely linked, which supports the validity of the meta-analysis (Lenstra *et al.*, 2012). The network further indicates that all eight Turkish breeds with diverse breeding purposes and appearances form a tight geographic cluster and confirm the findings of Bulut *et al.* (2016).

Inspection of allele frequencies of the Dutch goats reveals in addition to the two homozygous markers high-frequency alleles in nine marker that have low allele frequencies in other breeds. As the last authentic Dutch Landrace goats were kept in a zoo that also possessed cross-fertile ibex animals, ibex introgression may have occurred. However, comparison of allele frequencies of Dutch goats and four ibex populations for 37 markers (Table S4) did not show any sharing of major alleles and for all 10 markers clear differences in allele distributions, arguing against ibex introgression as explanation for the deviating allele frequencies in Dutch Landrace goats.

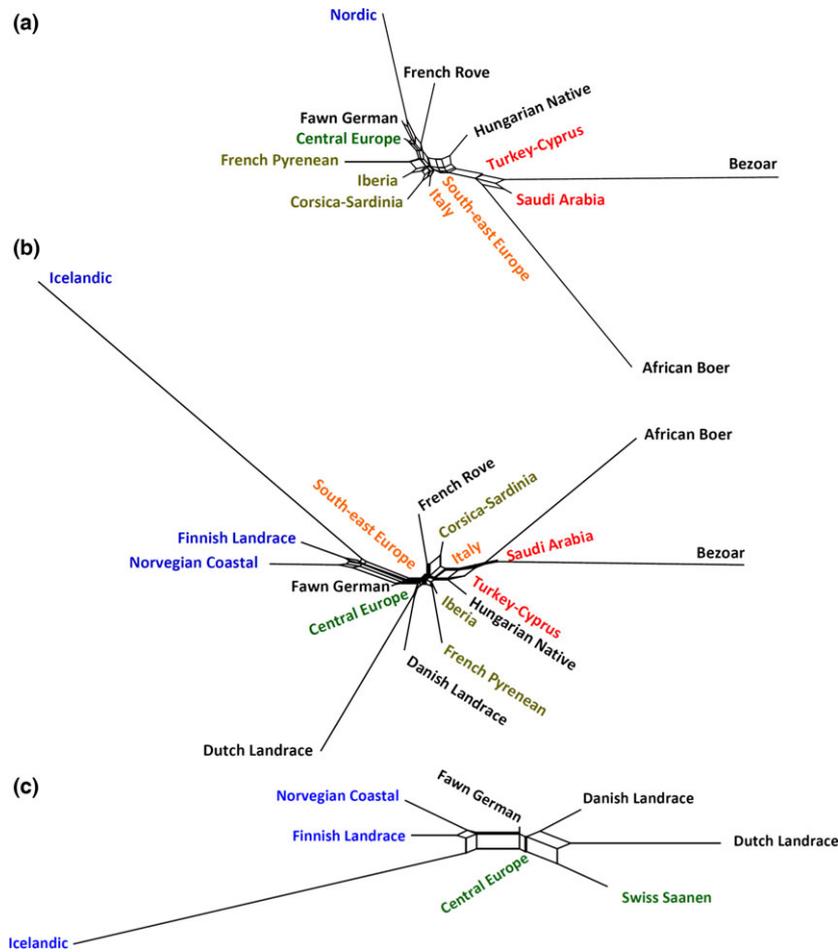


Figure 3 NeighborNetwork of Reynolds' distances (D_R) between breeds or regional clusters of breeds as defined in Table S3. Colours indicate regional clusters of related breeds (see Figure 1). Breeds that do not belong to a cluster or are intermediate between two clusters are indicated in black. (a) Clusters and intermediate breeds; (b) without the Nordic cluster but with the Nordic type of breeds; and (c) the Nordic breeds, Fawn German (*Buntes Deutsche Edelgeiss*) and Swiss Saanen relative to the central European cluster. Essentially, the same topology was obtained using Greek Goat instead of the central European cluster to indicate the phylogenetic root of the network.

Discussion

Our analysis of northern European breeds illustrates the strong geographic differentiation of the Eurasian goat populations. This is supported by a study of east Asian goats (Nomura *et al.*, 2012) and our meta-analysis of Turkish breeds, but is less evident in mitochondrial DNA data sets (Luikart *et al.* 2001; Naderi *et al.* 2008). We observed a decline of genetic diversity (Figure 1a), which probably indicates the effect of genetic drift by repeated founder effects during the gradual Neolithic introduction of livestock animals, starting in south-east Europe and finally reaching northern and western Europe (Groeneveld *et al.* 2010). The cline is stronger for central and northern European breeds than for Mediterranean breeds. This has been observed previously in cattle (Cymbron *et al.* 2005) and possibly reflects that the Danubian migration route that populated central and northern Europe (Tresset & Vigne 2011) involved either more numerous or more severe population bottlenecks than the Mediterranean route.

The extremely low diversity of Icelandic goats (H_E 0.279) is in agreement with (Baldursdottir *et al.* 2012) and reflects their isolation from other goat populations since ca. 1100 years. The Dutch Landrace goat is the second most inbred population with a H_E of 0.527. Strikingly, both populations and the Finnish and Danish Landrace goats combine a low genetic diversity with a considerable variation in coat colour and colour pattern, indicating that a low genetic diversity in an isolated population does not preclude the maintenance within the population of different visual phenotypes. Most northern-central European breeds with low H_E have low F_{IS} values as well, indicating an absence of significant genetic subdivision within the breeds with the highly fragmented Icelandic goat population (Baldursdottir *et al.* 2012) and the Pyrenean goats as notable exceptions.

Visualization of genetic distances in a NeighborNetwork extends the geographic clustering of European goats (Canon *et al.* 2006) with a separate cluster of Norwegian, Finnish and Icelandic goats (Figure 3a). However, the Danish and Dutch landraces do not

conform to the geographic pattern of breeds relationships. A separate analysis links the Danish and Dutch Landrace breeds to the network close to the central European breeds with only spurious relationships with each other (Figure 3b,c) or of the Dutch Landrace with the Swiss Saanen (Figure 3c and Figure S1).

We propose that a combination of mixed origin and severe population bottlenecks during the recovery of both north-continental breeds has effectively erased trace of their origin in the microsatellite data set. Admixture of Swiss Saanen and German Harz goats during the 19th century in the Danish population has been documented (<http://naturerhverv.dk/landbrug/genetiske-ressourcer/husdyr/genetiske-ressourcer/husdyrarter/faar-og-geder/#c9129>), but took place well before the decline of the population. The popular Saanen and Toggenburg were crossed into the Dutch Landrace in the beginning of the last century and further admixture may have occurred during the recovery of the breed; this might explain the sharing of a short branch in the networks in Figure 1c and Figure S1.

However, both breeds are characterized by large horns and diverse multicolour coats similar in appearance to the original landrace populations and the authentic Finnish and Icelandic breeds. The population size of the Danish Landrace is stable but marginal with only 400 animals. The 2000 Dutch Landrace goats on the other hand effectively fulfil their role as a traditional breed. This illustrates that conservation of phenotypic and molecular diversity should be considered separately (Hall *et al.* 2012). The examples of the Icelandic goats and several other livestock breeds (Hall 2004) also show that phenotypic and molecular variation is affected in different degrees by a low population size.

More in general, maintaining an authentic and variable phenotype does not guarantee the conservation of original wide genetic variation of the original authentic landrace (Hall *et al.* 2012). This raises the question whether for goat keepers and breeders pure genetic ancestry should be a prerequisite for the successful revival and maintenance of a breed. Instead, crossing with genetically related breeds with a similar appearance originating from a similar environment avoids the depleting effects of genetic drift and inbreeding. It may be argued that genetic purity is for heritage breeds less essential than an authentic appearance, even if expressed in another genetic context than the original breed. However, other traits of the original breed have to be conserved as well. In this respect, adaptation to local conditions and suitability for extensive management that are typical for

traditional livestock breeds are most important (Dohner 2001; Hall 2004).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Geographic origin and diversity statistics of goat breeds. H_E , expected heterozygosity; H_O , observed heterozygosity, F_{IS} , inbreeding coefficient, n.r., not recorded.

Table S2 Reynolds' genetic distances between breeds. For breed abbreviations, see Table S1.

Table S3 Combination of breeds in geographical clusters for NeighborNet analysis.

Table S4 Microsatellite allele frequencies of four ibex populations (Biebach & Keller 2009) and of the Dutch Landrace goat.

Figure S1 NeighborNetwork of Reynolds' distances (D_R) between goat populations.

Figure S2 NeighborNetwork of D_R distances showing a meta-analysis of our breed panel and a data set of five Turkish breeds indicated by asterisks and sharing 13 microsatellites with our panel. The duplicate samplings of the Angora breed are tightly linked, which supports the validity of the meta-analysis and indicates a close relationship of all sampled Turkish breeds.

Appendix

Members of the ECONOGENE Consortium are as follows:

Mahamoud Abo-Shehada, Paolo Ajmone Marsan, Jamil Al Tarrayrah, Antonella Angiolillo, Philip Baret, Roswitha Baumung, Albano Beja-Pereira, Marco Bertaglia, Salvatore Bordonaro, Horst Brandt, Mike