POSITION PAPER

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OneARK: Strengthening the links between animal production science and animal ecology

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Summary

1. Wild and farmed animals are key elements of natural and managed ecosystems that deliver functions such as pollination, pest control and nutrient cycling within the broader roles they play in contributing to biodiversity and to every category of ecosystem services. They are submitted to global changes with a profound impact on the natural range and viability of animal species, the emergence and spatial distribution of pathogens, land use, ecosystem services and farming sustainability. We urgently need to improve our understanding of how animal populations can respond adaptively and therefore sustainably to these new selective pressures.

2. In this context, we explored the common points between animal production science and animal ecology to identify promising avenues of synergy between communities through the transfer of concepts and/or methodologies, focusing on seven concepts that link both disciplines. Animal adaptability, animal diversity (both within and between species), selection, animal management, animal monitoring, agroecology and viability risks were identified as key concepts that should serve the cross-fertilization of both fields to improve ecosystem resilience and farming sustainability.

3. The need for breaking down interdisciplinary barriers is illustrated by two representative examples: i) the circulation and reassortment of pathogens between wild and domestic animals and ii) the role of animals in nutrient cycles; i.e. recycling nitrogen (N), phosphorus (P), and carbon (C) through, for example, contribution to soil fertility and carbon sequestration.

4. Our synthesis identifies the need for knowledge integration techniques supported by programs and policy tools that reverse the fragmentation of animal research towards a unification into a single Animal Research Kinship, OneARK, which sets new objectives for future science policy.

5. At the interface of animal ecology and animal production science, our article promotes an effective application of the agroecology concept to animals and the use of functional diversity to increase resilience in both wild and farmed systems. It also promotes the use of novel monitoring technologies to quantify animal welfare and factors affecting fitness. These measures are needed

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to evaluate viability risk, predict and potentially increase animal adaptability, and improve the management of wild and farmed systems, thereby responding to an increasing demand of society for the development of a sustainable management of systems.

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Keywords Adaptation, Agroecosystem, Bio-logging, Emergence, Functional diversity; Livestock, Phenotypic plasticity, Resilience, Sustainability, Zoonotic disease.

Introduction

Our planet is undergoing major global environmental changes mainly caused by a rapid increase in human population and concomitant agriculture industrialisation (specialization, concentration, intensification). These changes have a profound impact on biodiversity, on land use due to modified resource availability, as well as on emergence and spatial distribution of pathogens (Keesing et al. 2010). A primary concern is the extremely rapid rate of these changes, which apply strong and often novel selective pressures on animals, at scales rarely encountered over evolutionary time scales. These challenges are placing new demands on physiological and adaptive capacities (particularly phenotypic plasticity which allows for the compensation of rapid environmental changes when genetic adaptation is too slow), on the interactions among species, and ultimately on species persistence and biodiversity. The consequences are major in terms of conservation of biodiversity but will also have impacts on every category of ecosystem services: support (e.g. soil formation), production (e.g. milk, eggs and meat), regulation (e.g. pest control) and cultural, or on their combination (e.g. biodiversity-related ecotourism (Fuller et al., 2007). Thus, we have a responsibility to find new ways to better understand and preserve the functional diversity of ecosystems. These have been, and will continue to be, a major support of human endeavours.

Animals represent an enormous part of biodiversity, contributing 1.12 million species from a total of 1.43 million catalogued species throughout eukaryotic kingdoms (Mora et al., 2011). Only a very limited number of species are farmed but they contribute a significant amount of biomass. Wild and farmed animals are landscape shapers and ecosystem engineers that control the availability of resources by causing changes in biotic or abiotic materials. However, animals are also important vectors, intermediate hosts and reservoirs for microorganisms causing major infectious diseases (Woolhouse et al., 2005). Additionally, wild and farmed animals have always been a major source of proteins for human consumption.

It is increasingly recognized that there is a continuum between animals in managed ecosystems and animals in natural environments. No production system whatever its level of biosecurity is

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completely isolated from the surrounding environment. Likewise, today, no ecosystem is completely isolated from human influence, and increasingly ecosystems are subject to some degree of human management, or have limits imposed on them by human activity. Therefore, it is highly relevant to consider what the cross-fertilisation between the two communities of animal production science and animal ecology can bring.

A number of basic concepts appear at first sight to be fundamentally different between animal production science and ecology. However, when these concepts are given due consideration it transpires that they are actually more similar and not really in opposition. The aim of this paper is to explore the common points between animal production science and animal ecology. Better recognizing the similarities between the two communities will identify promising avenues of synergy by concept and/or methodology transfers between communities. We first discuss seven topics that are common to both communities but viewed from differing perspectives, in order to show their potential for synergy and then highlight these points using two examples. This prospective thinking for a community unification into a single Animal Research Kinship, i.e. OneARK, sets new objectives for future science policy.

Artificial selection versus natural selection

Selection denotes the fact that, among individuals born at a given generation, those that will survive to mate and procreate a new generation can be considered as "chosen" according to some of their characteristics. These characteristics typically impact on their survival, mating probability and their number of descendants. For domestic species, **artificial selection** depends on decisions taken by humans (breeding managers). For wild species, **natural selection** emerges from interactions with conspecifics, other species and the abiotic and stochastic environment.

Natural selection can act simultaneously on multiple traits, so that trade-offs are an important part of understanding adaptation and response to selection: natural selection maximises average fitness of the population, not trait values (Stearns, 1977). Another fundamental aspect is that natural selection varies spatially and temporally depending on the environment (Siepielski et al., 2013, 2017) so that traits may be positively selected in one environment and counter-selected in another. Investigating selection is thus complex notably because we need to assess the actual target of selection but also make sure that the covariances between trait and fitness are not only due to environmental covariance (Morrissey et al., 2010).

It is generally admitted that artificial selection started in the early stages of domestication, the first selected traits being favourability to the domestication process itself, e.g. docility. During the last three centuries, and especially during the last six decades, this artificial selection has become more and more organized and intense, targeting and maximising specific traits (e.g. dairy production, growth rate). Another consequence of domestication was to decrease the natural selection pressure because humans increasingly controlled the environment of animals. This is typified by the strong intensification of animal production.

After domestication, selection in different places and with different goals first led to a huge increase in diversity between populations (Darwin, 1859). However, the recent changes in livestock breeding led to the opposite, with (i) a decrease in the number of breeds for a given species (Sherf, 2000) and (ii) a reduction of within-population genetic variability in intensively selected populations (Danchin-Burge et al., 2012), which means a lower adaptive potential in the long run. In the short run, this selection of highly specialised and rather homogeneous "elite" breeding animals led to (i) the unwanted evolution of some functional traits due to unfavourable genetic correlations (e.g. milk yield and female fertility) (Oltenacu & Broom, 2010) and (ii) reduced robustness and flexibility *i.e.*, lower resilience to environmental variability, particularly to new stress and disease challenges. The multivariate nature of selection acknowledged by animal ecologists (Lande & Arnold, 1983) has promoted the development of artificial selection programs which include the use of selection on multiple traits (Puillet et al., 2016). Indeed, current livestock selection programs are increasingly seeking to optimise animal fitness in the production environment by putting more emphasis on functional traits and including robustness and adaptability traits alongside production (Berghof et al., 2019). Taking into account such trade-offs is particularly important in the context of global changes where resource availability and variability will be strongly affected.

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Such collaborative efforts are increasingly needed because the rapid and strong changes of environmental conditions generate strong selective pressures, so much so that humans are now considered as the greatest evolutionary force (Palumbi, 2001; Sarrazin et al 2016). Understanding how populations respond to these new selective pressures is a key issue in applied evolution and conservation. It is also a key issue for artificial selection since global changes are altering the environmental conditions under which artificial selection is operating. For example, because genotypes can perform differently under different environmental conditions (gene by environment interactions, G*E) there is a strong risk that individuals with high breeding values for production traits in protected environments will tend to be negatively impacted by adverse environments, leading to poorer breeding values for those animals that are most environmentally sensitive. Conversely, animals with poorer breeding values for production traits may be the individuals best equipped to deal with environmental perturbations, so that the selection criteria ought to be multivariate and in multiple environments. In terms of animal ecology, understanding how the environment affects selection pressures will be key to understanding potential adaptive responses (e.g. Siepielski et al. 2017). Animal ecology may also benefit from the rapid advances in quantifying the genetic bases of phenotypic/performance robustness of animals to environmental variability (quantitative genetics, epigenetic regulation), a field that is likely to advance much more rapidly in animal production science because of easier access to controlled genetic materials, advanced control of environmental backgrounds, rapid expansion of multivariate massive phenotyping (including omics), and the ability to account for social interactions between conspecifics (Wade et al. 2010). A major challenge is to understand how global environmental changes are going to affect selective pressures acting on both wild and domesticated populations. Determining the theoretical bases of how natural and artificial selections actually modulate adaptive (and therefore, sustainable) responses of these populations to these new selective pressures is a corner-stone objective. This will pave the way of resolving how we may improve (i) our management of agro- and wild ecosystems by increasing biodiversity and/or within populations' genotypic/phenotypic diversity, (ii) thereby improving resilience capacity of

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individuals, populations, and systems, and (iii) reducing viability-risks of our farmed and wild environments.

Viability risks for farmed systems versus natural ecosystems

Global changes pose a viability risk for both natural and farmed systems, although the "currencies" by which viability is judged have traditionally differed; it is largely about economics for farmed systems and about biodiversity and population persistence for natural ecosystems. The framework of ecosystem services links both types of systems by considering them as essential for sustainable development, but viability of natural populations for their own sake also needs to be integrated (Martin et al 2016). The most commonly used currency to assess viability in wild populations is the probability of extinction of a population over an arbitrarily chosen time period (e.g. 100 years in the UICN red list) or the median time to extinction. Several components of global change will affect viability of both natural and farmed systems.

The impacts of climate change emerge through both long-term changes in average conditions within local environments and an increase in the frequency of extreme events (Ummenhofer & Meehl, 2017). The former has received more attention so far. The effects of climate change can be mediated through many indirect effects such as the disruption of interaction between species because of changes of phenology or morphology (van Gils et al., 2016). A typical example is the earlier breeding of insectivorous birds so that the peak of offspring energetic needs coincides with the peak of food abundance (caterpillars, Visser et al., 1998): if the timing is mismatched then breeding success is low. These effects are more likely to be encountered in wild than farmed system where long-term changes in average environmental conditions will more frequently be experienced in terms of direct effects that alter resource availability. In farmed systems, the impact on animals will be less direct but in the longer term will impact farm management systems e.g. impacting the stocking densities of animals that are sustainable in extensive systems, and incurring greater costs for intensive systems (e.g. cooling systems). In managed populations, extreme events such as drought or flooding require the farmer to make costly, unplanned

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In contrast to wild animals in natural ecosystems that are fully in interaction with the environment, the magnitude of interactions of farmed animals with the environment spreads along a continuum, ranging from agro-ecosystems to landless livestock production. This gradient is driven by the form of the feeding system, opposing land sharing to land sparing, and the level of interaction the livestock population has *vis-a-vis* agricultural and natural system components (crops, forest, water, wildlife, etc.). Agro-ecosystems are defined by a high dependence on local resources, like land and water (pastoralism being its apogee). At the opposite end of the scale, landless livestock systems maximize their direct independence from environmental constraints by means of feed trade, thus establishing production systems with almost no direct relation (excluding by the market) between the places and times where livestock are reared, their food is produced, and where their products are consumed.¶
Gradients in degree of human intervention are also a common element of wild animal and natural ecosystem management. Indeed, not a single natural ecosystem is human-proof, at least since climate change started. More direct wild animal ecosystem management profiles can range from biodiversity reserves through natural parks, run as wildlife sanctuaries, to wildlife areas managed by local communities, which recognize combined wildlife, livestock, and rangeland services as essential for human groups, a vision emphasized in Southern Africa (Chomba et al., 2014; Jones et al., 2015). ¶
In the latter case there is a strong interaction between agricultural activity and ecosystem management. More generally, the frontier between the "wild" and the "farmed" animals is progressively being eroded, changing to situations where more coexistence and interactions are inevitable if we wish to reconcile preserving biodiversity and better resource sustainability. Achieving this in the design of these re-expanding agro-ecosystems imposes a tightening of the collaboration between animal production scientists and animal ecologists. An example of this is the "Natura 2000" policy to preserve biodiversity in Europe, often in human-made ecosystems. Furthermore, and in line with societal considerations, there is a visible shift in livestock and wildlife policy dialogue, moving beyond the simple support of resource sufficiency and food provision to now provide incentives for conservation and rehabilitation of functional integrity, and payment for environment services in production areas and at global Earth scale (Frost et al., 2008; Kammli et al., 2011).¶

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interventions (buying food, transporting animals) where possible. These clearly have economic consequences especially if possible interventions are limited and loss of animals occurs (e.g. rangeland grazing). In wild populations, effects of extreme events include both decreased survival (e.g. die-offs, McKechnie & Wolf, 2010) and reduced breeding success (Jenouvrier et al., 2015). Extreme events may generate very strong selection pressures leading to marked evolutionary shifts in wild populations (Grant et al., 2017). However, the impact of extreme events is particularly complex to anticipate, as they engage non-linear shifts in multi-species interactions.

Introduced exotic species, which may be pathogens, pathogen carriers, predators or directly competing species, represent another major viability risk to both farmed and wild populations (Bellard et al., 2016; Paini et al., 2016; see section on circulation of zoonotic pathogens). They are likely to be more prevalent and successful in highly anthropized habitats such as peri-urban and agricultural lands, and species of tropical origin benefit from the warming climate in temperate and boreal regions (Hufbauer et al 2012, Bellard et al. 2013).

Land use is another class of viability risks. There are direct economic impacts of human movement in terms of (i) the value of land or other shared resources such as water in zones where agricultural land is in competition with urban development, and (ii) in terms of rural depopulation (difficulties in recruiting labour, human isolation, costly supply chains) affecting ecological function of agro-landscapes (Sabatier et al., 2014). Extinction risks are further increased for wild populations due to competition with urban and agricultural land (e.g. palm oil, cocoa), and non-sustainable harvesting (Maxwell et al., 2016). To fully understand viability risks, all these factors and their interactions need to be taken into account.

There are also viability risks due to rigidity of human behavior. For wild animals, it relates to how human habits of farming landscape may evolve in response to recolonization by wild animal species like large carnivores, a question for which some straightforward solutions may exist (Kuijper et al. 2019). In farming this translates to, for example, continued use of inappropriate animal genetics through a failure to recognize the traits needed for durability in new conditions. Indeed, the loss of genetic diversity of domesticated breeds due to rigid selection of a very few

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breeds is a major issue being addressed by the FAO (FAO, 2015). Rigidity in farm management, such as failing to adapt fodder cropping practices to changing seasonal patterns, can also increase the viability risks for the animals that depend on this fodder. Rigidity of behaviour can apply not just to humans but also to animal species when one considers differences between generalist/specialist or plastic/non-plastic species (Clavel et al., 2011). For example, one issue is the existence of ecological traps where species respond to cues that were supposed to signal a high quality environment but that got uncorrelated from this environment, such as asphalt roads that may reflect light in the same manner as water bodies attracting some insects to breed (Schlaepfer et al., 2002). Ultimately, population viability will depend on the ability of organisms to respond adaptively to complex environmental changes inducing novel selective pressures.

Both farmed and wild populations share some of the same viability risks and ultimately must respond by adaptation (microevolution and/or plasticity). The degree of management of the animal populations within a given ecosystem will mainly affect the extent to which risks can be buffered by human intervention, e.g. deploying reproductive technologies developed in animal production science to aid in rewilding and to overcome habitat fragmentation. Biodiversity and economics are connected across the spectrum from farmed to natural ecosystems. Tools developed at the frontier between ecology and economics, such as coviability analyses (Mouysset et al., 2014), which aim at finding compromises where viability of both farmed and natural systems can co-exist by coupling economic and biodiversity models, will be important for the future.

Agro-ecosystems and farmed animal management versus ecosystems and wild animal management

In contrast to wild animals in natural ecosystems that are fully in interaction with the environment, the magnitude of interactions of farmed animals with the environment covers a spectrum, ranging from agro-ecosystems to landless livestock production. This gradient is driven by the form of the feeding system, opposing land sharing to land sparing, and the level of interaction the livestock population has *vis-a-vis* agricultural and natural system components

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(crops, forest, water, wildlife, etc.). Agro-ecosystems are defined by a high dependence on local resources, like land and water (with pastoralism being its apogee). At the opposite end of the scale, landless livestock systems maximize their direct independence from environmental constraints by means of a feed trade, thus establishing production systems with almost no direct relation (excluding by the market) between the places and times where livestock are reared, where their feed is produced, and where their products are consumed.

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Gradients in degree of human intervention are also a common element of wild animal and natural ecosystem management. Indeed, not a single natural ecosystem is human-proof, at least since climate change started. More direct wild animal ecosystem management profiles can range from biodiversity reserves through natural parks, run as wildlife sanctuaries, to wildlife areas managed by local communities, which recognize combined wildlife, livestock, and rangeland services as essential for human groups, a vision emphasized in Southern Africa (Chomba et al., 2014; Jones et al., 2015).

In the latter case there is a strong interaction between agricultural activity and ecosystem management. More generally, the frontier between the “wild” and the “farmed” animals is progressively being eroded, changing to situations where more coexistence and interactions are inevitable if we wish to reconcile preserving biodiversity and better resource sustainability. Achieving this in the design of these re-expanding agro-ecosystems imposes a tightening of the collaboration between animal production scientists and animal ecologists to reconcile opposing interests. Some examples of this are studies on heathlands or the policy of “Natura 2000” to preserve biodiversity in Europe, often in human-made ecosystems. The governance mode of Natura 2000 witnesses not only the inclusion of land users and civil society in taking decisions, but also the place of both animal scientists and animal ecologists in participation on scientific committees and their role in providing evidence through qualitative and quantitative evaluation of benefits, i.e. about the balance between provisioning services to local farming systems and markets and conservation services to the society (McCauley, 2008, Morán-Ordóñez et al., 2013). Furthermore, and in line with societal considerations, there is a visible shift in livestock and

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The key role of animal adaptability to connect evolutionary and animal production sciences

Adaptation processes are multifaceted, taking place at different spatial scales and with different temporal modalities (Gould & Lloyd, 1999). Evolutionary biologists, who mainly deal with natural populations, have focused on adaptation as a trait increasing relative fitness, *i.e.* which evolved via natural selection. Physiologists, who deal with laboratory and farmed strains, have focused on within lifetime reversible processes that allow individuals to adjust to their environment, with less focus on their heritability. These biological processes depend on the variability of the environment and adaptation can be described by the following continuum: (i) phenotypic flexibility of individuals leading to temporary/reversible changes, (ii) developmental plasticity leading to more permanent changes of phenotypes through physiological and/or epigenetic mechanisms, and (iii) intergenerational modification of allele frequencies through natural selection (Chevin & Beckerman, 2011). Integrating these different adaptive mechanisms has to be developed together at the interface with animal production science. Studying performance and behavioral changes induced by modifications in the farming environment would provide a great opportunity for evolutionary biologists to investigate the key mechanisms allowing individuals to maintain their performances over different abiotic conditions, complementing and providing a bridge between approaches in the lab and in the wild.

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The complex phenotypes underlying adaptability are forcing scientists to develop an integrated approach looking at multiple characters. The recent expansion of genomics, and other -omic data, offers new avenues to understand the mechanisms that shape adaptability (Valcu & Kempenaers, 2014). Studying organisms as a whole, taking into account functional links between traits is now made possible by combining –omic data with the characterization of physiological and performance traits (Prunet et al., 2012). This should uncover cell or physiological processes important for adaptability in both wild and farmed animals. However, such approaches often produce complex data on cell and physiological pathways that are concomitantly affected. Building an integrated phenotyping (Headon, 2013) that sorts out mechanisms underlying adaptability in an order of importance now needs to combine biological, bioinformatics and statistic knowledge.

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Important questions remain regarding the role of transgenerational adaptation pathways in fitting, in the long term, populations to their environment. Such phenotypic modulation has a predictive power and may help the offspring to be better adapted to future environmental conditions. Intergenerational plasticity encompasses various mechanisms, including epigenetic changes. These mechanisms are likely to sustain rapid adaptation and to promote survival of the next generation (Rey et al., 2016). Their understanding is also a key element for animal production science: it opens an innovative way to optimize productivity, *via* the modulation of farming conditions during reproduction and offspring growth.

This is not an exhaustive list of the research of interest that remains to be conducted on animal adaptability. However, it emphasizes that promoting the understanding of the link between adaptation and fitness (survival or health state) and of the inheritance of related processes will enhance our ability to predict adaptability of animal populations, living in the wild or under farming conditions.

The importance of animal diversity for system resilience

Ecological resilience focuses on the adaptive capacity of an ecosystem and is defined as the amount of disturbance this system can absorb while remaining within the same stability range and retaining the same function(s), achieved through reinforcing within-system structures, processes and reciprocal feedbacks (Holling, 1996; Kaarlejärvi et al., 2015; Gladstone-Gallagher et al., 2019).

Resilience strongly depends on the initial composition of the local ecological assemblage and the degree of disturbance (Sasaki et al., 2015). In highly disturbed areas, differences in the recovery trajectory of assemblages have been related to differences in the composition and the dispersal capacities of the surrounding species pool of colonists and the level of connectivity among populations, species and ecosystems (Allison, 2004). These factors influence both probability of species persistence by increasing the genetic diversity of local populations (Bach & Dahllöf, 2012) and capacity for recovery by providing sources of propagating organisms (de Juan et al., 2013).

Biodiversity, a key factor for improving the long-term resilience of ecosystems (Awiti, 2011; Mori et al., 2013; Oliver et al., 2015), is frequently associated with high functional redundancy (*i.e.* presence of several species able to perform similar functions) (Sasaki et al., 2015; Kaiser-Bunbury et al., 2017) and high species complementarity (Lindegren et al., 2016). Both taxonomic (TD) and functional (FD) diversities, but not species richness, adequately capture the aspects of biodiversity most relevant to ecosystem stability and functionality (Mori et al., 2013). TD enhances resilience because most of the rare species within an assemblage are considered as functionally similar to the dominant ones and able to compensate their potential loss under changing environmental conditions, thus maintaining ecosystem functions. However, the maintenance of a particular assemblage is not a necessary requirement for the resilience of ecosystem functions (Oliver et al. 2015). Functions could be resistant to change or recovered following disturbance with taxonomically different assemblages of species, while exhibiting rather similar sets of traits (Gladstone-Gallagher et al. 2019) or maintaining interactions with sufficient resemblance to the previous system so as to allow it to be recognizably similar (Bregman et al., 2017). FD improves resilience because a more diverse set of traits increases the variety of potential responses to disturbance (Messier et al., 2019. This then increases the likelihood that species can compensate function(s) lost during disturbance events (Moretti et al., 2006; Kühsel & Blüthgen, 2015). However, resilience is also likely to be scale-dependent (Shippers et al., 2015; Gladstone-Gallagher et al., 2019), *i.e.* a combination of traits providing resilience to small-scale disturbance can be ineffective against disturbance acting at largest scale. As a result,

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the link between biodiversity and resilience is sometimes weak (Bellwood et al., 2003). If the trait structure of highly diverse animal assemblages remains rather stable after moderate stress, further intensification of human pressure can substantially reduce the variety of traits and results in significant alteration of functional diversity (Bregman et al., 2017). This raises the question of how to manage resilience and ecosystem services (i.e. the varied benefits that humans freely gain from the natural environment and from properly-functioning managed ecosystems, including provisioning, regulating, cultural and habitat and ecosystem functioning services) in socio-ecological systems?

Conceptual frameworks, tools and indicators (Sasaki et al., 2015; Oliver et al., 2015) have been defined for quantifying the resilience of coastal fisheries, estuaries or agricultural landscapes (de Juan et al., 2013; Mijatović et al., 2013) based on structural and functional attributes; *e.g.* ecosystem elasticity or sensitivity and adaptive capacity (López et al., 2013). Trends in the frequency of animal species that provide key ecosystem functions in Great Britain, have highlighted that they are not equally impaired by global change, and conservation actions should focus on the functional groups for which there is clear evidence of resilience erosion (Oliver et al., 2015). Moreover, community field experiments have clearly shown that vegetation restoration can improve pollination, suggesting that the degradation of ecosystem functions is at least partially reversible (Kaiser-Bunbury et al., 2017) and that severe disturbance-driven reduction in ecosystem function does not preclude rapid ecosystem recovery.

Several pattern- or process-oriented strategies have been suggested (Pauly et al., 2002; Fischer et al., 2006) to enhance biodiversity and ecosystem resilience for an improved management of marine and terrestrial production systems including: (i) promoting structurally complex patches of resources throughout the system, and species of particular concern for functional diversity, but (ii) controlling over-abundant and alien species and minimizing threatening ecosystem processes. Implementing those strategies will result in more heterogeneous production areas, with structurally more complex mosaics of habitats. The resulting production areas are likely to sustain higher levels of animal diversity and will be more resilient to external disturbances.

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The concept of animal diversity can be applied in various ways within livestock farming systems. A first aspect of animal diversity is the diversity of species, with for instance a mixed farm exploiting sheep and cattle or an aquaculture farm exploiting different fish species. The benefit of species diversity in the farm is generally based on the ability of various species to exploit different resources. Sheep and cattle in grazing systems are using different patches of grass, with plant different selection strategies. The same type of complementarity is used in recirculated aquaculture systems with fishes that feed in different levels of the water column. Complementarity of species can also go beyond complementarity of resources used, with farming systems based on the complete trophic chain such as integrated multi-trophic aquaculture systems (IMTA). The benefit of species diversity in a farm can also rely on the diversity of products that are commercialized. For instance, small ruminants can be used as cash flow while larger ruminants have a role of savings.

A second aspect of animal diversity is the diversity of individuals of the same species. Animals may be diverse in terms of their adaptive profiles, with for instance a type of cows that copes with heat stress and another type that cope with feed shortage. Having these two types of individuals in a herd can enlarge the range of perturbations that the livestock system can absorb. Animals can also be diverse in terms of their lifetime trajectories, with for instance females that have different types of reproductive rhythms (e.g. extended lactation in dairy production, accelerated lambing in sheep production). This diversity of trajectories within the herd can be useful to cope with environmental challenges (portfolio effect) or to have different types of products answering to different market needs (e.g. heavy/light lambs).

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The concept of agro-ecology as a sustainable and responsible way forwards

Agro-ecology, a concept originally defined as "the application of ecological theory to the design and management of sustainable agricultural systems" (Altieri, 1987), has recently become a hot topic with the aim to optimize economic, ecological, and social dimensions to achieve sustainable food production. Understanding the mechanisms underlying the resilience of agro-ecosystems is critical for conserving biodiversity and ecosystem functions in the face of disturbances (Moretti et al., 2006) and for securing the production of essential ecosystem services. Surprisingly, the majority of research on agro-ecology has been in done in plant production. This concept now calls scientists from animal ecology and animal production domains to readily interact by developing more interdisciplinarity.

Thus, five key ecological processes were proposed to be adapted to the animal context (Dumont et al., 2013): 1) adopting management practices, including breeding, to improve animal resilience and health; 2) decreasing the external inputs needed for production, particularly use of resources that are directly useable by humans; 3) decreasing pollution by optimizing the metabolic functioning of farming systems, including consideration of animal manure as a resource; 4) enhancing diversity within animal production systems to strengthen farm resilience, and 5) preserving biological diversity in agroecosystems.

Even if agro-ecosystem resilience has been considered as a key driver of sustainable agriculture under increasing environmental uncertainty, only a very few studies have explicitly tested the resilience of productivity to disturbance. Taking agroecology forward as a shared discipline needs a number of challenges to be overcome; these relate to scientific problems (Carlisle, 2014; Dumont et al., 2013) and cultural issues. From an ecologist perspective, agroecosystems are often seen as being a special case study that offers the opportunity to test ecological principles in conditions that are less complex and more clearly controlled than purely natural ecosystems. From the perspective of an animal production scientist, agroecology is often perceived as a constraint problem, i.e. how to achieve economic performance without breaking some environmental "rules". An important objective to better understand the interactions between environmental and biological processes that control community resistance and resilience will be to move beyond these viewpoints and exploit the synergies that the biodiversity within agroecosystems can bring (Tabacchi et al., 2009; Tixier-Boichard et al., 2015). One example of a useful synergy is to view climatic events as manageable phenomena resulting from processes whose effects could be much more mitigated through the use of integrated ecosystem management and flexible diversification than through adaptation to severe stress (Carlisle, 2014). Thus, the notion of eco-efficiency may be a powerful tool (Keating et al., 2010). This implies enlarging traditional production-related efficiency definitions to include environmental (land, water, energy), ecological (biodiversity, resilience, conservation) and economic (labour, capital) dimensions. This eco-efficiency approach creates significant challenges for the integration of these multiple dimensions but there are promising avenues of research tackling this issue (Soteriades et al., 2016).

The commonality in the use of advanced technologies to monitor animals

In the context of agro-ecology, understanding the variability with which individuals respond to their environment is a key entry for understanding most of the issues raised above. Similarly, study of this variability also help to assess animal welfare at individual level, an issue which is now a necessary respond to the societal demand to improve animal welfare. Animal ecology and production science are both interested in explaining the variability with which individuals respond to their environment and have a lot to win from merging methodological approaches for quantifying this variability.

Recent technological advances allow ecologists studying free-ranging animals access to multiple parameters encompassing foraging patterns, social interactions, physiological parameters but also to monitor environmental variables or entire ecological communities (e.g; Rutz and Hays, 2019). These bio-logging technologies, recording from a distance several variables many times per seconds over periods up to years, now allow the quantification of energetic and behavioral variability between individuals (*e.g.* accelerometry, Gleiss et al., 2011).

Bio-logging is extensively used, as well, in animal production science and now recognized as field in its own right, in precision livestock farming (Wathes et al., 2008). It permits the monitoring of animals for signs of health problems, allowing timely intervention by the farm manager. The broad nature of the bio-logging data is increasingly useful, particularly with respect to phenotyping complex traits such as resilience and efficiency. Being able to achieve a sustainable balance

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This offers the potential to integrate multiple markers over long timescales to quantify factors affecting overall fitness. One promising step will be to combine diverse biomarkers to evaluate how environmental variations impact fitness and productivity over ages (a fundamental factor for selection in the wild) or over life stages (a key parameter to improve animal productivity). The use of non-invasive methodologies (using hairs, feathers, blood…) including biosensors raises the issue of integrating all this information in a valuable way. Consider for example animal resilience, the capacity to cope with short-term environmental fluctuations. There is no direct measure that encompasses all the facets of resilience, in other words it is a latent variable that can only be deduced by combining multiple (proxy) measures of its different aspects (see Højsgaard & Friggens, 2010 for a health-related example). This issue requires the development of new mathematical models on the ultimate consequence of, within and between individual differences in ecology (*e.g.* habitat use) and physiology (*i.e.* energy demands over different time scales).

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An important challenge for ecology and animal production science is to safeguard animal welfare and thus health status across the wide range of husbandry and production environments, and also among individuals of different sizes and/or ages. This can range from the surveillance of animals scattered across very extensive rangelands to the monitoring of stress within groups in indoors environments. Currently, most protocols for welfare assessment rely on human observation (i.e. limited duration and potentially subjective). In this context, bio-logging technologies developed to be implemented in large or small animals have considerable potential to provide continuous monitoring of welfare status, allowing early and rapid identification of changes in behavioral and physiological components (Borchers et al., 2016; Sadoul et al., 2014; Ripperger et al., 2016). We suggest that combining these different types of parameters offers a more complete way to quantify animal welfare, which better integrates animal coping ability to changing environments both in wild and farmed conditions.

Two topical examples of breaking down the interdisciplinary barriers

Elaboration of the above points, and the commonalities that emerge, reinforces the call to more explicitly link these two disciplines for a better understanding of animals as systems, and animals within ecosystems. The importance of making such links, and the benefits arising, is illustrated by considering the following examples:

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CIRCULATION AND REASSORTMENT OF POTENTIAL ZOONOTIC PATHOGENS BETWEEN WILD AND DOMESTIC POPULATIONS

Historically, animal domestication has indirectly mediated the transfer of infectious agents between wildlife and humans (Morand et al., 2014). If cases of domestic emergence are not refuted (Pearce-Duvet, 2006), almost three-quarters of emerging infectious diseases significant in terms of public health originate in wild animals (Woolhouse et al., 2005). The recent outbreak of highly pathogenic avian influenza (HPAI) H5N8 clade 2.3.4.4 in both wild and domestic birds in Europe is a major example of the “round trips” of viruses between wild and domestic populations. The ancestor of the H5N8 virus was first identified in January 2014 in domestic poultry in South Korea, then adapted to wild migrating aquatic birds and rapidly spread in 2014–2015 (Lycett et al., 2016). This virus affected poultry worldwide from fall 2016 to spring 2017. It caused a few domestic cases in northern Europe, mainly in gallinaceous populations and more rarely in domestic or wild ducks and geese population, which are commonly more resistant to HPAI. A

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H5N8-related virus appeared in June 2016 in Touva Republic (southern Siberia) causing high mortality in waterfowl (OIE 2016).

Crossing the species barrier favors transmission and circulation of pathogens and constitutes a major advantage for multi-host pathogens (generalists). Host switches rely on genetic changes including nucleotide substitutions, acquisition of mobile genetic elements, or important genome rearrangements through recombinations and reassortments. Influenza viruses are a remarkable example of genetic material exchange between viruses issued from domestic and wild animals. H5N8 is itself a long lasting descendant of the HPAI H5N1 virus, first detected in China in 1996 and responsible for epizootics in domestic birds and some human cases since 2003 (Lycett et al., 2016). The complete sequence of the H5N8 Siberian strain isolated from wild birds in June 2016 revealed many reassortments with other poultry viruses. This virus infected northern European wild and domestic whereas other reassortants infected birds in southern Europe birds in fall 2016 to spring 2017 (Anses, 2017). The emergence of novel pathogenic strains within a region concentrating high densities of a receptive population (fat liver ducks) made possible (i) the dissemination of the virus within domestic and wild bird populations (abundant opportunities for cross-species transmission) and (ii) its reassortment with other low pathogenic strains of influenza virus circulating in the domestic and wild bird populations, thereby creating high levels of genetic diversity that can in turn broaden host-spectra. This example of massive spreading of a wildlife virus within a domestic population is emblematic of the risk induced by massive change in “traditional” production methods. Thirty years ago, the traditional fat liver duck production involved small rearing farms (around 1000 free range ducks within rearing period) and force feeding was operated by so-called “electrical force feeders” which enabled a single operator to force feed only 200 birds a day. The appearance and spreading of ‘pneumatic force feeders” during the latter half of the 90’s, enabled a single operator to force feed around 1000 ducks a day. The enhanced productivity promotes a higher consumer for a lower price fat liver. It also increases the rearing production of ducks with a number of bird per flock frequently higher than 10 000 and with a higher density of ducks in the free-range pens. This increase in number and density of

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susceptible birds combined with the use of traditional rearing methods at "industrial" production levels are certainly risk factors for the spread of avian influenza. Production of genetic variants is a mechanism predicted to favor the emergence of zoonotic strains and is difficult to prevent but could be minimized by avoiding passages of the virus from bird to bird or between animal species. Fortunately, most of the time this has not led to pandemic viruses as avian influenza strains do not transfer easily from human to human due to the absence of important receptors in human bronchial tubes. Pigs are an exception to that as they are receptive to influenza viruses specific for pigs, humans and birds (Kaplan et al., 2017). As a consequence, when pigs are co-infected with viruses from different animal origins, they become gene reservoirs with the potential to facilitate reassortments and the emergence of pandemic viruses. Therefore, traditional farming systems mixing free range poultry and pigs in the same backyard close to human populations presents a risk for the emergence of new reassortants of influenza virus able to spread within human populations as pandemic viruses.

Together with emblematic examples of emerging and re-emerging vector-borne diseases in which wild and domestic animals play a key role as vectors, intermediate hosts and/or reservoirs (Boissier et al., 2016), influenza highlights the increasing globalization of health risks and the importance of the human-animal-ecosystem interface in the evolution and emergence of pathogens. It illustrates how a better knowledge of causes and consequences of certain human activities, lifestyles and behaviors in ecosystems is crucial for understanding disease dynamics and driving public policies. Therefore, health security must be understood on a global scale integrating human health, animal health, plant health, ecosystems health and biodiversity. This ambition requires breaking down the interdisciplinary barriers that separate human and veterinary medicine from ecological, evolutionary and environmental science. It calls upon the development of integrative approaches linking the study of proximal factors underlying pathogen emergence and host physiological and adaptive responses to stress to their consequences on ecosystems functioning and evolution (Destoumieux-Garzón et al., 2018).

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In that sense, several points discussed in this article may be considered to tackle epizooties and zoonotic diseases. This starts with a required knowledge on the ecology of pathogens of interest (environmental niches, hosts, reservoirs and vectors), which may be complex for multi-host pathogens. While reliable and efficient tools for pathogen monitoring are usually rapidly available, complex pathogen transmission routes are often poorly characterized. New technologies for the monitoring animal contact data, including social networks give now access to this knowledge. Network modeling should help the understanding transmission dynamics in wild animal and livestock populations, which is needed to predict and reduce pathogen transmission (Craft, 2015). Adapting livestock management according to ecological principles is also an important avenue to improve animal health. By reducing contacts, low density farming has been shown to limit pathogen transmission (Tendencia et al., 2011). Beyond respectful cultural practices, introducing genetic diversity in livestock should be considered as a sustainable way to reduce disease spread. Indeed, genetically homogenous populations (monocultures) are more vulnerable to infection than genetically diverse populations, which have the potential to buffer populations against epidemics in nature (King and Lively, 2012; Ekroth at al., 2019). Finally, new avenues remain to be explored to increase the adaptability of farmed animals. If selective breeding (artificial selection) remains largely used in animal farming, recent studies have shown that new prophylaxes that increase animal adaptability can be envisioned to confer resistant phenotypes to otherwise susceptible animals without affecting the genetic diversity of the livestock. Indeed, several invertebrates (e.g. oysters, shrimp, honey bees) can be protected from pathogen infections by immune priming, which confers the potential to control infections and limit pathogen transmission, even in species that cannot be vaccinated (Lafont M. et al., 2017). A high interest is currently paid to immune priming, which has proven to be trans-generational in a series of cultured invertebrate species (Tetreau et al., 2019). However, the epidemiological consequences of trans-generational immune priming and its impact on the evolution of parasite/pathogen virulence are still debated (Tidbury et al., 2012) and remain to be studied.

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THE ROLE OF ANIMALS IN THE NUTRIENT CYCLES IN TERRESTRIAL AND AQUATIC AGROECOSYSTEMS

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Pushed by a dynamic political agenda on climate change, the roles of animals on biogeochemical cycles, the livestock sector contribution to global anthropogenic GHG emissions (14,5% of CO_2, CH_4 and N_2O emission) and mitigation options were highlighted (Gerber et al., 2013). This incited animal production research to collaborate with environment science. Initial studies were restricted to closed farm systems and animals were seen as "*a system*" emitting nutrients and gases in the atmosphere. Moreover, some effort was given to modelling nutrient emissions associated to waste management (Génermont et al., 1997), proposing some treatment options (Martinez et al., 2009) and practices (Thu et al., 2012).

However, this first era of research focussed on partial and segmented analysis of systems, neglecting more complex sets of interactions and flows between ecosystem compartments (not only exchanges with the atmosphere). Research somehow neglected the role of wild and farmed animals in contributing to nutrient and carbon recycling to other compartments of the ecosystem like soil or crops, i.e. considering "*animals in their systems*", and yet there are clear examples. In Australia, changing dung resources thanks to import of bovine animals, has altered the provision of ecosystem services by local population of dung beetles, highlighting again the fact that ecological processes have to be studied in an holistic manner (Nichols et al., 2008). This case study provides evidence of the importance of considering interactions between wild and farmed animals and the need for collaboration, in this case between beetle ecologists and animal scientists.

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More recently there has been a marked increase of holistic and interdisciplinary research addressing biomass, nutrient and carbon recycling in soil-crop-animal systems at various scales, and their ecological, agronomic, environmental and economic impacts (Vayssières et al., 2009). Accordingly, animal science has adopted more holistic models, developing multi-dimensional impact assessment with metrics and methods derived from other disciplines including ecology, biogeochemistry, sociology and economics. Meanwhile, animal ecology and animal science have increasingly stressed the importance of considering the role of humans in their research, i.e. addressing sustainability and functioning of social ecological systems, a concept derived from new institutional economics (Ostrom, 2009).

In the terrestrial production context, research is now addressing animal effects on nutrient and carbon cycles in diverse agroecosystems. There are studies of the influence of specific management factors (e.g. ruminant grazing intensity) on nutrient recycling pathways, soil compaction and carbon stocks (de Faccio et al., 2010). In systems research on carbon balance, the use of pasture as the main source of feed was shown to be a non-negligible carbon sink under both semi-arid (e.g. Sahel) and humid environments (e.g. Amazonia) Some authors have addressed the importance of developing an ecosystem approach to better assess the real contribution of livestock (Assouma et al., 2017; Stahl et al., 2016) . Enteritic methane from ruminants, emission from manure deposition, emission by termites, and savannah fire have been accounted for as well as carbon sink function of soils and perennial ligneous vegetation in an annual cycle. The carbon balance was ultimately found to be slightly negative, i.e. emissions due to livestock activities are compensated by carbon sequestration in soil and trees at landscape level. Thus, when environmental impact assessments integrate all the compartments of the agro-ecosystem (biomass, soil, plants and animals in relation to the atmosphere), and both emission and sequestration, the results contrast with partial analysis that classed African pastoral ecosystems as high GHG contributors. Finally, recent work showed that the use of various metrics would slightly change the evaluated impact of ruminant's methane emission on global warming (Allen et al., 2018). These results come from another community and they also stress the need to include other disciplines i.e. climate and atmospheric science for evaluating environmental impact of animals GHG emissions on global warming.

In the aquatic production context, waste accounts for up to 75% of the nutrient discharge for Nitrogen and Phosphorus in conventional salmon and shrimp aquaculture. Therefore, biological and chemical filters have been developed to partially remove dissolved nutrients from waste. These various pathways of nutrient bioremediation have been increasingly embedded in diverse

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Integrated Multitrophic Aquaculture systems (IMTA), which are mostly adapted for land-based intensive aquaculture (fish, shrimp in ponds) (Troell et al., 2003). In such systems the addition of extractive organisms like seaweeds (macroalgae, culture of microalgae) (Milhazes-Cunha et al., 2017) or bivalves (shellfish) as biofilters to recycle wastewater, and reduce discharge and particulate and dissolved nutrient concentration was found promising (from 35 to 100% nitrogen removal). In open culture systems (fish cages) the setting up of IMTA is more complex and results are less clear. Accordingly, research is still on-going.

Such research needs continuity on the long term and design of new models (Lamprianidou et al., 2015). In particular, study of factors influencing reduction efficiency (seaweed species, capacity to uptake beyond physiological requirements, characteristics of production system and the environment, etc.) requires an interdisciplinary research approach (Troell et al., 2003). Similarly, increasing biomass recycling in terrestrial systems, or increasing carbon sequestration by soils and crops, is a long run and complex effort that argues for more global scientific collaboration.

Conclusions

This review highlights seven basic concepts that require cross-fertilization to respond to important societal challenges such as ecosystem resilience and farming sustainability. At the interface of animal ecology and animal production science, our article promotes an effective application of the agroecology concept to animals and the use of functional diversity to increase resilience in both wild and farmed systems. It also promotes the use of novel monitoring technologies to quantify animal welfare and factors affecting fitness. These measures are needed to evaluate viability risk, predict and potentially increase animal adaptability, and improve the management of wild and farmed systems, thereby responding to an increasing demand of Society for the development of a sustainable management of systems.

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This ambition requires interdisciplinary research: we need a new era of translational research before application of results. Animal ecology has particular strengths in the study of interactions between species, biodiversity, adaptive evolution in natural populations and ecosystem resilience but in-situ experiments considering broader system impacts are relatively rare. Animal production science has disciplinary strengths in selective breeding, production chains, economics and management. It also has a heritage of methods for combining these at farm- or regional systems levels. Therefore, the two disciplines have many complementary skills but a stronger synergy is lacking due to old habits, i.e. perceived differences in viewpoints on the goal of each discipline, different knowledge and scientific vocabulary (e.g. in quantitative genetics), and different policy masters. Nevertheless, there are substantial advantages to be gained for animal-related research and for society's interaction with animals, from an enhanced cross-fertilization between disciplines.

Modelling approaches have the power to integrate disciplinary visions and knowledge and to translate them into actionable research. However, so far, research has not reached the level of operationality required to fully "pilot" animal systems and agroecosystems. Further, implementation often involves socio-economic factors and innovation processes, which hampers the adoption of any proposed changes. Integration of knowledge holders from the society in the process of research is also needed to tackle anticipated challenges at the interface between science, policy and society. This needs the development of knowledge integration techniques and enhanced collective expertise backed by participatory modelling and science. Such a process begins by breaking down the disciplinary boundaries and promoting cross-fertilization between the animal ecology and animal production science disciplines. This should be accompanied by scientific vision, programs and policy tools that reverse the fragmentation of animal research across other themes, and instead create critical mass for animal science. The analogy to the emergence of One Health seems highly relevant, it is time for One Animal Research Kinship, OneARK!!

Authors' contributions. All authors contributed to the writing of the present article.

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Acknowledgements. Those issues have been discussed by the authors as members of the thematic group '*Animals in their environment*' from AllEnvi, the French national alliance for research on the environment. The authors declare no conflict of interest.

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