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Review

Domestic Herbivores, the Crucial Trophic Level for Sustainable Agriculture: Avenues for Reconnecting Livestock to Cropping Systems

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Abstract: Domestic herbivores have been closely associated with the historical evolution and development of agriculture systems worldwide as a complementary system for providing milk, meat, wool, leather, and animal power. However, their major role was to enhance and maintain agricultural soil fertility through the recycling of nutrients. In turn, cereal production increased, enabling to feed a progressively increasing human population living in expanding urban areas. Further, digestion of organic matter through the rumen microbiome can also be viewed as enhancing the soil microbiome activity. In particular, when animal droppings are deposited directly in grazing areas or applied to fields as manure, the mineralization–immobilization turnover determines the availability of nitrogen, phosphorus, potassium, and other nutrients in the plant rhizosphere. Recently, this close coupling between livestock production and cereal cropping systems has been disrupted as a consequence of the tremendous use of industrial mineral fertilizers. The intensification of production within these separate and disconnected systems has resulted in huge emissions of nitrogen (N) to the environment and a dramatic deterioration in the quality of soil, air, and ground- and surface water. Consequently, to reduce drastically the dependency of modern and intensified agriculture on the massive use of N and phosphorus (P) fertilizers, we argue that a close reconnection at the local scale, of herbivore livestock production systems with cereal-based cropping systems, would help farmers to maintain and recover the fertility of their soils. This would result in more diverse agricultural landscapes including, besides cereals, grasslands as well as forage and grain crops with a higher proportion of legume species. We developed two examples showing such a beneficial reconnection through (i) an agro-ecological scenario with profound agricultural structural changes on a European scale, and (ii) typical Brazilian integrated crop–livestock systems (ICLS). On the whole, despite domestic herbivores emit methane (CH_4), an important greenhouse gas, they participate to nutrient recycling, which can be viewed as a solution to maintaining long-term soil fertility in agro-ecosystems; at a moderate stocking density, ecosystem services provided by ruminants would be greater than the adverse effect of greenhouse gas (GHG).

Keywords: C, N, P biogeochemical cycles; crop–livestock system; grasslands; grazing; herbivores; soil fertility

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1. Introduction

World agriculture and human food systems are at the junction of two major United Nation Sustainable Development Goals [1] as they provide resources for human subsistence and welfare, but are also highly implicated in the perturbation of the major biogeochemical cycles of carbon (C), nitrogen (N), phosphorus (P), macro-nutrients such as potassium (K), calcium (Ca), magnesium (Mg), etc., and also micro- and oligo-elements necessary for plant growth and development. These cycles are strongly coupled with water and altogether associated with loss in biodiversity, environmental degradation, and climate change [2,3]. Reconciling the challenge of safe food production for an increasing human population, up to 9.5 billion in 2050, with the challenge of reducing drastically the adverse environmental impacts requires not only the redesign of agricultural production systems in a more sustainable way, but also the promotion of a transition of the whole food supply and demand system, including human diet and waste management [4]. Several studies [5–9] explored various scenarios of possible future global agricultural systems by changing cropping and livestock production systems and human diets toward a healthy plant-sourced–animal-sourced food equilibrium and concluded that a vast range of options exists for feeding the world, without expanding the global agricultural area. These studies demonstrated that new scenarios must be explored at the level of whole-agriculture systems, including cropping and livestock systems and their interactions, and must be extended to a scale large enough to avoid non-generalizable conclusions. For example, some overly restrictive studies analyzing the conversion from conventional to organic farming systems led to the conclusion of severe problems in food security, but they did not account for the necessary related change in human diet with less animal-sourced protein and the corresponding reduction in livestock production [10,11]. There is consensus that global transitioning towards a more plant-based diet is essential for maintaining planetary boundaries [12]. Nevertheless, some studies concluded on the need to reduce drastically herbivore livestock production because of their methane (CH_4) emissions; this is contradictory with greenhouse gas emissions resulting from ovo-lacto vegetarian diets (which require livestock production) which are ca. 35% lower than most current omnivore diets [12]. Therefore, it is important to have a more global approach considering the essential role that domestic herbivores could play in agriculture sustainability through their ability to recycle and transfer mineral nutrients across agro-ecosystems to maintain long-term soil fertility [13].

In business-as-usual scenarios, a large increase in food production by ca. 70% would be necessary to sustain the growth of the human population from 8 billion in 2022 to the expected 9.5 billion in 2050, as mentioned above [14,15]. Such a significant increase in agricultural production cannot be achieved by merely increasing cultivated land area because the corresponding deforestation would lead to high CO_2 emissions into the atmosphere and would accelerate dramatically the biodiversity crisis [16]. In particular, the reduction of available water resources in arid and semi-arid countries around the world rules out the expansion of cultivated areas in these regions. To feed an increasing world population with the current method of farming, once food losses and food wastes have been reduced, the only solution would be to continue to increase crop production per unit of cultivated land area using appropriate technologies. There are two ways to achieve such an increase in crop yield at global scale: (i) increasing the maximum yielding capacity (Ymax) of crops through crop genetic improvement and increasing the use of inputs (i.e., fertilizer, agrochemicals, water) necessary to reach this attainable Ymax; and/or (ii) reducing the yield gap that exists between the actual yielding capacity of low-productivity farming systems and Ymax in some regions. The first way seems very limited since the Ymax progression for the most important crop species such as wheat and rice are already plateauing and will become more and more limited by the ongoing climate change [17,18]. Moreover, the use of necessary inputs must be reduced drastically in order to limit the detrimental impacts of intensive/low-diversity agriculture on the environment. The second way, the yield gap resorption, cannot be achieved by simply following the same approach of the intensification of agriculture based on the increased use of external inputs such as fossil energy and N and P fertilizers without significantly amplifying the environmental impacts. In addition, in most countries around the world, from south to north, the majority of smallholder farmers is in an "intensification trap" because their socioeconomic and political conditions do not allow them to access investments that are necessary for reducing their yield gap [19].

Therefore, approaches to this global crisis through concepts that focused on a single domain (agriculture, environment, food supply and demand, human health, etc.) or a single subject analysis (climate change, water pollution, soil conservation, biodiversity, etc.), are too restrictive and superficial because the multiple trade-offs occurring among the different agro-system components are not properly taken into account. Today, agricultural systems must be viewed as components of more complex anthropogenic systems under the concept of "one health" [20,21] that fosters a holistic understanding of the multifunctionality of agriculture; i.e., not only as technical processes to produce food for society, but also as a way to provide a wide range of ecosystem services that will maintain natural resources and the environment and facilitate human welfare [22,23]. Farming and feeding systems are both interconnected at the nexus of food production–conservation of natural resources in the context of climate change [24].

Through this global approach, the analysis of the role and importance of domestic herbivores in farming and feeding systems must consider the numerous trade-offs between the positive aspects and negative impacts of livestock grazing systems. As pointed out at a global scale, intensive ruminant livestock systems in industrialized countries are responsible for high emissions of greenhouse gasses to the atmosphere [25], water nitrogen pollution (nitrate, [26]), and biodiversity erosion [27]. However, at the same time, these systems provide recycling of mineral nutrients that maintain soil fertility in cropping systems [28]. Intensive livestock production can be a source of diet-related diseases in developed countries when there is an excess of animal-sourced proteins in the human diet [29,30], but animal products are also a source of indispensable protein, vitamin B_{12}, and micronutrients (iron and selenium) in developing countries [31]. It is thus important to have a balanced estimation of the role of livestock production both in agricultural production systems and in human food supply, and demand chains in order to overcome these contradictions that create controversy when studies focus only on a specific problem disconnected from the whole system.

There is growing recognition that improving the environmental performance of livestock systems and establishing sustainable levels of animal-sourced food consumption are essential for the sustainability of the global food system [32]. From this point of view, it is fundamental to consider livestock production systems as composed of two components with each one having very different and fundamental functions: (i) domestic herbivores, and particularly ruminants, with the capacity to consume herbaceous vegetation and subsequently accelerate the recycling of mineral nutrients to maintain soil fertility and thereby also agricultural food production without being in direct competition with human food; and (ii) monogastric animals (pigs, poultry) being fed with grains (cereals and grain legumes) in direct competition with the human vegetal food supply. The conversion efficiency of plant proteins into animal proteins by monogastrics, although higher than that of ruminants, remains relatively low, about 6–7 kg of plant protein being required to produce 1 kg of animal protein. Consequently, monogastrics consume a much greater quantity of human-edible protein than they produce [33] while ruminants worldwide, on average, produce 40% more human-edible protein than they consume [34]. It would be also interesting to note that in Asia, the agriculture heritage of the rice–fish farming represents also a way for agriculture sustainability [35], but these systems are out of the scope of this review.

The objectives of the present opinion paper are to analyze the ecological roles of domestic herbivore livestock systems from a historical perspective and in the future adaptation of different forms of agriculture around the world; and to assess their contribution not only for feeding the human population and providing goods for the economy of societies, but also for fostering resilience in agro-ecosystems [36]. This resilience is achieved through a better coupling of the main biogeochemical cycles (C, N, P, micro- and oligo-elements, and water), the renewal, maintenance, and enhancement of soil fertility while minimizing the use of external fertilizers, and the capacity to sustain associated cropping systems to increase their productivity while reducing the use of external inputs [28]. Such a goal necessitates investigation of the continuum between plants, soils, herbivores, agriculture systems, and human diet to take into account the multiple trade-offs that exist among these different aspects in a more comprehensive way [37]. This integrated approach is necessary to counter the relatively hasty and incomplete analysis that has concluded on the need to exclude herbivore products from the human diet under the argument that ruminants emit CH_4 and contribute to the greenhouse effect. Further, this review aims to show that these CH_4 emissions are in fact part of a natural biogenic carbon cycle and thus must be considered as the "ecological way" of upcycling cellulose and converting it into human-edible products. We have to deal with biogenic CH_4 so as to benefit from all the other ecosystem services provided by integrating domestic herbivore livestock, grassland ecosystems, and forage production within sustainable agro-ecosystems [28].

2. Where Does Soil Fertility to Support Agricultural Production Come From?

An analysis of the sustainability of agricultural production systems cannot be made without a clear understanding of how soil fertility, i.e., the capacity of soils to provide available mineral nutrients to plants, is achieved and maintained in long-term trends in natural ecosystems. Thereafter, it is possible to analyze how soil fertility was enhanced by agricultural practices to support the increasing uptake and exportation of mineral elements as the productivity of the agro-system grew.

In an unmanaged natural ecosystem dominated by perennial herbaceous or woody species, the formation of new soil from the bedrock mobilizes P and K and other micro- and oligo-elements sequestered in primary minerals, creating a reservoir of plant-available nutrients in soil. These geochemical reactions are grouped under the concept of "weathering", which corresponds to the long-term pedogenesis processes [38–41]. The annual rate of input for each mineral element depends on local geological conditions (nature of the bedrock), long-term climate parameters, and vegetation type [42–44]. The other sources or inputs of P, K, and other minerals are (i) flooding, (ii) alluvial deposition, and/or (iii) atmospheric deposition of dissolved elements in rainfall or as (iv) dry eolian deposition [45,46]. However, in some places, wind erosion can cause nutrient losses and hence land degradation [47,48]. For N, the main input was achieved by non-symbiotic N_2 fixation of some soil microbes [49,50], and also by the contribution of certain N_2-fixing plant species [51,52], with the other sources of N being atmospheric deposition associated with rainfalls. All these inputs contributed toward enriching and maintaining N and minerals in ionic forms in soil solutions according to an equilibrium with soil colloids that determines their availability for root absorption and plant uptake. N, P, K, Ca, and Mg, among others, are assimilated for plant growth and CO_2 capture through photosynthesis and subsequently accumulate as a mineralomass within the primary production of ecosystems. In these natural terrestrial ecosystems, large herbivores species co-evolved with vegetation through their grazing and foraging activity, leading to plant community perturbations associated to defoliation; yet their dejection led to recycling of most of the nutrients of the mineralomass they have ingested.

Therefore, depending on the vegetation type, e.g., herbaceous or woody species, and its interaction with herbivores (grazing behavior), this mineralomass is subjected to two distinct ways of cycling, as presented in Figure 1:

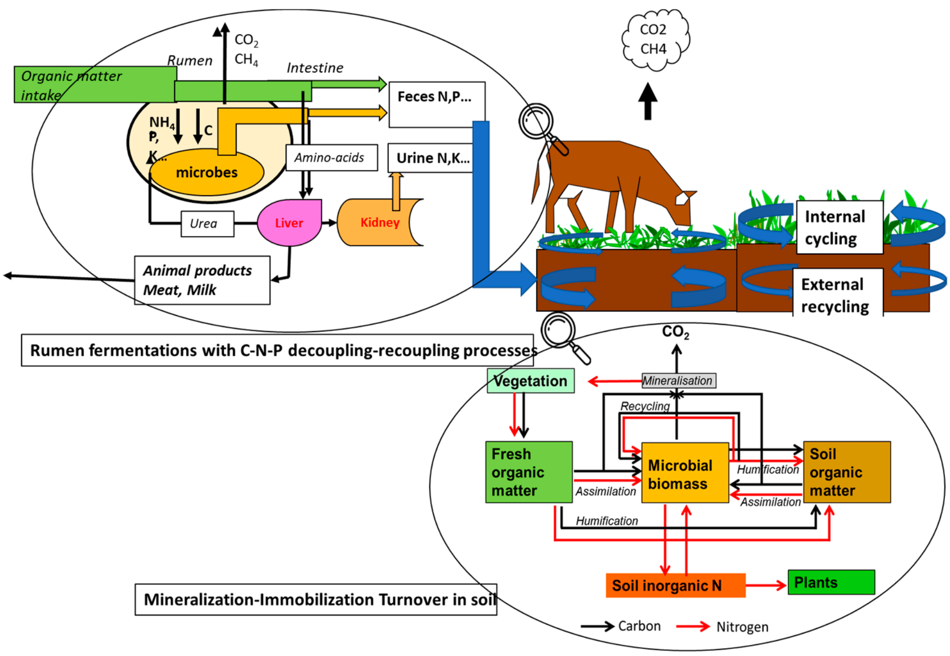

Figure 1. Schematic representation of the role of herbivores in "boosting" N, P, K recycling through ingestion, digestion, and excretion of organic matter, complementary to the mineralization–immobilization turnover (MIT) in the soil.

(i) An internal cycling in the plant corresponding to translocation of some organic mineral molecules with N, P, K, sulfur (S), and some others involved in plant metabolism from active plant organs (leaves and fine roots) during senescence to perennial storage organs (tap roots, trunks, rhizomes), representing a nutrient reserve for plant regrowth after defoliation and winter or drought damage. Hence, before returning to soil as litter, leaves have recycled at least two thirds of their N and P content [53,54]. Thus, the C/N ratio of mature green leaves of grass species is approximately 12–17, and this ratio increases to 24–33 for leaf litter [55,56]. In this way, perennial vegetation dominates natural plant communities because this internal recycling is very conservative.

(ii) An external recycling through leaf and root litter deposition in soil with the mineralization–immobilization turnover (MIT) of N, P, and other minerals in the rhizosphere, leading to a progressive decoupling of C from N and P and a smoothed restitution of mineral forms of these elements to soil solutions to be either absorbed by plants or reincorporated in new microbe bodies [57,58].

These two recycling pathways allow the ecosystem to be very conservative for mineral nutrient fluxes and thus for soil fertility. In such a perennial system, outputs are only limited to (i) lixiviation and losses of the more mobile minerals to the hydrosphere, mainly for N and S, to a lesser extent for K, Ca, Mg, and to a very small extent for P; (ii) atmospheric losses of N due to denitrification and ammonia volatilization; and (iii) soil particulate erosion. Hence, in many conditions, the annual input–output balance is slightly positive [41], leading to a progressive accumulation of mineralomass in soil–vegetation systems over the long term until a dynamic equilibrium is reached between (i) coupling of C–N–P and other minerals through plant autotrophy (photosynthesis and mineral absorption–assimilation) in organic matter synthesis and (ii) decoupling of C–N–P by the soil microbiome and living organism heterotrophy [59]. As the decoupling process (mineralization of soil organic matter) is mainly localized in the rhizosphere where soil microbes are fed by organic compounds exudated from plant roots [60,61], the available forms of N (NO_3^- and NH_4^+), P (PO_4H^- and $PO_4H_2^-$), and some other minerals are rapidly recoupled with C, either by microbe populations (bacteria and fungi) for their own biomass synthesis or by plant roots to be absorbed and assimilated. Thus, according to this rapid MIT leading to decoupling–recoupling of C–N–P, the residence time of available forms of nutrients in the soil solution is relatively low. Consequently, the probability of the loss of these soluble elements through lixiviation remains very low, as does the risk for atmospheric losses, as long as the concentration of NO_3^- and NH_4^+ in the soil solution remains low, e.g., without any mineral fertilizers generally applied to intensively cropped soils.

When herbivores consume a relatively significant proportion of the aboveground biomass accumulated in vegetation as green leaves and stems, they reduce the internal recycling of plant nutrients; however, as presented in Figure 1, the digestion of ingested plant tissues in the rumen accelerates the C–N–P decoupling process as most of the mineralomass ingested by animals is transferred to soil via feces deposition and urine patches with much lower C/N ratios. Ruminants excrete as much as 70–95% of the N they consume [13,62].

As a result, a new equilibrium can be achieved, depending on the herbivore stocking density, with a more rapid N, P, K recycling turnover rate. In this respect, herbivores can be viewed as playing a catalytic role in enhancing soil fertility in natural ecosystems. They mediate net nutrient recycling directly by affecting net primary productivity and altering the spatial distribution of plant biomass as well as the chemical composition of organic matter that enters the MIT process. Therefore, the herbivore zoogeochemical effects on ecosystem functioning are pivotal [63]. The emission of CH_4 due to the anaerobic digestion of cellulose in the rumen can be considered as the "ecosystem price" to pay in a natural biogenic cycle in order to obtain this ecosystem service of increasing soil fertility. Thus, the rumen can be considered as a "digestor" of organic matter for decoupling–recoupling C–N–P in parallel with the soil MIT: these two sub-systems of decoupling–recoupling lead to a more efficient N and mineral recycling at the scale of the whole agriculture system, and the herbivores are the main trophic connection level to these processes. However, because of this accelerated MIT, the risk for N losses within the environment increases gradually with rising stocking density and with the proportion of the primary production ingested by grazing animals [64]. As a consequence, the C–N–P decoupling capacity of domestic herbivores must be adjusted to the C–N–P recoupling capacity of the ecosystem (including carnivores in natural ecosystems). Thus, for a given local soil–climate condition, there is a local stocking density threshold [64] above which, in agro-ecosystems, the intensification of agricultural production would produce an excess of de-coupling and an excess of circulating N active compounds, leading to environmental losses and detrimental impacts. By contrast, an excessively low herbivore stocking density at local scale does not allow for a sufficient rate of C–N–P decoupling to match the C–N–P recoupling demand from vegetation, and the net primary production capacity is thus impaired.

3. Historical Analysis of the Role of Domestic Herbivores in Renewing Soil Fertility in Agricultural Systems

The emergence and development of agriculture in the neolithic period along the alluvial valleys of the Euphrates and Nile rivers was made possible by the continual renewal of soil fertility through regular loam deposition during annual floodings, providing mineral resources for grain production [65,66]. The extension of agriculture in other regions of the world, in which this very localized flooding fertilization was not possible, was achieved by adoption of the slash-and-burn cropping system by clearing and burning areas of vegetation (forest, savannas, or steppes) to replenish the nutrient availability in soils and to produce food [67,68]. These systems persist to this day in tropical forests where millions of people still rely on this type of agriculture to survive [69]. The soil fertility in these systems was maintained through short-term cultivation, from 1 to 3 years only, because of the rapid decline in soil fertility, followed by a long fallow period (several decades) that enabled a slow regeneration of natural vegetation and soil nutrient availability. As demonstrated by Mazoyer and Roudart [65], the sustainability of these systems collapsed rapidly when population density increased above a given threshold. This occurred because of the necessary acceleration of cropping–fallow rotations and, thus, the limited replenishment of soil nutrients that obliged human populations to expand land clearing areas, leading to deforestation and a substantial decline in soil fertility and food production capacities. This explains the significant deforestation in many regions of the world from 7000 to 3000 B.C. when the world population grew from 5 to 50 million [65]. In this way, forests regressed in more densely populated areas and were replaced by patchworks of herbaceous (savannas and steppes) and residual woody vegetation.

In these new agro-systems, the use of a swing plough enabled the development of biennial cropping–fallowing areas with the transfer of soil nutrients by domestic herbivores grazing in herbaceous areas and in parts of the residual forest areas; these animals were then kept in fallow areas overnight for excretion [65]. These systems developed in Mediterranean and temperate regions from 2000 B.C. until about 1000 A.D. They were based on interactions between three area components: (i) *ager,* corresponding to cropping–fallowing area cultivated by individual farmers; (ii) *saltus,* corresponding to a common pasture area with neighbors; and (iii) *silva,* corresponding to surrounding forest area providing energy, wood, and other resources for human populations (Figure 2).

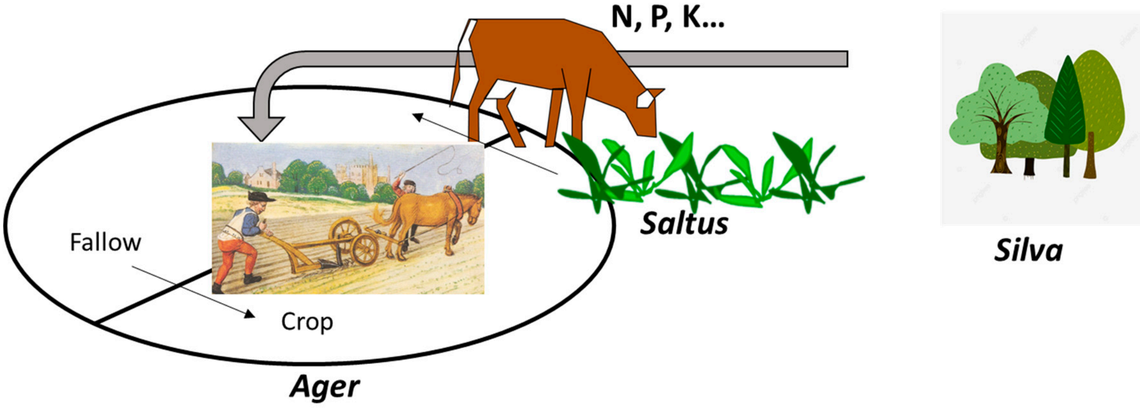

Figure 2. Representation of ancient agro-system based on biennial fallow–crop rotation in a cultivated area (Ager) with herbivores fed by grazing in common pasture areas (Saltus) and complementary forage resources from surrounding forests (Silva), providing mineral nutrient transfers for the renewal of soil fertility.

The role of domestic herbivores in the transfer of soil nutrients enabled an increase in soil fertility in *ager*, which led to a doubling of grain production per land area from ca. 0.5 to 1 t $a^{-1}year^{-1}$. Coupled with the increase in human labor productivity due to the accompanying harnessed cultivation, this progress in yield allowed a single-family farm to pass from strict autonomy to surplus production for feeding non-rural populations in developing urban areas [65].

According to the analysis by Mazoyer and Roudart [65], the productivity of human labor in these agro-systems, i.e., their capacity to produce food for non-rural human populations, was directly linked to their herbivore stocking density. Hence, for a family farm of five persons corresponding to a labor capacity of one farmer and family workers, the land area used was on average 6–7 ha of *ager*, 6–7 ha of *saltus*, and 1 ha of *silva* with about three livestock units that corresponded to the capacity to feed approximately 30 habitants per square kilometer, a common population density at that time. In less favorable climates (drought or more severe winter), this threshold was only 15–20 habitants/km^2 [65,70]. These agro-systems faced new limitations under temperate climates because the soil fertility transfer from *saltus* to *ager* remained relatively limited as the stocking density in *saltus* should have been adjusted to the lower level of herbage production during winter. Thus, a large *saltus* area was necessary to fertilize a relatively restricted *ager* surface. Moreover, the transfer of soil fertility from *saltus* to *ager* through herbivore droppings with this system remained fairly limited because only the droppings from the night were transferred. As a consequence, this agro-system had difficulties in providing food for an increasing non-rural population, thus leading to the severe food crisis that occurred in Europe during the 11th–14th centuries [65,71].

Progressive use of new tools for harvesting, tedding, transport, and storage of hay enabled the valorization of excess herbage produced during favorable seasons in *saltus* for feeding livestock in barns during winter; this, in turn, increased the quantity of animal droppings used to produce manure with indoor litters and therefore also increased the transfer of mineral nutrients for the fertilization of *ager* (see Figure 3). A more efficient incorporation in the soil of these high volumes of manure was also possible with the generalization of the use of the moldboard plow and, thus, a more sophisticated soil tillage. Depending on the region, this system evolved more or less rapidly to a triennial rotation: fallow–winter cereal–spring cereal. Hence, these advances led to an increase in cereal yield and in human labor efficiency, resulting in a dramatic increase in the capacity of agro-systems to feed non-rural human populations. Consequently, the threshold population density increased to 55 (in low-productivity soil and climate) and even 80 habitants.km^{-2} (in high-productivity soil and climate) during the late Middle Ages in Europe [65].

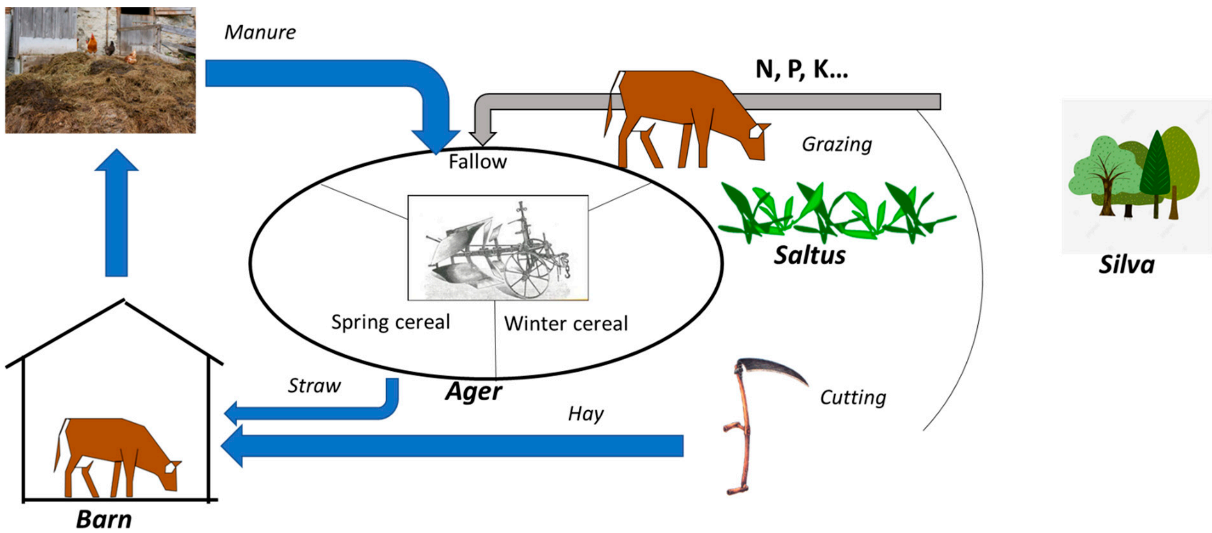

Figure 3. Representation of agro-system during the late Middle Ages in Europe based on triennial rotation with identification of fluxes of mineral nutrients through herbivores.

During the 16th–17th centuries, the First Agricultural Revolution in Europe was based on the suppression of fallow periods and the introduction of forage crops and artificial meadows with legume species (clover species, sainfoin, or alfalfa) within more diverse rotations in the *ager*, following the so-called Norfolk rotation system in the British Isles [72]. This made it possible to have a much higher increase in food production through more integrated livestock–cropping systems. Finally, productivity of cereal cropping increased rapidly from a maximum of 1 t.ha^{-1} to approximately 2 t.ha^{-1} of grain, mainly because of the high contribution of N_2 fixation by legume forage species [65]. Consequently, a large part of *saltus* was integrated within *ager*, changing from a common status to a private land status (see [73]), and thereby facilitating the adoption of improved agriculture practices.

This system expanded with different regional forms in West and Central Europe and brought about a population growth from 110 million to 300 million between 1750 and 1900 [65]. Nevertheless, these agro-systems remained limited by P and K deficiencies in soil.

This historical summary shows how the progressive integration of stocking herbivores in agricultural production systems helped renew soil fertility in order to increase food production and feed the growing human population. Thus, domestic herbivores were not only used to provide protein-rich food to complement the human diet that was based on cereal, but they contributed greatly to cereal production to feed the increasing human population throughout prehistoric and historic periods, despite the fact that P and K were mined and often exported to foreign markets [68,74].

In the early 20th century, this crop–livestock integration was gradually questioned in the Second Agricultural Revolution, initiated by the Haber–Bosch process industrialized in 1913, making it possible to synthesize ammonia directly from atmospheric N_2 together with the mining of P and K for the fertilizer industry. The generalization of the recourse to industrial fertilizers was also associated with the swift motorization and mechanization that occurred after the Second World War in North America and Europe and its rapid spread in many parts of the world. In the new agricultural system, the role of domestic herbivores for soil fertility renewal was progressively abandoned, and due to the gradual introduction of food exchange at a global level, farms and regions progressively specialized mainly in cereal production systems (or vineyards, orchards, and vegetable systems) in some favorable regions, or mainly in natural grassland-based meat and milk production systems in less favorable areas [65]. The consequences of this change were livestock decoupled from crops and nutrients not fluxing in circularity.

4. The Current Crisis in Industrialized Agriculture and the Need for Recoupling of Livestock and Crop Production

4.1. Ecosystem Services of Grasslands and Forage/Herbivores Associated with Arable Cropping Systems

Most of the negative environmental impacts of modern intensified agricultural systems are the consequence of the excessive use of energy and chemical inputs to achieve high levels of food production. As is widely reported in several publications [75–77], the causes of these environmental impacts are mainly linked to the simplification and homogeneity of land use systems at both the spatial and temporal scales. Hence, introduction of temporary grasslands and/or annual fodder crops as forage for feeding domestic herbivores is a source of diversification of cropping systems and a way to reduce some of the negative impacts of intensified arable cropping systems [78]. The most important effect is linked to the use of legume-rich meadows and forage species leading to a significant decrease in the use of external N fertilizers [79]. There is therefore a trade-off between the emission of CH_4 by herbivores and the reduction in greenhouse gas emissions linked to N fertilizer production, transport, and field application. In addition to this main effect, other ecosystem services must be taken into account when evaluating the role of herbivores in arable cropping systems: (i) soil C sequestration, nutrient cycling, and soil quality improvement [80]; (ii) weed control and reduction of herbicide use [81,82]; (iii) disruption of pathogen contamination at the temporal and spatial scale and reduction of fungicides and insecticides [83]; (iv) better control of water infiltration, evapotranspiration, run-off, and soil erosion [84]; (v) increase in system stability for environmental variability [85].

It is important to note here that all these ecosystem services are linked together and that most of them are the consequence of the remarkable capacity of domestic herbivores to convert non-edible biomass produced from grasslands and crop residues into human edible food, and thereby to not compete directly with human food consumption, in contrast to feed supplies for monogastric livestock [78]. A whole-system approach is therefore necessary for evaluating the role of herbivore livestock and for optimizing the trade-off between CH_4 biogenic emissions and their role in providing a large variety of ecosystem services. Grasslands and forage crops are important components of herbivore livestock systems, so that the animal itself cannot be separated from its feeding system, differently from monogastric livestock.

The diversity of grasslands contributes to diverse ecosystem services that are essential for humans [86]. Biodiversity is positively correlated with environmental indicators such as soil quality and prevention of erosion. Even temporary grasslands with low numbers of species, but with favorable agricultural management (e.g., moderate stocking density), can contribute toward reducing the risk of erosion, since vegetation cover is a main requirement for avoiding erosion and dense swards are generally the outcome of sound grazing management [87,88].

Moderate stocking densities also enable dense and taller swards to be more competitive with weeds [89]. They reported a lower number of weed species, a lower density of emerged weed seedlings, and a smaller weed seed bank when decreasing the stocking density in winter-grazed cover crops. Similar results were reported concerning a reduced size of the weed seed bank in integrated crop–livestock systems (ICLSs) compared to mono-cropping systems [90]. As a result, more diverse cropping systems, for example, using rotation or introduction of forage species or perennial species, may require smaller amounts of synthetic agrichemical inputs [91].

The need for a better understanding of how different grassland types in association with cropping systems affect surface/deep hydrology and water quality is gaining importance in the context of climate change. For instance, some authors have reported that the soil moisture content in deep soil layers (>30 cm) in ICLSs is higher than in exclusive grain production areas [92]. This result can be explained by the greater root production due to forage and grazing. Thus, during drought periods, the transfer of water from deeper soil layers to the dry surface may occur [93]. This is particularly important under future climate change scenarios, which project changes in the seasonal distribution of rainfall, with a greater frequency of summer droughts. Therefore, grassland when used as forage source for feeding domestic herbivores in cropping systems may influence the provision of relevant ecosystem services, especially those that do not have a clear market value such as water regulation [94].

4.2. Specialized Versus Integrated Crop–Livestock Farming Systems in Europe

The transition from the traditional mixed crop–livestock systems to the industrial fertilizer-based arable cropping systems is very well documented. In the case of France, agricultural statistics are available from the middle of the 19th century [95,96]. As presented in Figure 4, over a period of only 30 years, the mode of fertilization on arable land shifted from a dominance of manure and symbiotic N_2 fixation to chemical fertilizer applications.

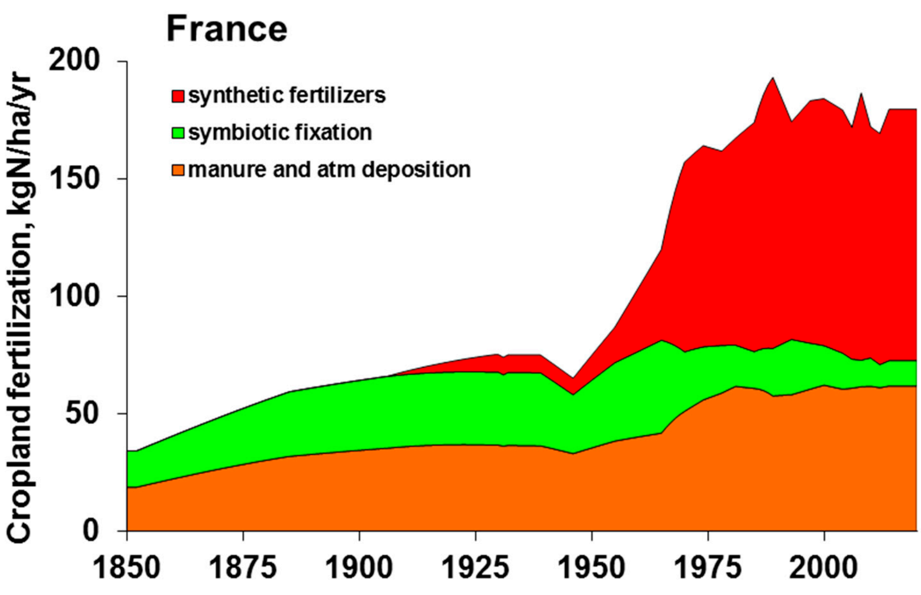

Figure 4. Average fertilization (total N input to cropland soils) in France from 1850 to 2020. The share of synthetic fertilizers became dominant from the early 1970s.

During the same period of agricultural "modernization," starting with the average diet of French people still based largely on cereals and on only about one third of animal proteins in the beginning of the 20th century, a rapid increase in meat and milk consumption occurred (Figure 5). Far from a spontaneous shift of consumers' preferences that the agro-food sector would have had to follow, the change was largely encouraged by proactive public policies often justified with the purpose of fighting against malnutrition diseases. However, many studies conclude that, today, the excess of animal product consumption is the cause of severe public health concerns [97].

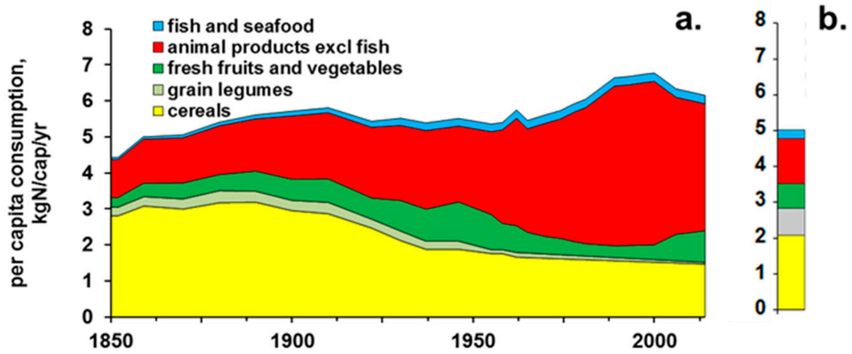

Figure 5. (**a**) Average human diet in terms of animal and vegetal proteins in France from 1850 to 2020. The share of animal proteins increased significantly from 1950. (**b**) Recommended healthy and fair diet as proposed by the EAT-Lancet Commission [97].

Together with the generalization of the use of industrial fertilizers and the increase in international trade of agriculture-based commodities, large regions have specialized their agriculture either into intensive livestock breeding systems largely dependent on feed import or into stockless cropping systems largely open to export and using no manure. The N flows across the territorial agro-food systems of 103 agricultural regions in Europe [98] were analyzed and classified according to a typology based on the degree of coupling between crop and livestock farming according to Table 1 [95]:

- **Intensive specialized livestock farming systems** are characterized by a high livestock density combined with a large share of imported feed to meet animal nutrition; in these systems, livestock farming is loosely connected to crop farming.
- **Specialized stockless cropping systems** refer to agro-food systems where crop production based on synthetic fertilizers is much more important in terms of material flow than livestock farming, which contributes only minimally to cropland fertilization.
- **Disconnected crop and livestock systems**, crop and livestock farming both co-exist but without strong connections in terms of manure used by cropland and local feed products in livestock feeding.
- **Mixed crop and livestock systems** have a high degree of coupling between crop and livestock farming activities because (i) manure provides a relatively high proportion of cropland soil fertilization, and (ii) local agricultural production provides a high share of animal nutrition. Within this category, **grass-based** and **fodder-based** systems can be distinguished according to the dominance of grass from permanent grassland or of fodder produced on arable land in livestock nutrition.

Furthermore, urban systems are those for which human food demand exceeds local food production (cropland production + livestock edible production), so that the import of food is a major structural component of the agro-food system.

The current distribution of these types of agro-food systems in Europe is shown in Figure 6 and Table 1 together with the decision tree on which the classification is based.

Interestingly, mixed crop–livestock systems (regrouping "Fodder-based mix crop and livestock" and "Grass-based mixed crop–livestock" in Table 1) still represent 29% of the total European agricultural land surface, produce 20% of vegetal-based food (either domestically consumed or exported) and 26% of animal-based food, while they are responsible for only 30% and 23% of N losses to either the atmosphere or the hydrosphere, respectively. Thus, these systems use proportionally fewer resources than disconnected systems, but they produce a similar relative share of food for human nutrition and generate relatively less pollution (Table 1a).

Table 1. Share of the different European agro-food system types to total food production, use of resources, and pollution generation (a) in the current (2014–2019) situation and (b) in an agro-ecological scenario at the 2050 horizon.

a. Current situation (2014–2019)						
Systems	**Intensive specialized Livestock**	**Specialized Stockless Cropping**	**Disconnected Crop and Livestock**	**Fodder-Based Mix Crop and Livestock**	**Grass-Based Mixed Crop–Livestock**	**Total**
Total area, Mha (%)	16.4 (9%)	48.9 (26%)	65.5 (35%)	38.0 (20%)	16.9 (9%)	185.8
Vegetal prod, GgN/yr (%)	564 (9%)	2511 (38%)	2165 (33%)	1062 (16%)	255 (4%)	6556
Animal food prod, GgN/yr (%)	667 (30%)	287 (13%)	713 (32%)	460 (21%)	113 (5%)	2240
Synth fertilizer use, GgN/yr (%)	1323 (11%)	4214 (34%)	4123 (34%)	1852 (15%)	756 (6%)	12,267
Losses to hydrosph, GgN/yr (%)	1381 (17%)	1892 (24%)	2894 (36%)	1361 (17%)	484 (6%)	8012
Losses to atmosph, GgN/yr (%)	670 (20%)	665 (19%)	1071 (31%)	749 (22%)	262 (8%)	3416
b. Agro-ecological scenario (2050)						
Systems	**Intensive specialized livestock**	**Specialized stockless cropping**	**Disconnected crop and livestock**	**Fodder-based mix crop and livestock**	**Grass-based mixed crop–livestock**	**Total**
Total area, Mha (%)	-	9.6 (5%)	7.4 (4%)	106.5 (57%)	62.4 (34%)	185.8
Vegetal food prod., GgN/yr (%)		53 (1%)	81 (2%)	3727 (77%)	997 (21%)	4858
Animal food prod, GgN/yr (%)	-	7 (1%)	17 (2%)	706 (63%)	387 (35%)	1117
Synth fertilizer use, GgN/yr (%)	-	-	-	-	-	-
Losses to hydrosph, GgN/yr (%)		105 (3%)	98 (3%)	1942 (56%)	1328 (38%)	3473
Losses to atmosph, GgN/yr (%)	-	16 (1%)	30 (2%)	1077 (62%)	614 (35%)	1735

Moreover, these systems, as currently operating, are not expressing all the potentialities that fully reconnected agro-systems would be able to exploit. Two situations of intensive specialized stockless cash crop farming systems in the French Paris Basin region have been studied [99,100]. In both situations, agricultural statistics from the past have made it possible to describe the traditional cropping system based on mixed crop–livestock farming as it was until about 1955 (Figure 7a) according to the GRAFS methodology [101,102]. This representation is in strong contrast to the current situation where the farming system has been simplified to the point of excluding livestock farming and is now fully dependent on external inputs of mineral fertilizers (Figure 7b). This change was accompanied by the emergence of severe water pollution problems linked to increased N leaching. In these regions, a few farms adopted organic farming practices based on long and diversified crop rotations, alternating fodder and grain legumes, cereals, and other crops. These practices, which enable independence from external sources of fertilization, were shown to considerably reduce N water contamination. However, the lack of a local outlet for alfalfa hay produced in these systems is a problem for the management and profitability of these organic farms. This solution could help in substituting the use of N-P external fertilizers for cropping systems by (i) a more important contribution of N_2 symbiotic fixation due to use of legume species as forage source; and (ii) the recycling of N-P in a more conservative way at the local level. The great advantage of such a substitution of mineral N by organic N is that in this last form, N is provided with a high degree of coupling with C, allowing a more direct use by soil microbes and then an activation of the MIT in soil (see Figure 1). By this way, a too high NO_3^- and NH_4^+ accumulation in soil is avoided, reducing then the risk for N leaching and N_2O emission as compared to the situation where N fertilizer is applied in mineral forms. So, it would be possible to maintain a sufficient overall agriculture productivity at the local scale with reduced environmental impact as compared to intensified and specialized systems. For achieving this recoupling between N and C, following the demonstration by Soussana and Lemaire in 2014, it is necessary to avoid a too high stocking density in grazed grasslands because of the excess of urine patches that do not allow rapid recoupling by MIT [64]. For a more intensified system with higher stocking density at the territory level, the use of manure from barns correctly enriched with straw to reach a more uniform C/N ratio of about 10–15, should be the best way for providing N, P, and other nutrients to crops without environment degradation [99,100].

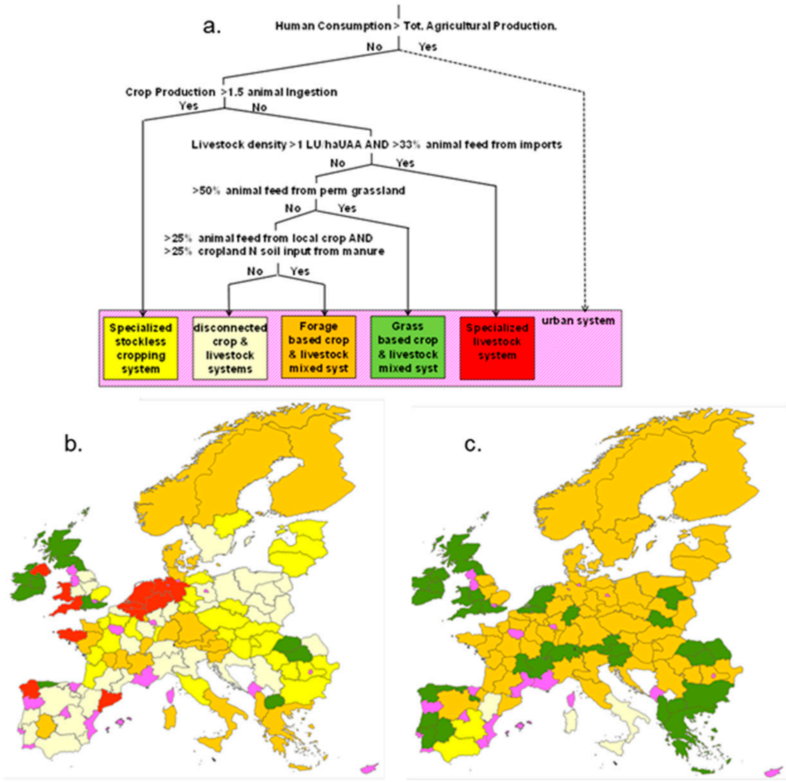

Figure 6. Typology of the agro-food system of 103 European agricultural regions. (**a**) Decision tree of the proposed typology. (**b**) Current situation. (**c**) An agro-ecological scenario for Europe at the 2050 horizon [95].

Livestock production systems have been stigmatized not only because of their CH_4 emission but also for their contribution to excess N and P into agro-ecosystems. However, these problems are only observed in situations with too high specialized livestock farms that go beyond the “environmental capacity threshold” for stocking density at the territory level that would excess the N-C and N-P recoupling capacity by vegetation [64]. So, the problem of eutrophication of the ecosystem in intensified agriculture regions needs a better integration of livestock systems with cropping system at the territory and landscape scale with a relatively homogeneous spatial repartition [76].

In an agro-ecological scenario established for Europe at the 2050 horizon [98], a full reconnection of crop and livestock farming was imposed, by sizing livestock numbers in each region on local feed resources (grass and fodder crops for ruminants, and cereals in excess of human needs, as well as waste from food industry transformation and consumption for monogastrics). The scenario also involves the generalization of diversified crop rotations rich in legume crops, as currently used in organic farming in the various regions of Europe, with no synthetic fertilizer application. Human diet was also adjusted according to the healthy and sustainable diet recommended by the EAT-Lancet Commission [97] (Figure 5b). In this scenario, by using all the potentialities of crop and livestock reconnection, symbiotic N_2 fixation by legumes is the main source of new N apart from recycling through livestock manure (Figure 6c). Such a scenario would clearly be able to feed the projected European population and even to export substantial amounts of animal and vegetal food outside Europe. It would result in much less environmental N loss (Table 1b).

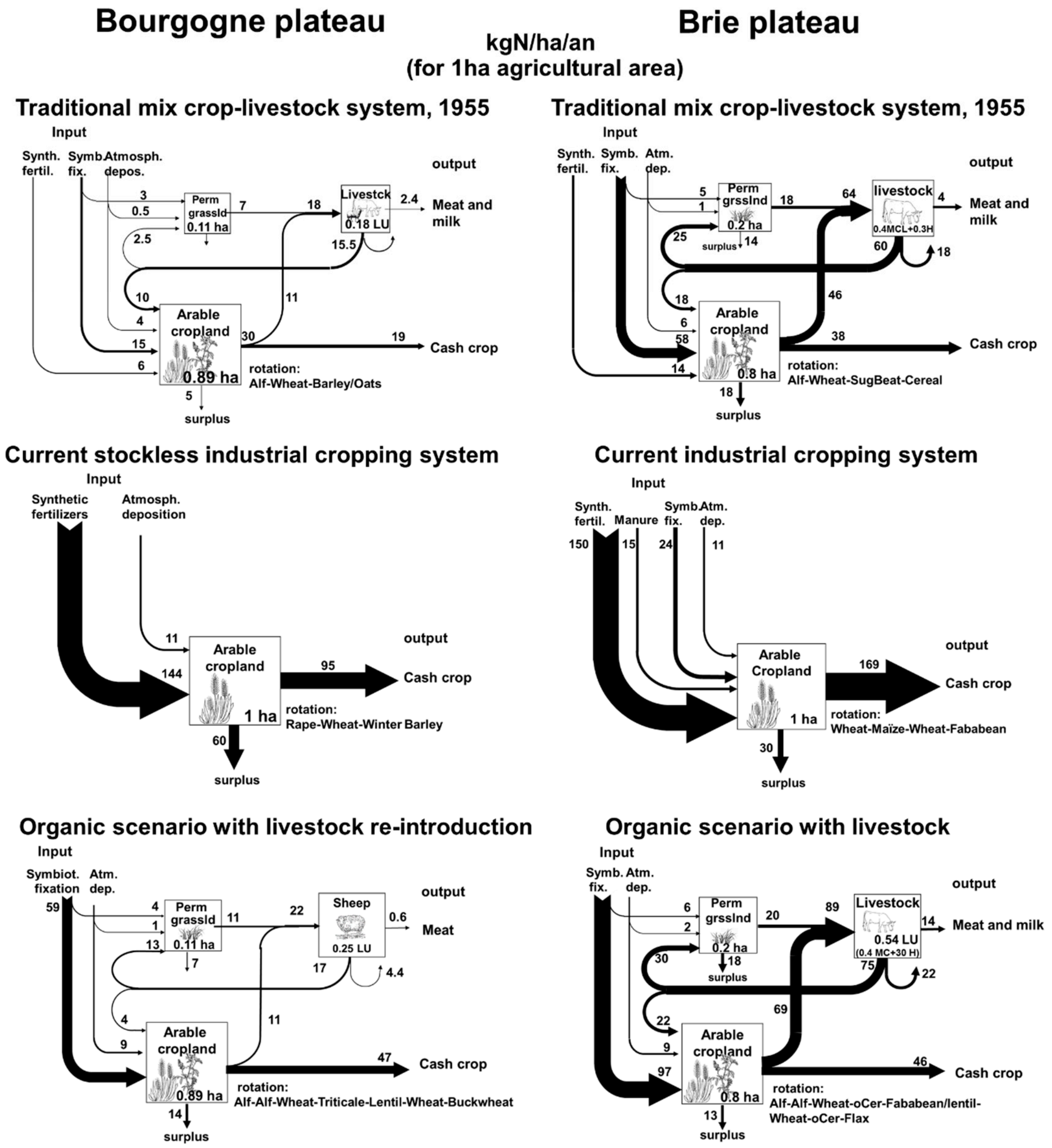

Figure 7. Nitrogen fluxes through the agro-system of two French regions (Plateau de Bourgogne and Brie). (**a**) Traditional mixed crop–livestock farming around 1950. (**b**) Specialized stockless cash crop farming typical of the 2010s. (**c**) Scenario of reintroduction of livestock with organic long crop rotation [99].

4.3. Some Examples of Soil Fertility Management in Integrated Crop–Livestock Systems in Brazil

An important concern with current agricultural systems is their reliance on and intensive use of chemical inputs. The first stage in a transition toward sustainable intensification can occur by increasing the efficiency of external input use to decrease production costs and environmental impacts [103–105]. This can be attained, for instance, by using technological innovations such as improved plant cultivars and animal genotypes [106]. However, this additive effect [107] is considered a fragile ecological organization process [108]. Efficiency is important, but it is not enough to accomplish long-term solutions.

Fostering biodiversity and stimulating interactions between different system components across multiple spatial and/or temporal scales, as reported in ICLSs [76], is part of holistic strategies to create long-term soil fertility [103]. The creation and enhancement of synergisms and emergent properties in ICLSs [108], due to the new complexity levels achieved, will contribute toward reducing, or replacing, external inputs. Such complex soil–plant–animal interactions necessitate a disruptive view of the nutrient demands of the system, where the classic pure crop-oriented models are no longer feasible. Therefore, a new approach to fertilization emerges, i.e., *system fertilization*, which considers nutrient cycling and exports, and the zoogeochemistry of grazing livestock, such as the conversion of plant organic nutrients into inorganic nutrients during the process of digestion [109] and the impacts on soil biology [110,111].

System fertilization is an approach based on the conceptual framework that fertilizer must be applied in the system phase or component that presents the lower nutrient extraction and the higher nutrient cycling capacity to maximize total system production [112]. For example, in a typical Brazilian ICLS, which alternates between a grain crop production phase with a higher nutrient exportation and an animal production phase with lower exportation, fertilizers should be entirely applied on pastures. System fertilization depends, therefore, on biological nutrient cycling from the crop and pasture phase in succession to achieve efficient nutrient use, and thereby reduce the requirement for mineral nutrient inputs, avoid losses, and maintain long soil fertility [113].

P and K soybean requirements applied on preceding Italian ryegrass did not affect the succeeding soybean yield and increased herbage production [114]. Fertilizers applied during the pasture phase are kept in the system by the decoupling–recoupling processes and then easily obtained by soybean in succession [115]. An increase in acid phosphatase activity was reported to be correlated with an increasing soybean yield, resulting from system fertilization and the livestock zoogeochemical effect [116]. When all nutrients (N, P, and K) are applied during the pasture phase, N increases the P and K demand [115], contributing to increasing the herbage accumulation rate and total herbage production, which in turn increase the stocking rate [114]. An increase in the stocking rate may not affect the live weight gain per animal if sound sward management targets are maintained [115], but it increases animal production per unit area and contributes to increased dung and urine deposition, resulting in a heavy cycling and a great source of available nutrients, which in turn may increase soil microbial biomass [110].

When the sequence is between crop and forage grasses, such as maize, oat, or Italian ryegrass, the N dynamics is pivotal. N application (200 kg $N.ha^{-1}$) in urea form in pastures during winter eliminates the application of N in maize sequence [117]. Assmann et al. [112] also demonstrated that after an application of 300 kg $N.ha^{-1}$ to cool-season pasture, no response in maize was observed to further N fertilization in the cropping phase. N system fertilization in ICLSs has several advantages, including: (i) lower exportation of N in cattle production, which ranges from 4% to 10% of N intake [118], leaving behind a large proportion of N available; (ii) reduction in N losses through volatilization due to the lower temperature during the winter pasture phase [119]; (iii) lower spacing between rows for pasture (17 cm) compared to corn (80 cm), and, thus, the urea applied to pasture may be less easily volatilized because of a faster uptake due to the dense root system and active canopy growth; and (iv) faster pasture litter decomposition [120] due the low C:N ratio, so that nutrients contained in the pasture litter are released and taken up quickly by the crop.

A vital element in this carryover effect relies on livestock grazing that "catalyze nutrient cycling". The MIT process for N and P by soil microbe communities and the rate of substrate decomposition during the grazing period are sped up and benefit the system provided the recoupling process is guaranteed by sound grazing management. Pastures preceding grain crops and system fertilization allow N to undergo a rapidly decoupling–recoupling process and possibly avoid losses that would otherwise occur with fallow periods. The synchronism (timing of the release of organically bound nutrients to coincide with crop demand) between nutrient release and plant demand is important for sustainability. Nutrient uncoupling in real time determines the efficiency of the nutritional resources used. In areas cultivated with pasture that received N fertilization, N-mineral contents in the soil tend to remain above the critical level for the establishment of grain crop [112].

Considering the complexity of ICLSs, the current fertilizer and liming recommendation model does not take into account nutrient cycling between different crop phases of rotation and the impact of zoogeochemistry on soil attributes (soil biology in particular). System fertilization is an approach that relies on biological nutrient cycling between phases of rotations to achieve a high nutrient-use efficiency, and thereby reduce mineral nutrient input requirements, avoid losses, and maintain long-term soil fertility. This approach is in contrast to the classic paradigm of individually driven crop fertilization where the residual effect of fertilizers is considered derisory and therefore ignored. Conversely, system fertilization considers all crops in the fertilization scheme with rotational carryover (i.e., either directly from inorganic forms or indirectly from organic N mineralization) as a key component.

Well-established ICLSs—i.e., with use of the no-till system, the presence of grazing animals in well-managed pastures in soils with high nutrient levels, and soil acidity neutralization—make it possible to achieve a well-functioning system fertilization strategy [114,121], improving land use sustainability and productivity, without increasing agriculture expansion and/or deforestation and with less dependence on external inputs. Diversification (e.g., with leguminous species in pastures), use of organic fertilizers, and new standard fertilization needs to be developed to improve the efficiency of and benefits from ICLSs.

4.4. Generalization at Worldwide Level

Most of the analyses reported above are mainly based on European, North American, and South American experiences. However, several works have also shown the interest for ICLSs in different other regions in the world, particularly in sub-Sahara Africa for developing local and efficient food production systems in smallholder farms [122–126]. The introduction of legume tree species as a source of N through N_2 fixation, and use of their leaves and/or pods for feeding domestic herds and the producing organic fertilizers for enhancing food crop production is also a highly recommended system [127,128]. In Sahelian regions of West Africa, introduction of alfalfa crop within rice or vegetable cropping system has been also tested as a way not only to improve soil fertility and productivity of food crops but also for providing forage resource for the local pastoral system and then to avoid a too long scarcity period during the dry season and the overgrazing of vegetation [129]. In Mediterranean countries such as in North Africa or in the Middle East, it has been shown that recoupling livestock with a cropping system is a necessity for restoration of overgrazed steppe vegetation and for enhancing productivity of the cereal cropping system [130]. In a similar climatic context, the integration of cereal cropping system with sheep livestock production in Western Australia has been considered as the mean for improving farm productivity and farm performance [131]. In Asia, crop–animal integration, including fish–rice systems (see [35] above), is also recommended for improving agricultural production and addressing food security, more particularly in China and India, but also Vietnam and Indonesia, for meeting the increasing meat demand in these regions [132,133]. For each climatic, edaphic, ecological, and socio-economic conditions across the world, it seems that the integration of animal herbivores within cropping systems, either the more industrialized or the more traditional ones, appears to be the way for enhancing agro-ecosystem diversity which is the prerequisite for reconciling the two objectives of food security and quality of environment.

5. Lessons Learned and Future Efforts

High food productivity to feed the human population requires a high flux of available nutrients, N, P, K, S, and other micro- and oligo-elements in soils as well as the continual renewal of their stocks in soil to compensate for their exportation with harvested agriculture products. To achieve the capacity of soil to provide and maintain these fluxes, intensive agriculture production systems have relied on the massive use of external fertilizers that inevitably lead to unwarrantable environmental emissions to surface and groundwater and to the atmosphere. Moreover, most of these fertilizer resources are limited (mining) or are obtained at a too-high cost in fossil energy sources and greenhouse gas emissions.

Thus, the only way to maintain a level of soil fertility high enough to satisfy food demand at a global level is to realize an efficient recycling of mineral nutrients within the agro-ecosystem, food system, and waste system in order to limit losses and achieve a neutral balance with natural inputs.

In the absence of domestic herbivores to "catalyze" this nutrient recycling, the ultimate solution would be to have a full recycling of human excreta [134] and waste [134,135]. However, such a system is difficult to establish because our systems to collect waste and human excreta mix organic sources of nutrients with a quantity of xenobiotics, heavy metals, toxins, and other polluting molecules. Moreover, the concentration of these waste collection systems in large urban areas does not facilitate the transfer of this resource into rural and agriculture areas.

Thus, the use of domestic herbivores in association with pastures integrated with crops must regain its importance as a solution to maintaining long-term soil fertility in agro-ecosystems. Therefore, livestock production systems must be re-integrated locally with arable cropping systems within an integrated food production system in which emerging synergies should be optimized to provide a more sustainable agro-ecosystem. Furthermore, livestock stocking density must be adjusted at local or regional scale to the degree needed to maintain soil fertility at the level required for food production. This threshold livestock stocking capacity must be determined according to specific local conditions—types of soil and types of arable cropping systems—which requires further experimental, bibliographical, and modeling research activities, taking into account not only herbivores but also monogastric production systems that are in competition with human populations for food. Moreover, at a global level, this threshold stocking density would involve a decrease in meat and milk consumption per capita in, e.g., Europe and North America, while allowing for an increase in meat and milk in the diet of populations currently affected by malnutrition.

This re-integration of herbivore livestock production with arable cropping systems, although very necessary from an ecological and environmental point of view, is sometimes not fully compatible with socio-economic and political constraints that favor a high specialization of food production and distribution systems, in addition to activism against animal production. Thus, without a clear identification of this locking and of the alternative socioeconomic systems that will have to be promoted—from agricultural production to food processing, distribution, and consumption systems—this necessity for integrated herbivore–cropping systems remains a sincere hope.

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