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Contributions of animal genetics to the agroecological transition of livestock farming systems

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■ Livestock systems are facing a major legitimacy crisis and must undergo in-depth changes in the future. Agroecology is a relevant framework to guide this evolution. Even though genetics has been associated in the past with the development of systems that are now being questioned, it can also play a role in their transition. For this to happen, animal genetics must contribute to research aimed at redesigning livestock farming systems.

Introduction

Livestock production underwent major changes during the 20th century in all industrialised countries[1], including France (Domingues *et al.*, 2019). The number of livestock farms has fallen sharply, and their average size has increased. Farms and territories have become more specialised, resulting in a relatively strong geographical separation between crop and livestock production. Other changes have concerned the feeding and reproduction of animals, the level of use of inputs (fertilisers, energy, medicines, etc.), selection methods and the dissemination of genetic progress. The **genetic improvement**[2] of animal populations (Box 1) has played a central role in this production intensification dynamic, allowing a very significant evolution in zootechnical performance (Hill and Kirkpatrick, 2010). The increasing standardisation and artificialisation of breeding conditions have led to the spread of a few highly productive and specialised breeds or lines, usually to the detriment of less productive local breeds adapted to their environment, some of which are now at risk of extinction (Verrier *et al.*, 2015). All these transformations were aimed at increasing the overall productivity of production factors, efficiency and economic competitiveness of agricultural enterprises in a context of increasing globalisation (Domingues *et al.*, 2019). They allowed access to animal products at a reasonable cost for the majority of consumers (Laisney, 2012).

However, these developments have had negative consequences for the environment, biodiversity, animal welfare, the socio-economic situation of many farmers and public health. The concentration of livestock in certain areas, such as northern Europe and western France (Roguet *et al.*, 2015), the massive import of feed resources (soy) from countries that heavily rely on deforestation (Rajão *et al.*, 2020), and the widespread use of inputs have led to significant water and soil pollution, increased greenhouse gas emissions, and have contributed to the collapse of biodiversity (Buckwell and Nadeu, 2018). In addition, the intensification of livestock production has led to the widespread adoption of practices that undermine animal welfare and/or raise important ethical questions, including: increased animal density in buildings without outside access or natural light, muti-

1 The scope of this article has been deliberately limited to livestock systems in Western countries with a temperate climate. The question of the agroecological transition of tropical livestock systems is of course important, but the issues, levers and modalities of this transition are partly different, and would justify a complementary analysis to that developed in this article.
2 Terms that appear in bold in the text when they first appear are defined in Box 1 (Glossary).

Box 1. ***Glossary.***

Genetic improvement (of livestock populations) : Human activity carried out by breeders organised collectively or by private companies, depending on the species. It is based on the concepts of (quantitative) genetics and statistics. Its objectives are to provide the industry with animals adapted to its needs by taking advantage of genetic differences within and/or between populations (or even species), by developing tools and by applying methods likely to lead to genetic progress consistent with predefined objectives (Source: http://www2.agroparistech.fr/svs/genere/uvf/AG/AGintro.htm).

Trade-off (biological compromise): A situation in which the improvement of one biological function is accompanied by a deterioration of another function (and *vice versa*). Various physiological and biological mechanisms can explain this phenomenon, e.g., if the functions compete for nutrients, or if there are physiological constraints (e.g., temporal or anatomical) on the co-expression of traits. From a genetic point of view, trade-offs sometimes result in unfavourable genetic correlations. Trade-offs are involved in adaptation processes in the broadest sense, including robustness (Source: Garland, 2014).

Feed efficiency: Feed efficiency, a term classically used in livestock production sciences to describe the efficiency of feed use by the animals, is generally understood using indicators such as the feed conversion ratio (FCR: quantity of feed required for the production by the animals of one kg of live weight, milk, eggs, etc.), or the average daily residual feed intake (ADRI: difference between actual consumption and the consumption predicted by taking the production and maintenance needs of the animals into account).

Effectiveness/Efficiency: Strictly speaking, effectiveness measures the gap between results and objectives. Efficiency, on the other hand, is generally defined as the ratio of outputs to resources. A process is more efficient if it is able to produce more from the same resources, or to produce the same amount with fewer resources. Based on these definitions, the two criteria defined in the previous section (FCR and ADRI) would also be *feed efficiency* criteria. In livestock production, improving one or the other of these two criteria has the same objectives: to reduce production costs and the impact of livestock production on natural resources (Source:Faverdin and Van Milgen, 2019).

Epigenetics : The study of changes in gene expression that are not accompanied by changes in the DNA sequence and can be transmitted during cell divisions. Unlike mutations that affect the DNA sequence, epigenetic changes are reversible (Source:Holliday, 1990).

Genetics : The life science that studies the variation and transmission of hereditary traits. Quantitative genetics, the theoretical basis of genetic improvement activities, deals with traits that can be objectively measured, and whose variation is generally continuous and due to the action of many genes (complex genetic determinism) (Source: http://silico.biotoul.fr/site/images/e/e0/Genetique-quantitative.pdf).

Genomics : Discipline whose objective is the exhaustive study of genomes, in particular, of all genes, their arrangement on the chromosomes, their sequence, their functions, their roles and their evolution (Source: Bidanel *et al.*, 2008).

Resilience : Ability of an animal or a system to absorb and/or respond to disturbances, particularly sudden and unpredictable ones (e.g., nutritional or health-related), by mobilising buffer capacities (temporary reallocation of resources), adaptation or transformation permitted by the complementarity and/or functional redundancy between the system's components. It is represented by the system's trajectory, which takes account of the extent of the deviation with respect to the initial state, and the kinetics of recovery towards this initial state or a new equilibrium state (Sources: Darnhofer, 2014; Sauvant and Martin, 2010; Dumont *et al.*, 2020b).

Resistance (of an animal to an infectious agent) : A set of mechanisms that limit the reproduction of a pathogen within a host by preventing the pathogen from entering the host or by inhibiting its replication (Source: Doeschl-Wilson and Kyriazakis, 2012).

Robustness (of an animal) : A robust animal is one that maintains its ability to transmit its genes to the next generation, despite various constraints imposed by the environment (availability of resources, infectious pressure, etc.). For domestic livestock, the functions of reproduction (fertility, prolificacy), production (of milk, meat, viable offspring, etc.) and health determine the longevity of the individual within the herd. Consequently, a robust livestock animal is able to maintain its (re) productive functions and a health status that is considered acceptable over its lifetime in a wide variety of environments (Sources: Blanc *et al.*, 2013; Knap, 2005).

Livestock production system : A set of dynamically interacting elements organised by humans according to their objectives, to produce (milk, meat, hides and skins, labour, manure, etc.) and to reproduce a group of domestic animals by valorising and renewing different resources (Source: Dedieu *et al.*, 2008).

Food system: The set of operating rules, organisational modes, technologies and practices that determine the consumption, production, processing, packaging, storage and distribution of food. Sustainable food systems ensure food security for all without compromising that of future generations. Agroecology aims to ensure food security at the level of territories while contributing to their social sustainability and the well-being of local populations (Source: Plumecocq (2018) *in* Dictionnaire d'Agroécologie).

Tolerance (of an animal to an infectious agent) : The ability of the host (of an animal) to limit the negative effects (reduction in zootechnical performances such as growth, feed efficiency, milk or egg production, fertility) of infection (infestation) with a pathogen, without affecting the infectious load (Source: Doeschl-Wilson and Kyriazakis, 2012).

Transition (agroecological) : Process by which the principles governing a system are radically modified, leading to a set of changes concerning both the values of the stakeholders and the techniques they use [...] (Source: Hazard (2017) *in* Dictionary of Agroecology).

lations such as tail docking, live castration of piglets or beak trimming of poultry, long-distance transport before slaughter, and the systematic elimination in some sectors of one of the sexes (Fraser and Nations, 2005). On the socio-economic level, the expansion and specialisation of farms and the search for efficiency through the continuous reduction of production costs have been accompanied by an increase in the average level of indebtedness of farmers. These changes, coupled with certain political, economic and commercial developments (globalisation, deregulation leading to instability in certain markets, changes in the balance of power within the sectors) have also led to increased insecurity for many French and European farmers (Nozières-Petit *et al.*, 2016). Finally, the extensive use of drugs and, in particular, antibiotics, has contributed to the emergence of resistant pathogens, constituting a serious threat to public health and requiring the implementation, since the 2010s, of public policies aimed at reducing their use (David *et al.*, 2019).

For all these reasons, European livestock farming is now facing an unprecedented crisis of environmental, social and economic legitimacy, and must undergo in-depth changes in the future (Peyraud *et al.*, 2019).

The types of changes to be considered depends on the objectives assigned to livestock farming and agricultural activities in general. According to the European Commission, the evolution of agriculture in the 21st century, including livestock farming, must result in the emergence of sustainable, equitable, healthy and environmentally-friendly **food systems.** This is the goal of the "Farm to Fork" strategy, which is at the core of the new "European Green Deal" that should guide European public policies over the next decades (European Union, 2020). These objectives are close to those of agroecology, defined by Gliessman (2006) as the application of ecological and social principles to the design and management of sustainable agricultural and food systems. Agroecology thus aims to (re)invent a sustainable, ecologically sound, economically viable and socially equitable agriculture (Wezel and Jauneau, 2011) by proposing long-term solutions to transform agricultural and food systems, taking their multiple dimensions into account (FAO, 2018). Such agroecological systems (1) make greater use of biological regulation, are productive but less dependent on inputs than conventional systems, (2) are linked to their physical environment and seek to enhance interactions between system components, (3) consider biodiversity as a resource and seek to preserve it, and (4) place food production, agroecosystem and food system integrity at the same level of priority.

In a study dedicated specifically to livestock farming, Dumont *et al.* (2013) proposed a conceptual framework for structuring reflections aimed at an **agroecological transition** of **livestock farming systems**. This conceptual framework is based on the following five principles:

(1) Developing integrated management practices to improve animal health.

(2) Enhancing the use of natural resources and co-products to reduce the inputs needed for production.

(3) Optimising the functioning of livestock systems to reduce pollution.

(4) Managing resource diversity and animal complementarity to strengthen the **resilience** of livestock systems.

(5) Adapting management practices to maintain biodiversity and provide associated ecosystem services.

In the remainder of this article (Part 1), we will examine the extent to which animal **genetics**[3] can contribute to each of the principles proposed by Dumont *et al.* (2013). We will then see (Part 2) that past and current contributions are generally related to only one or several principles, whereas they need to be mobilised together to overcome the environmental, social and economic crisis mentioned above. We will also see that most of these contributions aim at a "low" level of agroecological transition (or modernisation) (Duru *et al.*, 2014). We will show that integrating the "high" transition level, i.e., contributing to the redesign of livestock systems by conducting research and development projects in genetics designed for this purpose, is an important issue.

1. Contributions of animal genetics to agroecological principles for the evolution of livestock farming systems

■ 1.1. Developing integrated management practices to improve animal health

An "integrated" health management approach consists of combining preventive and curative actions that seek to limit the use of drugs (Fortun-Lamothe and Savietto, 2017). These actions may target: (1) the living environment and animal farming methods; (2) the pathogens, through vaccination and targeted use of drug treatments; and (3) the animals (hosts) themselves, which, depending on their genotype, are more or less **resistant**, **tolerant**, and/or **resilient**. It is natural that geneticists have focused their attention on the third aspect until now, in conjunction with the evolution of approaches concerning the other two fields of expertise.

3 Animal genetics is taken here in its broadest sense: in this article, we will consider research activities in genetics and genomics, as well as the genetic improvement of animal populations.

This field of research is currently mobilising a large scientific community, leading to significant scientific production. The research in progress concerns diseases that are well characterised from a clinical and etiological point of view, such as mastitis in dairy ruminants (Box 2), gastrointestinal parasitism in sheep (Moreno-Romieux *et al.,* 2017) and horses (Kornas *et al.,* 2015), respiratory diseases in rabbits (Shrestha *et al.,* 2020) and pigs (Boddicker *et al.,* 2014), various bacterial or viral diseases in trout (Fraslin *et al.,* 2019), and coccidiosis or salmonella carriage in chickens (Tran *et al.,* 2012). It also concerns diseases whose etiology is less well known, such as transmissible subacute spongiform encephalopathies, or non-specific health disorders (Gunia *et al.,* 2018). It aims at understanding the mechanisms involved in host resistance, checking the specificity or universality of these resistances (to different species or strains of infectious agents), and assessing the risk of asymptomatic carriage or resistance bypass by pathogens. Other research aims at evaluating the modalities and effectiveness of selection programmes aimed at reducing the incidence of certain diseases such as gastrointestinal parasitism (Aguerre *et al.,* 2018) or mastitis (Box 2). Finally, some research is aimed at defining original **robustness** criteria that can be selected for and that may contribute to improving the health status of animals or to maintaining a good health status during certain critical breeding phases (Revilla *et al.,* 2019).

Box 2. ***Genetic resistance to mastitis: state-of-the-art and mechanisms.***

Mastitis is an inflammation of the udder, mainly caused by bacteria and, principally, staphylococci.

The first genetic research on mastitis in dairy ruminants consisted of quantifying the genetic variability of resistance using indicators of the inflammatory state of the udder (somatic cell counts), or the occurrence of clinical cases, indicators that are easily measured on a large scale (Rupp and Boichard, 2003). Genetic evaluation of breeding stock was rapidly implemented in the main dairy breeds (production of genetic indexes for somatic cell counts or the occurrence of clinical cases), and these traits were integrated into the selection objectives in France, in conjunction with breeding organisations, during the years 2000 (cattle), 2005 (sheep) and 2016 (goats).

In parallel, transdisciplinary integrative biology approaches (immunogenetics, physiology, transcriptomics) were implemented, benefitting from original divergent selection experiments conducted in different experimental farms. This work initially demonstrated the effectiveness of selection based on somatic cell counts, associated with a decrease in the frequency of infections and the quantity of bacteria in the milk in sheep (Rupp *et al.,* 2009) and goat (Rupp *et al.,* 2019) models, thus invalidating the hypothesis that such selection would lead to degraded immunity in the animals. These experimental lines also allowed the study of the biological functions underlying the difference in resistance in the experimental lines produced. Transcriptomic analyses of different cell types of ewes from the divergent selection lines (Bonnefont *et al.,* 2012) confirm the importance of immune mechanisms in the genetic determinism of mastitis resistance and, in particular, the migration of immune cells (from blood to infected tissue) and the regulation of the inflammatory process in resistant ewes.

Moreover, complementary transcriptomic data in goats (Cremonesi *et al.,* 2012) and the meta-analysis of several experiments (Genini *et al.,* 2011) have highlighted the involvement of lipid biosynthesis pathways in the anti-infectious response, thus opening the way to the study of trade-offs between immunity and production traits. These first elements, as well as the emergence of questions on the adaptation capacities of animals in stress situations, motivated the study of the modulation of genetic resistance to mastitis in relation to food-borne energy stress. The work of Bouvier-Muller *et al.* (2018) clearly established a link between immunity and energy metabolism in the context of mastitis. These results reinforced the importance of the notions of trade-offs and synergies between the biological functions of an animal, and consideration of environmental conditions to study and optimise the genetic approach.

Finally, access to high-throughput genotyping tools (DNA chips) has made it possible to explore the genetic determinism of the mastitis resistance trait in greater depth and to identify, in the Lacaune breed, a mutation in the SOCS2 gene that explains nearly 20% of the genetic variability of the trait (Rupp *et al.,* 2015). Validation and detailed functional characterisation of this gene have highlighted its multiple effects, since the mutation associated with high susceptibility to mastitis is also responsible for positive effects on milk production and growth (Oget *et al.,* 2019a). The SOCS2 mutation currently represents a model for studying pleiotropy and how to implement balanced selection when several desirable traits present functional trade-offs (Oget *et al.,* 2019b).

Another strategy to improve resistance to infectious diseases in livestock is to incorporate immunocompetence criteria into breeding programmes. A considerable amount of research has been carried out in this area, particularly in chickens, rabbits and pigs (Mach *et al.,* 2013). This research has evolved in recent years to take the role played by symbiotic microorganisms (at the intestinal level, but also at the cutaneous, respiratory and mammary level, etc.) into account in the regulation of the host's immune response and to develop the "holobiont" concept (Calenge *et al.,* 2014).

In the field of animal health, it is also worth mentioning here the work carried out to understand the origin of and to manage the hereditary disorders that are segregating in breeding populations. Most of the anomalies described to date are due to mutations in a single gene, often (but not systematically) recessive, which are responsible for functional and/or morphological defects that can have lethal effects. In France, numerous results have been obtained in recent years in cattle within the framework of the ONAB (Observatoire National des Anomalies Bovines), the French national observatory of hereditary defects in the bovine species (Bourneuf *et al.,* 2017). Comparable work is being carried out in pigs, horses and small ruminants (Fabre *et al.,* 2020).

All of these projects are ongoing and will continue over the long term. Much knowledge remains to be acquired on these subjects. They will gradually be enriched by new data linked to the deployment of innovative technologies associated with precision livestock farming in experimental facilities and commercial farms (Faverdin *et al.,* 2020). These new data should make it possible to describe in greater detail the physiopathological mechanisms and the relationships between health and welfare. They are also essential for a better understanding of genotype×environment interactions that will certainly be important for these resistance, resilience and/or tolerance traits (Phocas *et al.,* 2017).

Research could also be initiated or expanded in other, relatively diverse areas:

- The study of the role of **epigenetics** in the regulation of host-pathogen interactions and immune response (Zhang and Cao, 2019) could be the focus of major research programmes in the coming years.

- The relationship between immunocompetence and resistance (or tolerance) should be more systematically and accurately studied.

- Based on new knowledge regarding the biological basis of resistance and/or tolerance and host-pathogen interactions, further modelling work could contribute to a better understanding of the zootechnical, epidemiological and economic effects of selection. Mathematical modelling could also be used to predict or explore ways in which selection can be effectively combined with other disease control strategies (Bishop, 2010).

- More attention could be paid in the future to the genetic and epigenetic determinants of "non-communicable" metabolic diseases (e.g., ketosis in dairy cows).

- Further work could be undertaken to better understand the adaptive capacity of animals to different sources of abiotic stresses that may induce health problems (e.g., temperature variations). The ability to cope with various sources of biotic and abiotic stresses could be considered in the context of the development of farming systems based on outdoor access for animals or, more generally, on less controlled environments in conjunction with reduced input use (see Chapter 1.2).

- Ongoing work aimed at better understanding the influence of the early environment on the construction and variability of phenotypes, and on the capacity of animals to adapt to their environment (using epigenetic mechanisms, in particular) should be continued (Pitel *et al.,* 2019). Such research could lead to proposals for innovative management methods that could improve the robustness or resilience of low-input breeding systems.

- Finally, the use of new techniques for targeted modification (or "editing") of genomes (CRISPR-Cas9 and other programmable nucleases; Ducos *et al.,* 2017) could also be considered to improve the resistance of animals to various infectious agents, from the perspective of integrated health management. This particular point is discussed in Box 3.

■ 1.2. Enhancing the use of natural resources and co-products to reduce the inputs needed for production

The development of livestock systems in the 20th century was accompanied by a significant increase in the inputs used for production.

Among these, feed inputs are particularly important for at least two reasons. The first reason is the considerable amount of plant output mobilised by livestock, leading to significant competition between animal feed and human food (Herrero *et al.,* 2015). In a context of high global population growth and global warming, controlling and, if possible, reducing this very strong impact of livestock on natural resources is a crucial issue. The second reason is the generally high share of feed in the production cost of animals, particularly monogastrics (65% in conventional pig farming, for example), which makes farms more vulnerable from an economic point of view. In a context of often difficult and fluctuating markets, controlling feed costs is a high priority for many farmers. This control requires the mobilisation of several levers.

One of these levers that has been of interest to geneticists for decades, is the improvement of animal **feed efficiency** (Phocas *et al.,* 2014). Essential work aimed at understanding the genetic determinism and at quantifying the genetic variability of different feed efficiency criteria such as **feed conversion ratio**, **average daily residual feed intake**, growth rate under feed restriction and digestive efficiency, has been underway for a long time. The search for biomarkers, which is crucial for these types of traits that are difficult and costly to evaluate, is the subject of a major research effort. Finally, other research aimed at analysing **trade-offs** and synergies between feed efficiency and robustness, or at developing relevant selection methods for these types of traits, is in progress. All of this research has resulted in considerable scientific production in various species: pigs (Gilbert *et al.,* 2017), rabbits (Drouilhet *et al.,* 2013), chickens (Mignon-Grasteau *et al.,* 2020), beef cattle (Martin *et al.,* 2019) and meat sheep (Tortereau *et al.,* 2020), etc. A very significant improvement in these feed efficiency criteria has been achieved. About half of this, in pigs, for example, can be attributed to genetic progress, and the other half to improved feed composition and feeding and housing strategies and techniques, in particular. Most of this work has been conducted using optimised feeds of high nutritional value. Other research has focused on the feed and/or

Box 3. ***Agroecology or technology, do we have to choose between them?***

The agroecological transition of livestock farming systems requires a detailed understanding of the complex regulations that operate within them. Producing the knowledge necessary to understand them and to *design* relevant systems involves a significant research effort, and can benefit from the most recent technological advances in various fields (electronics, digital technologies, biotechnologies, etc.). Some technologies can also play a useful role in the *management of* systems. This is the case, for example, of technologies that allow precise, real-time monitoring of the state of the system or its environment, making it possible to detect certain malfunctions at an early stage and to improve the use of resources: "precision" livestock farming and medicine approaches. The rational use of new technologies, at least some of them, is therefore not incompatible with the agroecological development of agricultural and livestock farming systems, provided that it does not compromise the autonomy of farmers and livestock breeders and does not place too great a mental burden on them.

The specific case of new genome biotechnologies: what role can they play in the agroecological transition of livestock systems?

New *"genome editing"* techniques, allowing targeted modifications (or "rewriting") of the genomes of all species of agronomic interest, were developed in the early 2010s (see the review by Ducos *et al.,* 2017). These techniques (CRISPR-Cas9 and other programmable nucleases) are often presented as essential if we are to meet the major challenges that livestock farming will have to face in the future: effectively managing animal health by limiting the use of drugs, reducing the ecological footprint of livestock farms, and eliminating practices that seriously affect animal welfare, among others. Although the relative simplicity and effectiveness of these new techniques undoubtedly offers excellent prospects, their commercial application in livestock farming raises many technical and/or ethical issues (Le Roy *et al.,* 2019; Ducos, 2020).

Some recent achievements have been highly publicised, particularly those related to health. This is the case, for example, of the production of pigs in which one of their genes (CD163) was altered so as to make them resistant to a viral disease for which "classic" control methods are not very effective, and which is responsible for considerable economic losses on a global scale (PRRS). Some published results show that such animals, produced by genetic manipulation of embryos and/or somatic cells in culture (followed in this case by cloning by nuclear transfer), are resistant to different viral strains. According to the authors of these studies, their commercialisation, which is technically feasible in the short term, would constitute an effective and rapid response to this major animal health problem, a response that is *a priori* compatible with the agroecological principle of integrated health management. However, using genetically modified animals that are temporarily resistant to a disease (or diseases) without questioning the elements of the design of the breeding systems that are the main causes of the severity and/or recurrence of these diseases (geographical concentration of farms, high densities of animals raised in confinement, low genetic diversity of these animals, the quest for very high zootechnical performance, etc.) seems to us to be at odds with the fundamental principles of agroecology. This could also lead to a delay in the necessary transition of these systems, whose predisposition to certain diseases is not their only weak point.

A more global reflection on the place and role of technological innovations in the transition towards a sustainable food system has been proposed by Herrero *et al.* (2020).

digestive efficiency of animals exposed to lower quality feed resources, e.g., chickens (Mignon-Grasteau *et al.,* 2004) and pigs (Déru *et al.,* 2020), or feed resources with a reduced impact on the environment and biodiversity, e.g., trout (Callet *et al.,* 2017). This research continues today and includes the study of the digestive microbiota (Borey *et al.,* 2020; Aliakbari *et al.,* 2021) and other non-genetic sources of heredity, such as epigenetics, behaviour and social interactions (David *et al.,* 2020), as well as feeding behaviour, animal activity and response to stress, greenhouse gas emissions (Renand *et al.,* 2019) and nitrogen and phosphorus discharges in effluents (Saintilan *et al.,* 2013), or the ability of animals to mobilise and restore their body reserves (Mace *et al.,* 2018). Much of this work has benefited from the significant developments in phenotyping technologies in recent years (e.g., individual feed and water consumption by animals reared in groups and/or outdoors, individual methane emissions and digestibility measurements made possible on large numbers of animals).

Further research will be required to study the genetics of adaptation to more disruptive diets, based to a much lesser degree on cereals and oilseeds that are directly consumable by humans. This will be particularly important to consider in monogastric animals, and especially in pigs. These animals are indeed likely to use biomass sources that have been little or not at all harnessed so far, such as (1) crop or intercrop products of agronomic interest that are difficult for humans or other livestock species to use; (2) by-products of the agriculture and agri-food industries; and (3) catering waste, which has considerable potential but would require a change in regulations to be available for use (Rauw *et al.,* 2020). An in-depth study of the impacts of the use of this type of feedstock on the health and digestive well-being of animals, as well as genotype×feed interactions, should be undertaken. In ruminants, especially dairy cattle, studies could focus on the determinism and genetic variability of criteria that characterise the ability of animals to efficiently use roughage from more diverse sources than at present, of lower and more variable quality, and whose availability will be subject to greater inter-annual variability, particularly due to climate change (Dellar *et al.,* 2018).

Energy, water and hormones are other inputs that are widely used in livestock production. Energy is used, for example, to control the atmosphere in livestock buildings. A better understanding of the genetic basis of thermoregulation (Gourdine *et al.,* 2019) and of the ability of animals to remain efficient in a wide range of temperatures is important for reducing energy expenditure (fluids) and, more broadly, the use of fossil fuels in livestock farming. Hormones are widely used for reproductive control in many sectors, and are even essential for maintaining certain types of management, such as batch management systems in pigs or off-season production in small ruminants. They are also crucial for the creation and dissemination of genetic progress in the vast majority of selection schemes. The search for alternatives to the use of hormones in livestock production has been the subject of a relatively large number of studies by physiologists (Pellicer-Rubio *et al.,* 2019). In comparison, the contribution of geneticists to this topic is more limited. We can nevertheless mention the studies on the genetic control of the ability to breed out of season and the response to the ram effect in ewes (Maatoug-Ouzini *et al.,* 2013), or the sexual receptivity of female rabbits (Theau-Clement *et al.,* 2015).

Reducing inputs by considering the total lifespan of animals on farms can also be considered *via* the reduction of losses associated with production, which can be assimilated to a waste of resources. For example, improving sexual precocity would make it possible to consider earlier breeding of heifers in beef cattle production systems, thus reducing the unproductive lifespan and the amount of agricultural resources mobilised by the rearing of replacement animals. Improving the longevity of breeding females such as dairy cows, sows, rabbits and laying hens would reduce the turnover rate of herds and save many animals' lives (and the resources mobilised to produce them). Reducing mortality rates at different ages would also contribute to this objective, while avoiding animal suffering. Understanding the genetic determinism and genetic variability of these traits in different selected populations and in different types of systems by attempting to understand the origin of possible trade-offs between biological functions is therefore important. Research in this area should be continued.

■ 1.3 Optimising the functioning of livestock systems to reduce pollution

If, at first glance, we only retain the end of the statement of this third principle ("reduce pollution"), we can consider that some of the studies mentioned in the previous section, aimed at reducing inputs per unit of production, are also interesting options for reducing the pollution represented by livestock effluents or greenhouse gas emissions.

Some scientists are considering the use of genome biotechnology for this purpose. For example, at the end of the 1990s, Canadian and Danish researchers began producing transgenic pigs that integrated genes coding for a bacterial phytase into their genome. They showed that these animals efficiently use the phosphorus provided by the plant phytates in the feed (which are usually poorly absorbed) and, consequently, require a reduced supply of bioavailable mineral phosphates, considerably reducing the pollution load of their effluents (Golovan *et al.,* 2001). Similar work has recently been replicated by Zhang *et al.* (2018), and other contributions using new genome editing techniques may soon follow. The evaluation of this type of approach compared to the use of microbial phytases incorporated in the diet, or to interventions aimed at selecting a more efficient microbiota, for example, remains to be done.

However, taken as a whole, the principle of "optimising the functioning of livestock systems" refers more specifically to the notion of "closing cycles" within diversified systems composed of complementary elements (Peyraud *et al.,* 2015). Mixed crop-livestock systems, when they are highly integrated as they were in Europe before the massive movement towards specialisation that took place during the 20th century, are emblematic of this third principle. These are largely autonomous systems that make little use of inputs, with high levels of coupling between crop and animal productions (Bonaudo *et al.,* 2014; Coquil *et al.,* 2019). The research needed to promote them mainly concerns the design of the systems themselves (at the farm and/or territorial scale; Ryschawy *et al.,* 2017). Contributions from animal genetics to this research have been relatively limited to date. However, research aimed at changing selection objectives in order to have more autonomous, adaptable and robust animals that can make the most of locally-produced heterogeneous resources (pastures, crop residues, various forage crops integrated into long rotations, etc.), or aimed at identifying genetic resources (breeds and/or crosses) with these characteristics, is nevertheless part of it (Phocas *et al.,* 2017).

■ 1.4 Managing resource diversity and animal complementarity to strengthen the resilience of livestock systems

The sheep experiment carried out at INRAE's La Fage Experimental Farm (Aveyron, France) is often cited as an example of a successful application of this fourth principle (for the "animal-resource complementarity" dimension; Thomas *et al.,* 2014). The animal production cycle (free-range lamb production from a flock of 280 meat-type ewes) and the feeding system (grazing on rangeland and forage crops) have indeed been designed and organised so that the needs of the animals and the resources offered by the agroecosystem are in balance, especially during the breeding period. This makes it possible to minimise the inputs required for production, to preserve an environment rich in biodiversity, and to generate a stable and satisfactory income. This success is partly based on the genotype of the animals selected for this experiment. Indeed, ewes of the Romane breed, a composite line resulting from Berrichon du Cher×Romanov crosses, are particularly well adapted at mobilising and restoring their body reserves, making it possible to cope with major fluctuations in forage resources during the year (González-García *et al.,* 2014), and have fleece characteristics that allow good lamb survival (Allain *et al.,* 2014). These abilities/characteristics have a genetic basis, which makes it possible to consider their selection for this type of system (Mace *et al.,* 2018). This example clearly illustrates the interest of integrating a genetic component at the design stage of innovative breeding systems and in the experiments aimed at studying them.

Beyond this particular example and the "complementarity" dimension between animals and resources, the general idea of the fourth principle is to rationalise diversity within systems in order to increase their resilience. The underlying assumption is that well-designed diversity, from a biological/genetic, technical, organisational or structural point of view, would increase the resilience of livestock systems (Box 1). For example, inter-individual variability within a mono-specific (mono- or multi-racial) herd could be a source of resilience in the face of variations in rearing conditions if all of the animals do not deal with the trade-offs between functions in the same way, and do not implement the same mechanisms of adaptation to particular constraints. Intra-herd diversity could also promote herd and social immunity, defined as the immune service provided by one animal to other animals. Combining several animal species in the same system can also have multiple interests: (1) valorisation of different feed resources, or with different temporalities, if the needs, strategies and feeding behaviours of the species reared in association are different and complementary; (2) reduction of competition for access to certain resources; (3) favourable effects on the epidemiological dynamics of certain diseases (parasitism; but possible concomitant risk of cross-transmission of other infectious agents) and on the biodiversity of forage areas; (4) securing income (Magne *et al.,* 2019; Mahieu *et al.,* 2020; Martin *et al.,* 2020).

While a large number of studies have been conducted in the field of crop production to explore the links between diversity, resilience and multi-performance, they remain relatively rare in the field of animal production (Dumont *et al.,* 2020b; Doré and Bellon, 2019). As summarised in the report resulting from the interdisciplinary prospective reflection for agroecology conducted at INRAE (Caquet *et al.,* 2019), the cognitive challenges are nevertheless important and numerous. They include:

(1) Accurately assessing the contribution of animal genetic diversity to the (multi)performance and resilience of agroecological systems, integrating the analysis of the relationship between diversity and ecosystem services (Leroy *et al.,* 2018).

(2) Developing a better understanding of the mechanisms of action of this diversity, as well as the effect of the range of diversity and the range of environmental variation on the magnitude of genetic×environmental interactions.

(3) Identifying the major traits of interest involved in interactions between animals. This includes modelling the influence of one animal on the performance of other animals within the same group.

(4) Defining the range of diversity that leads to the expression of mechanisms favourable to the development of more resilient production systems.

(5) Defining new criteria and developing new innovative selection and cross-breeding programmes that take the objectives of genetic diversity of the animals into account (see the next chapter).

These issues indicate that a contribution of animal genetics to the fourth principle requires going beyond selection and breeding approaches based on the search for an optimal animal with calibrated performances for standardised and controlled breeding environments, and adopting more systemic approaches to the functioning of breeding systems.

■ 1.5. Adapting management practices to maintain biodiversity and provide associated ecosystem services

The fifth principle of the conceptual framework proposed by Dumont *et al.* (2013) considers biodiversity in terms of (1) ecosystems, and (2) livestock populations.

First, the application of the fifth principle should lead to the implementation of livestock systems and practices that do not have negative impacts on the biodiversity of the agroecosystems they mobilise. These include those in which the animals live, but also those used to produce feed resources for them. Currently, the main way to promote biodiversity in agroecosystems is to use natural grasslands once again and to extend agroecological infrastructures (hedges, trees, etc.), in addition to adapting practices to enhance the value of forage areas in order to maintain biodiversity (Sabatier *et al.,* 2015). Conversely, livestock systems that mobilise feed resources produced from massive deforestation, or from monocultures which induce significant damage to vegetation or that require significant reliance on pesticides, should be banned, given the preponderant role of these practices in the collapse of biodiversity. This aspect should therefore be integrated into research on animal feed efficiency, for example. On the whole, research in animal genetics that contributes to this first aspect of the fifth principle is still largely insufficient in relation to the principle of agroecology, which considers food production and the integrity of agroecosystems to be of equal priority.

The fifth principle also includes objectives for preserving the diversity of animal populations themselves, referred to as "domestic biodiversity", which is important to consider but represents only a small part of the overall biodiversity of agroecosystems. The contribution of geneticists in this field has been and will remain important. Methods and tools to quantify, characterise and manage genetic diversity within (and between) populations have existed for a long time and are constantly being improved (Leroy *et al.,* 2013). Commercial breeding populations as well as local and heritage breeds have been targeted. This work has benefitted from the considerable evolution of genome analysis tools in recent years (genotyping and sequencing). Among INRAE's recent contributions, we can mention, at the international level: (1) the coordination of the European IMAGE project,[4] which aims to improve the management of gene banks for the *ex-situ in-vitro* conservation of genetic resources and to promote their use (CRB-anim in France);[5] (2) the participation in international projects such as "1,000 bovine genomes" (Daetwyler *et al.,* 2014), "1,000 Gallus genomes" (Tixier-Boichard *et al.,* 2020), and the coordination of the "1,000 goat genomes" project (VARGOAT)[6], making a major contribution to improving knowledge about genetic diversity within the species concerned; (3) the characterisation and genetic, zootechnical and economic evaluation of local European pig breeds (Muñoz *et al.,* 2019); and (4) work on the characterisation of the diversity and structure of European bee populations (Parejo *et al.,* 2016) and international goat populations (Stella *et al.,* 2018). At the national level, we can mention: (1) the study of the impact of genomic selection (selection based on a genomic evaluation of selection candidates; Le Roy *et al.,* 2019) on the diversity of the three main French dairy cattle breeds (Doublet *et al.,* 2019); (2) the development of a strategy for a conservation policy for local poultry breeds (Chiron *et al.,* 2018); and (3) the characterisation of genetic diversity within selected commercial trout lines (D'Ambrosio *et al.,* 2019). This inventory can be supplemented to include the methodological developments for the purpose of (1) reconstructing the demographic history of populations (Boitard *et al.,* 2016) and detecting selection signatures (Paris *et al.,* 2019), (2) preserving genetic diversity within populations under selection (Colleau *et al.,* 2017), and (3) optimising matings by taking non-additive genetic effects and inbreeding in cross-breeding programmes into account (González-Diéguez *et al.,* 2019).

4 4http://www.imageh2020.eu/
5 https://www.crb-anim.fr/
6 http://www.goatgenome.org/vargoats.html

2. From animal genetics research to the agroecological transition of livestock systems

The conceptual framework developed by Dumont *et al.* (2013), based on the five principles detailed above, is useful for methodically categorising the contributions of animal genetics to the agroecological transition of livestock systems. However, this analysis has certain limitations that are discussed below.

■ 2.1. Towards a joint and balanced mobilisation of the different principles

Some actions and/or research programmes have been associated in our presentation with one of these five principles, but also contribute to others (Figure 1). For example, improving animal genetic resistance to gastrointestinal parasites as part of integrated health management programmes (strong contribution to Principle 1) contributes to reducing the use of anthelmintics (drug inputs - contribution to Principle 2), while preserving soil biodiversity, entomo- and avifauna (more limited contribution to Principles 3 and 5) (Figure 1). Similarly, by improving the feed efficiency of animals, e.g., monogastrics, the quantities of inputs needed for production are reduced (per unit of production: meat, eggs, etc.; strong contribution to Principle 2), while reducing pollution (contribution to Principle 3) and the overall need to import raw materials from regions that are not very virtuous in terms of biodiversity preservation (for a given volume of production; more limited contribution to Principle 5). However, if the gain in feed efficiency is accompanied by an increase in the size of farms and the overall amount of plant output required to feed animals, and/or by a need for feed resources of higher nutritional quality, the favourable impact of the improvement in feed efficiency on the level of pollution or the preservation of biodiversity is likely to be partially or totally cancelled out.

Other research may mobilise several principles simultaneously. This is the case, for example, of studies conducted with the aim of jointly quantifying the economic and environmental consequences of selection based on particular traits (e.g., feed efficiency; Soleimani and Gilbert, 2020), or of studies that aim to analyse the economic and environmental impact of replacing the usual economic weights with environmental weights (or taking them into account together) within selection objectives (Besson *et al.,* 2020). This mainly mobilises Principles 2 and 3, but also contributes (albeit in a more limited way) to Principle 5 (Figure 1). Finally, some studies may mobilise all of the principles together. This includes: (1) the definition of new, more complete and balanced selection objectives adapted to "alternative" and diversified breeding systems, such as Organic Agriculture (Slagboom *et al.,* 2020); or (2) the definition of new selection objectives (and the development of related methods) that would make it possible to more explicitly take all the services and disservices of livestock farming at a territorial scale into account (Tixier-Boichard *et al.,* 2015).

Moreover, the in-depth modification of our agricultural systems faces many obstacles. Some of these are due to a lack of knowledge in various fields of the life sciences. The basic research effort currently underway in the field of genetics/genomics or, more generally, integrative biology, will probably lead to the production of knowledge that will be useful for the agroecological evolution of farming systems via its contribution to several principles of the conceptual framework and, potentially, to all of them (Clark *et al.,* 2020; Crespi *et al.,* 2020). This basic research effort should therefore be continued and expanded.

Overall, a joint and, if possible, balanced mobilisation of the different principles is necessary to implicate livestock systems in a genuine agroecological transition capable of responding to the legitimacy crisis mentioned in the introduction. Genetics research should be considered and developed with this in mind.

■ 2.2. From improving efficiency to redesigning livestock systems

As shown in Figure 1, some contributions may be associated with one or even several principles of the Dumont *et al.* (2013) conceptual framework, but are considered in the context of "conventional" livestock farming and not at all as part of a real agroecological transition or, if so, only marginally. This would be the case, for example, of work aimed at temporarily improving the genetic resistance of animals to a particular infectious agent (strong contribution to Principle 1, and more marginally to the other principles) without addressing the main factors that determine the level of risk or impact of the disease (Box 3). Beyond the five principles of the conceptual framework defined by Dumont *et al.* (2013), it seems therefore necessary to consider the level of transition (changes, transformations) that the different actions will generate. The use of the E/S/R (Efficiency/Substitution/Redesign) gradient proposed by Hill (1985) allows us to integrate this dimension into our analysis. On this gradient, some actions aim at a "simple" search

Figure 1. ***Examples of animal genetics contributions to the five agroecological principles[1] for livestock systems.[2, 3]***

[1]The five principles of the conceptual framework proposed by Dumont *et al.* (2013).
[2]The size of the circle indicates the extent of the contribution (actual or potential) of a research action/theme to the principle (see text as well).
[3]Research topics in bold and italics have been the subject of a limited amount of research to date.

for **efficiency** (E), without challenging the foundations, the components or the general design of the systems. This would be the case, for example, of the use of genetically improved animals to transform feed into muscle (carcass) in a more efficient way, without seeking to modify the type of feed used or the way the farms are run. Other actions aim at substituting (S), temporarily or permanently, certain components of a system with others that are better accepted and/or considered more "virtuous", but without questioning the general design of the systems either. This would be the case, for example, in arable farming regions, of the substitution of mineral fertilisers with organic fertilisers imported from livestock farming regions without questioning the structure of rotations, cropping systems or territorial specialisation. In animal production, this would be the case, for example, of a change in the raw materials used in the formulation of commercial feeds (replacement of soybean cakes with other locally-produced raw materials) without reconsidering quantitative production objectives or the management of livestock production units. Finally, the most advanced level of transition on this gradient involves a global and in-depth redesign of the systems. In a redesign approach, the joint implementation of several principles of the Dumont *et al.* (2013) conceptual framework is important (Dumont *et al.*, 2020a).

This E/S/R gradient is conceptually quite close to the idea of "weak" or "strong" agroecological modernisation of farming systems proposed by Duru *et al.* (2014). "Weak" agroecological modernisation refers to changes in practices leading to: (1) improved input efficiency (e.g., precision feeding); (2) the implementation of good practices such as material recycling or the use of precision farming (or medicine) technologies, to reduce the use of inputs (e.g., drugs) and their collateral effects (e.g., selection of resistant pathogens); or (3) the replacement of inputs by others, e.g., to reduce environmental impacts. "Strong" modernisation requires a paradigm shift and an in-depth redesign of systems based on the principles of agro-ecology. In a nutshell, using biodiversity to produce services, especially regulatory services, in order to limit inputs, reduces pollution and increases the resilience of systems.

"Weak" agroecological modernisation (E/S on the E/S/R gradient) is simpler to consider and implement. Indeed, in this case, we do not change the *previous* logic, but instead seek to reduce costs to improve the economic efficiency of the systems. However, the more effective these approaches are (or seem to be) in the short term, the more they lead to a lack of interest in the fundamental causes of the problems they are supposed to solve, and the more they delay the implementation of long-term solutions that generally require a "strong" rethinking of the structure, organisation and functioning of systems (Hill, 1985). As such, they can contribute to the socio-technical lock-in of systems, which makes their evolution all the more difficult. The idea of using genetically modified animals to solve (at least temporarily) a recurrent disease problem in livestock farming is a good illustration of this (Box 3).

The analysis of the numerous contributions of animal genetics to the different principles of the conceptual framework defined by Dumont *et al.* (2013) (see Part 1 and Figure 1) generally places them in a "low" agro-ecological modernisation (E/S) register. Animal genetics has had a positive impact on the economic and environmental sustainability of livestock farming systems in the past. By contributing to increased animal productivity, it made it possible to reduce or control production costs, as well as the amount of resources used to produce animal biomass (e.g., resources required to produce one kg of milk, meat or eggs) and the intensity of environmental impacts (greenhouse gases per kg of milk or meat). However, this contribution has mainly benefitted the dominant "conventional" livestock farming sector, and its positive effects have been more than offset by a very significant increase in the quantity of output produced. Animal genetics has thus accompanied the techno-industrial evolution of animal production systems that has taken place over the last few decades and that has led to the legitimacy crisis mentioned in the introduction. It has therefore also contributed, in part, to the socio-technical lock-in of these systems, making change difficult. This observation is now shared and discussed within the scientific community, and a desire to change research priorities and perspectives is gradually emerging.

Table 1 illustrates how some classic and important research topics in the field of animal genetics (on an international scale) could fit into the perspective of a "strong" agroecological transition of livestock systems.

■ 2.3 Agroecological transition, animal, human and environmental welfare

The fundamental ideas/concepts and seminal studies in the field of agroecology were contributed by researchers who were mainly interested in crop production. In 2014, only 5% of indexed publications in the field of agroecology explicitly referred to livestock in their keywords (Soussana *et al.*, 2014). The conceptual framework proposed by Dumont *et al.* (2013) for reflecting on the evolution of livestock systems was therefore quite logically based on principles inspired by those formulated by Altieri for cropping systems (Altieri, 2002). This probably explains why animal welfare, a major issue for the evolution of livestock production systems in the 21st century, has so far been given relatively little consideration in discussions aimed at an agroecological transition of livestock systems, which are relatively focused on environmental issues.

Table 1. ***Positioning of work in three major areas of animal genetics research on the Efficiency/Substitution/Redesign gradient. The current state of knowledge on each topic is considered to be very advanced (+++), advanced (++), under exploration (+) or largely unexplored (?).***

Themes/ Areas of research & development	**>> TRANSITION GRADIENT >>**		
	Efficiency (E) 	**Substitution (S)** 	**Redesign (R)** 
Feed efficiency	**+++** Selection to reduce the consumption of concentrates (reduction of inputs and of production costs)	**+** Selection to improve the ability of animals to valorise feed resources of lesser nutritional value that are less in competition with human food → alternative to concentrates	**+ / ?** Strategy(ies) to sustainably increase the efficiency at the farm level by mobilising several levers: - selection and management to improve efficiency at the level of the animal's career or of the herd (renewal management) - use of alternative feed resources (e.g., co-products, food waste) - implementation of diversified innovative systems based on a strong integration of agriculture and livestock production
Animal health	**+++** Selection to improve productivity of animals in highly controlled environments (i.e. sick animals are not productive, and *vice versa*)	**++ / +** Selection to improve resistance of animals to infectious and parasitic diseases and/or immunocompetence → alternative to the use of drugs, especially antibiotics and anthelmintics	**+ / ?** Integrated health management strategy to minimise the use of inputs by mobilising several complementary levers and ecosystem services: - association of several complementary animal species selected for their adaptation to the system (e.g., resistant or tolerant animals) - use of plants with health value - selective targeted treatments - rotational grazing
Production dynamics, diversity and system transition	**++** Selection to improve the efficiency of particular biological functions (milk persistency, longevity, etc.) Reducing the duration of non-productive periods	**+** Selection to improve the ability of animals to mobilise and restore their body reserves, to manage the trade-offs between functions → alternative to the control of the environment by farmers, based on an intensive use of inputs	**?** Management of the diversity and complementarity between animals, and between animals and the other components of the system (cross-breeding, innovative management of intra-herd diversity) to increase the resilience of the systems and minimise the use of inputs (including animals) Selection strategies based on multi-criteria objectives that integrate economic, social and environmental impacts (including biodiversity) of breeding, on a territorial scale

Good health is one of the necessary (but not sufficient) conditions for animal welfare. Lack of pain, injury and disease is one of the five "freedoms" on which most animal welfare assessment strategies are based (Mounier *et al.*, 2021). In order to more effectively integrate these highly connected notions of animal health and welfare into our analysis, we could have associated welfare in our presentation with the first principle of Dumont *et al.* (2013) (integrated animal health management), which is part of the *One Health* dynamic that promotes an integrated, systemic and unified approach to public, animal and environmental health. As an extension, it would be interesting to carefully analyse the extent to which certain contributions of genetics to the evolution of farming systems based on the principles of agroecology could be part of the *One Welfare* dynamic, which aims at developing a better understanding of the interconnections between animal welfare, human welfare and the environment (Garcia Pinillos *et al.,* 2016). An example that could well illustrate this point is the selection of robust animals, resistant to a range of infectious agents and therefore less sick (better animal welfare), that require less medical intervention (less drugs used, e.g., less antibiotics, and that therefore more effectively preserve the environment and public health) and allow a reduction in animals' mortality (contributing to the psychological well-being of farmers and in line with societal expectations). Another example would be the selection to increase the cognitive abilities of animals (e.g., learning abilities), enabling them to adapt to more diversified, exposed and more stimulating farming systems (in order to make better use of resources, to have positive interactions with other animal species sharing their environment and, in particular, with humans). Both animals and farmers could benefit from this for their health and well-being. This is a topic that deserves further discussion but is beyond the scope of this article.

Conclusion

Global population growth, the degradation of ecosystems and the threats posed to their integrity by climate change, as well as strong changes in societal expectations in certain countries, are some of the reasons that are now forcing us to reconsider certain choices that have structured our food systems for decades (Duru and Le Bras, 2020). Among these choices, the intensification of agricultural and livestock farming systems is now strongly challenged. Different transition paths are being considered. Some, such as sustainable intensification (or "industrial ecology", also mentioned in the article of Dumont *et al.,* 2013), extend the productivist paradigm of agricultural modernisation. Others, such as agroecology, propose a real shift. Even if some elements of convergence can be identified between these different orientations, debate is still intense between supporters of one or the other, including within the scientific community. Genetics, as a scientific discipline, is not the prerogative of only one of these models alone: it can be used for each of these transition paths.

Our literature review shows that the commitment to a strong agroecological transition of livestock systems requires the adoption of a holistic vision of these systems, without neglecting any dimension (social, environmental, health, ethical, economic, etc.). To support this transition, the research effort must be substantial (Dumont *et al.,* 2014) and necessarily interdisciplinary. Compagnone *et al.* (2018) have also suggested that conducting research aimed at the agroecological transition of systems requires a shift from a "scientific monoculture" to an "ecology of knowledge", integrating the diversity of knowledge from a broad and potentially renewed partnership. To become involved in work aimed at the agroecological redesign of livestock systems, geneticists will therefore have to consider the necessity of questioning some of their epistemological, theoretical, methodological and technical principles, as well as their research priorities, and to anticipate a certain renewal of their partnership, i.e., to question their "research frame of reference" (Hazard *et al.,* 2019). Major changes are therefore required, which will inevitably motivate new generations of researchers.

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Abstract

Livestock production systems have considerably evolved over the 20th century. Research in animal breeding and genetics and the implementation of genetic improvement programmes have played an important role in this evolution. Today, the dominant model, characterized by an intensive use of inputs, a very high degree of specialization of production systems and the search for ever lower production costs, is questioned. A now widely shared objective is to contribute to the emergence of sustainable, equitable, healthy and environmentally-friendly food systems. Agroecology is a means to achieve this goal and a guide to the necessary transition of livestock systems, to which animal genetics must contribute. Examples of past, current and potential contributions are presented and positioned according to five agroecological principles proposed as a guide to the evolution of livestock systems. Most of them, such as the selection of animals resistant to different infectious diseases or making a more efficient use of feed, correspond to low levels of agroecological transitions in that they do not question the foundations, components or general design of production systems. Further contributions aimed at a strong transition, based on an in-depth redesign of livestock systems, should be developed in the future.

Résumé

Contributions de la génétique animale à la transition agroécologique des systèmes d'élevage

Les filières et systèmes d'élevage ont considérablement évolué au cours du xxe siècle. La recherche en génétique animale et la mise en place des programmes d'amélioration génétique ont joué un rôle important dans cette évolution. Aujourd'hui, le modèle dominant, caractérisé par une utilisation intensive d'intrants, une très grande spécialisation des systèmes et la recherche de coûts de production toujours plus bas, est remis en cause. Un objectif désormais largement partagé est de contribuer à l'émergence de systèmes alimentaires durables, équitables, sains et respectueux de l'environnement. L'agroécologie est un moyen pour atteindre cet objectif et guider la nécessaire transition des systèmes d'élevage, à laquelle la génétique animale doit contribuer. Des exemples de contributions passées, actuelles et potentielles sont présentés et positionnés selon cinq principes d'agroécologie proposés pour guider l'évolution des systèmes d'élevage. La plupart, telles que la sélection d'animaux résistants à différentes maladies infectieuses ou valorisant de façon plus efficace leur alimentation, correspondent à des niveaux de transition agroécologique faible, dans la mesure où elles ne remettent pas en cause les fondements, les composantes ou la conception générale des systèmes. De nouvelles contributions, visant une transition forte, fondée sur une reconception en profondeur des systèmes d'élevage, sont à développer à l'avenir.

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