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ANIMAL HUSBANDRY & VETERINARY SCIENCE | REVIEW ARTICLE

Genetic diversity studies using microsatellite markers and their contribution in supporting sustainable sheep breeding programs: A review

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Abstract: Microsatellites have been widely accepted and employed as useful molecular markers for measuring genetic diversity and divergence within and among populations. The various parameters developed so far to measure genetic diversity within and among populations are observed and expected heterozygosities (H_o and H_e), the mean number of alleles per locus, polymorphic information content, genetic distance and phylogenetic or tree building approach. The objective of this review was therefore to quantify the genetic diversity studies of domestic sheep populations using microsatellite markers and their contribution in supporting sustainable sheep breeding programs. From the review, it is possible to see that there was high within population genetic variations in all the studied sheep populations, poor level of population differentiations and high levels of inbreeding. On the other hand, low estimates of heterozygosities and mean number of alleles and employing only few and weak markers were observed in some of the studies. The gaps observed in the previous genetic diversity studies of the sheep populations may demand further works to reveal more information on the population structures and to start appropriate and sustainable breeding programs.

Subjects: Agriculture & Environmental Sciences; Biodiversity; Animal Ecology

Keywords: genetic diversity; microsatellites; sheep; sustainable breeding

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PUBLIC INTEREST STATEMENT

In the past several years, microsatellite markers have been widely employed to quantify genetic diversity in the livestock sector. In this review, a comprehensive and current overview of numerous sheep genetic diversity studies have been organized and discussed in a holistic manner. Moreover, the gaps observed, with their implications and future prospects, have also been pinpointed. As conclusion, the authors provided different measures that can be adapted to enhance the contribution of genetic diversity studies in supporting sustainable sheep breeding programs.



Oumer Sheriff

1. Introduction

Domestic farm animals are crucial for food and agriculture, providing 30–40% of the agricultural sector's global economic value (FAO, 2000). Despite their invaluable contribution to the global economy, there is a rapid loss of genetic resource of farm animals and the world loses two breeds of its valuable domestic diversity every week (FAO, 2000). Hence, there should be an urgent mechanism to maintain and document the diversity of livestock genetic resources and design appropriate strategies for conservation and sustainable use, particularly in developing countries (Hannote & Jialin, 2005).

Maintenance of livestock genetic diversity is a key to the long-term survival of most species and should be done based on comprehensive information regarding the structure of the populations, including sources of genetic variability within and among populations. It also requires adequate implementation of conservation priorities and sustainable management programs (Sheriff, Belay, & Haile, 2013; Sheriff & Bireda, 2016; Mahmoudi, Babayev, Hayeri Khiavi, Pourhosein, & Daliri, 2011) and widely used to categorize livestock species in the world (Cardellino & Boyazoglu, 2009).

Genetic diversity (the variation of alleles and genotypes present in a population) provides a basis for adaptive and evolutionary processes (Frankham, Briscoe, & Ballou, 2002). The current pool of diversity in livestock has been created by the forces of both natural and artificial selection (Groeneveld et al., 2010). These forces encompass processes such as mutations, adaptations, segregation, selective breeding and genetic drift (Groeneveld et al., 2010). Future generations of domesticated species are wholly dependent on genetic variation which will be observed from genetic differences between breeds, between populations within a breed and between individuals within a population (Groeneveld et al., 2010).

Globally, sheep are the species with the highest number of recorded breeds contributing 25% to the total mammalian breeds adapted to a broad range of environments (Gizaw, 2008). The adaptation of different breeds to a broad range of agro-ecology provides the necessary variability that offers opportunities to meet the increased future demands for food and provide flexibility to respond to changed markets and needs (Wollny, 2003). To date, more than 1,078.2 million sheep populations are kept in different parts of the world with the following share in million: Asia (452.3), Africa (287.6), Northern America (6.9), Central America (8.1), Caribbean (3.1), South America (73.1), Europe (133.9) and Oceania (113.1) (Aziz, 2010).

Microsatellites have been widely accepted as useful tools for measuring genetic diversity and divergence within and among populations (FAO, 2011). So far, a number of genetic diversity studies on sheep have been conducted using microsatellite markers (Adamov, Mickov, Petkov, & Adamov, 2011). Their abundance, high level of repeat-number polymorphism, manifested as the occurrence of a large number of alleles per locus, and co-dominant inheritance has facilitated their extensive use in genome mapping, phylogenetic inference and population genetics in farm animals (FAO, 2011). However, most of the efforts of genetic diversity studies of sheep using microsatellite markers, conducted so far, may not be as supportive as expected in revealing the required information for designing appropriate and sustainable sheep breeding programs and conservation strategies. Therefore, the objective of this review was to quantify the genetic diversity studies using microsatellite markers and their contribution in supporting sustainable sheep breeding programs.

2. Genetic diversity and within population variation

Some of the parameters which can help to study genetic diversity within a population are the mean number of alleles per locus (MNA), the average expected and observed heterozygosity values (Halima, Lababidi, Rischkowsky, Baum, & Tibbo, 2012) and testing for deviations from Hardy-Weinberg equilibrium (HWE) per population. The deviation from HWE provides a lot of information about those primary forces viz., natural selection, mutation, genetic drift, nonrandom mating and genetic migration that derive evolutionary change (Ojango, Mpofu, Marshall, & Andersson-Eklund, 2011). On the other hand, the precision of estimated genetic diversity is a function of the number of

loci analyzed, the heterozygosity of these loci and the number of animals sampled in each population (Barker, 1994).

2.1. Estimation of MNA

The mean number of alleles is a good indicator of the genetic polymorphism within the population (Halima et al., 2012) and it depends on sample size of the population because of the potential presence of unique alleles in a population that may occur at low frequencies (Qwabe, 2011). The number of detected alleles may increase with an increase in population size. A high number of alleles imply more genetic variation (Nei, 1987). Mean number of alleles that indicate the genetic polymorphism within the studied microsatellites were reported for several sheep populations (Table 1).

The mean number of alleles (MNAs) (Table 1) showed relatively lower estimates for some Ethiopian, Chinese and South African sheep populations. For the other sheep populations, relatively encouraging estimates of MNA were reported. A high number of alleles imply more genetic variation (Nei, 1987) and it is the key relevance in conservation programs. However, though those reports explain the existence of high polymorphism, the average number of alleles depends on sample size; number of observed alleles tends to increase with increasing population size (Aljumaah, Musthafa, Al-Shaikh, Badri, & Hussein, 2012). Therefore it is important to sample population sizes that are more or less equal for comparison (Qwabe, 2011). However, some of the studies used not only very small number of animals which is quite far from FAO recommendation for microsatellite marker analysis (FAO, 2011), e.g. Hirbo, Muigai, Naqvi, Rege, and Hanotte (2006) used only nine animals to represent a population, but also they used unequal sample size. This may lead to biasedness in estimating genetic parameters such as HWE and MNA or there is no any technique indicated in the papers which was employed to handle such a limitation.

It was also observed that most of the sheep genetic diversity studies (Table 1) were undertaken by using few numbers of microsatellite markers. All the 30 microsatellites, the maximum coverage recommended by FAO (2011), were covered only for Merino derived and Albanian sheep breeds (Hoda & Ajmone-Marsan, 2012; Simone, Lasagna, Landi, Martinez, & Sarti, 2009). Genetic diversity studies with more number of microsatellite markers not only reveal more information on the population structures but also offer more opportunities to compare with results from previous studies undertaken with various subsets of the markers (FAO, 2011).

2.2. Estimation of observed (H_o) and expected (H_e) heterozygosities

Observed heterozygosity, the proportion of heterozygotes observed in a population, and expected heterozygosity, the proportion of heterozygotes expected in a population following the Hardy-Weinberg proportions (Ojango et al., 2011) are the most widely used parameters to measure genetic diversity in a population (Toro, Fernández, & Caballero, 2009). Literatures suggest that heterozygosity estimates having greater than 0.5 heterozygosity values are believed to be appropriate for genetic diversity studies (Dávila, Gil, Resino-Talavan, & Campo, 2009; Dorji, Duangjinda, & Phasuk, 2012). However, the heterozygosity estimates observed in some Indian, South African, Ethiopian, Chinese, Chilean, Kenyan and Nigerian sheep populations (Table 1) were below 0.5 or closer to the margin. This low heterozygosity estimates might be due to maintaining microsatellite loci which had registered values below 0.5 in the respective breeds during the analysis. On the other hand, very low heterozygosity estimates may be because of the effect of small population size, high selection pressure in closed population, inbreeding and minimal or null immigration of new genetic materials into the population (Canon et al., 2006). The heterozygosity (both observed and expected) estimates in the remaining sheep populations are relatively high concluding that the studied sheep populations have high amount of within population genetic diversity.

Most of the observed heterozygosity values are generally closer to, but lower than, the expected heterozygosity in most of the breeds and loci indicating no overall loss in heterozygosity (allele fixation) (Araujo et al., 2006) and the populations are at HWE.

Table 1. Estimated heterozygosities, mean number of alleles, polymorphic information content and level of inbreeding

Breed	Country of origin	H_e	H_o	MNA	PIC per locus	F_{IS}	MS (No.)	Author
Vembur sheep	India	0.73	0.52	5.88	0.69	0.29	25	Pramod et al. (2011)
Kail sheep	India	0.72	0.77	5.27	0.60	0.053	11	Ahmed et al. (2014)
Sheep breeds (7)	South Africa	0.63	0.45	5–16	0.95	NA	24	Buduram (2004)
Turkish breeds (4)	Turkey	0.87	0.66	7.04	NA	0.07	17	Yilmaz et al. (2015)
Turkish native and cross sheep (11)	Turkey	0.75	0.72	5.8–11.8	NA	0.09–0.16	15	Evren (2004)
Traditional sheep populations (14)	Ethiopia	0.66–0.75	NA	6.79	NA	F_{ST} (0.046)	17	Gizaw (2008)
Sheep breeds (3)	Ethiopia	0.50	0.33	3–23	0.69	0.236	22	Nigussie (2015)
Italian merino derived sheep (3)	Italy	0.64–0.75	0.61–0.70	5.17–8.43	NA	0.048–0.118	30	Simone et al. (2009)
Pelt sheep(3)	Iran	0.83	0.99	7.6	0.81	–0.19	15	Hatami et al. (2014)
Local Sheep (8)	China	0.54	0.59	3.8–5.4	0.49	0.404	10	Zenga et al. (2010)
Albanian Sheep (3)	Albania	0.75	0.72	8.54	0.72	0.041	31	Hoda and Ajmone-Marsan (2012)
Chilean sheep (4)	Chile	0.82	0.696	9–25	0.55–0.90	0.040	9	de la Barra et al. (2010)
Sheep populations (15)	Kenya	0.72	0.65	7.70	NA	0.109	15	Mukhongo et al. (2014)
Nigerian Indigenous Sheep (4)	Nigeria	0.78	0.49	8.64	0.85	0.34	15	Agaviezor et al. (2012)
Sheep breeds (3)	Saudi Arabia	0.59–0.82	0.65–0.989	11.47	0.75	0.031	17	Mahmoud et al. (2017)
Trans-caucasian, Asian, European and African sheep breeds (22)	*	0.62–0.81	0.60–0.77	6.71–9.36	NA	F_{ST} (0.06–0.10)	14	Hirbo et al. (2006)
Karakul sheep	Iran	0.831	0.989	8.07	0.81	–0.197	15	Nanekarani et al. (2011)
Romanian sheep breeds (4)	Romania	0.740	0.640	9.275	NA	NA	11	Hoda and Ajmone-Marsan (2012)
Namaqua Afrikaner (3)	South Africa	0.50	0.49	3.9	0.44	0.019	22	Qwabe (2011)
Sheep breeds (10)	**	0.74	0.59	5.4–6.0	NA	0.060	10	Farid et al. (2000)

MS = Microsatellite.

*Azerbaijan (5), Armenia (3), Georgia (2), Uzbekistan (1), Pakistan (2), Syria (1), China (1), India (1), Portugal (2), Barbados (1), UK (2) and Senegal (1).

**Canada, Iceland, USA, Denmark, UK and Kenya.

2.3. Estimation of polymorphic information content

Polymorphic information content (PIC) depicts the suitability of the markers and their primers used in the study for analyzing the genetic variability of a population. A marker with $PIC > 0.5$ can be considered as highly informative and highly polymorphic, whereas, $0.5 > PIC > 0.25$ recognized as reasonably informative and below 0.25 is measured as slightly informative (Marshall, Slate, Kruuk, & Pemberton, 1998). In line with this, highly polymorphic markers were employed for most of the sheep populations studied (Table 1) except the local sheep breeds in China $PIC = 0.492$. In fact, PIC is determined by heterozygosity and number of alleles (Aljumaah et al., 2012) and this makes microsatellite markers the choice for genetic characterization and diversity studies.

2.4. Level of inbreeding (F_{IS})

F_{IS} is estimated for populations which show significant deviation from the HWE and is significant for significant HWE estimation (Ojango et al., 2011). A high positive F_{IS} indicates a high degree of homozygosity and vice versa while negative values indicate low level of inbreeding (Dorji et al., 2012). Taking this background information in to consideration, moderate to high inbreeding levels were reported by various scholars for different sheep populations; for instance, three sheep breeds of Ethiopia ($F_{IS} = 0.236$) (Nigussie, 2015), Vembur ($F_{IS} = 0.29$) (Prasad, Rasberry, Butler, & Welch, 2011), Magra ($F_{IS} = 0.159$) (Arora & Bhatia, 2006) and Kheri ($F_{IS} = 0.128$) (Arora & Bhatia, 2006) sheep breeds of India, some Merino derived sheep breeds of Italy ($F_{IS} = 0.048-0.118$) (Simone et al., 2009), some Turkish sheep breeds ($F_{IS} = 0.09-0.16$) (Evren, 2004) eight local sheep breeds of China ($F_{IS} = 0.404$) (Zenga et al., 2010), fifteen sheep populations of Kenya ($F_{IS} = 0.109$) (Mukhongo, Mwai, Tapio, & Muigai, 2014) and Nigerian indigenous sheep ($F_{IS} = 0.34$) (Agaviezor et al., 2012). This might be because of the small sheep population size, closed breeding system and very limited number of breeding rams used for many consecutive years. The lowest heterozygosity and MNA estimates indicated in Table 1 above strengthen this justification.

However, tolerable mean values of F_{IS} (0.087) for Ganjam (Arora, Bhatia, & Jain, 2010), (0.0525) for Kail (Ahmed et al., 2014) and (0.0786) for Tamil Nadu (Kavitha, Vijayalakshmi, Sudhakar, & Narasimha, 2010) sheep breeds of India and F_{IS} (0.07) for Turkish breeds (Yilmaz et al., 2015) were reported by scholars. These moderate levels of inbreeding may be a result of moderate levels of mating between closely related individuals under field conditions and may be the uncontrolled and unplanned mating that caused high levels of inbreeding (Mekuriaw et al., 2016). On the contrary, F_{IS} (-0.19) (Hatami, Khomeini, & Mehran, 2014) and F_{IS} (-0.197) (Nanekarani, Amirinia, & Amirmozafari, 2011) depicting low levels of inbreeding and an excess of heterozygotes was reported for three Iranian sheep breeds and Karakul sheep breed of Iran, respectively.

3. Genetic distance and variation among populations

Kalinowski (2004) had suggested that the highest genetic distance (F_{ST}) to be higher than 0.25, moderate to be between 0.05 and 0.25 and the lowest estimate below 0.05. In relative to many reports, the genetic distance among most of the populations obtained by many of the scholars (Farid, O'Reilly, Dollard, & Kelsey, 2000 ($F_{ST} = 0.163$); Evren, 2004 ($F_{ST} = 0.002-0.146$); Hirbo et al., 2006 ($F_{ST} = -0.001-0.183$); Qwabe, 2011 ($F_{ST} = 0.105$); Agaviezor et al., 2012 ($F_{ST} = 0.088$); Hoda & Ajmone-Marsan, 2012 ($F_{ST} = 0.011$); Hatami et al., 2014 ($F_{ST} = 0.018$); Mukhongo et al., 2014 ($F_{ST} = 0.101$) and Ahmed et al., 2014 ($F_{ST} = 0.042$)) is almost negligible (<0.05) and/or moderate ($0.05 < F_{ST} < 0.25$) values. Some of the authors revealed significant genetic distance estimates among populations. This implies that there is relatively low to moderate genetic sub-differentiation among the sheep populations. A fixation index (F_{ST}) of about 0.15 is considered to be an indication of significant differentiation among populations (Frankham et al., 2002).

The average F_{ST} value over all microsatellite loci in the sheep populations in Ethiopia was reported to be 0.046, indicating a 4.6% of total genetic variation among populations and a 95.4% difference among individuals (Gizaw, 2008). The same author reported that lack of differentiation in those phenotypically different sub-populations could be due to gene flow between the areas having close geographical distance and similar ecology. Similarly, Nigussie (2015) noted that 3% of the total variation

occurred due to population subdivision, while 97% of the variation existed among individuals within the sheep populations, which might be due to migration of individuals from one sub-population to the other (Nigussie, 2015). Hailu et al. (2008) and Halima et al. (2012) also confirmed that the low genetic differentiations between sub-populations might be due to traditional uncontrolled mating practices and policies that facilitated or led to uncontrolled movement of animals through various market routes and agricultural extension systems in Ethiopia.

4. Identified gaps, their implications and future prospects

One of the gaps, identified so far, is related to the expected and observed heterozygosity estimates and microsatellite loci. It is generally suggested that microsatellite loci showing H_e and H_o estimates of less than 0.5 were not appropriate for heterozygosity evaluation. However, microsatellite loci with heterozygosity estimates less than 0.5 or close to that were used in some of the studies (Table 1).

Similarly, though FAO (2011) recommended the genetic diversity studies of livestock using all the 30 microsatellite markers, most of the sheep genetic diversity studies were undertaken by using a subset of the markers. For example, de la Barra, Uribe, Latorre, San Primitivo, and Arranz (2010) used only nine microsatellites to study four Chilean sheep breeds and Farid et al. (2000) used only 10 microsatellites to study ten sheep populations in Canada, Iceland, USA, Denmark, UK and Kenya. Hence, studying more number of microsatellite markers to reveal more information on the population structure is suggested in future sheep genetic diversity studies. If less than 30 microsatellites are to be used, it is important to be keen in selecting microsatellites to bring an appropriate recommendation that can support sustainable breeding strategies.

The mean number of alleles (MNA) in sheep genetic diversity studies in Ethiopia, China and South Africa (Nigussie, 2015; Qwabe, 2011; Zenga et al., 2010) were below the recommended value, the microsatellite loci for genetic diversity studies should have more than four alleles (FAO, 2011). This indicated that some of the microsatellite loci were not sufficiently polymorphic and were not appropriate for genetic diversity analysis.

Some of the diversity studies used not only very small number of sheep which is by far lower than the recommendation of FAO for microsatellite marker analysis (FAO, 2011), e.g. Hirbo et al. (2006) used only nine animals to represent a population, but also they used unequal sample size. This may lead to biasedness in estimating genetic parameters such as the MNA or there is no any technique indicated in the papers which was employed to handle such a limitation.

All these gaps point out that the microsatellites which were not sufficiently polymorphic could be dropped out and it is very important to be ardent in selecting them to bring the right recommendation that can support appropriate and sustainable sheep breeding programs.

5. Conclusion and recommendation

The results from this review indicated that the within population genetic diversity, in all sheep populations, is extremely higher than between population variation which might be due to the uncontrolled and random mating practiced among the breeding flock shaving close geographical distance and similar ecology. There was also poor level of population differentiations, high levels of inbreeding, low estimates of heterozygosities and MNA and markers which were not sufficiently polymorphic in most of the studies. All these results demand further works to reveal more information on the sheep population structures and help to start sustainable breeding programs and policies involving the decision on pure or cross breeding. Moreover, appropriate conservation activities on breeding farms have to be taken to avoid losses of genetic diversity and thereby to support the breeding programs. It is also suggested to set up an improvement scheme for the frequent exchange of rams among farms or flocks rearing the same breed, aimed to increase genetic diversity.

List of Abbreviations

FAO	Food and agricultural organization of the United Nations
F_{IS}	Level of inbreeding
F_{ST}	Genetic differentiation between subpopulations
H_e	Expected heterozygosity
H_o	Observed heterozygosity
HWE	Hardy–Weinberg equilibrium
MNA	Mean number of alleles per locus
PIC	Polymorphic information content

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Competing interests

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Authors' contributions

Mr Oumer Sheriff drafted and organized the manuscript while Dr Kefyalew Alemayehu participated in coordination and helped to draft the manuscript. Both the authors read and approved the final manuscript.

Availability of data and material

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Ethics approval and consent to participate

The review paper meets all applicable standards with regard to ethics and integrity. As a researcher and educator in animal breeding and genetics and along with the co-author, the paper has been submitted with full responsibility, following due ethical procedure, and there is no duplicate publication, fraud or plagiarism.

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