

Review

Conservation and Selection of Genes Related to Environmental Adaptation in Native Small Ruminant Breeds: A Review

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Abstract: Environmental stressors have, over generations, influenced the morphology, anatomy, behaviour, physiology, and genetic structure of small ruminants. The widespread dispersal of small ruminants over vast geographical areas occurred along with human migration, thereby promoting the adaptive process to different environmental conditions mainly through natural selection. Ongoing global warming prompted scientific efforts to deepen the knowledge and understanding of adaptation traits in small ruminants. Compared to other ruminants, sheep and goats seem to have a better adaptation ability to environmental stressors, as evident by their presence across different geographic areas on a global level. Adaptation to a specific environment leads to variations in precise genomic regions, allowing for the identification and selection of animals with a high capacity of adaptation to environmental stressors. Rapid development in sequencing technologies, together with bioinformatics tools, make it possible to analyse the genomic regions related to environmental adaptation. Hence, the aims of this review were (i) to outline the main steps of the evolution process in sheep and goat species, (ii) to summarise candidate genes related to environmental adaptation, and (iii) to evaluate both selection and conservation possibilities of these genes in native small ruminant breeds for future challenges to better face the global warming.

Keywords: sheep and goats; climate change; stressors; genetic adaptation



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1. Introduction

This review attempts to consolidate the existing knowledge present in the scientific literature on genes that have a potential role in the environmental adaptation of domesticated small ruminants within the perspective of climate change, and to highlight the underlying genes or variants that are responsible for the evolutionary process leading to differences and phenotypic changes.

Climate change is recognised as being a major threat to the sustainability of livestock systems on a global level. The impact of this phenomenon on environmental stressors, such as frequency and intensity of adverse weather events and the continuous changes in the agro-ecological landscape, raises concerns on the repercussions on the performance and productivity of indigenous livestock species.

The evolution of the domestic sheep and goat has been associated with marked phenotypic changes in morphology, behaviour, physiological adaptation, reproduction, and production parameters. Identifying the genes underlying these modifications will elucidate the genetic mechanism responsible for successful domestication and provide a

better understanding of the practical breeding strategies that need to be implemented to promote the improvement of productivity and resilience to the environmental challenges.

2. Domestication and Evolution of Native Small Ruminant Breeds

The domestication of species is usually accompanied with the simultaneous gradual changes in physiology, morphology, and behaviour traits compared with their wild ancestors, a process that is also known as the “domestication syndrome” [1]. In general, domestication is considered as a gradual and cumulative evolutionary process that, over time on a long-term basis, leads to the establishment of a new phenotype that has adapted to captivity and human control [2].

The genus *Ovis* comprises eight extant species, including the widespread domestic sheep (*O. aries*) (Figure 1): argali (*O. ammon*), Asiatic mouflon (*O. orientalis*), European mouflon (*O. musimon*), urial (*O. vignei*), bighorn sheep (*O. canadensis*), thinhorn sheep (*O. dalli*), and snow sheep (*O. nivicola*) [3].

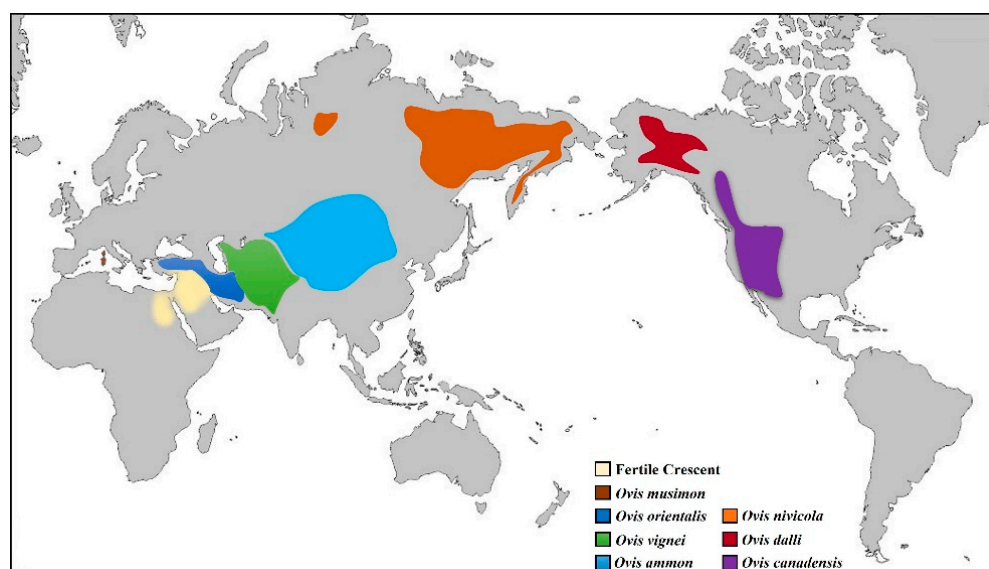


Figure 1. Global distributions of the seven wild *Ovis* species relative to the centre of domestication based on the IUCN Red List. Source: <https://www.iucnredlist.org> (accessed on 21 April 2022).

Meanwhile, in the genus *Capra*, the number of species and subspecies is still under debate, with estimates ranging from six to nine species [4,5]. Apart from the cosmopolitan domestic goat (*C. hircus*), Shackleton [5] reported a further nine wild species (Figure 2): Bezoar (*C. aegagrus*), Alpine ibex (*C. ibex*), Siberian ibex (*C. sibirica*), Nubian ibex (*C. nubiana*), Spanish ibex (*C. pyrenaica*), Markhor (*C. falconeri*), Walia ibex (*C. walie*), Kuban tur (*C. caucasica*), and Dagestan tur (*C. cylindricornis*).

The Asiatic mouflon (*Ovis orientalis*) and the Bezoar ibex (*Capra aegagrus*) branched out in the late Miocene era [6] to give rise to a type of sheep (*Ovis aries*) and goat (*Capra hircus*) that were domesticated around 10,000–12,000 years before present in Southeastern Anatolia, Mesopotamia, and Western Iran, commonly known as “The Fertile Crescent” [7–10]. From then on, sheep and goats dispersed throughout the region, occupying an important role in the Neolithic agricultural revolution, and thus contributing directly towards human settlement and civilization by providing a stable source of high-quality nutritional products based on milk and meat, with the additional benefit of also supplying wool and leather. The extraordinary adaptability capacity and hardiness to many biotic and abiotic stressors favoured the rapid geographic spread of sheep and goats [2].

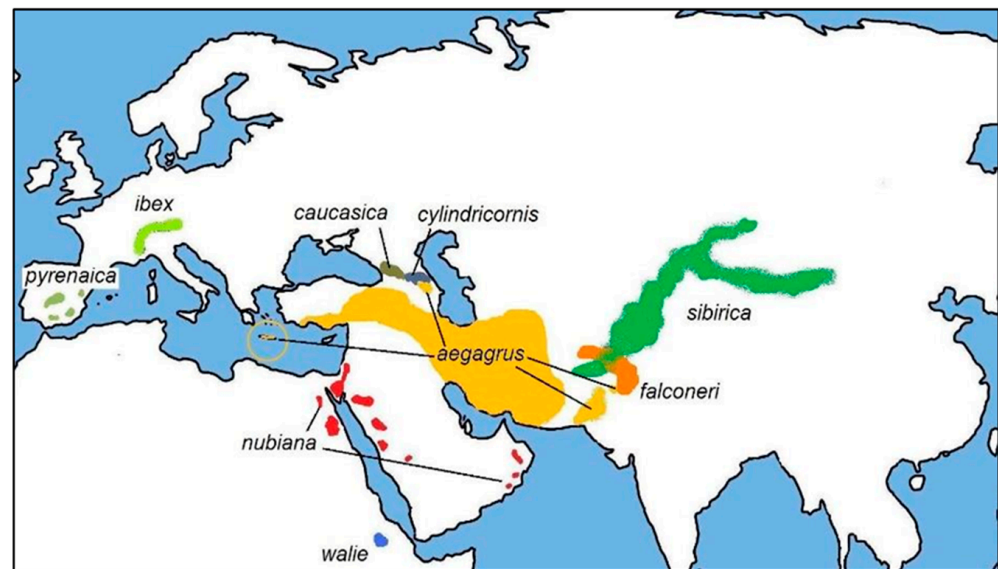


Figure 2. Geographic distribution of the nine wild *Capra* species. Source: https://www.wikiwand.com/en/Capra_genus (accessed on 21 April 2022).

Mitochondrial DNA (mtDNA) and nuclear genome analysis are very useful scientific investigative approaches to deepen the understanding of the history of modern domestic species through phylogenetic analysis [11]. The mtDNA technique allows for the identification of different maternal lineages present in modern breeds, which are assumed to be derived independently from the domestication process from the distinct original ancestral wild populations [12]. Therefore, based on this fact, it is obvious that, somehow, the phylogenetic history for sheep and goats differs.

In the case of sheep, from a mitochondrial point of view, it is evident that at least two independent domestication events took place, resulting in haplogroup A and B, which are the most frequent haplogroups on a global level [13]. According to several studies, the haplogroup B is related to the European mouflon (*Ovis aries musimon*) and currently is predominant in Europe [14], while the haplogroup A is mainly present in Asiatic breeds and descends from the Asiatic mouflon (*Ovis orientalis*) [13]. Different authors [9,14] have reported that the European mouflon (*Ovis aries musimon*), an indigenous breed found in the Mediterranean islands of Sardinia and Corsica, represents a primitive form of the Asiatic mouflon. Further studies have identified the existence of other sheep clades defined as C, D, and E. The haplogroup C is mainly present in China, whereas clades D and E, although scarce, have been observed in Caucasus and Turkish sheep [14,15]. Moreover, a recent study on whole genomes of domestic sheep and their wild relative species reported some independent events of adaptive introgression from the wild sheep population into the Asiatic and European mouflons, as well as the detection of shared introgressed regions from both *Ovis nivicola* and *Ovis ammon* into the Asiatic mouflon population before or during the domestication process. The European mouflons may have evolved through hybridization events, occurring around 6000–5000 years BP, between a sheep type that is now extinct in Europe and feral domesticated sheep [16]. The same study also revealed the subsequent introgressions from wild sheep to their sympatric domestic relatives after domestication. Another research, focused on the resequencing of the whole genome in wild and domestic sheep, confirmed that the modern European mouflon is the feral descendent of early domestic sheep, although the influence of Asiatic mouflon cannot be excluded due to a substantial influence of the urial on the current Asiatic mouflon [17]. Moreover, the authors affirmed that retained or introgressed wild gene variants in domestic sheep have contributed to the successful adaptation of sheep breeds in their respective local environments.

On the other hand, the process of the domestication of the goat involved multiple maternal origins. Studies on ancient genomes revealed a complex contribution of multiple and genetically divergent wild lineages to the early domestic breeds [18–20]. It is currently scientifically accepted that six divergent mtDNA haplogroups (A, B, C, D, F, and G) contributed to the early phylogeographic structure of domestic goats. During the post-Neolithic period, the domestic goats in the Near East and Iranian Plateau showed a collapse of their initial mtDNA pattern, leading to the widespread dominance of A lineages [18], which, today, characterize 91% of domestic goats on a global level [19]. The domestication processes of goat and their dispersal involved changes in several morphological and physiological traits. Zheng et al. [21] provided evidence of an ancient introgression event from a West Caucasian tur-like species into the domestic goats. In particular, these authors identified two genes, one related to pathogen resistance (*MUC6* gene) and the other to behaviour linked to neural functions (*STIM1-RRM1* gene), that emerged at least 7200 and 8100 years ago, respectively. Their current high frequencies in the modern domestic goat breeds increased with the expansion of the mitochondrial haplogroup A from the Neolithic period until present, probably resulting from the local genetic adaptations of goats.

3. Adaptation to Environmental Stressors in Native Small Ruminant Breeds

Collier et al. [22] gives a comprehensive description of the meaning of acclimation, acclimatization, and adaptation to environmental stressors. Stress is any environmental situation, while a stressor is any environmental factor that provokes an adaptation response to negative effects on various factors of health, welfare, production, and reproduction in livestock species [23]. In animal husbandry, stressors may originate from internal and/or external factors (Figure 3). Internal factors include animal activities and housing conditions, such as management and feeding practices, whereas the external factors consist of stressors outside of the barn condition, such as heat waves, drought, and forage deficiency [24,25]. Environmental stress factors occur when a given animal's environment changes and shows enormous diversity in terms of their severity and duration [26]. A stress may be chronic, such as in high stocking density situations and unsuitable barn design and construction that will evoke sustained and prolonged discomfort in herds one generation after another, or acute, as in the negative effects of transportation stress, which is abrupt, profound, and sustained over a short time period [27]. If chronic stress due to extreme or adverse surroundings persists over several generations, environmental adaptation is prone to occurring with the necessary modifications in animal's functional, structural, or behavioural traits that would favour its survival or reproduction. Exposure to different environmental conditions (abiotic and biotic factors) can induce a genotype to produce different phenotypes, and this ability is referred to as phenotypic plasticity. The plasticity can affect and modify the gene expression of animal organisms, especially to overcome negative environmental stressors [28]. This adaptation response will eventually become genetically "fixed" through the natural selection process. Compounding available knowledge of the different genetic parameters present in adapted animals will infer useful data on the genes that are associated with acclimation.

Environmental stressors due to climate change are the most important ecological factors determining the growth, development, and productivity of domestic animals [29]. Whether caused by natural phenomena or by human activities [28], the repercussions of climate change are not just limited to a significant decrease in livestock welfare and wellbeing [26], but will also have a negative impact on the environmental ecology through reducing pasture and water availability, and also with the potential introduction of new diseases and parasites [30].

Climate change, in addition to an increase in global warming, also manifests in an increase in frequency in extreme weather events and conditions, such as unexpected and unpredictable rainfall patterns, drought, and heat waves. The gradual yearly increase in ambient temperatures is being reported as causing particular damages to the thermal comfort zone in farm animals [26,28]. Under normal environmental conditions, livestock

maintain a balance between heat gain and heat loss, a physiological process referred to as thermoregulation. Excessive heat loss or gain by the animal leads to cold stress and heat stress, respectively [31,32]. An increase in heat load mainly occurs due to the heat increment associated with metabolic activities and exposure to high ambient temperature. Heat-stressed animals will consume less feed and drink more to compensate for metabolic heat production, and they will also move to avoid direct exposure to sun while seeking air flow to facilitate heat dissipation [26,30]. Although these responses may lessen the negative effects of heat stress, they are associated with a decrease in production and reproductive efficiency in small ruminants, particularly due to low feed intake [33]. On the other hand, livestock species all over the world have managed to survive and maintain their production and reproductive parameters in the presence of numerous environmental stressors following an adaptation and acclimation process that occurred over centuries and was facilitated through favourable animal husbandry practices.

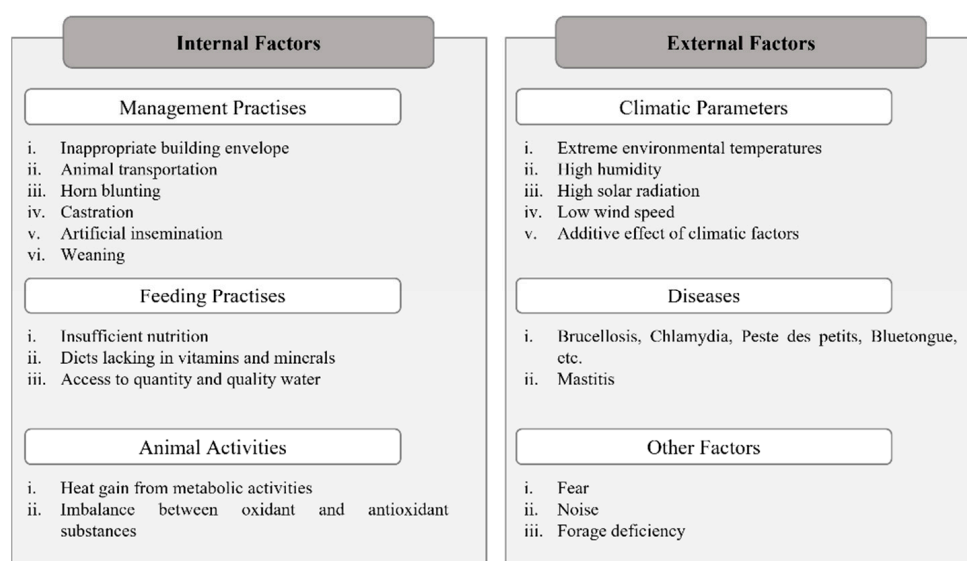


Figure 3. An overview of stressors in small ruminants. Source: data revised from [23,26,28].

Adaptation capacity is the response process at morphological, anatomical, physiological, and genetic bases against different environmental conditions to maintain welfare, survivability, and reproduction in animals [24,34]. Small ruminants are deemed to have a better adaptation capacity than other ruminants in terms of heat stress (Figure 4), since they possess some unique adaptive traits that allowed them to be the most acclimatised and geographically widespread animal species [34]. Indeed, native small ruminants developed adaptation traits to specific environments over generation via the natural selection process [35].

Additionally, these indigenous breeds could develop adaptation against a novel environment by acclimation, i.e., the animal's ability to co-ordinate compensatory phenotypic response alterations due to a single stressor in the environment acting alone [36]. Climate change is an excellent example of a stressor that evokes acclimation in native small ruminants. In rangeland-based small ruminant farming systems, the native herds graze during the season in which grass is available, thereby decreasing feed cost but, simultaneously, also exposing animals to high temperatures and direct solar radiation. Compared to the exotic or high-yielding breeds, indigenous animals generate less heat from metabolic activities and, in so doing, these native breeds are less likely to be affected by high temperature and heat stress on rangeland-based production systems. Furthermore, climate change emerged gradually over various generations, thereby allowing these native breeds to gradually develop an adaptation against heat stress due to this phenomenon.

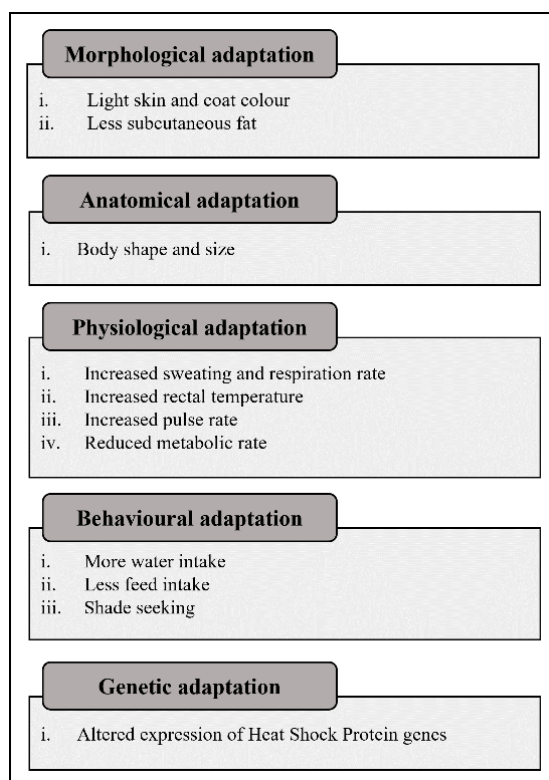


Figure 4. Adaptation against heat stress in small ruminants. Source: data revised from [24,33,34].

The human stewardship element in managing animal husbandry plays a key role in diminishing the negative repercussions arising from climate change. For example, in the poultry and broiler sector, farmers may develop and maintain a microclimate within a totally environmentally controlled building envelope in which ambient conditions, such as temperature, humidity, air flow, and lightning, are pre-set at optimum levels for production. Unfortunately, creating a microclimate for native small ruminant breeds is not practical nor feasible, since they are kept on grassland ranges and the economic burden is too heavy to be sustained. Instead, efforts could focus to increase resistance to thermal stress with the implementation of breeding practices in which thermo-tolerant animals are selected as mating animals within a properly structured breeding program that aims to concentrate and promote these traits.

4. Genes Involved in Environmental Adaptation and Acclimation

Climate is the single most important ecological factor that determines the growth, development, and productivity of domestic animals [29]. The economic impacts of climate changes on livestock production have been discussed in various studies [37–42]. Global warming and its direct link to climate change brings with it great challenges, since it adversely affects the yield, durability, and living conditions of small ruminant animals, especially those reared on pasture. Acclimation includes the biological response to immediate or long-lasting environmental stressors and phenotypic changes. When stressors persist for several generations, the biological response will become genetically stable through a process of selection, either natural or as influenced by humans, and the animal will eventually adapt to the environment [22]. Small ruminants, such as sheep and goats, possess a high level of adaptability to a wide range of agro-ecological regions. Moreover, goats have a relatively high capacity for disease resistance, allowing them to thrive better in harsh conditions [43].

Different strategies should be developed and implemented at the international level to counteract the negative effects of climate change on livestock. Crossbreeding of native sheep and goats with high-yielding breeds may play an important role in the mitigation

process [43]. Recent advances in molecular genomic expression technologies make it possible to identify candidate gene regions associated with thermo-tolerance [44]. The inclusion of such genetic information in the design of breeding programs may be instrumental in developing heat-resistant breeds. In addition, genes related to acclimation and environmental adaptation should be highlighted so that high-yielding animals with a resistance to stressors linked to changing climate and harsh environmental conditions will be developed following genomic selection procedures. Currently, there are no clear data on how these animals will adapt and survive in new and changing environments, although identifying genes associated with the genetic architecture of adaptation is crucial for selection programs.

Some gene regions identified to be associated with environmental adaptation and acclimation in small ruminants are summarized in Table 1.

Table 1. Genes involved in environmental adaptation and acclimation.

| Features | Species | Breed | Related Gene | Detection Method | References |
|---|----------------|--|--|------------------|------------|
| Coat Colour | Sheep | Crioula sheep | <i>MC1R, ASIP, TYRP1</i> | Sequencing | [45] |
| High-altitude hypoxia adaptation | Sheep | Tibetan sheep | <i>EPAS1, CRYAA, LONP1, NF1, DPP4, SOD1, PPARG, SOCS2</i> | Sequencing | [46] |
| Adaptation to cold climate | Sheep | Russian sheep | <i>NEB, APOB</i> | SNP array | [47] |
| Protection against pulmonary injuries | Sheep | Nepal, Asian and Middle East breeds | <i>FGF-7</i> | SNP array | [48] |
| Coat Colour | Sheep | Lezgin, Karachaev, Karakul, Edilbai, Romanov, Russian | <i>KIT, KITLG</i> | SNP array | [49] |
| Reproduction | | Longhaired, Groznensk, Salsk, Volgograd, Buubei, Tuva, Altai | <i>CMTM6, HTRA1, GNAQ, UBQLN1, IFT88</i> | | |
| Environmental adaptations | | Mountain, Krasnoyarsk, Baikal, and Kulundin | <i>EGFR, HSPH1, NMUR1, EDNRB, PRL, TSHR, ADAMTS5</i> | | |
| Coat Colour | | | <i>ASIP, MC1R, TYRP1, MITF, EDN3, BNC2</i> | | |
| Stature and morphology | Sheep | French sheep | <i>NPR2, MSTN (GDF-8), LCORL, NCAPG, ALX4, EXT2, PALLD</i> | SNP array | [50] |
| Horns | | | <i>RXFP2</i> | | |
| Wool | | | <i>IRF2BP2</i> | | |
| Energy and regulation activities | Sheep | Autochthonous sheep | <i>TBC1D12</i> | SNP array | [51] |
| Cold tolerance | Sheep | Worldwide Sheep Populations | <i>TRPM8</i> | Sequencing | [52] |
| Heat Stress | Sheep | Chokla, Magra, Marwari, and Madras Red | <i>HSP90AA1, HSPA1A, HSPA8</i> | RT-PCR | [53] |
| | | Tibetan sheep | <i>HSP27, HSP60</i> | RT-PCR | [54] |
| Altitude adaptation | Sheep | Ethiopian sheep populations | <i>PLCB1, PLCE1, FHAD1, GNA12, KLF12, SUSD4, ZNF407</i> | Sequencing | [55] |
| | | Barbari, Jakhrana, Sirohi and Jamunapari | <i>ENOX2</i> | RT-PCR | [56] |
| Heat Stress | Goat | Barki | <i>EIF2B3</i> | SNP array | [57] |
| | | Karamojong | <i>KPNA4, MTOR, SH2B1, MAPK3</i> | SNP array | [58] |
| | | Barbari | <i>HSP90, HSP70</i> | RT-PCR | [59] |
| | | Barbari, Sirohi, and Jhakrana | <i>HSP60, HSP70, HSP90</i> | RT-PCR | [60] |
| Coat Colour | Goat | Osmanabadi, Malabari, and Salem Black | <i>HSP70</i> | RT-PCR | [61] |
| | | Unspecified | <i>ADAMTS20, MC1R, ASIP, SOX18, TIMP3, GPR37L1, INS</i> | SNP array | [62] |
| Against oxidative stress | Sheep and Goat | Barki | <i>BMP2, FGF</i> | SNP array | [57] |
| Adaptation to hot arid environments | | Barki | <i>FGF2, GNAI3, PLCB1, BMP2, BMP4, GJA3, GJB2, MYH, TRHDE, ALDH1A3, GRIA1, IL2, IL7, IL21, IL1R1</i> | SNP array | [57] |
| Thermo-tolerance (melanogenesis), body size and development, energy, and digestive metabolism | Sheep and Goat | Barki | | | |

Heat shock proteins (HSPs) are directly associated with exposure to heat stress caused by metabolic activity and environmental temperature affect. The imbalance caused by the

higher metabolic heat production than heat dissipation capacity of animals will cause an internal heat load that manifests itself as heat stress. The first biological response of animals exposed to heat stress is an increase in respiratory rate, rectal temperature, and heart rate, while, at the same time, they will decrease feed intake, thereby compromising production parameters, i.e., live weight gain, milk yield, reproductive performance, and health [33]. Fortunately, animals react to heat stress by synthesizing HSPs that are classified as HSP100, HSP90, HSP70, HSP60, HSP47, and other small HSP proteins that are ranked according to their molecular weight [30,63]. During the exposure to high temperatures, protein damages, heavy metals, traumas, and starvation, the expression levels of HSP genes increase in order to maintain homeostasis in live cells [64]. Being a family of large proteins, HSPs allow cells to gradually develop tolerance and adaptation against changing environment condition [65]. Indeed, Kumar et al. [60] reported higher expression of *HSP60*, *HSP70*, and *HSP90* genes in peripheral blood mononuclear cells of heat-susceptible goat breeds (Sirhi/Jhakarana), while lower expression profiles were highlighted in the Barbari breed, which is known to be heat-tolerant. Moreover, higher expression of *HSP60*, *HSP70*, and *HSP90* was observed during summer months when compared to thermo-neutral conditions and winter seasons [60]. Similarly, Banerjee et al. [66] reported high expression of several gene regions belonging to the HSP70 family (*HSPA1A*, *HSPA8*, and *HSPA6*) in peripheral blood mononuclear cells of Indian goat breeds (Sirohi, Barbari, Gaddi, and Chegu) during summer season. Besides, the authors indicated that the expression of *HSP70* may be utilised as a stress marker in different species in order to face challenges caused by climate change. Numerous studies have also revealed that the expression patterns of HSPs are a useful indicator to estimate intensity and duration of heat stress in small ruminants [53,67–70].

Moreover, heat stress may also be suppressed or triggered by coat colour, since it is related to sunlight absorption and reflection based on fleece size, length, and depth, as well as colour type [71,72]. Coat and skin colour in mammals are affected by two main sets of genes: one involving pigment synthesis and the other involved in replacing melanocytes [73]. So far, more than 300 genes have been identified as having a direct and indirect effect on pigmentation [74]. Many of these genes are involved in the production or regulation of the two pigments, pheomelanin and eumelanin [73]. Melanocortin 1 receptor (*MC1R*), agouti signalling protein (*ASIP*), proto-oncogene, receptor tyrosine kinase (*KIT*), and tyrosinase (*TYR*) are all involved in the regulation of melanin production [62]. Dark coats are known to absorb more thermal radiation and, thus, animals with such a coat are more susceptible to heat stress than light coat ones [75]. In fact, Ross et al. [76] reported lower rectal temperature and respiratory rate in Blackbelly sheep under heat stress conditions. Variations in the genomic region related to the capacity for adaptation to environmental stressors may be used in selection strategies to develop tolerance and resistance against these challenges. Therefore, in view of the future prospects of global warming and climate change, heat-tolerant small ruminant breeds will occupy an increasingly important role in the production of animal-derived protein.

5. Conservation Strategies and Current Selection Practices for Genes Related to Environmental Adaptation

Since the onset of domestication, the genetic diversity found in livestock species is the compound result of several factors, such as mutation, adaptation, isolation, migration, and breeder's preference, all of which are of great importance for sustainability and future challenges [77,78]. Genetic diversity defines the total genomic information in a certain species, including all breeds, subpopulations, and varieties that fall within that particular species [79,80]. Genetic variability, a prerequisite for conservation genetics, plays a key role in supplying and meeting demands for animal-derived products in different climatic regions and zones across the world, and is also essential for the potential adaptation to future changing environmental conditions [81,82].

The present efforts of both producers and scientists have mainly focused on climate change caused by global warming rather than addressing the decrease in natural resources and other environmental stressors [42,83,84].

Over the last two decades, climate change caused by global warming has been closely followed and monitored by scientists from all corners of the world. Since 1975, the global ambient temperature has increased steadily at an average rate of 0.15–0.20 °C per decade and it is predicted to rise by a further 2–3 °C by 2100 [83,85]. Furthermore, it is being speculated that the expected climate change phenomena will also cause a significant reduction in biodiversity and will increase the occurrence of some diseases and pathogens [86]. In this regard, small ruminants are being incorporated in research projects aimed at investigating the capacity of farm animals to increase their adaptation capacity against extreme environmental conditions, such as high temperature, heat waves, and drought.

Since more than 1,000 sheep and 500 goat breeds are reared in a wide spectrum of agro-ecological zones across the globe, it is of uttermost importance to involve these small ruminants in research studies focused on environmental adaptation [87,88]. The existence of a significant number of subgroups (types and varieties) due to crossbreeding practices further supports this view. Ever since the domestication of the small ruminants, genotypic variations have evolved in response to the different geographical and climatic conditions, as well as to the different management practices, thus offering enormous opportunities to develop adaptation in small ruminants [82]. It is also noteworthy to mention that native breeds that have existed in a particular geographic region for a long period of time, eventually become part of the ecological value of that specific geographic landscape. Today, native breeds having a high adaptation capacity are preferred by breeders [89–91].

The first step in enhancing environmental adaptations in structured breeding programs is to detect the genomic regions associated with resistance to environmental stressors. Over the last 30 years, PCR-based molecular techniques (RFLP, AFLP, microsatellites, etc.) have been utilized in animal genetics studies [91–93]. These techniques were mainly used to conduct conservation programs [94] via limited loci across the genome to detect quantitative trait loci (QTLs) [95] and to increase the frequency of the desired genotype combinations across populations by using the marker-assisted selection (MAS) [96]. However, analysis of a limited number of loci in specific traits, such as environmental adaptation, which is shaped by many genes, is a considerable obstacle for success in both conservation and selection studies [97].

The rapid development of SNP chips and DNA sequencing technologies for livestock species offers a novel and important opportunity to overcome these obstacles. For instance, microsatellite-based QTL studies have been mainly carried out via 30–100 loci, whereas 50,000–100,000 SNPs could be detected by SNP arrays or next-generation sequencing (NGS) technologies (GBS, RADseq, and ddRADseq) [98]. Similar genetic information is obtained by a single microsatellite and three SNPs [99,100]. Compared to traditional genetic markers including microsatellites, SNP arrays and NGS are powerful tools for genomic studies due to their abundance across the genome. Indeed, high-density genomic data obtained from SNP arrays and NGS technologies are commonly used to reveal genomic regions associated with environmental adaptation [55,101,102]. Genomic regions related to environmental adaptation detected by selection signatures and genome-wide association study (GWAS) could be integrated in the genomic selection (GS) practices [103]. These developments in genotyping have significantly facilitated studies that analyse the whole genome in livestock, as well as in many other fields of science.

Many studies aimed at detecting genomic regions related to environmental adaptation are available. Recently, much research has detected candidate genes related to high altitude [101,104,105], climate change [47,55,105], and disease resistance [104] in small ruminants by screening the genome for selection signatures using SNP arrays. Similarly, via high-density genomic data from NGS technologies, numerous candidate genes related to environmental adaptation (high altitude, climate change, disease resistance, etc.) have been investigated in small ruminants [49,56,106,107].

In conservation programs, SNP arrays are more useful than traditional molecular markers, while they have some disadvantages compared to NGS technologies. First of all, SNP arrays are developed based on a reference genome, which limits the detection of some unique SNPs and rare variants related to environmental adaptation in native small ruminant breeds and varieties. In addition, the creation of SNP arrays on exons, ignoring rare variants (frequency less than 5%), and working based on nucleotide hybridisation leads to SNP errors and filtration-induced locus losses. Unlike SNP arrays, the whole genome sequencing technique (WGS) is complete genome sequence containing all the polymorphism present on the genome. Thus, WGS does not have the problem of ascertainment biases. Therefore, WGS analysis, even when allowing for the detection of unique SNPs and rare variants, is the more powerful genotyping tool to reveal the total genetic diversity, as well as conservation genetics [108,109].

After detection of candidate genes related to environmental adaptation, the priority should be given to the conservation of these variations in small ruminants. In particular, conservation programs should start from the populations holding a high genetic variation and a low inbreeding level. Meanwhile, it is important to consider not only breeds but also varieties in which unique genotype combinations with low frequencies may be available for environmental adaptation [77,81,94].

Consequently, the frequency of desired gene combinations could be increased in the next generation by applying suitable selection strategies, which should also be feasible in terms of aim, time, and affordability. In small ruminants, genetic improvement is comparatively low in traditional selection practices due to low heritability of quantitative traits, such as longevity and disease resistance. On the other hand, MAS and GS practices are fast and may yield more genetic improvement per generations [110,111].

It is worth noting that ongoing traditional selection practices could be easily supported by MAS in which genes related to environmental adaptation are considered. This method allows the development of new selection criteria, not only for the economically important traits, but also for traits against environmental stressors. Although the traditional selection practices supported by MAS are affordable and easily adaptable, genetic improvement will still be insufficient due to the consideration of a low number of genes [112].

In the last decade, GS practices offer huge opportunities to improve several traits in livestock species. Since genomic breeding value (GBV) is estimated for each animal across the entire genome, success in selection and genetic gain has been significantly increased in quantitative traits, such as meat and milk yield and environmental adaptation [113–115]. While GS practices are promising to increase economically important traits and environmental adaptation simultaneously, economic burdens of NGS technologies still cannot be afforded by smallholder farmers [116]. Further, in underdeveloped and developing countries, the number of qualified scientists who have the ability and/or the facilities to conduct bioinformatics analyses via high-density genomic data may be low. Moreover, it is a known fact that there are multiple difficulties for breeders or breeders' associations, especially in developing countries. Although selection for genes related to environmental adaptation is possible for sheep and goats, there are other limiting factors to be considered due to difficulty in collecting phenotypes and pedigree information and the costs of applying breeding schemes, especially in developing countries [117]. Moreover, an accurate pedigree is mandatory for a correct implementation of breeding programs. Even in dairy cattle, which have a well-established breeding program, a high misidentification rate has been referred [118] and these pedigree errors are probably even higher in sheep and goats.

However, the decrease in the cost of SNP arrays or NGS technologies in the near future will lead to a rapid increase in GS studies in farm animals and not only restricted to research flocks.

6. Conclusions

In conclusion, this manuscript aimed at reviewing the genes related to environmental adaptation in small ruminants by considering the reason for their conservation status, as

well as usefulness in selection practices. High-density genomic data, via SNP arrays and whole genome resequencing, are promising tools to increase adaptation capacity against environmental stressors in native small ruminant populations. These informative data sets are commonly utilised to estimate genetic diversity and inbreeding level, as well as analysing the genomic regions associated to environmental adaptation in local populations. Identifying breeds with a high ability to adapt to changing environmental conditions with global climate change is of great importance for the sustainability of animal husbandry.

Basically, environmental adaptation could be improved by considering related genes in crossbreeding practices. Alternatively, the frequencies of the tolerant animals may be increased by MAS and GS studies in native sheep and goat populations. Conservation of genomic variations in related genes will not only allow animals to develop adaptation against future challenges, but also will support farmers in their efforts for the sustainable use of local populations. Particularly, due to the exposure of animals to high temperatures via ongoing global warming, the conservation of the genomic variations related to environmental adaptation will be inevitable for countries in the future.

This review may serve as a guideline for the development of conservation and management practices to reduce negative effects of the increased environmental stressors in local small ruminants.

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