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Food securers or invasive aliens? Trends and consequences of non-native livestock introgression in developing countries

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ABSTRACT

Importation of livestock genetic resources from industrialized countries for introgression of specific traits and other forms of crossbreeding is often indicative of a shift in production systems toward greater intensification and specialization. In developing countries, imported genetic resources are regarded as both a solution to improve the performance of local livestock and as one of the main threats to local populations. Using international databases, censuses and technical reports, we investigate ongoing trends and consequences of these two phenomena in 40 countries from Africa, Asia and Latin America. In these countries, the share of locally adapted breeds within species has decreased by an average of 0.76% per year over the last 20 years. The corresponding increase has been distributed between pure exotic breeds and crossbred animals, with differences across regions. In several countries, increased utilization of exotic cattle breeds and crossbreeding has been accompanied by a trend in increased milk yield per cow. The shift from local genetic resources to crossbred and exotic animals must be considered in the context of challenges such as food security, erosion of agrobiodiversity, interactions with other agricultural production, reduction of poverty and provision of ecosystem services, as well as resilience to and mitigation of climate change.

1. Introduction

Global production of livestock is expected to increase substantially, driven by increasing demand from developing regions. By 2030, global milk and meat production are expected to be 33 and 19 percent, respectively, above current levels (FAO, 2018). In this context, and considering limited availability of land, water and other natural resources, livestock farmers from those developing regions need to increase the production and productivity of their animals (Mayberry et al., 2017). Genetic improvement is an important lever for improvement of livestock production traits (Miglior et al., 2017; Tallentire et al., 2016). Livestock in industrialized countries have undergone generations of intense selection and their genetic merit for production in their usual production environment usually is superior to local breeds in developing countries. Therefore, crossbreeding and replacement of local livestock by exotic breeds are often seen as attractive solutions to close yield gaps.

Crossbreeding strategies usually require less investment in capital, infrastructure and technical know-how than within-breed genetic improvement (Leroy et al., 2016a). As a consequence, national livestock authorities in developing countries frequently integrate the extensive use of exotic livestock in their development strategies aiming at increasing the productivity of their livestock production systems (see for instance DAPH, 2010; GOI, 2013; Shapiro et al., 2015, 2017). Abundant literature documents the theoretical and practical impacts of crossbreeding and breed replacement at the local level (Galukande et al., 2013; Getachew et al., 2016; Roschinsky et al., 2015; Wilkes et al., 2017). Various studies have shown that in appropriate production environments, milk yield of crossbred cattle can be 2 to 2.6 times greater than of pure indigenous breeds, with associated increases in farmers' income (Galukande et al., 2013; Hegde, 2018).

On the other hand, outcomes of the many initiatives to replace and/or crossbreed local livestock breeds have been variable (Madalena et al., 2002; Marshall, 2014). Failures generally relate to limited adaptedness of exotic livestock breeds, poor infrastructure and technical capacity, lack of long-term commitment of institutional partners, and limited preparatory involvement of the small-scale livestock keepers (Lemke

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Box 1
Terminologies used for breeds and populations.

Breed: either a sub-specific group of domestic livestock with definable and identifiable external characteristics that enable it to be separated by visual appraisal from other similarly defined groups within the same species, or a group for which geographical and/or cultural separation from phenotypically similar groups has led to acceptance of its separate identity.

Crossbred: animals produced through the mating of individuals from different breeds, either following a specific strategy (such as terminal crossing, rotational crossing or synthetic breed creation) or through an indiscriminate process. Synthetic breeds are excluded from this definition once the population has reached an equilibrium state at which all animals have the same proportion of genetics from the original breeds. In this study, the crossbred category is restricted to the cross between locally adapted and exotic breeds.

Exotic: animals originating from breeds that have not been continuously present in a country for sufficient time to be adapted to the prevailing environmental conditions. Exotic breeds comprise both Recently Introduced Breeds and Continually Imported Breeds. In this study, exotic breeds correspond essentially to highly productive breeds originating from developed countries.

Local: breeds that occur only in one country.

Locally adapted: breeds which have been in the country for a sufficient time to be genetically adapted to one or more of traditional production systems or environments in the country. Indigenous Breeds, also termed autochthonous or native breeds and originating from, adapted to and utilized in a particular geographical region, form a sub-set of the Locally Adapted Breeds.

National breed population: a subpopulation of a breed found in a given country.

International transboundary: breeds that occur in more than one country in more than one region.

Regional transboundary: breeds that occur in more than one country in one region.

Source: adapted from FAO (2012).

et al., 2007; Leroy et al., 2016a). Murray et al. (2013) showed that exotic breeds of cattle and their crossbreeds with Zebu cattle show reduced resistance to endemic diseases.

The use of exotic breeds and indiscriminate crossbreeding have been reported as the two main factors causing erosion of local genetic resources (FAO et al., 2015). Animal genetic resources are an essential component of sustainable food systems. Therefore, monitoring and maintaining locally adapted livestock are essential. The putative importance of local breeds is reflected in the UN Sustainable Development Goals (SDG), for which Target 2.5 addresses maintenance of the genetic diversity of domesticated animals (https://unstats.un.org/sdgs/metadata?Text=&Goal=2&Target=2.5, FAO, 2019).

Despite the abundance of literature on individual projects, little is known on the trends and consequences of crossbreeding and breed replacement on a larger scale. Using data from international databases, agricultural censuses and technical reports, we investigate the recent trend in the global share of locally adapted, crossbred and exotic livestock in 40 countries. We also investigate the relationship between those proportions and estimates of average milk yield per cow for 11 countries, as well as the trends of 190 national breed populations considered as locally adapted, and discuss issues regarding sustainability.

2. Material and methods

2.1. Data

To obtain data on the relative importance of locally adapted, crossbred and exotic livestock populations, information from agricultural censuses and technical reports from the years between 2000 and 2019 were used. These data originated from 40 African, Asian, and Latin American countries and the five main livestock species (cattle, chicken, goat, pig, sheep) (see Supplementary Table 1). In two countries (Senegal and Niger), the Domestic Animal Diversity Information System (DAD-IS) was used as the source of information, because the DAD-IS breed population data corresponded closely to the total species population reported in FAOSTAT (http://www.fao.org/faostat) for ruminants (±5%), This decision was made following discussion with corresponding National Coordinators officially nominated by these countries as focal points for animal genetic resources.

From those different sources, 479 Country/Species/Year combinations were formed, representing 83 Country/Species combinations (see Supplementary Table 1). The classification system differed according to countries and species and the three following categories were used in our analysis (see Box 1 for terminologies):

- Exotic: defined according to countries as exotic, foreign, broilers and layers, specific improved breeds (such as Holstein, Dorper, Boer …) or any terms other than crossbred and local.: 59 Country/Species combinations.
- Crossbred: defined according to countries as crossbred, crossed, hybrid, or improved local (presumably through introgression by exotic breeds): 35 Country/Species combinations.
- Locally adapted: defined by countries as local, indigenous, native, locally adapted, backyard, and/or with a specific name implying that breed is of local origin (e.g. Criollo, Desi or Tswana): 79 Country/Species combinations.

In some cases, only one category was differentiated from the other two (i.e. Locally adapted versus non-locally adapted or exotic versus non-exotic). For this reason, the three categories were analyzed independently from each other.

Average milk yields (Number of L per cow and per year) for cattle were extracted from FAOSTAT or provided by National Coordinators to compute linear regressions on either the proportion of exotic breeds or the proportion of exotic + crossbred (according to data available) for 11 countries that had provided either information on populations described as dairy cattle (Algeria, Chile, Egypt, Ethiopia, Iran, Morocco, Tunisia) or on general cattle populations oriented toward milk (Bhutan, India, Nepal, and Jordan) (see Supplementary Table 2).

To analyze demographic trends at breed level, a third data set was extracted from DAD-IS, containing information on the population size of national breed populations reported at different points in time during the period 2000–2019. Only data from local breeds or regional transboundary breeds were included as proxies for locally adapted breeds, as in DAD-IS information regarding geographical adaptation is provided for fewer than 20% of national breed populations from Africa, Asia, and

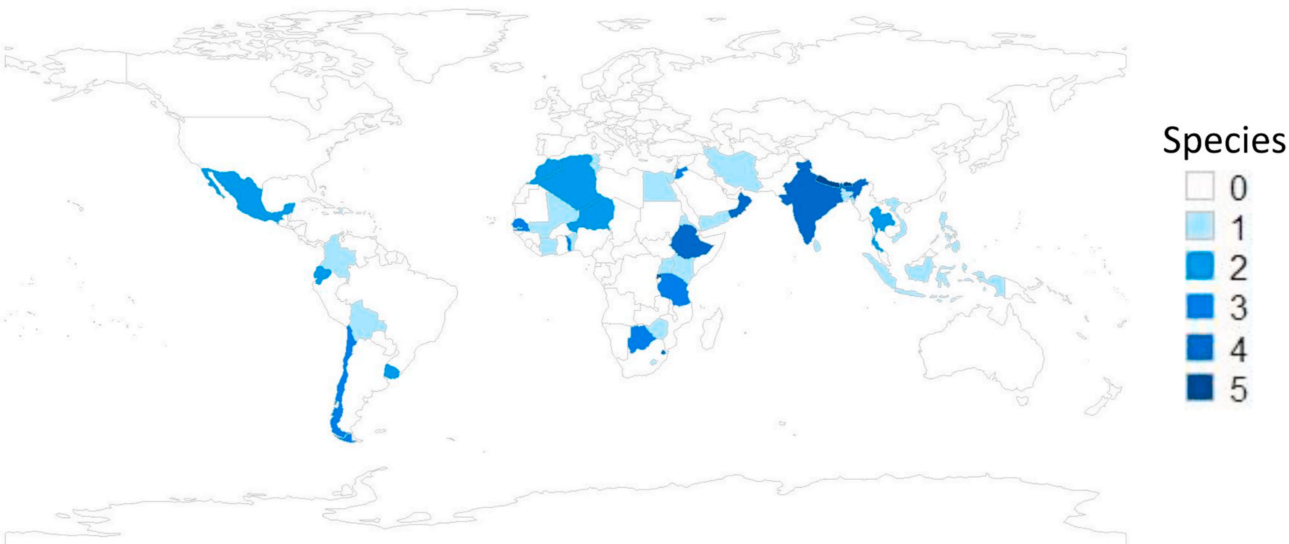

Fig. 1. Map of the countries providing information on trends in locally adapted, crossbred and exotic livestock for the five species.

Latin America. 190 national breed populations with at least two population size estimates (as the average of minimal and maximal population sizes provided in DAD-IS) were extracted from 29 countries of those three regions (11 in Africa, 9 in Asia, 21 in Latin America), for a total of 877 population size estimates *(to be confirmed)*.

2.2. Statistical analysis

The proportions of the species populations belonging to each of the three categories were analyzed independently for each category, considering a linear mixed-effect model (R lme function). The three Regions and five Species were included as explanatory factors. Year, as well as interactions of Year x Region and Year x Species were considered as covariables. Species/Country combination was added as a random effect, as well as an autocorrelation structure component of order 1 with the Year covariate (corCAR1). Explanatory variables were removed stepwise until minimizing the Bayesian Information Criterion (BIC), but keeping Region, Year and Species/Country random effects as explanatory variables.

A linear mixed model was also utilized for the second data set containing milk yield per cow per year as the dependent variable (R lme function). In absence of information on animal husbandry (e.g. diet and veterinary care) and production environment, Year was used as a proxy and considered in the model as a covariable. The proportion of exotic/crossbred animals was used also as a covariable, while an explanatory factor indicating whether animals were 100% exotics or a combination of exotics and crossbreds was also included. Country was included as a random effect, as well an autocorrelation structure component of order 1 with Year covariate (corCAR1). Explanatory variables were removed stepwise until minimizing the BIC, keeping Year, proportion of exotic/crossbred animals and Country random effects in the model as explanatory variables.

Considering the large differences in population sizes among DAD-IS national breed populations, the third data set was simplified by computing the linear regression coefficient of population size over years for each national breed population, then comparing the number of populations with a positive trend (i.e. positive regression coefficient) to the numbers of populations with null or negative trends, according to Regions.

3. Results

3.1. Situation and trends

The 83 country x species cases studied here covered the past 20 years and originated from Africa (20 countries), Asia (13 countries) and Latin America (7 countries) (See Fig. 1), and from the five main livestock species, with 23 cases for cattle, 25 for chicken, 12 for goat, 9 for pig,

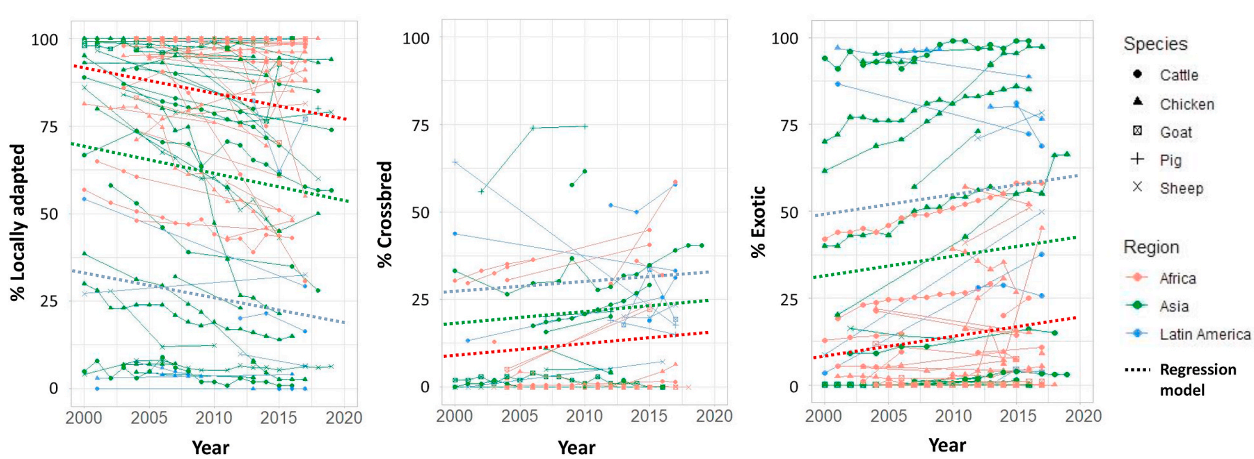

Fig. 2. Trends in locally adapted, crossbred and exotic share of livestock in countries. Dotted lines represent the statistical regression model.

Table 1
Regression coefficients and Least Square Means (LSMeans) for the proportions of local, crossbred and exotic livestock within national breed populations in the year 2019.

Category	Year (%)	Region effect (%)					
		Africa		Asia		Latin America	
		Estimate	LSMeans (2019)	Estimate	LSMeans (2019)	Estimate	LSMeans (2019)
Locally adapted breeds	−0.76***	0[a]	77.3	−21.9[b]	55.4	−59.1[b]	18.2
Crossbred	0.35***	0[a]	15.0	10.0[a]	25.0	14.2[a]	29.2
Exotic	0.48***	0[a]	16.7	28.3[b]	44.9	44.3[c]	70

***P < 0.001. Small letters represent non-significantly differentiated regions at P = 0.05.

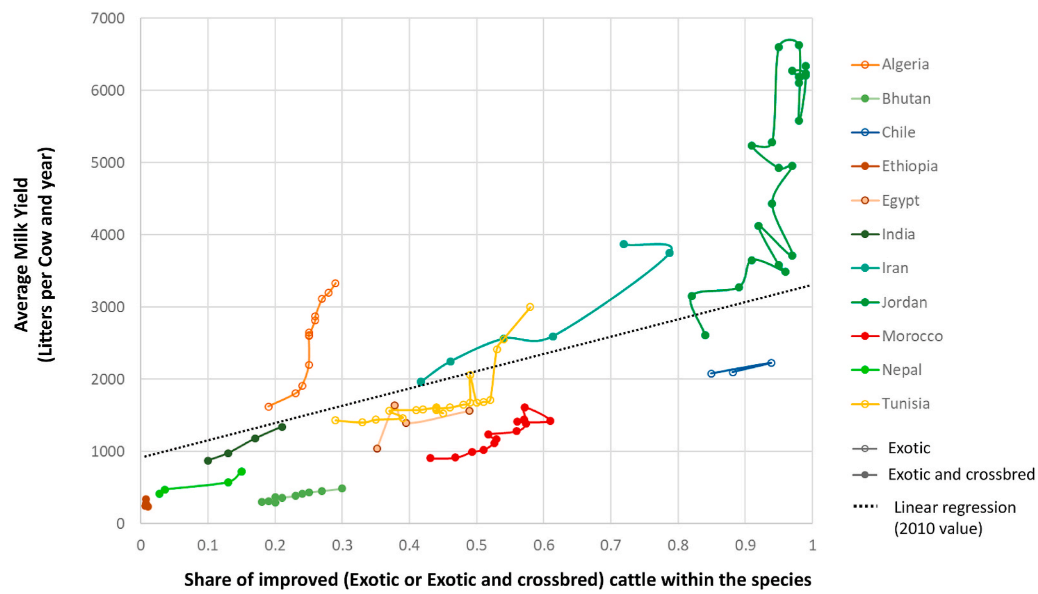

Fig. 3. Relation between crossbred/exotic share and milk yield in cattle. Dots are linked according to chronological order, while the dotted lines represent linear regression of average milk yield over proportion of improved cattle.

and 14 for sheep. The different cases represented a wide range of situations and contexts, with shares of national species populations ranging from 0 to 100% for locally adapted breeds, from 0 to 74% for crossbreds, and from 0 to 99% for exotic breeds, according to years, species and countries (Fig. 2). According to the models utilized, the trends observed revealed that the average share of locally adapted breeds has decreased by 0.76% per year, compared to yearly increases of 0.35% for crossbreds and 0.47% for exotic breeds (Table 1). The 2019 estimates for the respective proportions of locally adapted, crossbred and exotic breeds were 77.3, 15.0 and 16.5% for Africa; 55.4, 25.0 and 45.2% for Asia; and 18.2, 29.2 and 60.8% for Latin America. The three estimates within a region do not correspond to the exact same combinations of countries and species, so they do not sum to 100%. Proportions of locally adapted (exotic) breeds were significantly greater (smaller) in Africa than in Asia and Latin America (P < 0.01).

3.2. Impacts on milk yield

At the national level, our results on impacts of proportions of non-local genetics on milk yield from 11 countries suggest very different outcomes depending on the country, as illustrated by Fig. 3. In Ethiopia for instance, the share of exotic and crossbred dairy cows has remained very small, increasing from 0.7 to 1% between 2005 and 2011, with average milk yield remaining low at around 250 L per cow per year. In contrast, data from Jordan show the results of efforts to intensify the dairy industry that initiated in the 1970s (Alqaisi et al., 2010). The share of exotic and crossbred cattle (almost entirely purebred Holstein) was already 94% in 2000 and increased to 99% by 2016. Annual milk yield

Table 2
Proportion of local and regional national breed population with population size reported to increase over the period 2000–2019, and Tropical Livestock Unit (TLU) increase between 2000 and 2017.

	Africa	Asia	Latin America
Number of local regional breeds considered	74	95	21
Percentage with population size increasing	74.3%[a]	53.7%[b]	38.1%[b]
TLU increase 2000–2017	+56%	+9%	+18%

The same letters represent non-significantly differentiated regions at P = 0.05.

per cow passed above 4000 L during this period, i.e. values comparable to some European countries. Our analyses demonstrate a positive relationship between the relative proportion of crossbred and exotic breeds among all dairy cattle and average milk yield. Both time and the percentage of exotic/crossbred livestock were found to have a significant relationship with average milk yield, which increased by 50.3 L per year (P = 0.011) and 23.6 L per % of increase in improved/crossbred livestock (P = 0.007).

3.3. Demographic trends of locally adapted breeds

To assess more precisely the consequences for local livestock, we estimated the proportion of local and regional transboundary breeds with positive demographic trends, using 190 national breed populations extracted from DAD-IS.

A large majority (74.3%) of local national breed populations from Africa showed positive trends in population size (Table 2), which was significantly higher ($P < 0.001$) than in Asia (53.7%) and Latin America (38.1%). Between 2000 and 2017, the absolute number of livestock, measured in terms of Tropical Livestock Units (TLU) to account for species differences, increased at a much higher rate in Africa (+56%) than in Asia (+9%) and Latin America (+18%). In the case of Africa, the absolute increase in TLUs compensated for the relative decrease in the proportion of locally adapted breeds such that populations of most local breeds did not decrease in size. By contrast, in Latin America, a majority of local and regional breeds decreased in population size despite increases in the overall livestock population.

4. Discussion

4.1. Trends in locally adapted, crossbred and exotic breeds

In the last hundred years, multiple initiatives to improve food security in developing countries have aimed to cross or replace local livestock populations with more productive ones (Madalena et al., 2002; Marshall, 2014; Leroy et al., 2016a). Our results show that this trend is still ongoing and that locally adapted livestock still represent the largest share of livestock populations in Africa and Asia, while exotic breeds have become the majority in Latin America. Various factors may be responsible for these regional differences. For example, many African countries lack the logistic capacity to allow the diffusion, use and maintenance of exotic germplasm. In Latin America, the locally adapted Criollo breeds are themselves the products of crosses among various populations imported over the last centuries, so continued importation and crossing may be more culturally and scientifically accepted than in other regions.

The regression model that optimised the BIC did not include a species effect, although it's plausible that species-based economic, technological and logistic differences across production systems (such as artificial insemination in cattle, or provision of fertilised chicken eggs) could allow crossbreeding and breed replacement to occur more quickly for some species. Heterogeneity in the yield gaps between industrialized and developing countries may also play a role in species differences, as selection programmes for chickens, pigs and dairy cattle tend to be more advanced in industrialized countries relative to those for sheep, goats and beef cattle.

Interpretations of the definitions of exotic, crossbred and locally adapted animals and knowledge of genetic composition may vary among countries and among people within countries and even evolve through time, impacting the classification of breeds into the different categories and thus perhaps affecting our results. Genomics may offer a solution to inconsistencies in definition of breed type, which could consequently improve the inferences if our study were to be repeated in the future. Depending on species, breeds and locations, extent of influence from exotic (generally of European descent) breeds due to recent admixture has been found to range from negligible to predominant in local populations (Leroy et al., 2012; Murray et al., 2013; Buzanskas et al., 2017; Selepe et al., 2018; Ben Jemaa et al., 2019; Zhang et al., 2019). Although incomparably more precise to assess genetic origins of individuals than other sources of information, molecular approaches are currently limited in their coverage of livestock populations. Nevertheless, both molecular and census studies describe a wide diversity of situations according to species and countries.

4.2. Consequences for livestock production, poverty reduction and food security

The aim of the various crossbreeding, introgression and breed replacement projects has generally been to improve the production and productivity of local livestock (i.e. milk and egg production, growth, or prolificacy for instance) and in turn to increase both livestock production at the national level and income of farmers. This strategy is supported by the results of a wide number of studies showing positive impacts of crossbreeding on productive traits at local level, both in research stations and on farms (Galukande et al., 2013; Getachew et al., 2016).

Within countries, our results showed a positive association between average milk yield per cow and the proportion of exotic or crossbred genetics the national herd. Those results must be considered with caution, however, and cannot be entirely attributed to genetic differences, given the fact that the model did not directly account for factors such as changes in production systems and environment/inputs (e.g. quality and quantity of feed, health care and housing), which are likely to have occurred and contributed positively to the average milk yield of animals. In absence of information about possible changes in inputs and the costs related to such changes, conclusions on the impact of these trends in terms of costs and benefits and more generally in terms of the overall economic efficiency of the system (Acosta and De los Santos-Montero, 2019) cannot be drawn. Karugia et al. (2001) concluded that crossbreeding of cattle had a positive effect on the Kenyan economy and social welfare, although they speculated that the introduction of exotic genes may have not been beneficial at farm level, because improved animal productivity also involved accrued input costs. By contrast, Hegde (2018) reported positive economic impacts of crossbreeding for Indian cattle farmers, with the number of above-poverty-line families increasing by 262% over a ten-year period. In Senegal, Marshall et al. (2017) found that under good management, 50% indigenous Zebu by *Bos taurus* crossbreds for dairy production provided greater net economic benefits to households than did alternative options involving pure indigenous, highly introgressed (with Bos Taurus) or alternative crosses. Most studies concur with the notion that the success or failure of crossbreeding is associated with financial and logistic conditions enabling access to inputs and extension services. Overall, Marshall (2014) concluded that the socio-economic benefits to households of keeping a specific breed type depend largely on the production systemsand also vary according to the type of livestock keepers within a system.

A related factor to consider is that exotic livestock and their crosses require greater nutritional inputs to achieve their genetic potential for milk or meat production. Above a certain level of genetic potential for production, ruminant-livestock producers in mixed crop-livestock systems may have difficulty to produce the sufficient high quality forage and may need to purchase feed (McDermott et al., 2010). On a larger scale, this may have consequences on the dependency of countries on importation of nitrogen and other nutrients, which constitutes a growing issue for many regions with developing or emerging economies (Lassaletta et al., 2014).

4.3. Consequences for locally adapted breeds

Our results suggest that in Africa, and to a lesser extent in Asia, the general increase in the overall livestock population over the past 20 years has compensated for the decreasing proportion of locally adapted animals within species, allowing sizes of local populations to remain relatively stable. On the other hand, the population sizes of a majority of local and regional breeds have decreased in Latin America, while the overall livestock population has increased less in size than in Africa.

The increased presence of exotic and crossbred animals does not necessarily mean replacement of local populations, especially if the new animals are not raised in the same production environments (for instance, if new, peri-urban farms are developed). However, even if the importation of exotic animals is not intended to directly replace locally adapted breeds, they may nevertheless remain a threat as they enter in competition with traditional breeds and herds for resources and market share.

Erosion of the diversity of local animal genetic resources is especially problematic given the phenotypes of interest that are possessed by those breeds (Leroy et al., 2016b) and the ecosystem services they and their production systems provide (Leroy et al., 2018). In relation to their

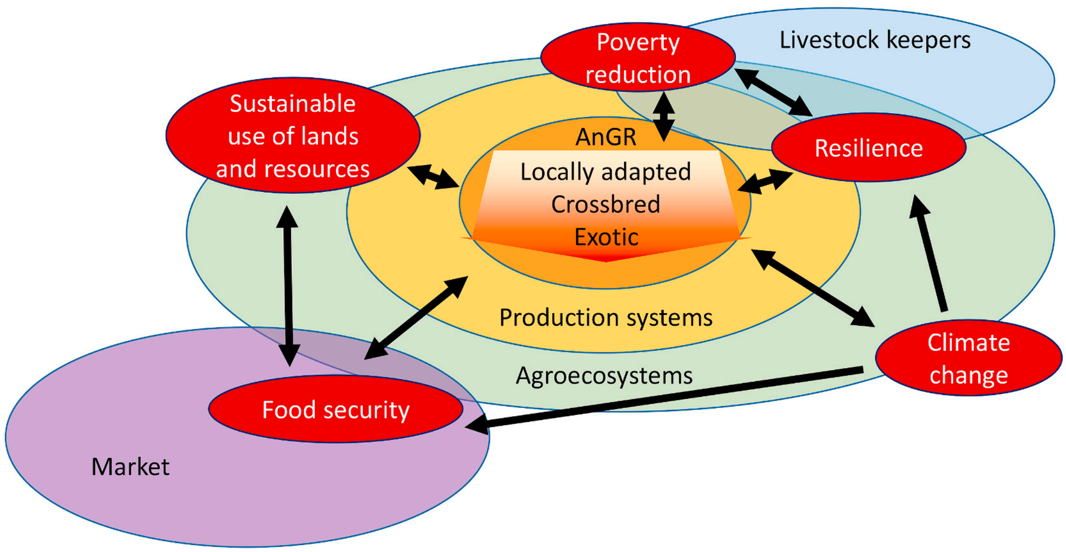

Fig. 4. Connection of Animal Genetic Resources and various challenges related to sustainability.

capacity to withstand endemic diseases and harsh climate conditions, survive on low-quality diets and walk long distances to access food and water, locally adapted ruminant breeds are especially well suited for the valorization and maintenance of pastoral rangelands, which constitute a large share of the global agricultural area (2 billion ha, of which 1.3 billion ha is not convertible to cropland according to Mottet et al., 2017) and therefore of critical importance for food security and livelihoods.

More generally, the increased number of crossbred and exotic animals is indicative of a shift in production systems toward greater intensification and specialization. This process may impact negatively on landscapes and use of resources, as illustrated by Magnani et al. (2019a). They showed that the sedentarisation of pastoralists and promotion of exotic breeds over local ones resulted in land fragmentation of the middle valley of the Senegal River. Also, considering the specific adaptive potential and robustness of locally adapted breeds, breed replacement may reduce the resilience of livestock production systems. The use of mixed herds and modifying herd composition to favour more resistant species or breeds are components of a classical strategy of herders facing long-term droughts (Blench and Marriage, 1999) and the use of locally adapted breeds has been suggested as an option to cope with constraints (drought, feed shortage, disease) induced by climate change (Musemwa et al. 2012; Bettridge et al., 2018). Considering the short and long term impact that the COVID 19 pandemic will have on food and agriculture in general and livestock in particular (e.g. shortage of labor and animal feed, Zhang, 2020), both the adaptedness of locally adapted breeds to less-intensive and/or short supply chains, and their general resistance to zoonotic diseases (Marshall et al., 2019) give them potential competitive advantages relative to exotic ones.

Considering the specific issue of mitigation of climate change, locally adapted breeds tend to perform poorly relative to exotic breeds with regard to intensity of GHG emissions, due to their inferior production. However, standard measures of intensity are somewhat biased, as they typically consider only the ratio of GHG emissions to yield of a single commodity, ignoring other ecosystem services usually associated with locally adapted breeds and their production systems. Single-commodity measures of GHG intensity also fail to account for the differences among breeds in their ability to survive while consuming poor quality forage and converting it into human-edible food (Hoffmann, 2010).

5. Conclusion

In the Second Report on the State of the World's Animal Genetic Resources for Food and Agriculture (FAO et al., 2015), countries, especially those of developing regions, reported indiscriminate crossbreeding and introduction or increased use of exotic breeds as the two main causes of genetic erosion. Our results provide for the first time an objective assessment of the situation and the rate at which the relative proportion of locally adapted genetic resources is decreasing in those regions. We also discuss how this phenomenon connects to various challenges on the national scale, such as food production and security as well as agrobiodiversity. These discussions are far from exhaustive, however, inasmuch as locally adapted livestock breeds and their production systems are also associated with various aspects of sustainability, including poverty reduction, resilience to climate change and landscape management. Our analyses are also limited to the national scale, whereas local-level heterogeneity in constraints associated with environmental conditions and access to markets influence the fit of a given genetic resource to a certain locale. For instance, Herold et al. (2010) proposed a stratified organizational scheme for pig production in Vietnam, with farmers close to markets raising crossbreds of exotic males and locally adapted sows, the latter of which would be provided by farmers from more remote areas, for whom crossbred genotypes would be of limited interest due to environmental constraints and lack of access to inputs such as high-energy feeds and veterinary care.

Strategic planning is required to ensure the conservation of the unique alleles possessed by the local breeds, either by complementary *in situ* or *ex situ* conservation of the breeds themselves or by breeding programmes to ensure conservation of these alleles in the gene pools of new synthetic breeds. Moreover, because of the influence that context has on the success of using exotic breeds, a livestock development policy involving these genetic resources requires strategic thinking that goes beyond the simple technical dimension of breed improvement or conservation (Magnani et al., 2019b). As illustrated by Fig. 4, animal genetic resources can be regarded as the centre of a complex social, environmental and economic system, so policies need to address the challenges related to sustainability in a holistic manner, accepting trade-offs where necessary, and considering, at different scales, the relationships and dynamics between the animals, their herders, the production systems, agroecosystems, and the market.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gfs.2020.100420.

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The views expressed in this information product are those of the authors and do not necessarily reflect the views or policies of FAO.

Authors contribution

G.L., P·B., B·B., and R.W. designed the study. G.L., C.R.P. collected the data. G.L. and F.J. conducted the statistical analysis. P.B., B·B., and R.W. assisted with data preparation and interpretation. G.L. wrote the manuscript, which was edited and approved by all authors.

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