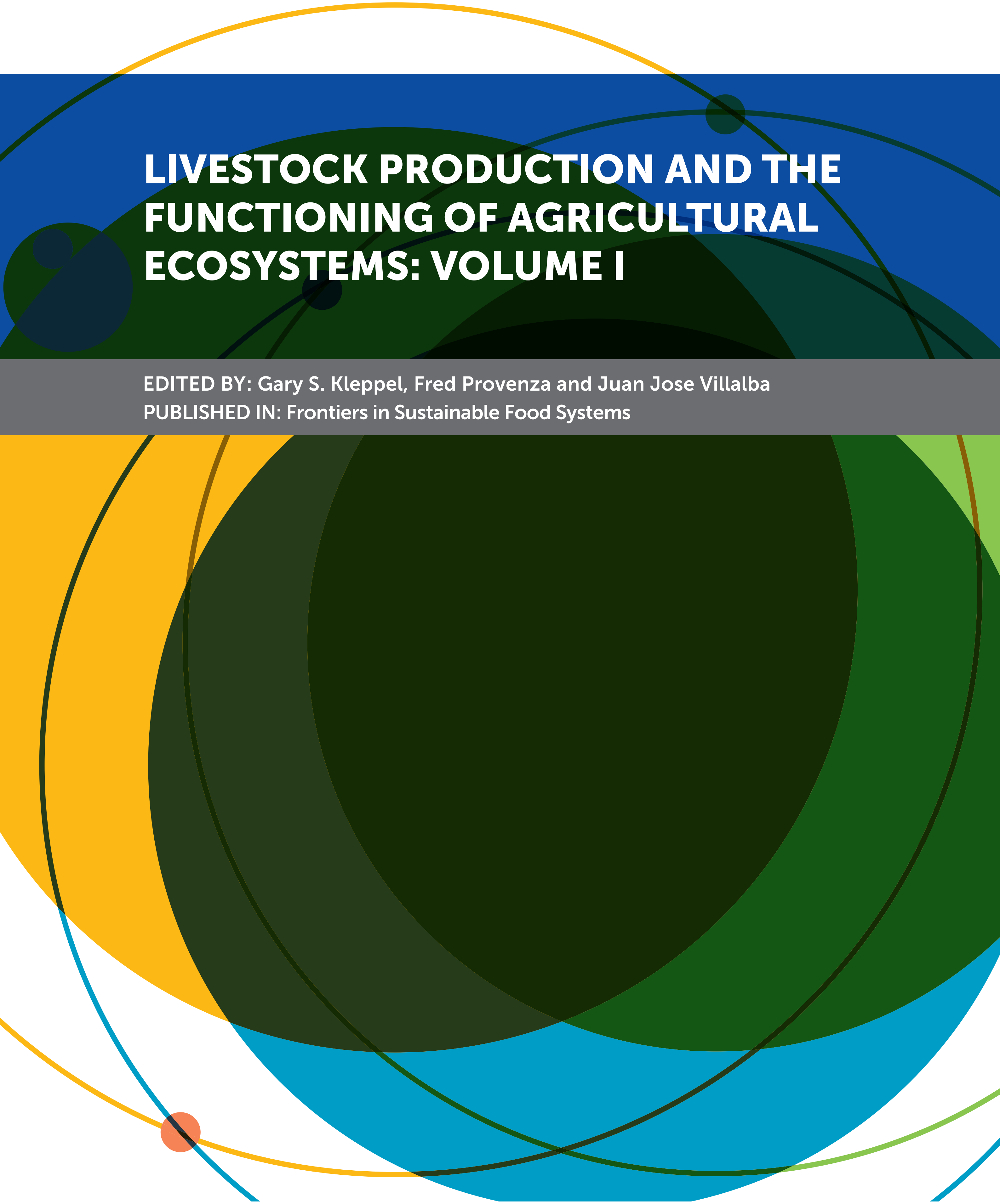

LIVESTOCK PRODUCTION AND THE FUNCTIONING OF AGRICULTURAL ECOSYSTEMS: VOLUME I

EDITED BY: Gary S. Kleppel, Fred Provenza and Juan Jose Villalba
PUBLISHED IN: Frontiers in Sustainable Food Systems

frontiers Research Topics

ISSN 1664-8714
ISBN 978-2-88971-218-2
DOI 10.3389/978-2-88971-218-2

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LIVESTOCK PRODUCTION AND THE FUNCTIONING OF AGRICULTURAL ECOSYSTEMS: VOLUME I

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Citation: Kleppel, G. S., Provenza, F., Villalba, J. J., eds. (2021). Livestock Production and the Functioning of Agricultural Ecosystems: Volume I. Lausanne: Frontiers Media SA. doi: 10.3389/978-2-88971-218-2

Table of Contents

frontiers
in Sustainable Food Systems

EDITORIAL
published: 21 June 2021
doi: 10.3389/fsufs.2021.690016

Editorial: Livestock Production and the Functioning of Agricultural Ecosystems

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Keywords: livestock management, grazing impacts, health and meat, livestock and social welfare, integrated agriculture

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Specialty section:
This article was submitted to Agroecology and Ecosystem Services, a section of the journal Frontiers in Sustainable Food Systems

Received: *01 April 2021*
Accepted: *14 May 2021*
Published: *21 June 2021*

Citation:
Kleppel GS, Provenza FD and Villalba JJ (2021) Editorial: Livestock Production and the Functioning of Agricultural Ecosystems. Front. Sustain. Food Syst. 5:690016. doi: 10.3389/fsufs.2021.690016

Editorial on the Research Topic

Livestock Production and the Functioning of Agricultural Ecosystems

Approximately 37% (5.1×10^7 km^2) of the Earth's land mass is used for agriculture, but only about 11% of that is capable of large-scale crop production (World Bank, 2021a,b). As such, about 26% of the Earth's agricultural land can only be used to produce animals. Despite trends toward veganism in some countries, the consumption of meat is increasing globally, and sustained consumption of the vegan diet is rare (Lal; van Vliet et al.). Although domestication of animals began nearly 11,000 years ago, our species' relationship with livestock has been challenging from the beginning. From the first efforts at domestication to the present day, livestock have been zoonotic disease vectors (Diamond, 1998). Livestock management has challenged the integrity of ecosystems globally (Kleppel; Teague and Kreuter) and has created social, animal welfare and public health concerns in both developed and developing countries. Clearly, the relationship between humans and the animals we raise for food is paradoxical. On the one hand, they are the source of nourishment, particularly protein, for most of the people on this planet. On the other, they and the practices used to raise them are major contributors to the pollution of surface waters, the degradation of air quality, the emission of greenhouse gases, the destruction of soil, vegetation and biodiversity, and the incitement of social unrest. While it is unlikely that any of this would or could compel *Homo sapiens* to turn again to a hunter-gatherer lifestyle, it is worth considering animal agriculture from both positive and negative perspectives, endeavoring to resolve those aspects of practice that threaten our environment and social systems, and to replace them with beneficial practices and approaches to produce food for a rapidly growing, but endangered human population on this fragile planet.

To respond to this challenge, we have compiled a collection of research and review articles dedicated to the many facets of *Livestock Production and the Functioning of Agricultural Ecosystems*. In fact, livestock and humans can contribute to meeting such challenges by integrating key principles underlying the adaptive and dynamic interactions of plants, animals, and humans with their environment into existing and novel management practices that foster ecosystem health and biodiversity. The nine papers presented here address the topic from different perspectives, providing readers with a range of questions and challenges associated with animal agriculture. The subjects examined in this issue are wide ranging, from the benefits of non-fiber carbohydrates in forage for beef cattle, to the comparison of different philosophies of pasture and rangeland management, to the resolution of conflicts between herders and crop farmers, as well as herders and lions, to the benefits of an omnivorous over an herbivorous diet. Several themes emerge from this compendium. Pre-eminent among them are the: (i) importance of biodiversity in animal agriculture, (ii) impacts of different management approaches to livestock and the environment, and (iii) effects of animal agriculture on human well-being and wildlife conservation. There are numerous overlaps among themes. For instance, biodiverse livestock operations may not only help mitigate certain climate change impacts, but they may increase economic stability, particularly in the developing world.

The theme of *biodiversity* is central to articles by Lal, Dumont et al., and Rowntree et al., who consider the implications of animal-crop-tree farming, and multi-animal species integration from different perspectives. As Dumont et al. point out, "… the diversity of system components and interactions among these components can increase productivity, resource-use efficiency and farm resilience." These ideas are captured in the life cycle assessment conducted by Rowntree et al. on a farm that practices multi-species rotational grazing in Clay County, Georgia, USA. They are extended further by Lal, who demonstrates the links between integrated agriculture, environmental quality and social well-being within the context of the UN's Sustainable Development Goals.

The second theme, *the environmental and nutritional impacts of different management approaches*, focuses on forage quality and emerging livestock and grazing-land management approaches. Villalba et al. remind readers of the importance of non-structural or non-fiber carbohydrates in beef cattle nutrition and they recommend the incorporation of such nutritional sources, particularly legumes, into forages for livestock on pasture. Teague and Kreuter, and Kleppel focus on regenerative methods of livestock production. Regenerative agriculture emphasizes soil health and the restoration of ecosystem services. Kleppel compares the environmental impacts of regenerative and conventional animal agriculture, the latter being associated with practices that have become mainstream since the end of World War II. He suggests that relative to conventional practice, regenerative techniques favor restoration and maintenance of environmental quality and ecosystem services. Teague and Kreuter emphasize that, "[s]cientists partnering with farmers and ranchers… who have improved their… resource base and excel financially have documented… sound environmental, social, and economic outcomes."

The third emergent theme in this issue, *the effects of animal agriculture on human well-being and wildlife conservation*, focuses on human health, and on interactions among disparate human communities, and humans and non-humans. van Vliet et al. present a comprehensive analysis of the nutritional importance of the omnivorous human diet, making the case for the synergistic nutritional complementarity of plant- and animal-based foods. They extend the discussion to popular plant-based meat alternatives, showing that extensive processing and lack of animal-based nutrients prevents them from being nutritionally complete substitutes for animal foods. Jablonski et al. describe the resolution of stress between Maasai herders and African lions, caused by increased lion depredation on livestock, by identifying and correcting weaknesses in herding practices. Similarly, Alary et al. document the reduction of stress between Bedouin herders who have long used the western edge of the Nile Delta to graze their livestock and newly arrived farmers seeking to cultivate the land.

Ultimately, this volume speaks to the breadth of researchable questions associated with animal agriculture, the integrated context of thematic areas within the discipline, and the obvious role that livestock production can play, not only in the food supply, but to human health, social welfare, and the future of Earth's ecosystems. Animal agriculture is in a state of transition. Changes are occurring in the ways we manage livestock and produce food and fiber from them. Answers to many of the questions raised in these papers remain elusive. Many will be controversial. But if good research raises more questions than it answers, then this issue should prove a useful stimulus for new research into the 11,000-year old practice of cultivating animals for food and fiber.

AUTHOR CONTRIBUTIONS

GK, FP, and JV contributed substantively to the production of this document. GK prepared the initial draft of this Editorial. FP and JV reviewed and revised the draft. All authors approved the submitted version of the article.

ACKNOWLEDGMENTS

We are grateful to the authors who contributed manuscripts to this issue, and to the many reviewers and paper editors, who contributed their time and efforts to ensure the success and quality of the peer review process.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Sustainable Food Systems

REVIEW
published: 16 July 2020
doi: 10.3389/fsufs.2020.00109

Incorporating Diversity Into Animal Production Systems Can Increase Their Performance and Strengthen Their Resilience

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Specialty section:
This article was submitted to
Agroecology and Ecosystem
Services,
a section of the journal
Frontiers in Sustainable Food
Systems

Received: 20 March 2020
Accepted: 16 June 2020
Published: 16 July 2020

Citation:
Dumont B, Puillet L, Martin G, Savietto D, Aubin J, Ingrand S, Niderkorn V, Steinmetz L and Thomas M (2020) Incorporating Diversity Into Animal Production Systems Can Increase Their Performance and Strengthen Their Resilience.
Front. Sustain. Food Syst. 4:109.
doi: 10.3389/fsufs.2020.00109

Animal production systems (APSs) have long been transformed through intensification, specialization and geographical concentration, leading them to become major anthropogenic drivers of pollution, climate change, and biodiversity loss. Agroecology, organic farming and sustainable intensification have been proposed as alternative models to invert those trends. Diversity is highly valued in agroecology and organic farming, in which it is assumed not only to increase farm performance but also to strengthen farm resilience. Here, we examine how the diversity of system components and interactions among these components can increase productivity, resource-use efficiency and farm resilience in aquaculture, rabbit, monogastric and ruminant systems. In doing so, we reveal that the same processes can occur in very different systems. For instance, the higher performance of multi-species aquaculture or ruminant grazing systems results from (i) the complementary feeding habits of animal species that exploit resources from different ecological niches more efficiently; and (ii) facilitation or competitive exclusion, which results in a species increasing or decreasing resource availability for another species. The benefits of diversity are observed not only in relatively extensive systems but also in intensive indoor systems. For instance, genetic diversity is associated with herd and social immunity in rabbit production, while trade-offs between life functions play a major role in dairy herd performance. In the last section, we discuss how management options nested in system component diversity and their interactions can enhance system resilience. Strategic and tactical management of APS diversity can promote farm buffering and adaptive capabilities, respectively, via the abovementioned processes. By stabilizing the farm financial situation and facilitating access to short supply channels, transformative changes, such as a diversification of the animal species bred or development of a processing enterprise on farm, expand options for increasing the resilience of APSs to market price fluctuations and climatic shocks. However, the need for new technical skills and sometimes high initial investments can act as strong inhibitors of farm diversification. We conclude with a description of some of the research or action that is needed for these principles to be more widely implemented in commercial farms.

Keywords: agroecology, aquaculture, grazing, livestock, management

INTRODUCTION

The livestock sector has received particular attention in the news and scientific media and is considered a major anthropogenic driver of climate change, water pollution, and biodiversity losses. Although the best transition options are still strongly debated, there is a consensus on the need for animal production systems (APSs) to reduce the use of inputs, to emit less greenhouse gasses (GHG) and to increase their mitigation potential, e.g., through carbon sequestration in grassland and crop soils (Food Agriculture and Organisation, 2013). Over the past 60 years, APSs have been primarily transformed through the top-down structuring of linear value chains, intensification, specialization and geographical concentration (Thornton, 2010). When intensification and specialization were the two primary drivers of APSs, the focus was primarily on short-term efficiency to make the best use of high-yielding breeds and cultivars under optimal production conditions. Intensification led to a dramatic reduction in within-system diversity, i.e., the diversity of animal species and breeds, the genetic diversity within breeds, the diversity of feed resources, and even the diversity of management practices. Recently, the methods (van der Werf et al., 2020) and frameworks (Ryschawy et al., 2019) for analyzing system sustainability have increasingly accounted for a wider perspective on the functions and services livestock farming systems provide to society. A number of these functions and ecosystem services (recycling of nutrients, forage yield, pollination, etc.) are closely linked to agrobiodiversity, and their persistence depends largely on maintaining biological diversity in APSs (Kremen et al., 2012; Carvalho et al., 2018; Haughey et al., 2018; Wang et al., 2019; Yang et al., 2019).

Incorporating diversity in APSs is thus highly valued in agroecology (Dumont et al., 2013, 2018) and organic farming (Ponisio et al., 2015) the two main forms of APSs that attempt to step away from highly specialized conventional models. Sustainable intensification of tropical forage-based systems is likely to increase their productivity, while saving land from further deforestation (Silva et al., 2017; zu Ermgassen et al., 2018). Incorporating diversity in these systems mainly relies on the integration of forage leys into cropping systems to enhance the coupling of carbon and nitrogen cycles within grasslands and soils, while minimizing environmental losses toward the atmosphere and hydrosphere (Carvalho et al., 2018; Dumont et al., 2018). Beyond this, the value of diversity in agroecological or organic farming systems is based on the need to fortify their internal capacity to face perturbations because these systems are not secured with external inputs (e.g., concentrated feed and veterinary products) as they are in conventional systems (Bommarco et al., 2013). For instance, individual response variability and interactions among system components could enhance the long-term herd (Blanc et al., 2013; Magne et al., 2016) and system performances (Tichit et al., 2011; Kremen et al., 2012; Ponisio et al., 2015; Diakité et al., 2019). In addition, rearing different species in a pastoral system could be seen as a risk-spreading strategy against disease outbreaks, feed shortages and market price fluctuations (Mace, 1990; Nozières et al., 2011; Joly et al., 2019). Within-farm diversity is thus assumed to affect not only the system's productive yield but also its stability and ability to cope with uncertainty (Altieri et al., 2015; Sneessens et al., 2019). Therefore, the primary outcome related to an increase in system diversity may be an increase in system resilience.

Resilience focuses on the capacity of a system to absorb perturbations and reorganize while undergoing changes to maintain its function (Walker et al., 2004). As a system is indeed not organized around a unique equilibrium, Darnhofer (2014) discussed that resilience covers the buffer, adaptive and transformative capabilities of a given system. Buffer capability denotes the ability of a system to assimilate a perturbation without changing its structure or function; adaptive capability, that of adjusting to change while staying in the current stability domain; and transformative capability implies transition to a new system. These three capabilities may also operate in synergy at the farm scale since gradual and marginal changes may accumulate and, ultimately, hinder a transformative change (Darnhofer, 2014; Vermeulen et al., 2018). Among the underlying mechanisms, the 'portfolio effect' states that communities with high species diversity are likely to include complementary species that can adapt to any condition of a fluctuating environment. Consequently, the number of species *per se* would have a positive effect on the system resilience (Figge, 2004; Volaire et al., 2014). Functional diversity is also likely to increase system resilience through redundancy mechanisms since the collapse of any species can be offset by another species with similar characteristics (Biggs et al., 2012).

Thus, at this stage, we have knowledge of the underlying mechanisms supporting farm resilience properties and theoretical assumptions on the role of diversity for resilience. However, as there is a lack of experimental evidence, it is far from clear how these concepts are applicable in different types of APSs. In this paper, we therefore examine empirical evidence and model outputs related to how within-farm diversity can enhance the production of goods and services and strengthen farm resilience in APSs with different types of productions covering a large gradient of intensification (i.e., relying on increasing levels of inputs to produce food on a given area of land). In the first section, we focus on the mechanisms expressed within the system components, including grassland diversity and the inter-individual variability between animals in herds and flocks. In the second section, we focus on interactions between system components and analyze how appropriate combinations of plant and animal production and of livestock species can increase farm production and benefit animal health. In the third section, we address how to manage system resilience by discussing how the capabilities proposed by Darnhofer (2014) could be enhanced by farm-scale diversity. Integrating economic and social dimensions through sales management and farmers' securitization strategies results in a broader analysis of how farm-scale diversity allows for the adaptation of APSs to risks and uncertainties.

VALUING DIVERSITY OF SYSTEM COMPONENTS

Grasslands

There has been an important research effort to determine how multispecies grasslands could benefit sward productivity, animal performance, and farm fodder autonomy and resilience in grassland-based systems. A review by Cardinale et al. (2007) revealed that mixtures of species produce an average of 1.7 times more biomass than that of species monocultures. These authors also showed that the contribution of biological processes involving multiple species equals or exceeds the contribution of the most productive species, with an increase over time. Finn et al. (2013) extended this result to the case of intensively managed temperate grasslands; the yields of pastures made up of a variety of annual species was 30% higher than those of pastures that only had a single annual species and exceeded those of the best monoculture in approximately 60% of the sites (**Figure 1**). Finn et al. (2013) attributed this higher yield to the complementarity of the resource acquisition (e.g., nitrogen capture by N_2-fixing legumes and rooting depth) and conservation strategies among plant species. In ecology, traits related to leaf functions such as photosynthesis efficiency, carbohydrate metabolism, nitrogen consumption allow plant species to be ranked according to their strategies for the acquisition and conservation of resources (Wright et al., 2004). These mixtures benefited from the presence of grasses that rapidly acquire supplied N, and maintained resistance to weed invasion for at least 3 years. Plant diversity also secures the system against seasonal and long-term climatic variability by limiting the impacts of climatic disturbance on forage yield and by increasing grassland resilience to drought conditions (Volaire et al., 2014). This results from the complementarity of plant traits and strategies, such as dehydration avoidance, dehydration tolerance and summer dormancy, within species-rich communities. Yield stability also increased when a plant species assemblage increased from one to four species in intensively managed swards, under drought and post-drought periods of two consecutive years. This is likely due to the high degree of species asynchrony increasing the temporal stability (Haughey et al., 2018).

Rotationally grazing on sown swards with increasing botanical complexity (in terms of the number of species and functional types) has been shown to improve animal performance in dairy cows (Roca-Fernández et al., 2016) and sheep (Grace et al., 2019). Grazing sheep on multispecies swards reduced the requirements for mineral fertilization and chemical anthelmintics, due to the availability of N-fixing legumes and the presence of tannin-rich plants, respectively (Grace et al., 2019). In dairy cows, improved animal performance resulted from the cumulative effect of improved pasture nutritive value and increased daily intake (Roca-Fernández et al., 2016). Such an increase in daily intake happens through a higher feeding motivation in association with a more diverse diet (Ginane et al., 2002) rather than through associative effects between grasses and legumes on dry matter digestibility (Niderkorn et al., 2017). Diversified natural grasslands also have the potential to combine high digestibility with a reduction in enteric methane and nitrogen losses in urine (Macheboeuf et al., 2014). Knowledge of the individual and associative effects of plants containing bioactive compounds (polyphenolic compounds, alkaloids, and terpene compounds) is still scarce. Some legumes containing condensed tannins, including species such as *Onobrychis viciifolia* and *Hedysarum coronarium*, have also been used to control strongyle larval development in small ruminants (Hoste et al., 2006) and horses (Collas et al., 2018) but these compounds are toxic to animals when consumed in large amounts. Further research is thus needed to balance their positive and toxic effects in a way that benefits animal health and performance without impairing their digestive efficiency.

Animal Inter-Individual Variability

The intrinsic individual variability in animals within a herd or a flock is a source of diversity, which has a key role in the production process (Tichit et al., 2011) and may also have positive effects on system resilience. Such positive effects are grounded in the diversity of the trade-offs between life functions that induce specific adaptive responses of animals to suboptimal environments. For instance, a multi-trait and dynamic method was proposed by Ollion et al. (2016) to describe the trade-offs between life functions in dairy cows. These authors used phenotypic traits during the first 13 weeks postpartum, when dairy cows experience a negative energy balance, and distinguished four trade-off profiles independently of the cattle breed (i.e., Holstein, Montbéliarde and Normande) and cow age (parity order). Profile one (n = 53 cows) corresponded to high yielding cows [average weekly milk yield (AMY): 487 kg]. These animals mobilized much of their body reserves to sustain their milk yield at the expense of fertility [the pregnancy rate (PR) during current lactation was 64%]. The three other profiles corresponded to cows with a lower milk yield and contrasted reproduction performance (**Figure 2**). Cows in profile two (n = 111; AMY: 320 kg) mobilized body reserves but were able to maintain an acceptable PR at 71%. Profile three (n = 67; AMY: 331 kg) corresponded to cows with a low body condition and high body reserve mobilization resulting in very thin animals at the start of the breeding period. Their fertility was thus very low (PR: 30%). Profile four (n = 103; AMY: 331 kg) corresponded to cows with the most stable body condition score and the best fertility among all the profiles (PR: 92%). Each profile

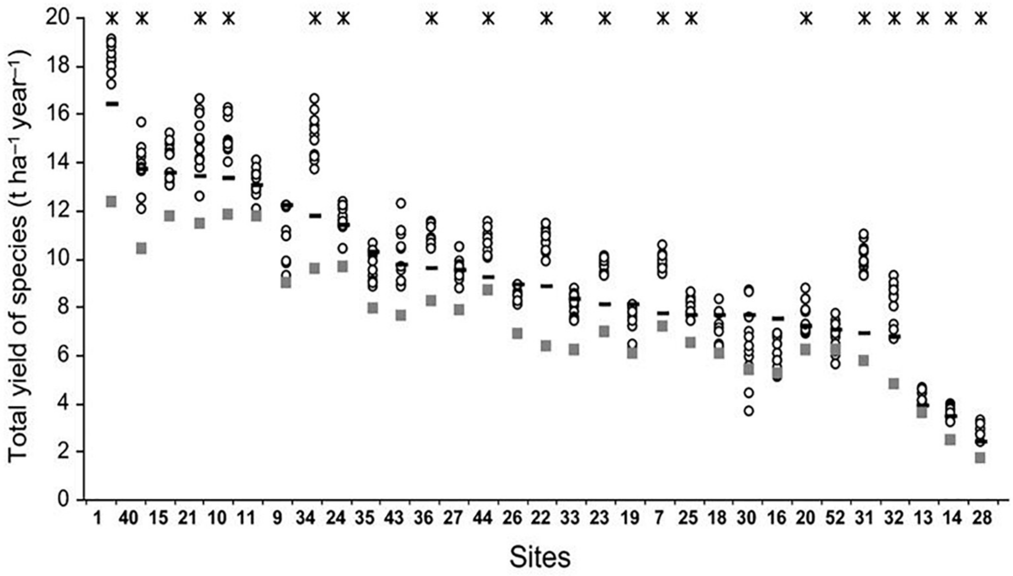

FIGURE 1 | Average annual total yield at each of 31 sites of a 3-years pan–European experiment in 17 countries testing whether higher yields, compared with monocultures, can be achieved with grass–legume mixtures containing four species [adapted from Finn et al. (2013)]. At each site open circles represent mixture yields, horizontal bar the yield of the best performing monoculture, gray square mean monoculture performance, and asterisk sites where mixture yields exceeded those of the best monoculture.

was linked to a specific adaptive response by the daily milk yield to perturbation, cows with profiles 2 and 4 showing no fluctuation (**Figure 2**). At herd level, the diversity of trade-offs and adaptive response of animals is assumed to buffer the effect of random environmental perturbations in the long term. This assumption was tested by Blanc et al. (2013) who simulated the annual milk yield produced by dairy herds composed of cows with either a single or different types of theoretical adaptive profiles (the ability to cope with feed shortages, heat stress or diseases). One simulated perturbation occurred every 3 years over a 50-year period and it was randomly related to either feed availability, heat or diseases. Simulation runs were repeated 50 times to account for the random effect of perturbation sequences. After 50-years, the results showed that while the annual milk yield was very stable across groups, the inter-annual variability was 25% less in the herd composed of cows with diverse adaptive profiles.

Beyond this modeling work, Magne et al. (2016) analyzed the productive performances of 22 multi-breed dairy herds from southern France and compared them with those of single-breed specialist (Holstein) or generalist (Montbeliarde or Simmental) herds from the same area. They concluded that multi-breed dairy herds experienced better trade-offs than single-breed herds among milk yield, milk solids, herd reproduction and concentrate-conversion efficiency. However, experimental evidence that herd composition could be a factor in enhancing system resilience remains scarce, which highlights the need for more research on the technical and economic performances of varying the proportion of specialist and generalist individuals or breeds in mixed herds. Benefiting from this diversity requires the ability to adequately phenotype dairy cows to characterize their trade-offs between life functions and identify their response profiles to perturbations (Friggens et al., 2017).

Some effects of the genetic structure of animal groups are also expected in pigs, poultry, and rabbits, where genetic variability is usually ‘concentrated’ at the individual level (**Figure 3**). Purebred, specialized paternal, and maternal lines are crossed to produce the animals found in most commercial farms (Phocas et al., 2016). This organization allows the valorization of the complementarity between lines. It benefits from heterosis and leads to a homogeneous population of highly productive individuals. In sire lines, selection focuses on improving feed-use efficiency and increasing growth rate and carcass lean meat content (muscle depth), while accounting for the meat technological quality, for instance in boars. In maternal lines, the priority is to increase prolificacy (i.e., the number of young alive at parturition) while accounting for maternal abilities, for instance in sows (Phocas et al., 2016). Breed-related resistance to diseases (e.g., to swine fever) is also known in pigs (Depner et al., 1997), stressing opportunities offered by using the available genetic material in a combined and more rational way. Group diversity is assumed to limit the use of chemical drugs and animal mortality (Hamilton et al., 1990; Pekkala et al., 2014). In the case of intensive rabbit production, disease occurrence is a major challenge. Increasing herd genetic diversity by crossing specialized lines or raising lines from distinct genetic

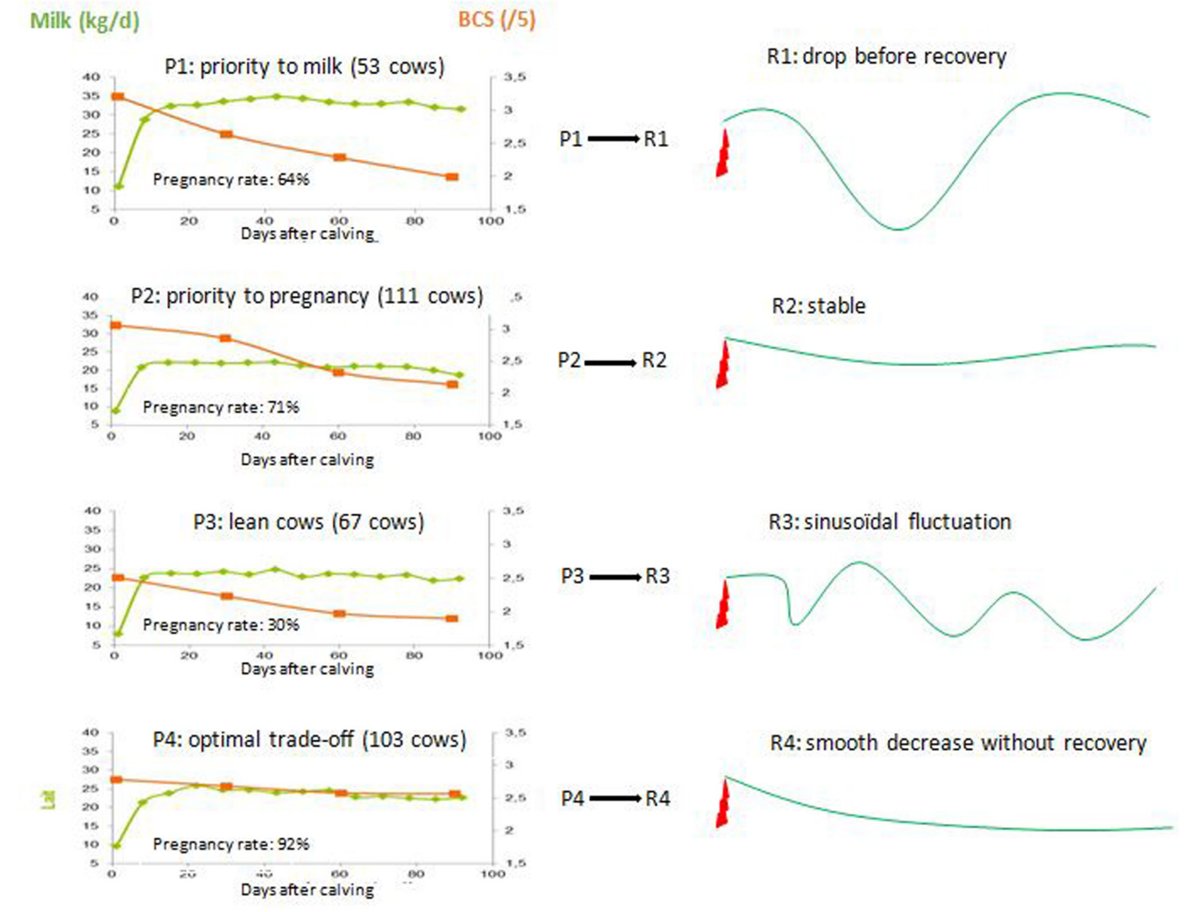

FIGURE 2 | Relationships between four individual trade-off profiles (P1-4 accounting for daily milk yield in green, body condition score in orange, and pregnancy rate during current lactation) of dairy cows measured in early lactation when competition between the functions is the highest, with their milk yield response (R1-4) to a perturbation (adapted from Ollion et al., 2016).

backgrounds together is assumed to provide benefits in terms of not only the complementarity of productive and adaptive traits from different lines and heterosis but also the herd and social immunity. While herd immunity refers to a reduction in disease transmission as the number of susceptible individuals in a population decreases (Fine, 1993) social immunity goes beyond that definition. It encompasses any type of immunity services provided by one individual to the others (Cotter and Kilner, 2010), such as the transmission of immunoglobulins via lactation, or self and collective grooming behavior. The results of a series of experiments conducted on rabbit lines affected by a rapidly spreading pathogen called epizootic rabbit enteropathy are demonstrative of herd immunity. In studying the effect of eight weaning diets on the health of rabbits from a unique crossbred line, Martínez-Vallespín et al. (2011) reported a mean mortality rate of 54.6% (±15.4%). The post-weaning mortality was reduced to 16.5% (±6.4%) (Savietto et al., 2012) and to 8.7% (±5.5%) (García-Quirós et al., 2014) within a mixed-breed population of three genotypes. In this last experiment, one of the genotypes was a long-lived and productive line in which post-weaning mortality was as low as 3.6%. These results suggest that beyond genetic susceptibility to diseases, the increase in genetic diversity at the herd level matters.

VALUING INTERACTIONS AMONG SYSTEM COMPONENTS

Combining Plant and Animal Production

Interactions between system components primarily refer to how context-appropriate combinations of plant and animal production could increase farm-scale productivity and resource-use efficiency. For instance, in a network of 66 beef cattle farms of the Charolais area, organic farmers who grow crops on farms to feed cattle and efficiently exploit the diversity of feed resources had good technical performances (e.g., the highest percentage of calves weaned per cow service), and the lowest GHG emissions and non-renewable energy consumption per hectare (Veysset et al., 2014). Conversely, conventional mixed crop–livestock farmers that sell both meat and cereals were, on average, less efficient than the specialized grassland-based farmers. This example reveals that farm-scale diversity is not

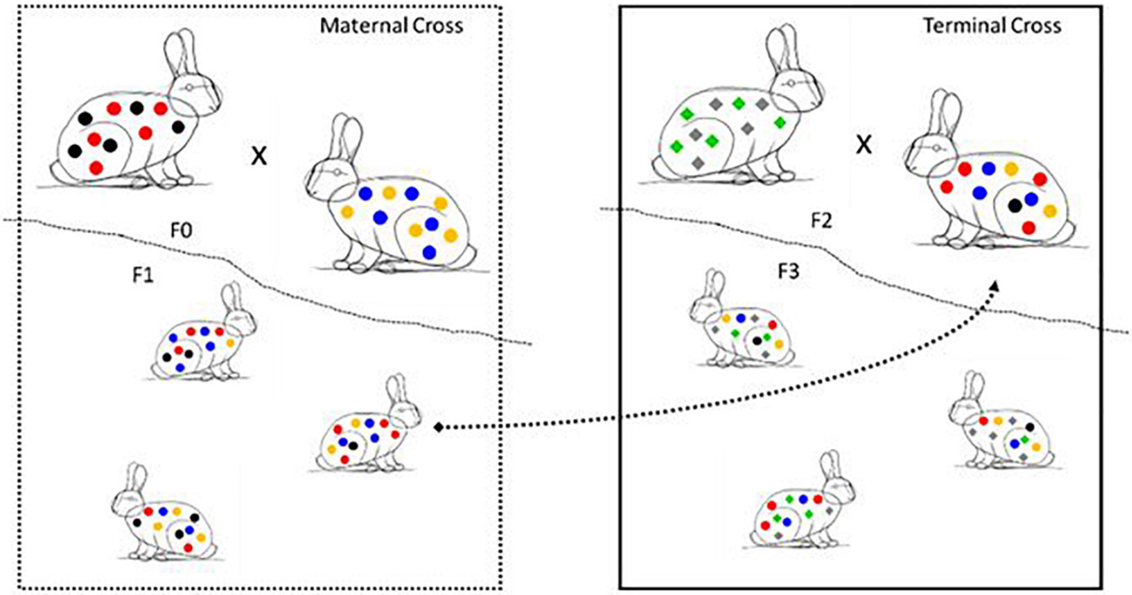

FIGURE 3 | Schematic representation of crossing specialized maternal lines (generation F0) for further crossing with a paternal line (generation F2). Genetic diversity is represented by colored shapes (circles for maternal lines and diamonds for the paternal line).

sufficient to increase resource-use efficiency and that interactions between components of APSs are needed.

There are some other demonstrations of the benefits of resource diversification on farm self-sufficiency, environmental performance and farm resilience in ruminant systems. In Australia, increasing the length of the alfalfa phase in the rotation decreased the variability in production and ecosystem services value (Kragt and Robertson, 2014). This is because annual crops display more inter-annual variation in production due to variations in timing and amount of rainfall than perennial pastures. Another farm-scale simulation analyzed the forage autonomy of four dairy farms located on a NW-SE diagonal across France over a succession of 4 years and under varying weather conditions (Martin and Magne, 2015). A change in the variety of and balance between crops and grasslands grown on the farms was shown to promote redundancy in forage resources and to buffer year-to-year variations in forage yields. Crop diversification increased the self-sufficiency for forage and resilience of dairy farms after two unfavorable years, while changing the calving period only had a minor additional effect. There are benefits of grazing cover crops in rotation with cash crops for primary and secondary production and for soil physical, chemical, and biological parameters (Carvalho et al., 2018). However, careful management of grazing intensity is needed as overgrazing can lead to soil deterioration. In organic farms, crop rotations are 15% longer than those in conventional systems and result in higher diversity and more even crop species distributions (Barbieri et al., 2017). These changes are largely driven by a higher abundance of temporary fodders and cover crops. Indeed, several legume or non-legume cover crops have a high nutritive value for ruminants and provide ecosystem services, such as soil fertility and weed control. Some of them also have the potential to decrease GHG emissions by the animals (Maxin et al., 2020). In silvopastoral systems, trees buffer crops and grasslands from large fluctuations in temperature, reduce soil evaporation and increase soil water infiltration. Farms with several vegetation strata, including trees, showed buffered forage yields in cases of severe droughts and an 80–90% productivity recovery 40 days after a hurricane (Altieri et al., 2015). There could thus be a wide range of conditions under which multispecies plant communities represent an efficient adaptation strategy against climatic events. An important challenge will be the development of innovative forage systems that intercrop plant species at different strata in temperate areas, notably in agroforestry systems, which are perceived by stakeholders to improve not only the environmental performance of livestock farming systems but also animal health and welfare (García de Jalón et al., 2018).

Multi-Species Animal Production Systems

The higher performance of multi-species APSs is assumed to result from (i) the complementary feeding habits of animal species that exploit trophic resources from different ecological niches more efficiently and (ii) facilitation or competitive exclusion, which results in an animal species increasing or decreasing the resource availability for another species. Aquaculture is a good illustration of these ideas, as manipulating combinations of species of carps and small indigenous fish enhances fish production in the polyculture systems of southern or South-eastern Asia (Milstein, 2005; Milstein et al., 2006; Wahab et al., 2011). This performance largely results from differences in the feeding strategies of fish species that are mixed, for instance, a combination of filter, herbivorous, and bottom feeders (Milstein, 2005 **Figure 4**). Mixing species that exploit the same resource at different times and/or in different spaces (so that they do not compete directly) can lead to the same benefit. For instance, farming sterlets (*Acipenser ruthenus*) with juvenile pikeperch (*Sander lucioperca*) in a recirculating aquaculture system increases the feed-use efficiency and reduces the labor needed for tank maintenance (Kozlowski et al., 2014). This efficiency occurs because the pikeperch consume feed floating in the water column, while the sterlets feed on the food that sinks to the bottom. One species can even enhance the food availability for another species through the facilitation process. For instance, Milstein et al. (2006) found a 50% increase in biomass production and a higher growth rate of rohu (*Labeo rohita*) when they are raised with common carp (*Cyprinus carpio*), a bottom-feeder, because common carp improve the nutrient re-circulation in the water column through the bioturbation of sediments when feeding on benthic organisms. The physical movement of the sediments favors phytoplankton development and thus increases the feed resources available in the water column where the rohu feed. Finally, differences in fish adaptive profiles can buffer a pond ecosystem, such as when local fish species reared in polyculture systems in Mexico were able to resist hypoxia and desiccation under conditions that caused massive mortality of carp (Moctezuma-Malagón et al., 2008).

There are thus strong analogies to what is observed in grassland-based systems, in which a combination of livestock species with complementary ecological niches also increases the overall use of pastures. The results of a meta-analysis reveal a positive effect of mixed grazing of sheep and cattle on the daily live weight gain of sheep, while cattle live weight gain was similar in mixed and monospecific grazing systems. On average, sheep grazed with cows grew 14.5 g/day faster than those grazed alone, resulting in higher meat production per hectare compared with that of a monospecific grazing system (d'Alexis et al., 2014). In another survey conducted over 5 years on permanent grasslands in Germany, lamb production also showed the highest benefits under mixed grazing, with a 17% increase in liveweight gain (Jerrentrup et al., 2020). Mixed grazing significantly increased daily average liveweight gains of suckler cows, but not that of calves. Mixed system productivity was also higher, which confirms the advantages of combining livestock species, attributed to complementary pasture use. This complementarity between grazing species could, however, lead to overgrazing as observed across nine Uruguayan farms where sheep to cow ratio was negatively correlated with cow pregnancy rate (Modernel et al., 2019). Due to their nutritional requirements and morphological capacities, cattle and sheep exhibit distinct grazing behaviors (Dumont et al., 1995) and have complementary effects on the vegetation structure, which can benefit pasture nutritive value (Jerrentrup et al., 2020) and biodiversity. For instance, mixed grazing with sheep and cattle not only improved livestock production but also provided

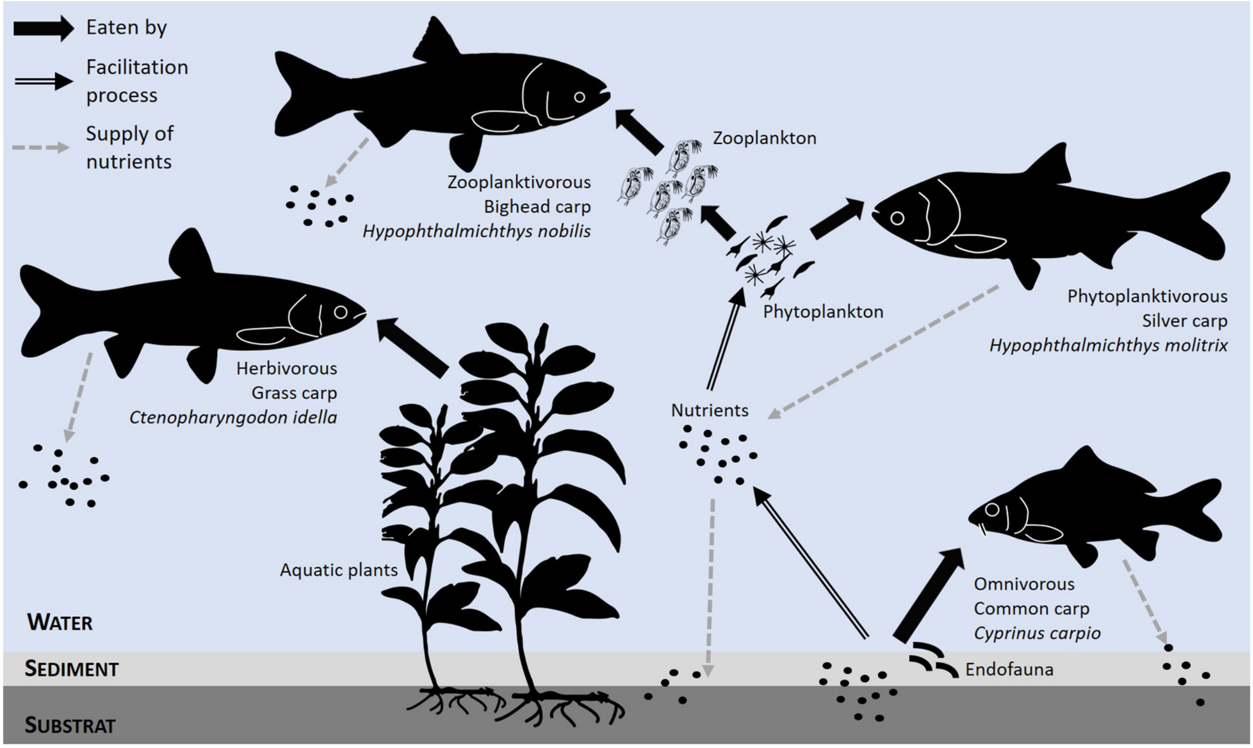

FIGURE 4 | An example of manipulation of the trophic network in the polyculture of cyprinidae, with two objectives: (i) the trophic complementarity of fish species, leading to an effective use of available food resources, and (ii) the exploitation of the facilitation process occurring through the bioturbation of sediments that promotes plankton development on which other fish species rely [adapted from Milstein (2005)].

suitable habitats for butterflies in Welsh upland pastures (Fraser et al., 2014). A recent study extended this finding across six groups of above-ground and below-ground organisms (plants, herbivorous insects, predatory insects, soil bacteria, fungi, and nematodes), and it suggested that mixed grazing is likely to provide enhanced levels of ecosystem services (Wang et al., 2019). Thanks to their two sets of incisors, horses graze close to the ground and maintain relatively stable open patches with specific plant communities (Ménard et al., 2002; Fleurance et al., 2016). Patch stability is likely to impact ecosystem functioning for agricultural (maintaining sward nutritive value) or conservation purposes (Dumont et al., 2012). Another key process is the competitive exclusion of cattle by horses: as cattle were not able to meet their daily requirements on the short lawns they switched to tall grass areas where they limited the development of competitive and unpalatable grasses on horse latrine areas. Consequently, co-grazing cattle and horses produced more species-rich vegetation communities than cattle or horses grazing alone (Loucougaray et al., 2004). Species combinations between ruminants and monogastrics (e.g., cattle and pigs or poultry) remain largely ignored, although they may have some potential due to their complementary diet compositions and resource-acquisition strategies (Sehested et al., 2004; Martin et al., 2020).

Polyculture fish production systems and mixed grazing systems can also achieve higher performance as a result of processes that benefit animal health. These benefits can be direct or indirect. An example of a direct effect comes from salmon farms, in which some fishes (e.g., wrasses and lump-suckers), named 'cleaner fishes,' benefit Atlantic salmon by removing ectoparasites, such as sea lice (Skiftesvik et al., 2013). In polyculture systems, a small proportion of carnivorous fishes can also contribute to the system performance by feeding preferentially on weak and ill individuals, thus limiting the pathogen load and diffusion. Such system could, however, be considered unacceptable from an animal welfare point of view. Some observations suggest that mixed grazing of pastures may directly reduce predation risks in poultry when grazed with cattle (Martin et al., 2020) or sheep, e.g., when grazed with donkeys or llamas in traditional pastoral systems (Smith et al., 2000). An indirect effect is the control of gastrointestinal parasites on pastures grazed by several herbivore species as the result of a dilution effect. Most nematode species exhibit high specificity for their hosts and are unable to complete their lifecycle when swallowed by a non-susceptible species. Mixed grazing, thus, appears to be an efficient strategy for reducing nematode infection in small ruminants (Marley et al., 2006; Mahieu, 2013) and young saddle horses (Forteau et al., 2020). This dilution effect is likely to decrease treatment frequency, and thus drug resistance, veterinary costs and environmental side effects of drug metabolites on dung beetle assemblages (Sands and Wall, 2018). The various benefits of mixing different animal species on the same farm should not overshadow the health hazards that they can induce and that need to be carefully evaluated. Cross species transmissions have been reported for bacterial diseases between co-grazing sheep and cattle (Moloney and Whittington, 2008; Rodgo et al., 2012). Another example in more intensive systems comes from the observation that some infectious agents, such as influenza viruses, can adapt to different species, increase their virulence after recombination and even be transmitted from animal reservoirs to humans (Kuiken et al., 2006).

MANAGING FOR RESILIENCE: DIVERSITY ALLOWS FOR ADAPTING TO RISKS AND UNCERTAINTIES

Is Resilience a Manageable Property of Animal Production Systems?

The first two sections of this paper have shown the extent to which valuing diversity of system components and interactions among them can increase the performance patterns of APSs (especially their productivity and resource-use efficiency) and strengthen their resilience, mainly via more stable production and reduced sensitivity to hazards (e.g., diseases). Such expected benefits depend on the implementation of fine-tuned management practices in time and space to take advantage of underlying ecological mechanisms, such as niche complementarity and facilitation. Otherwise, trade-offs may occur among organizational levels and between system performance patterns (e.g., productivity and efficiency) and system resilience (Peterson et al., 2018). This raises the question of how to manage resilience in APSs.

The buffer, adaptive and transformative capabilities of any resilient system (Darnhofer, 2014) refer to different types of management decisions. Buffer capability involves strategic decisions at the current farm configuration stage. Such decisions apply both when defining the level of within-farm diversity (e.g., sowing multispecies pastures or using different breeds in mixed herds) and when planning interactions among system components (e.g., co-grazing or feeding animals with crop residues; **Table 1**). Adaptive capability involves tactical decisions aimed at adjusting to hazards and changes. It is not always easy to modify the level of within-farm diversity in the course of a year, but interactions among system components can be revised and combined with other components (e.g., selling animals to reduce stocking density) to mitigate the effects of hazards and changes. Transformative capability involves strategic decisions and implies a transition to a new system. It involves a full reconfiguration of the farm layout, e.g., introducing aquaculture into existing integrated farming systems (Dumont et al., 2013), which drastically modifies both the level of within-farm diversity and the interactions among the system components.

Consistently managing these three capabilities remains a challenge. This partly relates to our limited knowledge of how management options nested in the APS diversity can enhance system resilience beyond the buffering capability discussed in the two previous sections. It is likely that managing for resilience based on the within-farm diversity of APSs will result in a greater management complexity for the farmer (Kingwell, 2011; Dumont et al., 2013) and require additional technical skills, for instance, for managing a new livestock species. García de Jalón et al. (2018) reported that increased complexity of work, management costs

TABLE 1 | A typology of resilience factors [according to Darnhofer (2014)] related to on-farm diversity with examples.

	Feed resource	Animal	Farm management
Buffer capability	• Sow multispecies swards. • Keep a diversity of permanent pastures. • Sow temporary fodders and cover crops in crop rotations.	• Use different breeds/lines in mixed herds. • Breed fish species with different ecological niches.	• Graze different livestock species on the same plots. • Increase crop–livestock interactions, i.e., use crop residues to feed animals and manure to fertilize crops.
Adaptive capability	• Use dual purpose crops. • Use tree foliage (e.g., *Fraxinus excelsior* L.) to feed animals.	• Lengthen animal productive lifespan.	• Sell animals to reduce stocking density. • Adapt the type of product sold to market conditions. • Modify equilibrium between herds in multispecies farms.
Transformative capability	• Exchange feeds, straw and manure with local specialized crop farmers.	• Graze animals on cover crops.	• Introduce aquaculture into existing integrated farming systems. • Add pigs/poultry (short production cycles) to cattle farms to achieve more regular cash inflows. • Develop a processing enterprise (e.g., sausages) and sales on farm. • Develop agritourism.

and administrative burden were the most limiting factors for the transition to agroforestry systems.

Additionally, despite several scientific indicator frameworks (Cabell and Oelofse, 2012; Speranza et al., 2014) farmers lack simple and reliable indicators to monitor the resilience of their farms over time and relate it to the implemented adaptations and/or transformations (Peterson et al., 2018). Two types of indicators are needed. Indicators relying on "fast" variables, e.g., the presence of parasites in animal dung (Forteau et al., 2020) and stocked biomass in pastures (Do Carmo et al., 2016), are of interest to farmers for managing hazards in the course of a year (Walker et al., 2012). The dynamics of these fast variables are dependent on other system variables that change much more slowly, e.g., soil nitrogen availability and soil organic matter content (Wang et al., 2019) and are therefore referred to as "slow" variables (Walker et al., 2012). These slow variables are excellent indicators of the medium- to long-term resilience of farms.

Promoting Buffer Capability via the Management of APS Diversity

Buffer capability is sometimes referred to as robustness or resistance in the literature (de Goede et al., 2013). It can be enhanced by planning within-farm diversity, which can in turn improve farmer profit (**Table 1**). For instance, replacing ryegrass-clover mixtures with multispecies pastures, including species such as chicory and alfalfa, increased profit in New Zealand dairy farms due to the increased biomass harvested on the farms. Nitrate leaching also decreased from 61 to 34 kg N/ha, indicating that multispecies swards can be a cost-effective way to reduce nitrogen leaching and achieve win–win options for grazing systems in terms of economic and environmental performance (Romera et al., 2017). Related to animal management, Diakité et al. (2019) assessed the profit stability of mixed dairy and beef cattle farms compared to that of specialized farms against variations in milk and meat prices. These authors simulated mixed farms and specialized cattle farms (dairy or beef) in the upland Auvergne area (France), while accounting for pasture agronomic potential, field configurations and animal productivity. The model outputs revealed that mixed cattle farming would be an effective strategy to manage market risks, as it provides a good balance between higher annual net profit and less variability in net profit (**Figure 5**). As discussed in the previous section, grazing different animal species on the same plots offers various levers to increase the buffer capability of multi-species APSs. Co-grazing cattle and sheep has also been shown to improve the abundance and diversity of six groups of above-ground and below-ground organisms (plants, herbivorous insects, predatory insects, soil bacteria, fungi, and nematodes; Wang et al., 2019). This confirms that APS diversity is a key aspect to consider in system design in order to come to win–wins balancing productive and environmental goals.

Buffer capability can also be promoted by planning interactions among system components. Sneessens et al. (2019) analyzed the economic results of 208 French crop–livestock farms over a 14-year period. Farms that were more diverse and had more crop–livestock interactions had higher and less variable annual income. They experienced fewer economic disruptions and required less time to recover after a disruption. Farmers promoting interactions among crop and livestock components within a farm had lower expenses in terms of energy per hectare, water per hectare, and feed concentrate consumption per animal, thereby displaying better environmental performance patterns. In the beef-farm network of the Charolais area, the higher resource-use efficiency of organic beef farmers that fed their cattle with grasslands, grain produced on-farm and crop residues decreased production costs by 30–35% and increased the net-income per worker by 20% (Veysset et al., 2014). Such a reduction in market dependency via increased self-sufficiency and high resource-use efficiency was also reported in Mediterranean pastoral systems (Bernues et al., 2011) and in organic dairy cattle farms (Perrin et al., 2020).

Although APS diversity and interactions among system components are needed to promote system buffer capability and enhance farmer profit and economic-environmental trade-offs, there is a theoretical diversity optimum beyond which system resilience would be compromised by the level of APS diversity and interactions (**Figure 6**). Biggs et al. (2012) suggested that though low levels of diversity limit options for adapting to change, high levels of diversity in interconnected farming systems would be too complex to manage due to an inability to integrate all the possibilities and parameters into an analysis, leading to system stagnation. Social lock-ins occurring at the implementation stage can thus compromise the achievement of better trade-offs among economic and environmental performance expected at the farming design stage.

Promoting Adaptive Capability via the Management of APS Diversity

Adaptive capability is sometimes referred to as flexibility (Astigarraga and Ingrand, 2011; Nozières et al., 2011) in the

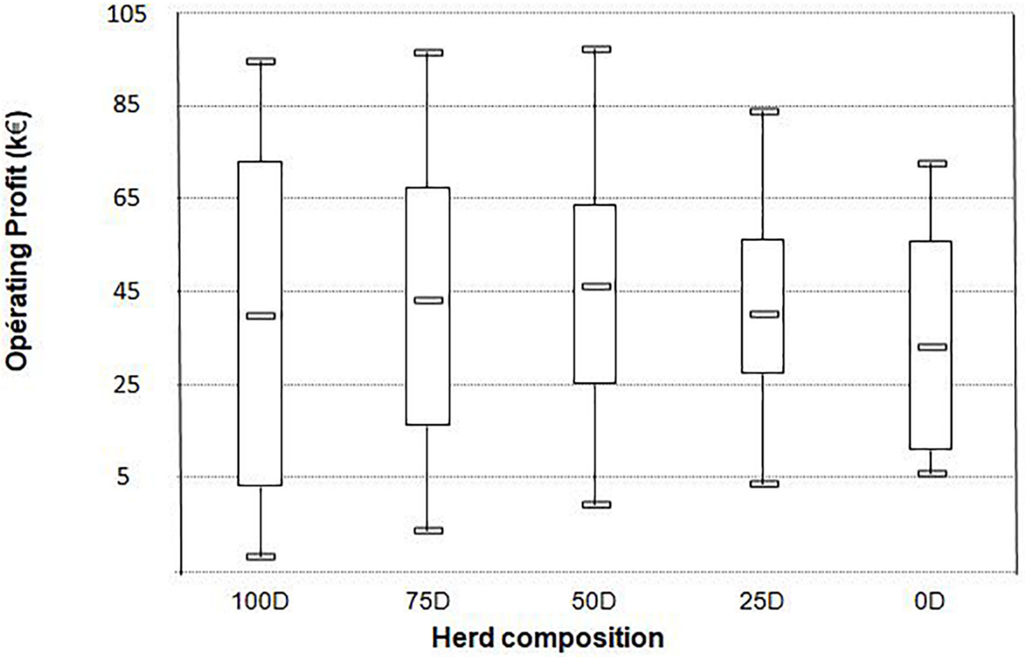

FIGURE 5 | Boxplots of net profit from 27 simulations in scenarios of a mixed dairy-beef farm in French Massif central, in which prices of milk, beef, and concentrate feed varied simultaneously among three levels [adapted from Diakité et al. (2019)]. D represents the relative proportions of dairy cows, so that 75D is a 75–25% dairy-beef combination. Net profit was on average higher in the 50–50% dairy-beef combination (50D), while profit variability was the lesser in the 25–75% dairy-beef combination (25D).

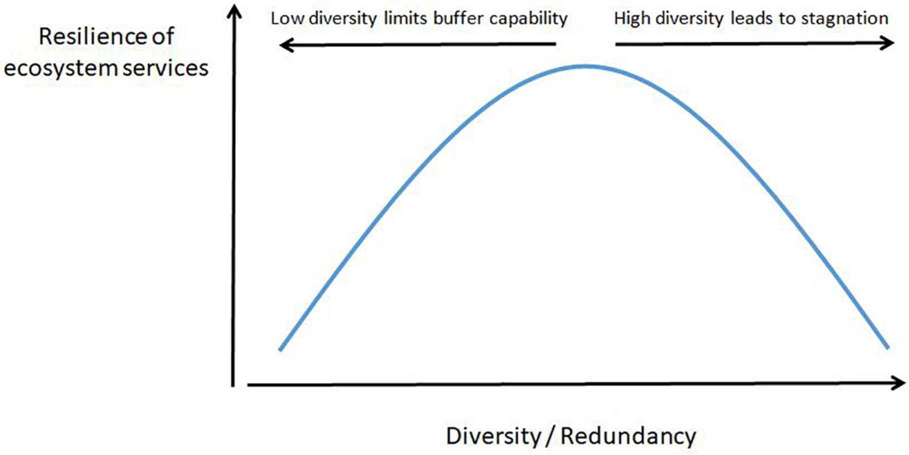

FIGURE 6 | Theoretical relationship between system diversity/redundancy and the resilience of ecosystem services [adapted from Biggs et al. (2012)]. The shape of this curves suggests an optimum beyond which system resilience would be compromised by the level of APS diversity and interactions.

literature and could be promoted by within-farm diversity. When focusing on the pasture and crop component, dual purpose crops (**Table 1**) can be used by farmers to adapt to the conditions of a specific year. This practice consists of grazing the crop during the early vegetative stages and harvesting grain at maturity. The use of dual-purpose crops has a limited impact on yield (−7 ± 25% across 270 experiments; Harrison et al., 2011) and avoids using extra area to feed livestock, thereby limiting feed-food competition and the environmental footprint of livestock farming. In the case of a feed shortage, it is also possible to feed ruminants tree foliage [e.g., from ash (*Fraxinus excelsior* L.) in temperate areas or *Leucaena leucocephala* in the tropics] as part of their daily diet, with similar environmental side-effects than dual-purpose crops.

When focusing on the animal component, farmers can lengthen the animal productivity lifespan (thus enhancing diversity in animal age classes) and thus increase production efficiency, as the proportion of the animal lifespan during which it is non-productive is proportionally lower. At the farm scale, it is also possible to adapt the type of product sold to the market conditions. For instance, in Limousin, France, calves can be sold as lean male calves just after weaning or as young heifers for fattening, fattened heifers or as reproductive females (Astigarraga and Ingrand, 2011). Selling animals to decrease stocking density is a classical way to adapt to unfavorable grass growth (**Table 1**). In Uruguayan grasslands, decreasing beef farm stocking density was shown to increase farm technical and economic performances and alleviate the effects of climatic variability (Do Carmo et al., 2016) thus increasing farm resilience. In multi-species herbivore systems, the breeder can also adapt to climatic shocks or price fluctuations in the short and medium term by juggling the relative weights of the two herds (Nozières et al., 2011). After considerable herd mortality, adaptive capability consists of selling part of the resistant, slow-growing species that survived to buy animals from less resistant but fast-growing species. For instance, Mongolian herders temporarily replace their camels and horses by goats after substantial winter die-offs (Joly et al., 2019). Similar trait-based exchange strategies involving camels and small ruminants are used in sub-Saharan Africa to mitigate the effects of severe droughts (Mace, 1990).

Promoting Transformative Capability via the Management of APS Diversity

Transformative capability can also be promoted by enhancing within-farm diversity. Hansson et al. (2010) described two ways to transform a farm through diversification toward enhanced resilience: either by adding a new activity (fattening, adding a new species, etc.) within conventional APS or by developing a para-agricultural activity using the farm's resources, such as a processing enterprise (farm-made cheese, processing pork into sausages, etc.) or agritourism (**Table 1**). López-i-Gelats et al. (2011) reported these two farm trajectories in the Pyrenees with some farms relying on agricultural diversification (via the management of APS diversity) and others implementing farmland diversification (i.e., the shift away from the production of food to exploit the multifunctional nature of agriculture, e.g., through agritourism). They also identified a further level of diversification, labor diversification, which relates to the shift from family labor toward off-farm employment.

According to Chavas (2008) diversification of APS could generate two forms of benefits that could strengthen farm resilience: 'the presence of economies of scope, reflecting the reduced cost associated with producing multiple outputs, and the risk-reducing effects of diversification.' However, we still lack evidence of the economic benefits of transformative farm diversification, especially from a resilience perspective. For instance, in the Charolais area, conventional mixed crop–livestock farmers who sell both meat and cereals seemed unable to take advantage of economies of scope due to the lack of interactions between the crop and beef components of their systems (Veysset et al., 2014). This may relate to the above-mentioned social lock-ins especially management complexity. The risk-reducing effect of transformative diversification was, however, mentioned by Valenti et al. (2018) as a factor of resilience in aquaculture. In a multispecies livestock system, adding pigs or poultry, which have a short production cycle, to a beef or dairy cattle system (i.e., a long production cycle) could lead to more regular cash inflows and more stable incomes thereby indirectly enhancing farm resilience (**Table 1**). Together with a reliance on different global markets (i.e., pork and milk/dairy), such a transformative diversification of APS is assumed to stabilize farm financial situations and can thus be seen as part of the securitization strategy of farmers. In multispecies livestock systems, pork and poultry, for which there is a high consumer demand across Europe (Centner, 2019; Rauw et al., 2020) could be used as call-products to attract and retain local customers; this again enhances farm resilience. It was thus recently shown that there is a demand among consumers from central France for beef-pork-vegetable 'baskets,' which benefits the commercialization of local beef products (Vollet and Said, 2018). Having a diversified range of products for sale also facilitates the use of short supply channels and may contribute to enhancing customers' interest in local products. However, meat processing on-farm usually requires a major initial investment. Developing a new production line can also lead to the need to hire new farm workers, as introducing a new livestock species to a farm requires additional technical skills. These investments imply taking a financial risk and may thus prevent farm diversification, and its positive effects on resilience. Still some of these transformative diversification pathways are well-documented. For instance, combining pig and cattle production (mainly dairy cattle) at the farm level is common in France, where 38% of pig farms (corresponding to 27% of pork production) are associated with ruminants (Dourmad et al., 2018).

CONCLUSION

In this paper, we have discussed examples from various types of APSs, including aquaculture, rabbit, monogastric, and ruminant systems. In addition to theoretical developments, evidence reveals that the benefits of diversity are grounded in the inter-individual, inter-breed or inter-specific variability in response to environmental conditions. The benefits of diversity were observed not only in relatively extensive systems but also in intensive indoor systems for fish, rabbit, and dairy production. Therefore, the level of system intensification does not seem to prevent the use of inter-individual diversity as a driver for resource-use efficiency and farm resilience. This, however, requires that animals are phenotyped to capture the trade-offs between their life functions and to describe their adaptive capacities. The benefits of diversity also arise from a network of interactions generating emergent properties at the farming system level. Management practices can modulate the scale and direction of interactions among plants and animals or among animal components so that synergies occur.

These findings allow us to define a number of research priorities. It is still necessary to address the empirical evidence on the linkages between APS diversity and resilience under a larger range of conditions. This involves monitoring system resilience based on long-term farm surveys and the prioritization of individual life functions throughout animal productive lifespans, e.g., across all subsequent lactation cycles. This could be achieved through the coordinated use of European[1] or global research infrastructures. To ensure general insights, a common set of indicators across a range of experimental or commercial farms still needs to be defined, together with a standardized description of APSs, especially their diversity and the perturbations they face. Once this indicator issue has been solved (and more data are available), a research avenue will be to carry out a meta-analysis of the effects of diversity on farm performance and resilience. Simulation modeling could also allow extrapolation of the findings from these surveys and experiments by directly exploring the strength, direction, and synergic effects of inter-individual, inter-breed, inter-specific, and crop–livestock interactions. A further step will be to include the knowledge of the linkages between APS diversity and resilience into co-designed approaches. These can be used to guide farmers toward adaptive or transformative changes, leading to the increased use of the potentialities of APS diversity.

AUTHOR CONTRIBUTIONS

BD led the writing and revision process, with all co-authors agreeing on manuscript structure, contributing to manuscript development, and reviewing the final version of the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

This position manuscript was initiated by INRAE Phase Division on Animal Husbandry and Livestock Farming Systems.

ACKNOWLEDGMENTS

We are grateful to Frédéric Joly, Bénédicte Lebret, and Claire Mosnier for helpful comments on a first draft of the manuscript. We also benefited from fruitful discussions with colleagues from PSDR4-Auvergne 2015–2020 project new-DEAL, and from the MIX-ENABLE project provided by transnational funding bodies, being partners of the H2020 ERA net project, CORE Organic Cofund, with the cofund from the European Commission.

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[1] https://www.smartcow.eu/

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Sustainable Food Systems

REVIEW
published: 29 July 2020
doi: 10.3389/fsufs.2020.00113

Integrating Animal Husbandry With Crops and Trees

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Per capita intake of animal protein is expected to increase globally through 2050, and the rate of increase will be more in developing or emerging economies than in developed countries. Global meat consumption between 1980 and 2050 is projected to increase from 133 million to 452 million tons, and 86% (279 million tons) of the increase will occur in developing countries. Animal-based agricultural systems occupy 45% of the global land area and contribute a large proportion of agricultural emissions. In addition to being a major source of nitrous oxide (N_2O), methane (CH_4), and other greenhouse gases (GHGs), livestock also use 8% of the global water withdrawal. The animal sector is dominated by resource-poor and small landholders of developing countries. Adverse effects of livestock on the environment are caused by the way animal husbandry is practiced, in no small part because animals are not integrated with other agricultural and forestry-based practices. Thus, improving and sustaining the livestock sector is critical to advancing the Sustainable Development Goals (SDGs) of the United Nations, especially SDG #1 (No Poverty), SDG #2 (Zero Hunger), SDG #6 (Clean Water and Sanitation), and SDG #13 (Climate Action). Separating raising of livestock from cultivating seasonal crops and perennial trees has decoupled the biogeochemical/biogeophysical cycling of carbon (C), water (H_2O), nitrogen (N), phosphorus (P), and sulfur (S). This decoupling is a causative factor of the increase in emissions of N_2O and CH_4, eutrophication and contamination of water resources, degradation of rangelands, and decline in its biodiversity. Therefore, identifying and adopting systems that integrate livestock with crops and trees are critical for reducing the environmental footprint of animal-based dietary products. Incorporating pastures/forages in the rotation cycle along with controlled grazing, called ley farming, and agroforestry, such as alley cropping, are examples of integrated farming systems. Other strategies of reducing the environmental footprint comprise the following: reducing enteric fermentation by precision feeding and matching dietary protein to animal need, processing CH_4 and N_2O emissions for other uses, and managing manure and other animal waste prudently. Other important considerations are adopting multiple GHG perspectives and minimizing gas swapping, reducing wastage of animal products, decreasing the use of antibiotics, and restoring rangeland for sequestration of atmospheric CO_2 as soil organic matter.

Keywords: gaseous emissions, food security, ecological footprint, sustainable development goals, waste management, farming systems

OPEN ACCESS

Edited by:
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Reviewed by:
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Specialty section:
This article was submitted to Agroecology and Ecosystem Services, a section of the journal Frontiers in Sustainable Food Systems

Received: *17 March 2020*
Accepted: *23 June 2020*
Published: *29 July 2020*

Citation:
Lal R (2020) Integrating Animal Husbandry With Crops and Trees. Front. Sustain. Food Syst. 4:113. doi: 10.3389/fsufs.2020.00113

INTRODUCTION

The domestication of animals, which started as early as the 12th millennium circa BP (Zeder, 2008), began with dogs and was followed by that of ruminants (i.e., goats, sheep, cattle). Chickens were domesticated about 10,000 years ago, followed by oxen and horses as beasts of burden for plowing and transportation (Rutledge and McDaniel, 2011). Over millennia, the cultivation of crops was closely integrated with that of raising livestock. Since the mid-twentieth century, however, the separation of raising livestock from the growing of crops has caused environmental issues such as the degradation of soil health, eutrophication of water, emission of greenhouse gases (GHGs) into the atmosphere, and loss of biodiversity (Peyraud et al., 2014).

Raising livestock separately may not be a sustainable option (Broom et al., 2013) economically, pedologically or ecologically. In view of the numerous demands of the growing and increasingly affluent human population, achieving food and nutritional security is seemingly at odds with the necessity of reducing the negative environmental footprint of agriculture. An important cause of this dilemma may be the simplification of agro-ecosystems, and the attendant decline in diversity of farming systems at the soil scape, landscape, and the farm scale (Lemaire et al., 2014). The adverse effects of livestock on the environment are attributed to the way in which the animals are raised, and such issues can be addressed (Dalibard, 1995). In some climates and landscapes, separating livestock from crops and trees is an important cause of the decline in diversity at the farm scale, with the attendant adverse impacts on the environment. Such a simplification and loss of biodiversity also leads to decoupling of the cycling of carbon (C) from those of water (H_2O), nitrogen (N), phosphorus (P), and sulfur (S) (Lal, 2010). Cycles of N and C, closely connected to livestock's role in land use and land use change (Steinfeld et al., 2006), may be decoupled by this simplification of the farming system. Emission of GHGs (i.e., CH_4) is exacerbated when ruminants are concentrated, which tends to uncouple the C and N cycle by releasing the digestible C as CO_2 and CH_4 and digestible N in waste as N_2O (Soussana and Lemaire, 2014). The risks of uncoupling, which has severe implications to climate change because CH_4 and N_2O have a high global warming potential (GWP), can be minimized by integrating livestock with crops and trees. Practices such as establishing vegetation buffers on agricultural fields to enhance biodiversity and conserve soil and water (i.e., agroforestry or alley cropping), can also reduce the environmental footprint of livestock raised on the same land unit (Goldstein et al., 2012).

The objectives of this article are to discuss: (1) the potential and challenges of increasing food and nutrition for the growing human population by raising livestock, (2) the livestock sector and the Sustainable Development Goals (SDGs) of the United Nations, (3) the conceptual basis of integrating livestock with crops and trees to increase the biodiversity of farming systems, (4) the options for sustainable management of grasslands for food and climate security, (5) the potential of integration of livestock with crops and trees to sequester carbon and reduce gaseous emissions, and (6) improved management of livestock in the tropics.

THE POTENTIAL AND CHALLENGES OF INCREASING FOOD AND NUTRITION FOR THE GROWING HUMAN POPULATION BY RAISING LIVESTOCK

Fears of widespread famine were aggravated by the rapid population growth during the 1950s and 1960s (Ehrlich, 1968). The human population of 2.56 billion (B) in 1950 increased to 3.04 B in 1960, 3.71 B in 1970, and 4.34 B in 1980 at the 10-year growth rate of 18.9, 22.0, and 20.2%, respectively. The fears of widespread famine were averted by the spectacular increase in yields of cereal crops, achieved through the Green Revolution during the 1960s (Pingali, 2012). However, the world population has increased to 7.8 B in 2020 and is projected to be 9.8 B by 2050 and 11.2 B by 2100 (UN, 2019b). Whereas 820 million people are prone to undernourishment (FAO, 2017), about 2 B are suffering from malnourishment because of deficiencies in protein, micronutrients, and vitamins (Ritchie and Roser, 2019). However, the livestock sector can play an important role in eliminating hunger and malnourishment.

Since the 1960s, large parts of natural lands have been converted into agro-ecosystems to feed the growing world population. In addition to reducing biodiversity, conversion of natural ecosystems at a larger scale has also depleted and contaminated water resources, polluted air, and exacerbated the emission of GHGs into the atmosphere. There has also been a growing interest in increasing animal products to address malnourishment. The global population of livestock (i.e., cattle, sheep, goats, pigs, poultry) has increased drastically since the 1950s. This increase in both populations (i.e., human and animals) has also led to a growing concern whether the biosphere has the capacity to support such large populations of domesticated livestock and people.

The human population has increased from about 10–20 million at the dawn of settled agriculture to about 7.8 B ($\sim$10,000 times) in 2020 (UN, 2019a), and there is an equally alarming growth of the population of domesticated livestock. While the cattle population has declined from a of high of 1.4 B in 2011, it still remains at $\sim$1 B in 2019 (The Economist, 2011; Shahbandeh, 2019). The global average stock of chicken is estimated at 19 B, and that of sheep and pigs at about 1 B. Global demand for animal-based produce is projected to double by 2050 (Herrero et al., 2009) because of the increasing affluence and the change in dietary preferences (Rojas-Downing et al., 2017). The global population of bovines is projected to increase from 1.9 B in 2010 to 2.4 B in 2030, 2.6 B in 2040, and 2.64 B in 2050 (Rosegrant et al., 2009; Thornton, 2010). The human population is increasing at an average global annual rate of 1.2%, but the population of domesticated livestock is increasing at an annual rate of 2.4%. The geographical distributions of livestock population also vary widely depending on biophysical, socio-economic, and cultural factors (Gilbert et al., 2018).

Along with the livestock population, the amount of livestock produce is also growing rapidly. Between 2000 and 2050, global production is projected to increase from 229 to 465 million tons of meat and 580 to 1043 million tons of milk (FAO, 2006; Steinfeld et al., 2006). More than 60 B land animals are used worldwide for meat, egg, and dairy production, and the global population of livestock may exceed 100 B by 2050 (Yitbarek, 2019), when the world's meat production is projected to double (FAO, 2019). All trends from 1980 to 2002 indicate that meat consumption increased from 47 million to 132 million tons in developing countries (NAS, 2015). All trends from 1980 to 2050 indicate that meat consumption is projected to increase from 86 million to 120 million tons in developed countries and 47 million to 326 million tons in developing countries (NAS, 2015). By 2050, the increase in meat production may be 290% for pig meat, 200% for sheep and goats, 180% for beef and buffalo meat, 180% for milk, 700% for poultry meat, and 90% for egg (Yitbarek, 2019). Similar to meat products, production of milk is also increasing globally. With a current average milk consumption of 100 kg per person per year (Reay and Reay, 2019), the projected increase in population will increase milk production as well. Each liter of fresh milk is equivalent to 3 kg of GHG emissions (Reay and Reay, 2019).

The strong nexus between livestock and anthropogenic climate change can neither be denied nor ignored. Indeed, livestock impact climate change, and the rapidly changing climate is also impacting livestock. It is precisely in this context that integrating livestock with crops and trees can play an important role in re-greening of the planet (Janzen, 2011). Harnessing the positive effects of livestock-based farming systems (e.g., nutritious food, eliminating hunger and hidden hunger) can lead to sustainable management of crops and trees and reduce the environmental footprint of farming (Herrero et al., 2009). In addition, sustainable management of rangelands by adopting ecologically based principles of animal husbandry can strengthen the provisioning of ecosystem services (ESs) from these fragile and ecologically-sensitive but economically important ecoregions (Havstad et al., 2007).

LIVESTOCK SECTOR AND SUSTAINABLE DEVELOPMENT GOALS OF THE UNITED NATIONS

The highly dynamic livestock sector is rapidly changing in response to the ever-increasing demands of the growing population, especially in developing countries. Thus, judicious management and eco-intensification of livestock-based systems can also address the daunting challenge of advancing the SDGs of the United Nations (**Figure 1**) because site-specific integration of crops with livestock is critical to advancing several SDGs. Specifically, prudent management of livestock can advance SDG #1 (No Poverty) by improving income of small landholders as well as that of commercial farmers. For small landholders in developing countries, livestock are not only a source of nourishment, they are also a source of renewable energy through draft animals, use of dung as household fuel, and also a source of manure as an amendment for crops. In addition to addressing the vulnerability of 820 million under-nourished people, most of them concentrated in South Asia and Sub-Saharan Africa (FAO, 2017), judicious production and use of animal-based diet can also alleviate malnutrition (hidden hunger) affecting 2 B people globally. Thus, livestock are critical to advancing SDG #2 (Zero Hunger).

The livestock industry, which consumes 8% of the global water supply (Schlink et al., 2010), has a strong impact on SDG #6 (Clean Water and Sanitation). Livestock production involves the use of both blue and green water (Falkenmark, 2003). Nearly one-third of the total water footprint of agriculture in the world is related to animal products (Mekonnen and Hoekstra, 2012), and beef has a larger water footprint than poultry and pork (Gerbens-Leenes et al., 2013). Therefore, reducing the water footprint of livestock, an important consideration of eco-intensification of livestock-based systems (Doreau et al., 2012), can advance SDG #6. Judicious management of livestock and rangelands is critical to improving the quality and renewability of water through buildup of soil organic matter content that can enhance soil water storage and denature and filter pollutants.

In addition to water, reducing emissions of GHGs from the livestock sector is pertinent to advancing SDG #13 (Climate Action). Because of its importance, the interaction between climate change and the livestock sector is now widely recognized (Thornton et al., 2009). Livestock are responsible for a large part of agricultural emissions (Gill et al., 2010; Havlík et al., 2014). Agriculture contributes about 10–12% of the current anthropogenic emissions. Some estimate that direct livestock non-carbon dioxide emissions caused about 19% of the total modeled warming of 0.81^{O}C from all anthropogenic emissions in 2010 (Reisinger and Clark, 2018). GHG emission per unit of livestock product is more in ruminants than that in monogastric animals (Gill et al., 2010). Because of the high global warming potential (GWP) of CH_4 and N_2O, it is appropriate to combine the cumulative effect of all GHGs into CO_2-equivalent (Pitesky et al., 2009).

CONCEPTUAL BASIS OF INTEGRATING LIVESTOCK WITH CROPS AND TREES

Livestock use 30% of the Earth's entire land surface as permanent pastures; 33% of arable land is used to produce feed for the livestock (FAO, 2006), and thus livestock have a large environmental footprint (Smith et al., 2013). Pelletier and Tyedmers (2010) projected that the livestock sector will even more strongly impact the environment by 2050 with regards to three issues: (i) climate change, (ii) reactive nitrogen mobilization, and (iii) appropriation of plant biomass at a global scale. Pelletier and Tyedmers also predicted that the livestock sector alone may overshoot humanity's "safe operating space" by 2050 in each of these three domains. While (FAO, 2006) estimates in the report "Livestock's Long Shadow" have been strongly debated (Maday, 2019), emissions of GHGs from the livestock sector, especially that of CH_4 and N_2O, can be reduced and managed by adapting the integrated systems presented herein.

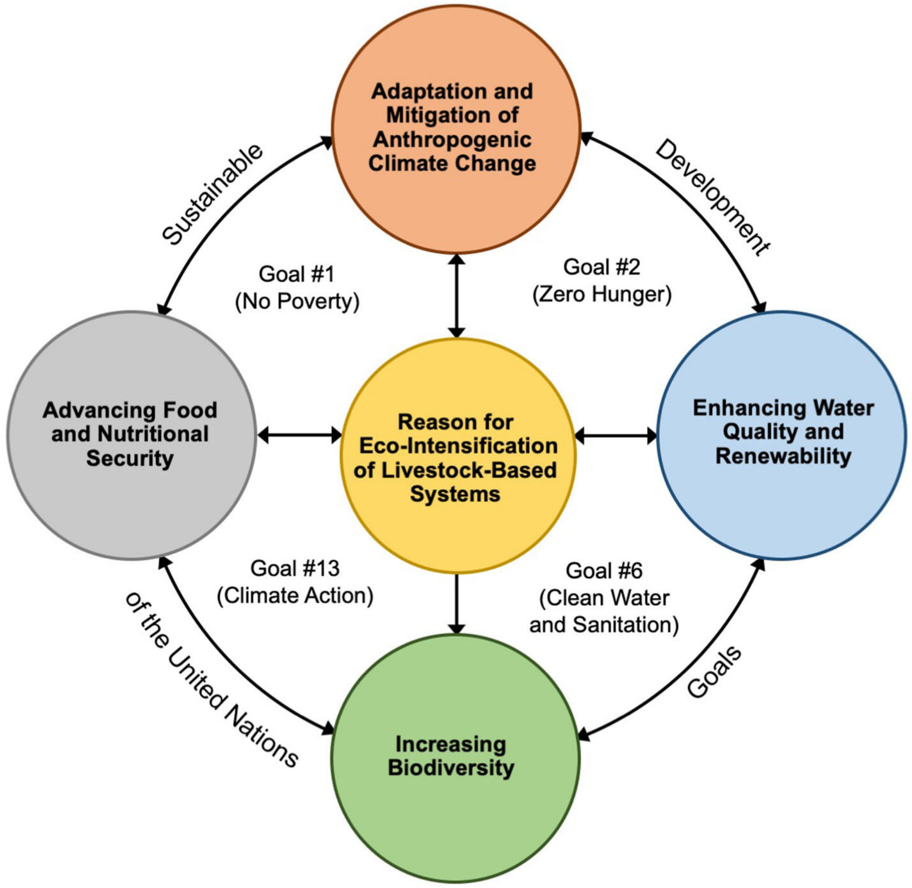

FIGURE 1 | Eco-intensification of livestock-based systems to advance the Sustainable Development Goals of the United Nations.

It is also pertinent to carefully choose site-specific sustainable livestock production to reduce or mitigate emissions, and to develop policies that promote climate change adaptation and mitigation options (Rojas-Downing et al., 2017). Some concerns about the impacts of animal-based diet (Pitesky et al., 2009; Gerber et al., 2013b; Eshel et al., 2014; Hedenus et al., 2014) can be addressed through a judicious integration of crops with livestock. The latter can lead to an increase in the quantity and quality of food production and economic returns while also reducing pressure on land and water resources (Franzluebbers, 2007; Provenza et al., 2019).

Most emissions from the livestock sector occur in commodity (meat, milk) production or the supply-side. However, gaseous emissions are also affected by the demand-side, or the consumer population, which is not only growing in numbers but is also undergoing a nutrition transition in favor of the animal-based diet. Therefore, several studies have suggested that merely addressing the supply-side emissions from the livestock sector may be insufficient to limit the temperature rise to $<2^{\circ}$C, and addressing the demand-side is also necessary (Kiff et al., 2016; Scherer and Verburg, 2017). Indeed, demand-side mitigation measures—including preferences for a plant-based diet, along with eating more poultry and fish than red meat, or grass-fed rather than grain-fed meat – have a greater potential to reduce emissions (1.5–15.6 Gt CO_2-eq /yr) (1 Gt = gigaton = billion ton) than do supply-side measures (1.5–4.3 Gt CO_2-eq/yr) (Smith et al., 2013). An integrated and judicious management of crops and livestock may mitigate some of the negative environmental impacts on the supply-side when crops are grown separately from that of raising the livestock (Herrero and Thornton, 2013).

Ruminant production systems are under pressure for several reasons: (i) methane emission, (ii) inefficient use of land, (iii) feed-food competition, and (iv) weakening of key ecosystems services through large-scale conversion of grasslands to crop production for livestock. However, livestock can produce human food of high nutritional quality from marginal lands that are mostly unsuitable for crop production. Thus, a viable strategy may involve the following: (i) raising animals from feed that is non-edible for humans, (ii) grazing livestock on land not suitable for crop production, and (iii) reducing emissions of GHGs (CH_4, N_2O). Some site-specific grassland-based ruminant production systems are much more efficient than concentrate-based systems for producing protein (Peyraud and Peeters, 2016). The challenge

TABLE 1 | Examples of integrated livestock systems with crops and trees (Compiled from Kang et al., 1990; Leakey, 1996; McCown, 1996; Bajracharya et al., 1998; Garrett et al., 2004; Fike et al., 2016; Jose and Dollinger, 2019; Munsell and Chamberlain, 2019; USDA-NRCS, 2020).

Integrated system	Description
Sod-based	2–10 years of sod rotated with 1–8 years of cropping, or sod-inter-cropping
Cover crops as forage	Cover crop grazing by livestock to accomplish both production and soil conservation objectives
Ley farming	The growing of grass or legumes in rotation with grain crops as a soil conservation measure and to enhance soil fertility
Pasture cropping	Land management system that integrates cropping with pasture production and allows grain cultivation as a part of perennial agriculture
Dual purpose cereal crops	Growing of cereals (i.e., wheat, rye) as pastures from late autumn to early spring and then harvesting for grains
Agroforestry	Intentional integration of trees, forages, crops, and livestock with specifically designed spatial arrangements
Alley cropping	Planting rows of trees at wide spacings and on contour with grain crops grown in the alleyways between the rows. Trees are specifically chosen for fodder, biological nitrogen fixation, fuel wood, or fiber.

lies in developing sustainable systems of forage production that also lead to positive responses to societal demands for consuming more natural products (Peyraud and Peeters, 2016).

Site-specific options for integrated crop-livestock systems can also achieve synergies between agricultural production and environmental quality (Lemaire et al., 2014). **Table 1** outlines examples of sustainable intensification of livestock-based systems, involving judicious combinations of sod/forages with crops and trees, which address some concerns of ruminant production systems. The term "sod" refers to the soil surface when covered with grass, sward, or turf. By using grassland-based ruminant-livestock systems (GRLS) models of African Guinea Savanna, Bateki et al. (2019) observed that sustainable intensification of livestock, integrated with crops and trees, could increase food security of the growing African population.

Agroforestry is a set of technologies in which trees are sequentially or simultaneously integrated with crops and/or livestock in a wide range of integrated systems (Leakey, 1996). Alley cropping is a system of planting trees on the contour at a wide spacing (4–10 m apart) with a food crop grown in the alley ways between the rows of trees. Planting several rows of trees and shrubs, which can also be used as forage, is a system that integrates livestock with both crops and trees. Trees can also be harvested as a source of fuel wood. Such a complex system is an example of an agro-silvopastorial system (Okali and Sumberg, 1985; Kang et al., 1990). In temperate alley cropping systems, tree species may include hard wood veneer or lumber species; softwood species for fiber production, or fruits and nuts for food (USDA, 2020). Trees grown on the contour can also be used as filter strip and for contour farming in strip cropping (USDA-NRCS, 2020). Grain crops (i.e., corn, soybean, cowpeas) are grown when the trees are young. When the ground is shaded, forages can be harvested and cattle grazed, and the prunings can also be used as green manure for cereals (i.e., corn). Leguminous trees serve as a source of nitrogen to enhance soil fertility.

Models are needed for simultaneous quantification of C and N flows and how they are affected by different livestock-crop-tree management systems. Several whole-farm based models have tried to estimate gaseous emissions (Snow et al., 2014; Bateki et al., 2019), but there is a need for more data on nutrient and C flows at the field level (Snow et al., 2014).

OPTIONS FOR SUSTAINABLE MANAGEMENT OF GRASSLANDS FOR FOOD AND CLIMATE SECURITY

Site-specific options are needed for sustainable intensification of livestock systems in diverse socio-economic and biophysical regions prone to climate change. For example, livestock-based systems occupy 45% of the global land area; grasslands/savannas suitable for grazing cover 37% of Earth's surface area (NAS, 2015). These ecosystems are highly diverse and occur within the seasonally dry tropical to sub-tropical equatorial regions (Whitley et al., 2017). Savanna ecoregions, open-canopy and fire-dependent biomes, are also prone to climate change that may alter phenology, root-water access and fire dynamics (Whitley et al., 2017). Principal environmental drivers affecting biomass/feedstock productivity in savanna regions are water and nutrient availability, vapor pressure deficit, solar radiation and fire (Devi Kanniah et al., 2010). Therefore, understanding these controls and their management through eco- intensification is critical for enhancing net primary productivity (NPP) under the changing global environment (Kanniah et al., 2013). Important controls include restoring soil functions, conserving water to minimize the risks of drought, and adopting improved species of forages and meat of better nutritional quality (Herrero and Thornton, 2013; Provenza et al., 2019).

Climate change is already adversely impacting agro-pastoral production in Africa (Stige et al., 2006; O'Mara, 2012). Under these conditions, Teague et al. (2011) observed that multi-paddock (MP) grazing may be an option for sustainable intensification. Teague and colleagues reported that MP grazing at a high stocking rate increased SOC content and cation exchange capacity of soil compared with light continuous and heavy continuous grazing. Similarly, Kleppel (2019) reported that microbial biomass in MP grazed soils was higher, more diverse, and contained relatively more fungal than bacterial biomass than did conventional management and hay field. A 2-year study in South Africa by Chaplot et al. (2016) showed that topsoil SOC stocks were significantly increased in soil with either livestock exclosure and NPK fertilization or high density and short duration grazing compared with annual burning, livestock exclosure and livestock exclosure with topsoil tillage. This was accomplished by high intensity, short duration grazing

TABLE 2 | Global land area under grasslands and the estimates of C sequestration (Adapted from Grace et al., 2006; Lal, 2008).

Ecosystem	Area (10^6 km^2)	Estimated carbon sink (Gt C/y)	Average carbon sink (ton C/ha·y)
Tropical savannas and grasslands	27.6	0.39	0.14
Temperate grasslands	15.0	0.21	0.14
Tropical forests	10.4	0.35	0.34
Boreal forests	13.7	0.47	0.34
Mediterranean shrublands	2.8	0.11	0.38
Crops	13.5	0.20	0.07
Deserts	27.7	0.20	0.07
Total	149.1	2.55	—

Gt = gigaton = billion ton.

(HDSD, 1200 cows per ha for only 3 days per year) followed by complete exclosure for the remainng 362 days each year (Chaplot et al., 2016). On the basis of a global assessment of holistic planned grazing, however, Hawkins (2017) concluded that only rangelands with higher precipitation have the resources to support MP grazing at a high stocking rate.

THE POTENTIAL FOR INTEGRATING LIVESTOCK WITH CROPS AND TREES TO SEQUESTER CARBON AND REDUCE GASEOUS EMISSIONS

Restoration and sustainable management of grasslands can play an important role in adaptation and mitigation of climate change (Lal, 2008). Technical potential of C sequestration in global savannas, through land restoration and integrated management of livestock with crops and trees, can be as much as 2.55 Gt C/y (**Table 2**). Pertinent animal feeding strategies (e.g, use of flax seeds, protein-intensive forages) can reduce enteric CH_4 and NH_3 emissions (Yáñez-Ruiz et al., 2018). Above all, carbon sequestration in grass—by planting species with high biomass production and biological nitrogen fixation, such as trees like *Acacia albida* and *Leucaena leucocephala* in west Africa (Kang et al., 1990; Pieri and Gething, 1992; Soussana et al., 2010)—is an important option to reduce net emissions from the livestock sector. In addition, recycling of livestock manure in a whole-farm perspective (Petersen et al., 2007) can reduce the input of fertilizers in croplands.

Adaptation and mitigation of climate change in the livestock sector requires translating of science into action by policy interventions that remove barriers to implementing proven technologies (Smith et al., 2007). Appropriate policy interventions are especially important in developing countries for achieving sustainable management of rangeland because of ecologically fragile and climatologically harsh environments. In India, for example, total annual CH_4 emissions, estimated at 9–10 Tg (Tg = teragram = 1 million ton) from enteric fermentation and animal waste (Sirohi and Michaelowa, 2007), can be reduced by appropriate policy interventions such as payments for provisioning of ecosystem services.

The goal of enhancing and sustaining agricultural production for meeting the needs of the growing population while reducing the environmental footprint of agriculture necessitates local and site-specific integration of cropping with livestock systems. Soil C sequestration and decrease in gaseous emissions are in accord with SDG #13 of the U.N. Therefore, site-specific technologies for integrating livestock with crops and trees (**Table 1**) are needed to: (i) better moderate coupled biogeochemical cycles and reduce fluxes of pollutants into the atmosphere and the hydrosphere, (ii) create a more diversified and structured landscape mosaic that supports diverse habitats, and (iii) enhance capacity of the system to adapt to extreme events associated with climate change and alterations in the socio-economic and human dimensions (Lemaire et al., 2014). It is precisely in this context that management of grasslands can strengthen the coupled cycling of carbon (C) with those of H_2O, N, P, and S within vegetation, soil organic matter (SOM) stock and soil biota in general, but the soil microbial biomass in particular (Lemaire et al., 2014).

The schematic in **Figure 2** depicts the pathways of decreasing the environmental footprint of livestock products. Conceptually, choosing a livestock product with a lower emission footprint for a diet would reduce the overall negative impact on climate and the environment. The environmental footprint of a dietary product can be expressed in three ways (de Vries and de Boer, 2010): (i) per kg of product, (ii) per kg of protein, and (iii) per kg of average daily intake of each livestock product. Based on the lifecycle analysis (LCA) of 16 studies conducted in OECD (Organization for Economic Cooperation and Development) countries, de Vries and de Boer (2010) determined that the land and energy use and the GWP for 1 kg of product followed the order of beef > pork > poultry. This order was based on differences in feed efficiency, enteric CH_4 emission, and reproduction rates. Similar trends were reported by (Eshel et al., 2014).

Emissions of all gases (CO_2, CH_4, N_2O) are used to compute CO_2 equivalents (Lal, 2004). Direct emissions of CH_4 and N_2O in the livestock sector must be reduced. In this context, a multiple GHG perspective must be adopted (**Figure 3**) because CH_4 has a GWP of 21 and N_2O of 310. Because of the high GWP of CH_4 in both confined and grazing systems, steps must be taken to develop credible methods of measuring CH_4 emission by ruminants (Hill et al., 2016), and to reduce enteric fermentation by ruminants (Grossi et al., 2018). Precision feeding, matching feed intake with the need of the animal (Gerber et al., 2013a), and the choice of forages can also reduce the gaseous footprint. For example, the combination of highly digestible forages (Haque, 2018; van Gastelen et al., 2019) that contain secondary compounds such as tannins (Roca-Fernández et al., 2020) can also reuce methane emissions. The multiple GHG perspective is an important strategy that can address the potential pollution swapping—a reduction in one gas can lead to emission of another (Gerber et al., 2013a). Thus, a full accounting of all GHGs is required (Soussana et al., 2007).

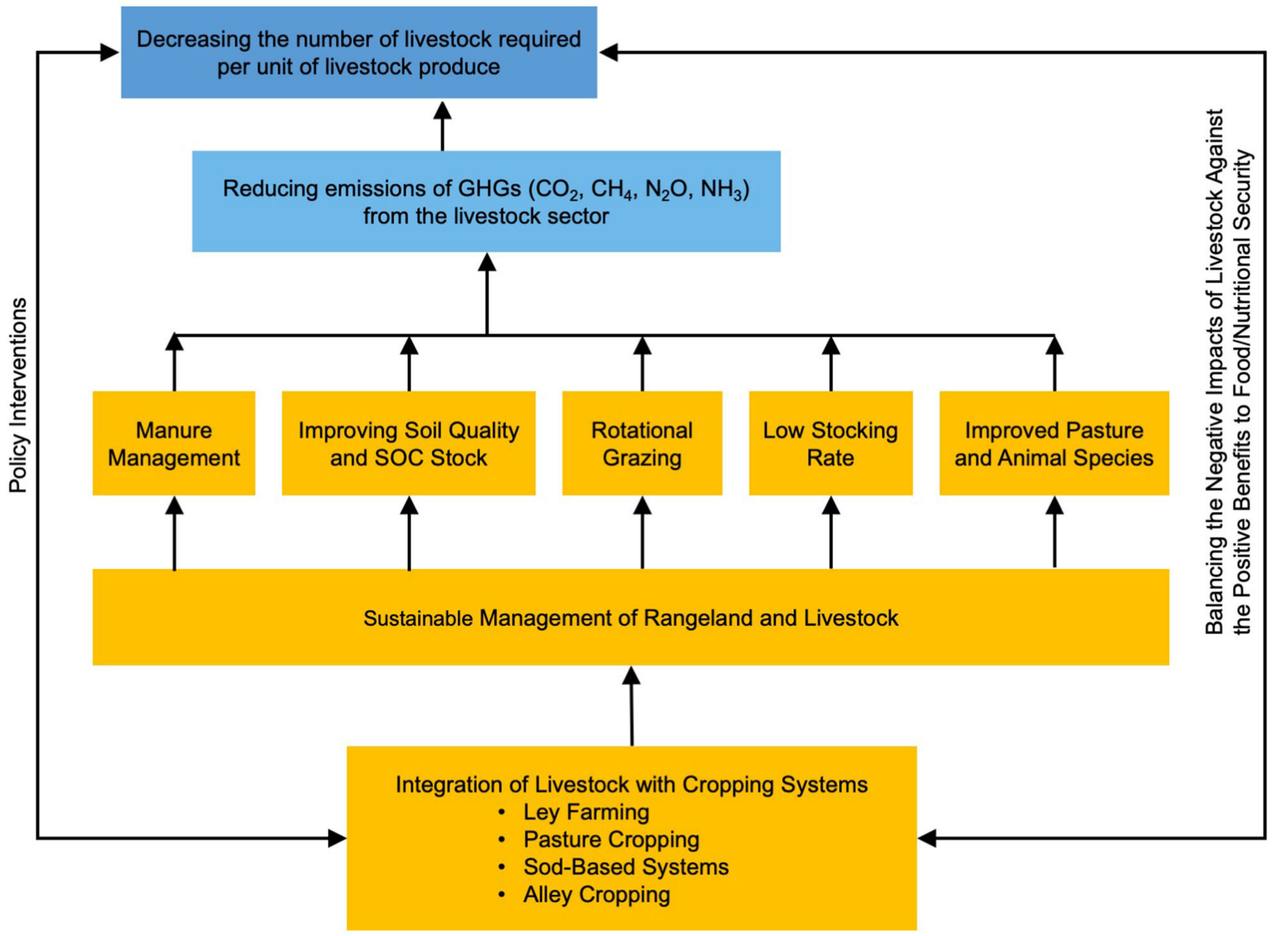

FIGURE 2 | A flow chart depicting the integration of livestock with arable land use for decreasing the number of livestock required (SOC, soil organic carbon; GHGs, greenhouse gases).

IMPROVED MANAGEMENT OF LIVESTOCK IN THE TROPICS

Livestock are an important component of agroecosystems in the tropics and adopting innovative livestock/farming approaches can enhance production and reduce environmental footprints. Judiciously combining crops with livestock within the same landscape has numerous co-benefits (Gil et al., 2015). For example, ley farming (Carberry et al., 1996; McCown, 1996), involving light grazing of legumes grown in rotation with crops, is a pertinent strategy for integrating crops and livestock. Built on the concept of ley farming, pasture cropping is a farmer-initiated concept of sowing a winter-active cereal into a summer-active native perennial pasture (Millar and Badgery, 2009). Self-regenerating annual legume pastures (Puckridge and French, 1983) can enhance soil fertility and increase cereal yield, along with more forage for sheep and cattle production. Ley farming, developed in Southern Australia since the 1930s, is also relevant to similar regions in Sub-Saharan Africa, South/Central Asia, and the Caribbean. However, soil/site specific choices of legumes and grazing patterns/intensity must be identified.

The numerous benefits of ley farming include (Bell et al., 2010): (i) enhancing soil N for the next crop, (ii) sequestering SOC and off-setting emissions, (iii) controlling weeds and other pests, (iv) minimizing risks of runoff, soil erosion, and deep drainage, (v) increasing livestock production, and (vi) sustaining crop yield. However, several challenges exist. Successfully implementing ley farming includes a critical appraisal of the following (Bell et al., 2010): (i) addressing difficulties with pasture establishment, (ii) suppressing/removing pasture plants before seeding crops, and (iii) reducing competition for water and some plant nutrients. Site-specific choice of pasture species is critical.

Integrating livestock with cropland and forestland can also be a prudent complimentary strategy. For example, growing Acacia albida (*Faidherbia albida*) as a permanent tree crop on farmlands (cereals, vegetables, and livestock) is a traditional agroforestry system in Sub-Saharan Africa (Poschen, 1986; Weil and Mughogho, 1993; Wanyancha et al., 1994). *Faidherbia* sp. has been widely used for enhancing soil fertility and as a source of

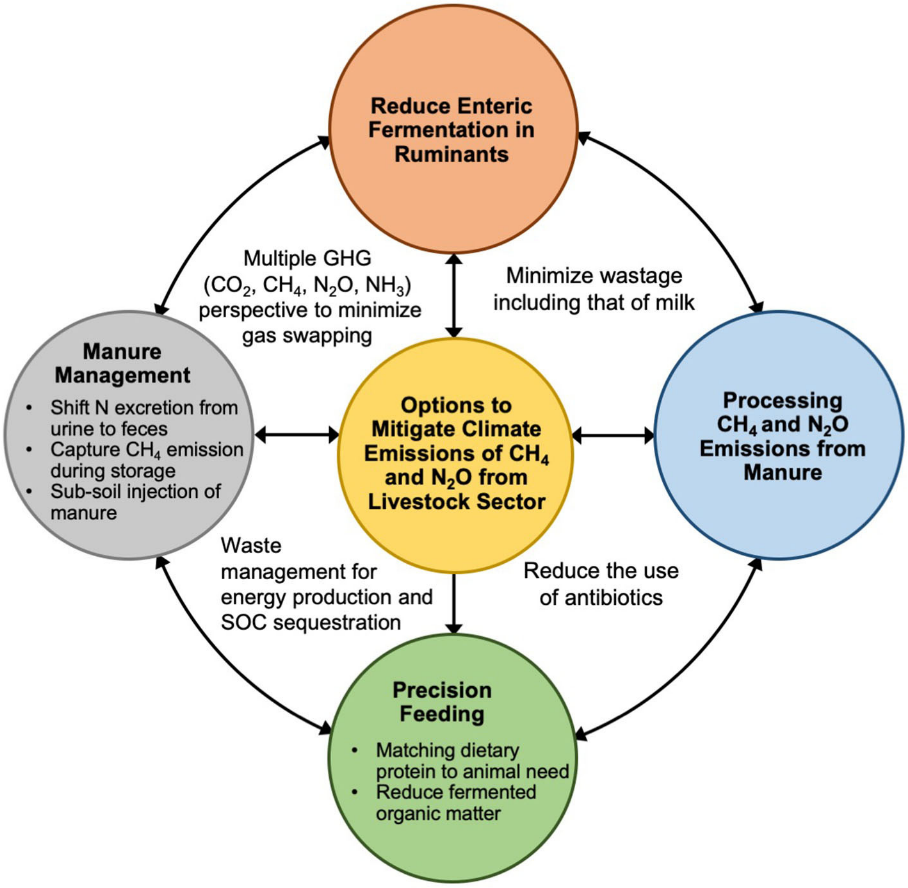

FIGURE 3 | Measures to reduce emissions of greenhouse gases (GHGs) from the livestock sector (SOC, soil organic carbon).

shade and shelter for livestock in Sub-Saharan Africa (Pieri and Gething, 1992).

Widespread adoption of integrated systems can reduce the risks of rangeland degradation, as seen in China (Hou et al., 2008). India provides an example of how integrated systems can reduce land area under pasture. With 2.3% of the global land area, India supports 18% of the human and 11% of the world's livestock population: the latter consists of 536 million animals and 740 million poultry in 2019, which are raised on only 12.3 M ha of land under permanent pastures and grazing land (TAAS, 2019).

Successfully integrating crops with livestock has numerous economic, ecological, and other benefits (**Figure 4**), especially in developing countries of the tropics (Herrero et al., 2013). Important among these are: (i) creating another income stream for farmers and alleviating rural poverty (De Haan et al., 2001), (ii) developing a safety net for the poor and especially women farmers, (iii) enhancing assets for farmers, and (iv) alleviating malnourishment (**Figure 4**). However, livestock need additional land, water, nutrients, and forage resources. Therefore, judicious management of the growth of this sector is critical, especially for reducing environmental footprints. These technical dimensions must be objectively considered within the context of institutional support (market) and the human dimensions (Tarawali et al., 2011).

CONCLUSIONS

Intensive farming, which is designed to produce large amounts of economic food to meet the demands of the growing and increasingly affluent human population by using high inputs on small areas, has its merits and demerits. Intensification of crops and livestock systems have drastically increased per capita food production since the 1960s. However, the environmental footprint of livestock sector must be reduced by decreasing soil degradation, increasing water and nutrient use efficiency, reducing eutrophication of water, decreasing pollution of air, and minimizing the risks to global warming. Despite the successes in food production, there are 820 M people vulnerable to undernourishment and more than 2 B to malnourishment caused by the deficiency of protein, micro-nutrients and vitamins. The proportion of vulnerable population may increase as a result of the COVID-19 pandemic. Thus, the objective of sustainable agriculture is

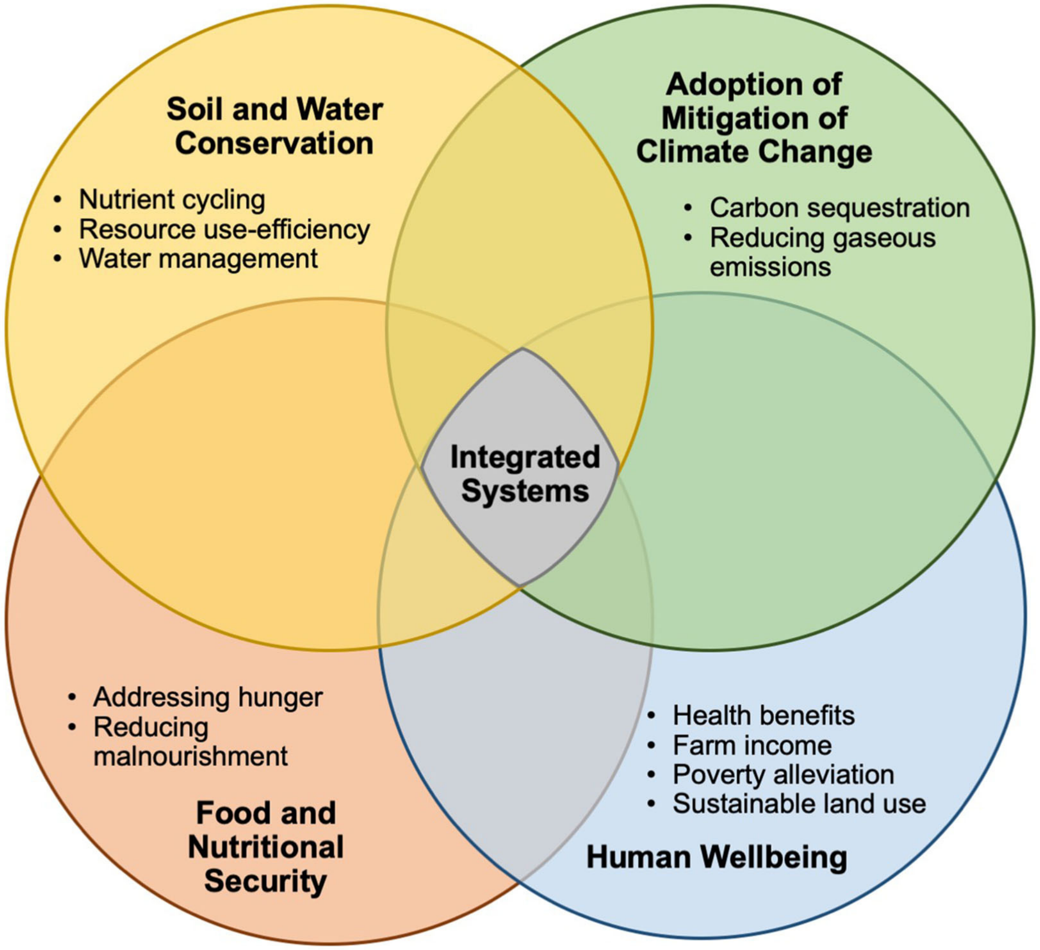

FIGURE 4 | Ecological and socio-economic benefits of integrating livestock with crops and trees.

to adopt technologies that increase production, reduce the environmental footprint of food production systems (IPBES, 2019; IPCC, 2019; UNEP, 2019), and also minimize any risks of diseases and infections through intensive livestock farming (Sigsgaard and Balmes, 2017; Smit and Heederik, 2017).

A feasible option to produce the required amount of nutritious food while restoring and sustaining the environment is through site-specific integration of livestock with crops and trees. Such an approach of eco-intensification would simultaneously achieve several overlapping and interconnected SDGs including #2 (Zero Hunger), #3 (Good Health and Wellbeing), #6 (Clean Water and Sanitation), #13 (Climate Action) and #15 (Life on Land). Ignoring such an option would aggravate risks of environmental pollution, exacerbate perpetuation of natural ecosystems, increase harmful interactions between humans and the wildlife, and even aggravate the frequency and intensity of tragedies such as the COVID-19 pandemic (Lal, 2020b). Some recommendations of the Conference of Parties (COP) of the United Nations Framework Convention to Combat Climate Change (UNFCCC) are also in accord with the strategies of integrating livestock with crops and trees. Examples of these are the "4 Per 1,000" initiative launched at COP21 in Paris in 2015 and "Adapting African Agriculture"of COP 22 in Marrakech (Lal, 2019, 2020a). The scientific community and land managers should seize the opportunity to adopt innovative options such as those outlined in this article and promote sustainable agricultural practices which reconcile the need for producing more and nutritious food with the absolute necessity of improving the environment. Integrating livestock with crops and trees can reduce direct non-CO_2 emissions and achieve the COP21 mitigation goal of limiting global warming to 2°C.

These efforts can be enhanced through research priorities identified by The Committee on Consideration for the Future of Animal Science Research (NAS, 2015). They include: (1) identifying appropriate mixes of intensification and extensification required to simultaneously increase production and reduce environmental footprints in different regions throughout the world, (2) enhancing sustainability of medium- and smaller-scale producers, (3) developing policy interventions to optimize demand for animal products, and (4) evaluating environmental impacts of diverse livestock-based production systems.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Sustainable Food Systems

ORIGINAL RESEARCH
published: 14 August 2020
doi: 10.3389/fsufs.2020.00118

Ecological Doctors in Maasailand: Identifying Herding Best Practices to Improve Livestock Management and Reduce Carnivore Conflict

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Ilkisonko Maasai pastoralists in the Amboseli ecosystem of southern Kenya earn livestock-based livelihoods in a difficult environment exacerbated by a range of challenges. In this setting, many stakeholders, including the Maasai themselves, have come to see traditional extensive pastoralism as essential to long-term social–ecological resilience. This includes the maintenance of communal land tenure, which protects both unfragmented landscapes and the cultural practices necessary to thrive therein. This land tenure system has also been well-documented to support diverse wildlife populations, including large carnivores such as the African lion. Lion Guardians is a conservation organization working on the group ranches of the Amboseli ecosystem to reduce human–lion conflict using culturally appropriate strategies, with a 13-year track record of reductions in lion killing as compared to other conflict mitigation approaches. However, in recent years, they have noted a marked increase in the amount of lost livestock. Lion Guardians' data indicate that untended livestock account for >80% of lion attacks, making them a primary driver of human–lion conflict in the ecosystem. In this paper, we present the results of a community-based qualitative study aimed at identifying the causes of lost livestock, in pursuit of win–win solutions for people and lions. Using an iterative multistage research process, we conducted interviews with more than 120 Maasai community members. Finding general agreement that lost livestock are a problem and that poor herding practices are the primary cause, we next sought to identify both herder and herder-mentor best practices. For this, we focused on the knowledge of elders and "master herders," those identified by their communities as especially adept and responsible herders. In creating these lists, we learned that herding best practices relevant to carnivore-conflict prevention are inseparable from those related to pasture management and livestock productivity and largely inseparable from traditional Maasai culture. This means that good herders, who have been called "ecological doctors," can support the vitality of not only plants and pastures but also lions, ecosystems, and entire human cultures.

Keywords: pastoralism, grazing management, African lion, human–wildlife conflict, Kenya, cattle, carnivore

Edited by:
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Specialty section:
This article was submitted to Agroecology and Ecosystem Services, a section of the journal Frontiers in Sustainable Food Systems

Received: *23 February 2020*
Accepted: *29 June 2020*
Published: *14 August 2020*

Citation:
Jablonski KE, Merishi J, Dolrenry S and Hazzah L (2020) Ecological Doctors in Maasailand: Identifying Herding Best Practices to Improve Livestock Management and Reduce Carnivore Conflict. Front. Sustain. Food Syst. 4:118. doi: 10.3389/fsufs.2020.00118

INTRODUCTION

Paralleling the situation of pastoralists in semiarid rangelands worldwide, Ilkisonko Maasai pastoralists in the Amboseli ecosystem of southern Kenya must navigate growing challenges to secure a livestock-based livelihood (BurnSilver and Mwangi, 2007; Reid et al., 2014; Galvin et al., 2015). These challenges include a highly variable climate, heterogeneous distribution of resources, conflict with wildlife, and population growth (Homewood et al., 2009). Additionally, for more than a century, Maasai across the region have been forced to adapt to repeated changes in government land tenure policy (including land seizure), misguided non-governmental organization interventions, incursions into communally held lands by outsiders, and, more recently, anthropogenic climate change (Fratkin and Mearns, 2003; Galvin, 2009; Bobadoye et al., 2016).

In this complex environment and amid growing sociocultural change, many pastoralists and affiliated stakeholders have come to see traditional extensive pastoralist culture as essential to long-term social–ecological resilience (Lesorogol, 2008; Groom and Western, 2013). This includes maintenance of communal land tenure as well as the associated preservation of unfragmented landscapes and the dynamic cultural practices necessary to thrive in them (Scoones and Graham, 1994). Apart from the inherent value of maintaining Maasai culture and the ecological value of maintaining pastoral mobility amid heterogeneously distributed forage, the protection of traditional extensive pastoral practices also holds promise to assist in maintaining viable wildlife populations outside of protected areas, including large carnivores such as the African lion (*Panthera leo* L.; Ellis and Swift, 1988; Boone and Hobbs, 2004; Mwebi, 2007; Groom and Western, 2013; Schuette et al., 2013).

This last assertion is perhaps counterintuitive. After all, lion killing resulting from depredation of livestock is one of the chief causes of the drastic and ongoing decline in lion populations across Africa (Woodroffe and Ginsberg, 1998; Ogada et al., 2003; Woodroffe and Frank, 2005; Hazzah et al., 2009). This has led many to conclude that the best way to conserve lion populations is to exclude pastoralists from vast areas in order to minimize interactions among livestock and lions (Packer et al., 2013).

However, historical and recent evidence indicate that a combination of effective livestock husbandry practices and culturally mediated tolerance can ensure the long-term viability of lion populations outside protected areas, a necessity if the species is to survive (Ogada et al., 2003; Hazzah et al., 2009; Dolrenry et al., 2014). We do not romanticize Maasai pastoralists or the challenges they face, which include overstocking of livestock and mismanagement of pasture resources. Nevertheless, we contend that traditional livestock husbandry practices, including herding, are not antithetical but instead essential to lion conservation in that they help prevent the vicious cycle of conflict that reduces tolerance and leads to lion killing.

Lion Guardians and Lost Livestock

Lion Guardians (LG) is a conservation organization working to enact culturally appropriate long-term solutions for people and lions to thrive together in the pastoral areas of East Africa. In the Amboseli ecosystem, the organization employs a team of more than 50 Maasai *ilmurran*, young warriors on whom their communities traditionally relied to kill problem lions, especially those that target livestock. Instead of hunting lions, these young men now work as "lion guardians" to monitor lions, mediate conflict, and serve as community liaisons. In combination with extensive community engagement by LG staff, this holistic approach has a lengthy record of significant reductions in lion killing compared to other conflict mitigation strategies (Hazzah et al., 2014). However, in the course of their work, LG staff, including many local Maasai, have identified one persistent cause of conflict that seems to be worsening despite their success—lost livestock.

Lost livestock leave the protection of the *boma* (night pen or *kraal*) with a herder in the morning but stray during the day and are often lost in the bush overnight. LG data show that lost livestock account for >80% of lion attacks on livestock in the Amboseli ecosystem, and the lion guardians have reported returning >15,000 lost livestock to owners each year. Lost livestock are also predated by other large carnivores such as spotted hyenas (*Crocuta crocuta* Erxleben), leopards (*Panthera pardus* L.), and cheetahs (*Acinonyx jubatus* Schreber). However, the reasons that Maasai herders lose livestock and how this might be prevented are poorly understood.

In this paper, we present the results of a qualitative study aimed at identifying community perceptions of causes and trends related to lost livestock in the Amboseli ecosystem. Our primary objective for the study was to seek solutions to the challenge of lost livestock in a way that provided value to both pastoralists and conservationists. We thus used the research process to identify management practices that could lead to win–win outcomes related to lost livestock. We ultimately came to focus on descriptions of herding best practices by elders and "master herders," those identified by their communities as being especially adept and responsible herders. By placing lessons from these experts in context with broader community perspectives, we were able to inform ongoing lion conservation efforts while focusing on outcomes of interest to Maasai research partners.

Fundamental to this work is the 13-year record of successful engagement and cooperation between Lion Guardians and the Ilkisonko Maasai communities of the Amboseli ecosystem and that most of the organization's staff are themselves Maasai. LG is embedded in the social–ecological landscape in which it operates, with a headquarters deep in the "bush" and a commitment to the local communities that extends well beyond lion conservation. Local Maasai were thus fundamentally engaged in the research, as well as within the iterative process wherein we continuously adapted our design to best meet the needs of the communities. Particularly, coauthor JM, an Ilkisonko Maasai from the Olgulului–Ololarashi Group Ranch, coled the design of the study and led or co-led as well as translated the interviews.

Study Area and Background

The study area was within the Amboseli ecosystem, a 5,975-km^2 region of semiarid grasslands and savannahs north of Mt. Kilimanjaro and west of the Chyulu Hills (**Figure 1**). Although

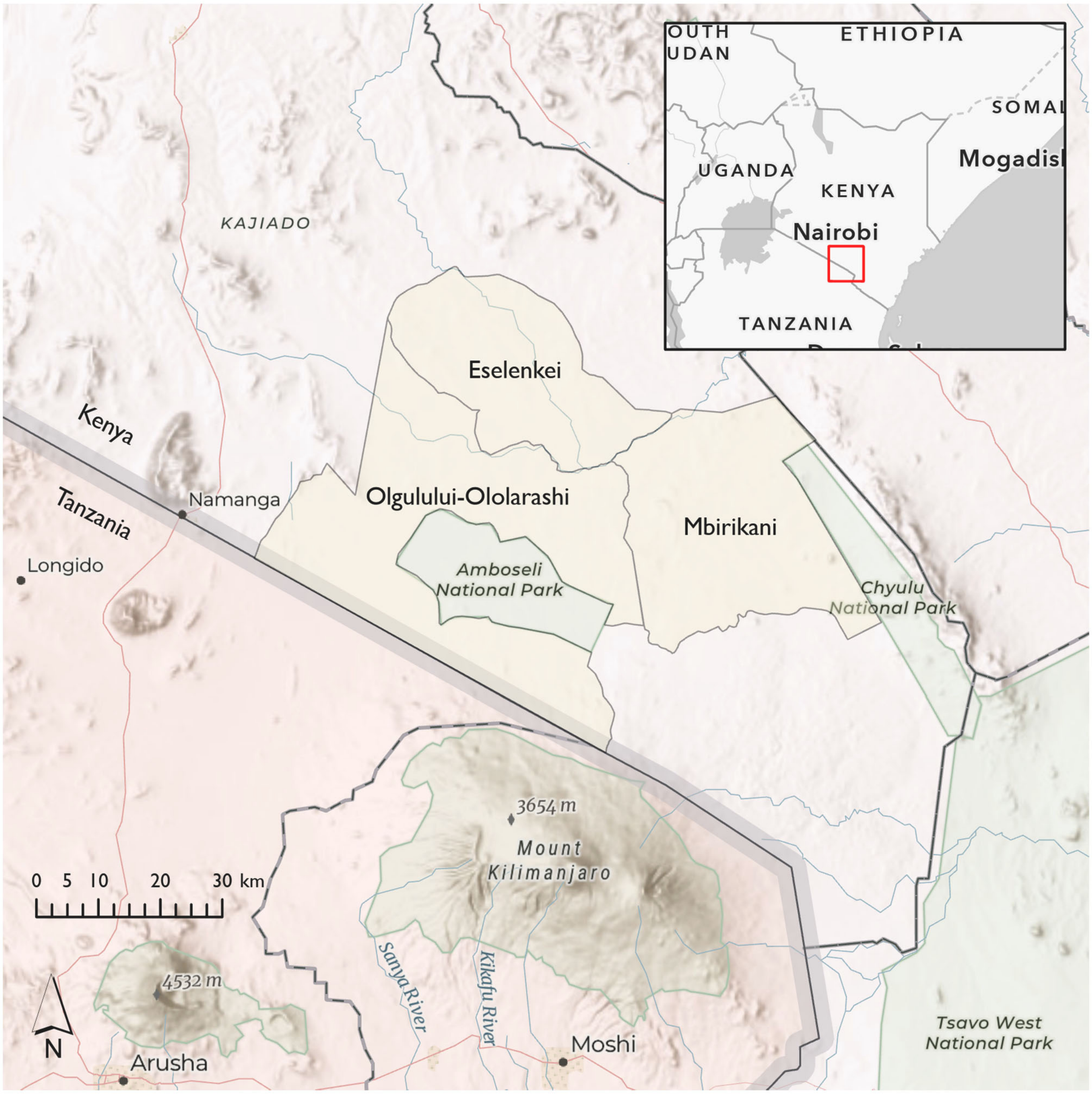

FIGURE 1 | Location of the study area, including the three Maasai group ranches.

Amboseli National Park is at the heart of the region, land tenure in the ecosystem is dominated by Maasai group ranches, which are communally owned and collectively managed. We focused our work on three of these group ranches: Eselenkei Group Ranch (748 km^2), Mbirikani Group Ranch (1,229 km^2), and Olgulului–Ololarashi Group Ranch (1,427 km^2) where LG has had a long-term presence, with guardian working territories covering most of the landscape.

An accurate human population count is difficult, as Kenyan national census boundaries do not overlap well with group ranch boundaries, but residents of the three group ranches likely number in excess of 30,000. Although income sources are increasingly diversifying, livestock such as cattle, sheep, and goats are the major livelihood source in the region, with an estimated 100,000 livestock spread across the three group ranches (BurnSilver, 2009; Hazzah et al., 2014). Nearly all livestock still rely on traditional pastoral extensive grazing for 100% of their feed, although some intensification has occurred in other aspects of livestock production, including the use of "improved" breeds and selling of animals (BurnSilver, 2009).

This extensive grazing is managed by herders, such that men and boys are responsible for cattle, which range further from the *boma*, and women and girls are responsible for sheep and goats, which stay close to home. The herder is responsible for watching over the herd from sunup to sundown, guiding them to good foraging areas and water and protecting them from predation or theft. Decisions about which areas are open to grazing and which are closed, as well as when herders can move cattle to temporary *bomas* to access forage located far from home, are made by elders. While open access (at least for other Ilkisonko Maasai) is the expectation for this decision making, it is subject to community-based negotiation, and resource use is carefully monitored and reported on by community members (Galaty, 1992). It is important to note that these livestock management practices are situated within a rapidly changing sociocultural landscape where economies, education, social networks, and land tenure are in flux (Homewood et al., 2009; Butt, 2015).

The group ranches also support diverse wildlife assemblages, including large herbivores such as zebra (*Equus quagga* Boddaert), wildebeest (*Connochaetes taurnius* Burchell), Thompson's gazelle (*Eudorcas thomsonii* Gunther), Grant's gazelle (*Nanger granti* Brooke), giraffe (*Giraffa camelopardalis* L.), and elephant (*Loxodonta africana* Blumenbach). Resident large carnivores include lion, spotted hyena, leopard, cheetah, black-backed jackal (*Canis mesomelas* Schreber), and the rare African wild dog (*Lycaon pictus* Temminck). Despite growing challenges, the continued coexistence of significant human, livestock, and wildlife populations makes the Amboseli ecosystem one of the world's great examples of conservation outside protected areas.

Maasai and lions interact within a complex cultural web of awe, fear, respect, and violence, wherein the lion is uniquely valued among all wildlife (Goldman et al., 2010). Although Maasai certainly resent and retaliate against lions that kill livestock, this is merely one aspect of a relationship that is continuously negotiated, across time and space with individual humans and lions, and mediated through social networks across Maasai communities (Hazzah et al., 2009; Goldman et al., 2010; Despret and Meuret, 2016; Dhee et al., 2019). It is thus important to recognize that lion killing by Maasai is motivated by diverse attitudes and experiences and is unlikely to ever be precipitated by a single livestock depredation event (Hazzah et al., 2017). Nonetheless, numerous studies have found a clear connection between livestock depredation by lions and lion killing by Maasai (Kissui, 2008; Ontiri et al., 2019).

METHODS

Throughout, this work was situated within a social–ecological framework wherein we sought to understand both social and ecological factors related to lost livestock in order to help "create beneficial feedback loops such that…ecological objectives are met in ways that benefit livestock operators and the broader society" (Hruska et al., 2017, p. 296). To do so, we used constructivist qualitative methods, which recognize human realities as complex and dynamic and acknowledge the researcher's role in constructing a story from data. Data collection was therefore iterative, interactive, and pragmatic, with analysis informing further data collection in cooperation with participants, with an aim toward thematic saturation (Saldaña, 2011; Denzin and Lincoln, 2018). We then used thematic analysis to encode responses in a collaborative process with research partners (Braun and Clarke, 2006).

We also structured the work to adhere to guidelines for responsible research practice with Indigenous communities (David-Chavez and Gavin, 2018). This means that the local Maasai were included in the decision to initiate the study; were continually engaged in study design, implementation, and analysis; and are leading the effort to appropriately disseminate results, among other important considerations. Overall, we worked to be non-extractive, with a focus on generating knowledge that will be useful to Maasai pastoralists rather than merely scientifically novel (Reid et al., 2016). At the same time, we approached the research participants as intelligent livestock producers with useful information that other livestock producers can learn from to improve their outcomes. This research was conducted with an exemption under Colorado State University IRB Protocol 204-18H.

Data Collection

We collected data in three stages. In all stages, participants were informed that participation was completely voluntary and anonymous and that the interview could be halted at any point. For LG staff, because of potential reluctance to criticize conservation groups in general and LG specifically, we took care to emphasize anonymity and address any questions or concerns. As is typical in Maasai culture, interviews were usually preceded by an often-lengthy conversation about families, weather, and recent events. Additionally, participants were encouraged to ask questions of the researchers. We kept detailed notes of all interviews in all stages. Some interviews were recorded but, on the advice of JM, this was often foregone when he determined that doing so might make participants reticent.

Stage 1 of data collection consisted of semistructured interviews of 21 LG staff in December of 2017 to build a baseline level of understanding about lost livestock trends and drivers, and to pilot and refine questions. Six of the interview subjects in this stage were English-speaking staff, three of whom are Maasai, while 15 were field-based lion guardians who did not speak English, were young men from all three group ranches, and were interviewed in groups of one to four. All lion guardians interviewed had experience tending livestock, and we believe their responses were generally more representative of the view of community members rather than conservation staff. Interviews lasted between ∼40 and 90 min, with an average of 1 h for individuals and slightly longer for groups.

The second stage of data collection used flexible, open-ended questionnaire-based interviews to learn more about lost livestock trends and drivers from a diverse set of 80 Maa-speaking Ilkisonko Maasai community members spread across the three group ranches. We interviewed participants individually and sought a range of ages and locations as well as gender diversity, with a target of 20–30 min per interview. This work was

TABLE 1 | Questions used in questionnaire-based interviews.

Question
1. Are lost livestock a problem in your area/community? Why or why not?
2. Are numbers of lost livestock increasing? Why or why not?
3. Why do livestock get lost?
4. Do certain types of herds lose livestock more often?
5. Do certain types of herders lose livestock more often?
6. What strategies are used (or could be used) to prevent lost livestock?
7. When livestock are discovered to be lost, what happens? Has this changed?
8. What strategies are used (or could be used) to find lost livestock?

completed in November of 2018. **Table 1** shows the questions included in the questionnaire.

Finally, using lessons learned from the first two stages of data collection, we conducted 12 semistructured interviews aimed at identifying herding best practices in January of 2019. All interview subjects were Ilkisonko Maasai community members with significant herding experience and knowledge, and most had been identified in stage 2 as excellent herders by other community members. In five interviews, only one respondent was present; in two, multiple people were present but only one responded to questions; and in five instances, there were multiple people that responded to questions, although a single respondent (usually the eldest male) led the responses with others occasionally contributing. These interviews lasted from 53 to 140 min.

All interviews were translated from Maa by a Maasai LG staff member (all but four by JM). For the semistructured interviews, KJ and JM collaborated to pose questions to participants, with JM translating and providing continual feedback and suggestions. For the questionnaire, KJ wrote the questions, JM translated them to Maa, and then a third Maa speaker translated them back to English to confirm that the interpretation in Maa was as desired. All quotations in this paper are translated from Maa.

Data Analysis

Thematic coding of responses followed a continuous iterative process whereby we developed initial general themes focused on our main questions and then examined the interview data in more depth, looking for additional themes, refining as we proceeded. For the semistructured interviews, we used these findings to improve or develop new questions as data collection proceeded, while the questionnaire remained consistent. We used the results from stage 1 to guide us in creating the questionnaire, both in further exploring areas where more information was needed and identifying new questions.

To analyze the questionnaire data, which were collected solely by JM, KJ, and JM jointly followed the coding process for each of the questions, together reviewing the results, identifying themes, and then iteratively refining those until we were satisfied that we had captured all relevant themes. For the semistructured interviews focused on herding best practices, we again followed the iterative coding process but with an *a priori* focus on identifying clear and actionable best practices. For example, while some participants identified national government policy changes as necessary, we did not focus on these. We also reviewed the results from the previous two stages to identify herding best practices. In the end, we were confident that, among our >120 participants, we had reached thematic saturation regarding lost livestock and herding best practices. The data collection and analysis process is illustrated in **Figure 2**.

RESULTS

Stage 1: Interviews of Lion Guardians Staff

A core question of the work was whether lost livestock are occurring more frequently across the region, as Lion Guardians' internal data indicate. Although the LG staff certainly had opinions about this (they generally felt that they are, although this was not uniform), we decided that there was too much potential intraorganizational bias to make conclusions about lost livestock trends from these interviews. Nevertheless, the findings from this stage exist within the context of increasing lost livestock, the reality of which we explored in more depth in stage 2 with community members.

As long-time observers of relationships among people, livestock, and wildlife in the region, both the Maasai and non-Maasai staff shared a wealth of knowledge about the causes of lost livestock conflict, noting that it has always been present. During this stage, we identified two core lost-livestock themes that would form the basis for the rest of the study, as well as several other factors that increase the likelihood of lost livestock, decrease the capacity to find them once lost, and increase the risk of predation of lost animals.

We also confirmed that although all livestock are important to Maasai livelihoods and all are predated by carnivores, cattle have the most social value and, because they graze farthest from home, are most likely to be predated when lost. As such, cattle and cattle herders were the dominant focus of the responses in all stages.

Declining Herder Skill and Dedication

The first of the core themes was that declining herder skill and dedication is causing an increase in lost livestock. Within this theme, we identified several driving factors for two main categories of herders: family herders and paid herders. Traditionally, family herders progress from children with responsibility over young sheep and goats to teens tending adult cattle, improving their herding skills and bush knowledge as they grow into skilled herders. Paid herders are usually adults from outside the family who are hired to tend to livestock.

Among family herders, many participants noted that children have always been "full of fun" and prone to distraction and thus prone to losing livestock. However, increased primary school attendance by children, which became compulsory in Kenya in 2003, has led to decreased interest in and knowledge about herding. Additionally, with adults seeking more diverse sources of income, they have less time to train the children that are available to herd. Several participants noted that children are no longer punished for bad herding as they once were.

With more children in school and increasingly uninterested in herding, participants noted that herds are frequently tended

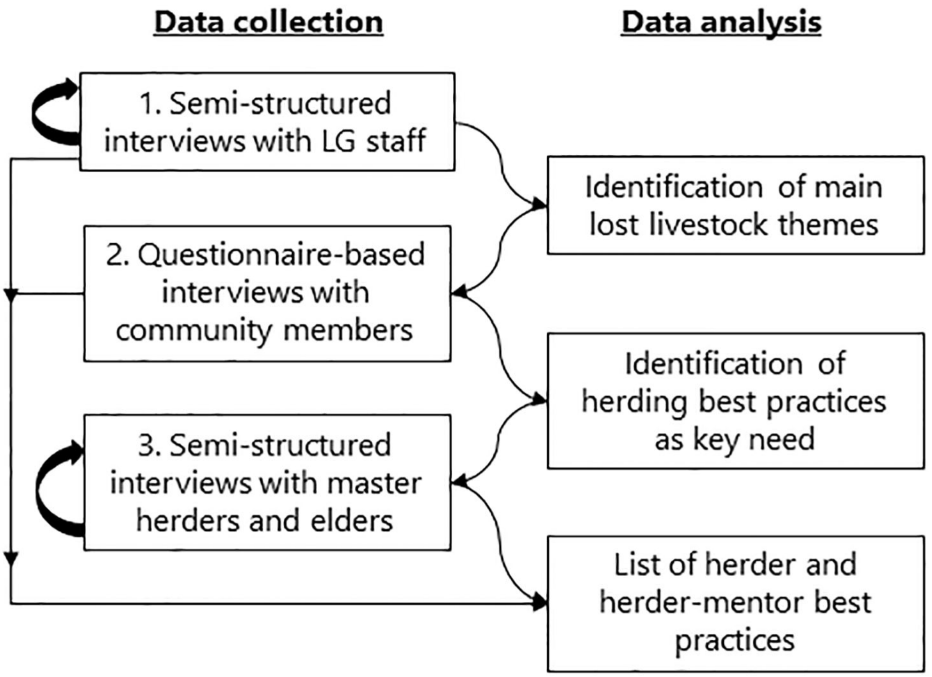

FIGURE 2 | The iterative data collection and analysis process, wherein each stage built upon what came before. Stages 1 and 3 were internally iterative, such that the conversation evolved as we proceeded. The data analysis column shows the key finding from each stage but is not comprehensive. All data collection stages informed the generation of herder and herder-mentor best practice lists.

by too few herders for the number of livestock and that young, inexperienced herders are often placed in charge of herds for which they are ill prepared. In the past, a large cattle herd may have been tended by an *ilmurran* warrior and two younger apprentice herders, while now, it is common to see a single young boy tending a large herd.

The alternative, when a family can afford it, is to hire a paid herder. However, with fewer children learning the trade and fewer viewing herding, which requires long days in the hot sun amid dangerous wildlife, as a desirable profession, good paid herders are increasingly scarce. Even when paid herders are available, many noted that it is difficult to evaluate their skill and dedication, especially if they are from outside the community. Dedication, which refers to the herder's personal devotion to the livestock and the family that depends on them, was frequently highlighted as especially important in both family and paid herders, and especially difficult to find in a paid herder. This was exacerbated by the tendency to pay herders poorly, perhaps in anticipation of poor performance.

Decreased Capacity to Search for and Find Lost Livestock

Because lost livestock have always been a challenge, and because livestock are so valued in Maasai society, the search for lost livestock is a well-known event in Maasai life. Traditionally, when a herder reported lost livestock, members of the community would rally to collectively search for them, with an elder perhaps performing *oenet*, a traditional practice intended to help guide lost livestock home. Participants consistently reported that it is increasingly difficult to mobilize community members and that *oenet* is now rarely practiced.

One reason that it is difficult to rally support to search for livestock is that *ilmurran* warriors, who used to be a "search army," are now less interested and available. Major causes of this include the declining interest in livestock and the bush noted above, as well as diversified livelihoods. However, several participants also noted that the legal prohibition on lion killing discourages warriors from joining a search, as searches no longer have the same potential to lead to a lion hunt, which can confer great prestige on a warrior who spears a lion.

Additional factors in the decreased capacity to search for and find lost livestock include fewer adults available to search and poor herders failing to note where the lost livestock were last seen. Of note regarding adult searchers is that several participants told us that there is a declining sense of community and so people are less willing to help look for livestock that they do not own. Lastly, a few participants noted that compensation from conservation organizations for livestock killed by predators may reduce the drive to search for lost livestock, although they stressed that this is only the case with sick or otherwise less-valued animals.

Other Factors

Several other potential factors were noted as contributing to lost livestock conflict but were viewed as less actionable by participants. For example, most noted that livestock are more likely to be lost in areas of dense vegetation and during times of

TABLE 2 | Profile of the 80 participants in the questionnaire-based interviews.

		Gender		Age		
Group ranch	**Count**	**Male**	**Female**	**Min**	**Max**	**Mean**
Eselenkei	24	21	3	18	76	38.6
Mbirikani	26	17	9	18	92	45.1
Olgulului–Ololarashi	30	23	7	24	80	41.3
Total	80	61	19	18	92	41.7

drought when livestock range farther from home and from the herder to find forage. However, participants saw these as cyclical and unavoidable causes of lost livestock. Carnivore abundance, distribution, and behavior were also identified as sources of conflict but were likewise seen as less tractable.

Finally, a few participants raised the issue of broad level herd and forage management as driving lost livestock. For one, overall livestock numbers have increased in the region, increasing the number of lost livestock. Participants also suggested that poor community-level enforcement of grazing restrictions means that herds and herders must travel farther to reach forage, increasing the likelihood of losing livestock. The effects of this poor management are exacerbated by drought.

Stage 2: Questionnaire Interviews of Community Members

To build upon and more broadly examine the findings from stage 1, we conducted questionnaire-based interviews with 80 Ilkisonko Maasai community members (**Table 2**) from across the three group ranches (**Figure 3**). Overall, 61 participants self-identified as men and 19 as women, with a minimum age of 18 and a maximum of 92.

Are Lost Livestock a Problem, and Are They Increasing?

For the question, "Are lost livestock a problem in your community?," 60 participants said that they are, while 20 said they are not. Responses were consistent across the different group ranches and for age and gender. For those that said lost livestock are a problem, reasons given ranged from their frequency of occurrence (60%) to the likelihood of lost animals being killed by predators (38%—note that more than one response was often given):

> *It is a big problem and predators are taking advantage of the situation. Most of the livestock that get lost are killed by predators. This is a big loss to pastoralists. (Older woman, Mbrikani GR)*

> *It is a big problem—livestock are reported lost daily across the village. (Middle-aged man, Eselenkei GR)*

For those who said that lost livestock are not a problem, the most common response was that they are not occurring frequently (35%), while many also noted that the problem varies according to either pasture availability (25%), vegetation density (20%), seasonal/drought conditions (20%), the availability (5%), and skill (10%) of herders, or the likelihood that predators will kill lost animals (10%), which they described as not currently problems in their area.

When asked if lost livestock are occurring more frequently in their area, 42 participants said yes while 38 said no. While responses were consistent across age and gender, 70% of participants from Olgulului–Ololarashi GR said they are increasing, much higher than on Eselenkei GR (46%) or Mbirikani GR (38%). Of those that said lost livestock are increasing, 50% said that this is due to a lack of adequate herders. Other reasons include declining herder skill and dedication (14%), failing to properly value livestock (12%), and a variety of environmental factors such as increasing drought and predator pressure.

> *Lost livestock are increasing because of the following reasons: In the past herding was done by livestock owners, nowadays it is done by paid herders. Most herds nowadays lack herders because of school and the lack of ability to pay herders. Also, there is a high presence of predators. (Older woman, Olgulului-Ololarashi GR)*

Of those that said lost livestock are not increasing over time, the most commonly given reason was that lost livestock occur cyclically due to forage heterogeneity (21%) or drought (18%) and so may rise and fall but, over the long run, have remained consistent. A few said that numbers have fallen over time due to an increased percentage of adults herding because children are in school (3%) or due to smaller herd sizes as livestock become less important (3%).

> *The numbers have been consistent over the years. The numbers are high during drought and somehow drop when rain comes and there is enough pasture. (Young man, Mbirikani GR)*

Overall, 44% of participants said that lost livestock are a problem and are increasing, 31% said they are a problem but not increasing, and 9% said they are increasing but not a problem in their community. This leaves only 13 of 80 participants (16%) who said that lost livestock are not a problem and are not increasing.

Why Do Livestock Get Lost?

Three questions focused on the causes of lost livestock, with prompting questions related to types of herds and types of herders that might lose livestock more frequently. The most common responses to the open-ended question related to herder skill and dedication (55%), with lack of herders (31%) also prominently noted. Other common responses related to heterogeneity in the distribution of forage and water causing livestock to wander (45%) and dense vegetation causing herders to lose track of some livestock (34%).

When prompted for the characteristics of herds that might lose animals more frequently, the most common response (40%) was that there are no consistent differences. Large herds (26%) were the most common affirmative response, with others mentioning herds of sheep and goats, herds of calves, and herds

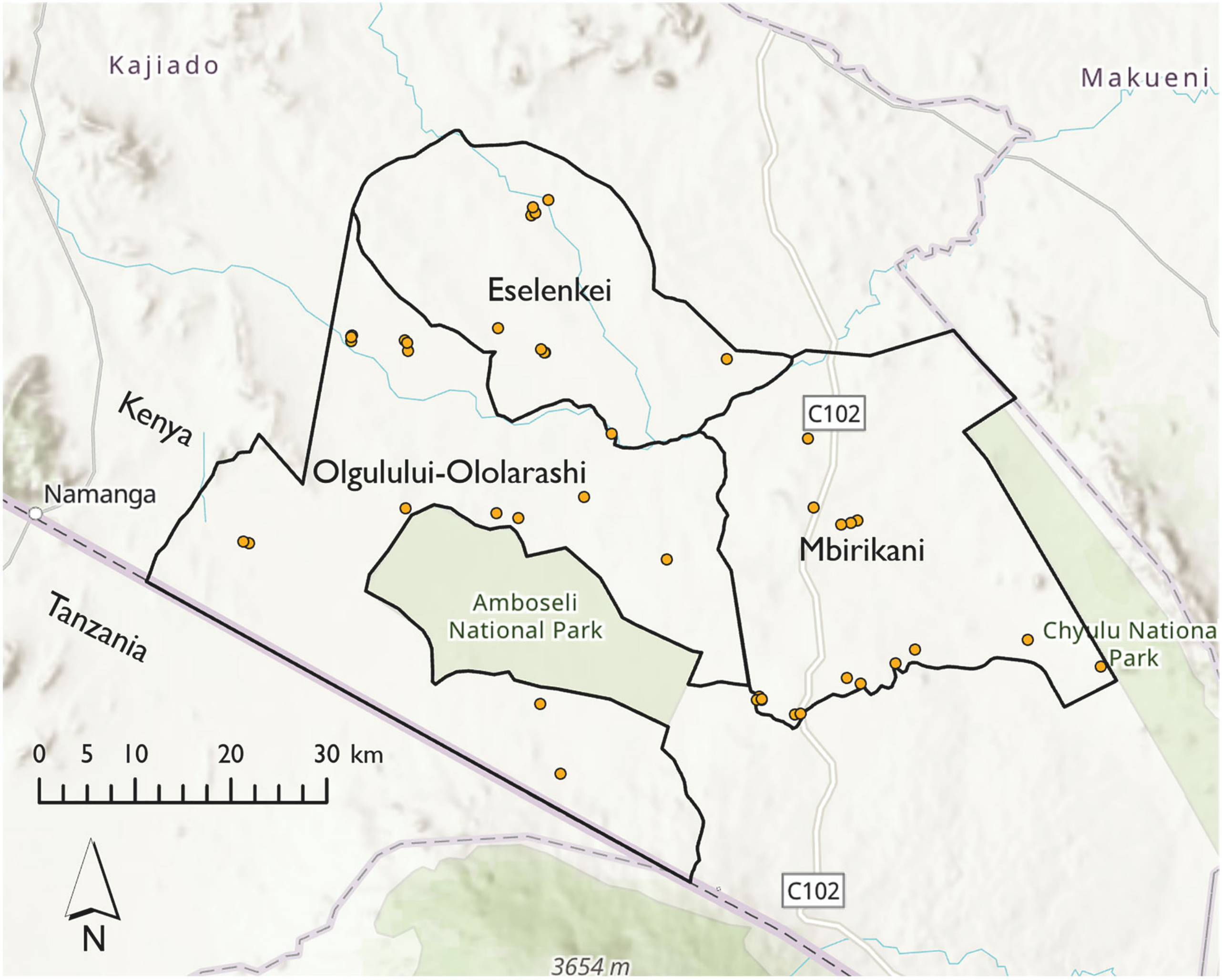

FIGURE 3 | Questionnaire participant locations. Note that multiple questionnaire interviews were often completed in a single location and that points do not necessarily mark the exact location that the person lives but rather where they were interviewed.

with many "rogue" livestock, those individual animals that have the tendency to lag or otherwise stray from the herd.

When prompted for the characteristics of herders that might lose animals more frequently, there was a broad range of opinions, with many participants sharing lengthy thoughts on the subject. The most common responses related to herders who were deemed "unreliable" (36%), did not value livestock (35%), or otherwise showed poor character.

> *Most paid herders are not good herders since there is no sense of ownership of the livestock. School children are not good herders either because they care more about books than livestock. They play while herding! (Middle-aged man, Eselenkei GR)*

Others noted that herders who have not received proper training (13%) and therefore lack skill (13%), those too young for the herd they have been assigned (15%), or those who are treated (4%) or paid (11%) poorly are most likely to lose livestock. Overall, 89% of participants reported that adult family members are always good herders, while only 13% said the same of paid herders or school children.

> *School children are not good herders because of school and lack of punishment. Most people no longer take time to mentor their children to be good herders. (Middle-aged woman, Eselenkei GR)*

How Can Lost Livestock Be Prevented?

We next asked about strategies that are used (or could be used) to prevent lost livestock. Reliable herders (41%) was the most common answer, with the related proper mentorship of herders (31%), adequate number of herders for the herd (21%), herders of the proper age (20%), and punishment of poor family herders (13%) also mentioned.

> *The owner must talk to the herder on how to be a responsible herder and, if needed, change their responsibility from a challenging*

> *herd to a less challenging herd, for example from herding cows to herding calves. Involve mature herders in herding. (Young man, Olgulului–Ololarashi GR)*

Many participants also referenced specific best practices for herders. These include working with an elder to select areas with adequate forage and less dense shrubs and trees (28%), properly timing the grazing day to ensure the herd returns well before sunset (10%), using bells on animals, especially rogue livestock (6%), and proper pay for paid herders (4%).

> *Allow paid herders to have their own livestock in the herd. This increases their sense of ownership. Put bells on livestock to aid in identifying and also hearing livestock from afar or in dense brush. (Middle-aged man, Olgulului–Ololarashi GR)*

Searching for Lost Livestock

Because owners are typically notified of lost livestock when a herder returns home in the late afternoon or dusk, the most common responses for what to do when this happens were to immediately mobilize neighbors to help (45%) and start searching as soon as possible (79%). *Oenet* was mentioned by 10% of participants. The main recommended strategy for searching for lost livestock was finding and following animal tracks (59%), which requires identifying the last point the lost animals were seen (19%). Others mentioned listening for bells (13%), strategically dividing the search team (10%), and prioritizing areas where predators are known to be (5%).

In response to the prompt of whether searching for lost livestock has changed, 45% were unsure, 29% said no, and 26% said that it has. Of those who felt that it has not changed, many noted that people still help when livestock are lost, with a few noting that mobile phones have made it easier. Of those that felt that it has changed, nine indicated that there has been a loss of communal feeling among the Maasai.

> *Nothing has changed since people are still united in the search for lost livestock. (Young man, Olgulului–Ololarashi GR)*
> *Mobile phones have made mobilizing a search party easier. (Middle-aged man, Eselenkei GR)*
> *People still help each other to search for lost livestock, However, sufficient notice is needed since people are busy these days. (Young man, Eselenkei GR)*
> *In the past, livestock were considered property of the community. Thus, everyone participated in the search for the lost livestock in their village. Nowadays, things have changed. People don't want to help each other. Everyone is on their own. (Older woman, Mbirikani GR)*

Stage 3: Identifying Herding Best Practices

The results from stages 1 and 2 made it clear that most pastoralists in the region see lost livestock as a problem in their community and that most see the main cause of lost livestock as poor herding practices. A slim majority felt that lost livestock have been increasing, and there was a consensus that, although the search for lost livestock has seen changes, it is not the main impediment to reducing lost livestock conflict.

As we discussed these issues with community members, it became clear that a large increase in school attendance in recent decades has led to a gap in the transmission of traditional herding knowledge. There is still a living generation of elders who learned to herd through a long apprenticeship, but many feel that the younger generations are not interested in learning what they know. We thus sought to document this knowledge to assist in its transmission and preservation.

During stage 2, we asked participants to identify any master herders in their area. In stage 3, we sought out these experts as well as elders with the reputation of having significant herding knowledge. The main question in these interviews was a "grand tour" question where we asked the respondent to walk us through a day in the life of a good herder. Using these interviews and our previously collected data, which often contained discussion of herding practices, we created a list of five herder best practices. Because we learned that mentorship of herders is also an essential element of a strong herding culture, we also created a list of five herder-mentor best practices.

Herder Best Practices

Practice 1: know your herd

As noted by Galaty (1989), Maasai pastoralists have a remarkable capacity to recognize individuals among herds of hundreds of cattle and, even more impressively, to identify a single missing animal among hundreds present. This is achieved through a system of symbolic organization of herds wherein "multiple dimensions of cultural classification provide for cognitive organization and redundancy" (Galaty, 1989). This is not a numerical count; in fact, one master herder told us that counting is taboo. We found this cognitive capacity to be alive and well in older generations but consistently lamented as lacking in younger generations.

Specifically, participants described using cattle matrilineal "houses," markings and colors, breeding status and health, and behavioral tendencies in naming and classifying animals. Many also described the need to continually update which animals are leaders and which are likely to lag, including those that might not usually lag but are sick or pregnant. If using bells, the animals they are placed on should be continually reviewed. The participants also noted that a good herder will know which animals are likely to be in the middle of the herd or at the side of the herd, as this knowledge may be useful at strategic moments, such as when moving through thick brush or away from a crowded watering location.

Practice 2: morning routine

The most frequently mentioned distinguishing feature of good herders was the tendency to awaken early and examine the herd immediately. Walking among the herd, the herder should mentally update animal health and reproductive status and clear up any concerns that may have arisen during the night. As in Galaty (1989), a few participants mentioned that concerns about missing or sick animals regularly arise in dreams.

Next, the herder should conduct the morning briefing with the herder-mentor. During this conversation, they will discuss the daily route, including areas with good forage, watering locations, and potential challenges or threats. The master herders noted that a good herder will aim to arrive at the mid-day watering location slightly early, before the bulk of the local herds has arrived and created a risk of losing animals in the chaos. The herder and herder-mentor should also discuss which animals may present difficulty during the day and decide whether to leave any behind that may be too sick or likely to give birth.

> *A good herder wakes very early in the morning and, before he takes breakfast, he goes straight to the livestock and checks the status of each animal. He will observe which are sick, which are limping, and which might give birth. He can then go for his meal… Different seasons of year have their own rhythm. When things are green, herders need not be in a rush, but when it is dry the herder must get the animals out very early. (Master herder, Olgulului–Ololarashi GR)*

Practice 3: keep the herd close (physically and mentally)

The practices of a good herder in the field are complex, place based, and spatiotemporally dynamic (Meuret and Provenza, 2015). We cannot hope in this brief space to capture the range of place-specific practices that Maasai master herders use to find good forage, move animals efficiently and safely across varied terrain, avoid dangerous wildlife, and otherwise maintain healthy, well-fed livestock across the seasons. Instead, we focus on some key general practices.

All participants noted that herders must stay physically and, more importantly, mentally active throughout the day. Throughout this research, napping herders were objects of scorn and identified as regular sources of lost livestock. Other key behaviors are carrying a walking stick, whistling to keep livestock and wildlife aware of your presence and location, and shouting in densely vegetated areas to keep your livestock moving and alert.

The master herders noted that a good herder will continually and strategically reposition oneself in relation to the herd and its location on the landscape. This includes leading the herd through dense brush, pushing the herd from behind when leaving a crowded watering location, and staying toward the middle when moving through open areas. The herder should continually adjust the cohesion of the herd to keep them as close together as the forage resource will allow, recognizing that when forage is sparse, it may be necessary to allow them to spread out to find adequate nutrition.

Building on practice 1, herders should perform a herd check whenever arriving at pasture, ensuring that all livestock have arrived. Because the herd will then settle to graze, the herder can track down laggards before they become lost. Lastly, herders should always be wildlife aware, especially when moving the herd. Large carnivores, as well as elephants and Cape buffalo (*Syncerus caffer* Sparrman), present a threat to the herd and to the herder, and careful attention and strong bush skills can prevent most negative encounters.

> *A good herder is always passionate about herding and a good herder always values the livestock. While out in the bush, because you value your livestock and are passionate, you will use practices that ensure you keep a close eye on livestock, get to water on time, and find good pasture. (Master herder, Olgulului–Ololarashi GR)*

Practice 4: return early with full bellies

The strategic timing of leaving and returning was so frequently mentioned that it emerged as a best practice. The distance that a herd will travel during a day depends on many factors, including forage availability and proximity, water locations, and community grazing management. When forage is plentiful, many master herders noted that a herd can leave later in the morning and return earlier in the evening and still be adequately nourished. When there is a dearth of forage, particularly during drought, a herd may graze the whole day and not obtain enough food.

It is therefore essential for the herder to carefully consider the day's route and create a plan to obtain adequate forage for the animals while returning home when there is still plenty of daylight. This allows the herder and herder-mentor to identify any missing animals and begin a search before the danger of darkness sets in. However, there is an inherent tension between full bellies and an early return, and this practice will test the skill of the best herders and the knowledge of the best mentors, especially during drought.

Practice 5: evening routine

Just as it is important to start each day with herd assessment and route planning, it is important to end each day with another round of herd assessment as well as consideration of lessons learned from the day's activities. Most master herders stressed the necessity of the herder and herder-mentor reviewing the day together, including areas of good forage, route timing, and herd behavior, in preparation for the next day. They also stressed the importance of honest communication, as herders that are fearful of reprisal may not share all relevant information, making effective strategizing difficult.

As the day draws to a close, good herders will once again walk among the herd, observing animal health and behavior. If the herd has been carefully observed and kept close throughout the day, any lost animals should have already been noticed. However, participants did note that lost animals are occasionally identified at this point, and a search can still occur. If all animals are present and these five practices were followed, the herder can then rest well knowing that they have been good livestock stewards and set the stage for another productive day.

Herder-Mentor Best Practices

Practice 1: mentorship system

The biggest concern among elders was that a centuries-old traditional system for mentoring young herders is rapidly breaking down, despite livestock still being the most important component of Maasai livelihoods. In this system, children are taught to value livestock and their important role in Maasai culture. As a Maasai saying states, "You can't love the milk if you don't love the cow."

Young herders work with a mentor, often a parent but sometimes a sibling or relative, as they move through progressively more difficult assignments—baby sheep and goats to calves to adult sheep and goats to cows and bulls. Through a long apprenticeship they acquire the skills to know their herd and navigate the bush, developing into not only good herders but respected community members. One master herder stressed to us that he had little formal education but was nonetheless one of the most respected members of his age set, which he attributed almost entirely to his skill as a herder.

The most important ingredient in this mentorship system is time. Good herding requires intimate knowledge of the changing environment across the seasons and years, the dynamics of livestock as individuals and groups, the personalities and behaviors of the local wildlife, and, ultimately, the proper place of the herd and herder in the world. These kinds of knowledge only emerge through a long conversation between child and elder, human, and environment. The elders despaired that this conversation is increasingly fractured and perhaps irrecoverable.

> *School-going children are losing their chance to learn herding, they only have a few days on weekends and holidays, and this is important but not enough. In the past, children spent lots of time with adults learning to herd. Now, my grandsons only know the classroom… The whole process is missing. The abarani [*those especially skilled at cattle recognition*] are gone. (Elder, Eselenkei GR)*

Practice 2: the right herder for the right herd

The master herders noted that the dearth of herders in the area is demonstrating the importance of placing the right herder with the right herd. In addition to properly correlating skill with herd type, participants indicated that herds should be properly sized. Although it was a matter of some disagreement, roughly 200 cows emerged as the maximum that is manageable by one good mature herder. Assistance with larger herds can be provided by younger apprentice herders under the tutelage of the mature herder.

Strategic splitting and mixing of herds was noted as one way to ensure proper herder coverage. For example, larger herds can be split into groups of older and younger cattle such that the older group is larger but equally manageable given the slower movements of the older animals. Other commonly noted elements of properly equipping a herder for the job were providing the herder with a mobile phone, purchasing bells for indicator animals, and properly rewarding paid herders, including with livestock of their own that can then be included in the herd.

Practice 3: morning routine

Because livelihoods are diversifying, many participants observed that herder-mentors are less engaged in the morning routine, as they have often already left the *boma*. However, their role in this routine is essential. One master herder shared that a beloved memory of his deceased father was when he would awaken as a young herder and find his father already walking among the herd in the gathering light, carefully checking each animal. Herder-mentors should walk through the herd with the herder, sharing what they see and listening to what the herder sees.

Discussion of the day's route is the most important part of the herder-mentor's morning routine. Based on the previous day's experiences, the two should walk through the plan for the current day. Many participants stressed that this conversation must be a two-way street wherein the herder-mentor trusts the herder to make decisions. Lastly, many noted that herder-mentors should walk out with herders as they leave the *boma*, observing the herd as they move and offering any final notes to the herder.

Practice 4: evening routine

The entire community becomes more active as the time approaches for the herds to return from the day's grazing. Herder-mentors should use this time to begin to walk out in the direction from which their herd will come, meeting the herders on their way in. Most importantly, the herder-mentor can use this time to learn from the herder if any individuals are missing and check the herd on their own. Walking in with the herd, the herder-mentor can see if bellies are full and ask the herder about the day while the events are still fresh in mind. Once the livestock are settled in the *boma*, the herder-mentor can check them again and then engage in a more leisurely conversation with the herder.

> *It is a routine that the livestock owners and elders should go into the bush and meet the livestock as they are coming home, the reason being that it gives you time to check the herd and respond if needed. Mostly it is just the senior elders who still do this, the younger ones are too busy with business errands. This is a big mistake, and they only realize animals are missing after it is too late… Maybe they only realize when they are in deep sleep, and they will not sleep well! (Elder, Olgulului–Ololarashi GR)*

Practice 5: respect grazing committees and other rules

Regulation of grazing is largely managed through local networks of elders. One such manifestation of this is the grazing committees, which are formally organized groups that meet to determine when and where herds can graze. This includes allowing herders to move to temporary *bomas*, granting permission for outsiders to graze in the area, and opening reserved areas to grazing. Many participants throughout the study noted that these formal committees are currently resurgent in the region and that they are increasingly involving younger community members, including herders, in their deliberations.

Herder-mentors should ensure that herders are aware of areas that are restricted for grazing and encourage them to observe and report on violations of these restrictions. Herder-mentors should provide input to the grazing committees and attend meetings when appropriate. Herders themselves, especially as they mature, can also provide input and may even be invited to join the committee itself, as had two of the master herders that we spoke with, to their great pleasure.

DISCUSSION

In this study, we aimed to capture the causes of and potential solutions to lost livestock, a social–ecological challenge that leads to damaged livelihoods and dead lions. Perhaps unsurprisingly, in the process, we learned that the challenge of lost livestock is inseparable from the whole of Maasai livestock herding practices and, ultimately, traditional Maasai culture. As observed by Despret and Meuret (2016, p. 25–26), pastoralism is an endeavor that knits together ecology and cosmology into an unbreakable net, "forming a cosmoecology of multiple beings, gods, animals, humans, living, and dead, each bearing the consequences of the others' ways of living and dying." We should not be surprised that this holds true among the "people of the cattle," the Maasai.

We learned that working to prevent livestock–lion conflict by limiting lost livestock also requires us to assist in preserving traditional herding knowledge. Good herders lose fewer livestock but require a long-term intensive apprenticeship with their elders, as herding knowledge is fundamentally place based and ungeneralizable. As we have done here, we can potentially assist this knowledge transfer through the application of a "usable science" (Meiman et al., 2016), but this cannot take the place of a practical education in the particulars of place, people, and animals.

The alternative to herding is the model of commercial ranching practiced worldwide in which fences and other technologies take the place of herders. While these systems may be more effective at producing high-quality livestock products, they have also proved broadly devastating to pastoral peoples, large carnivores, and other wildlife (LaRocque, 2014). Meuret and Provenza (2014) describe herders as "ecological doctors," and we submit that their patients include not only plants but also lions, ecosystems, and entire cultures.

Throughout this work, we have been faced with the difficult reality that increased schooling, as Galaty (1989) observed, "is progressively altering the nature of the cognitive experiences of young Maasai, thus transforming the basis of knowledge on which pastoral practice has for so long rested." Clearly, this is not a new phenomenon, but our research suggests that the loss of the "cognitive concomitants of pastoralism" engendered by schooling is approaching a threshold among the Ilkisonko Maasai of the Amboseli ecosystem. Knowledge that has been developed and passed down across centuries is now being irretrievably lost with the death of every elder.

We are not in a position to judge the worthiness of schooling for Maasai children. However, we can encourage those that value lion conservation to also value good herding. As demonstrated by the work of Lion Guardians, there is great leverage in seeking conservation solutions that are embedded within pastoralist culture. We believe that supporting traditional herding practices presents a tremendous opportunity to demonstrate that there is no necessary paradox in seeking gains in both livestock-based livelihoods and lion populations.

Future work on Maasai herding practices should aim to grow our understanding of the fine-scale practices used by effective herders in the field. Because we did not target the transient population of paid herders and because they have growing importance in livestock management, the addition of their perspective on the questions we have asked would be instructive. Additionally, although we aimed to represent a broad range of perspectives, a study targeting Maasai women could shed important light on their all-important knowledge, especially as it relates to herding of sheep and goats. Lastly, young herders under the age of 18 were not included in this study due to privacy concerns, but their voices are certainly worth hearing.

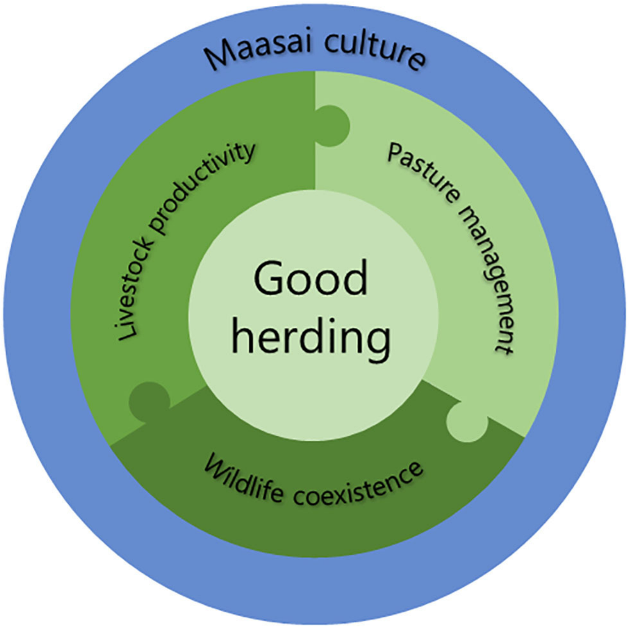

FIGURE 4 | Good herding simultaneously and synergistically achieves livestock productivity, effective pasture management, and wildlife coexistence. These outcomes are inextricably bound and are held together by traditional Maasai culture. At the same time, good herding also supports traditional Maasai culture by safeguarding livestock-based livelihoods and connecting the generations.

CONCLUSIONS

Lion Guardians data show that lost livestock are a significant driver of livestock–lion conflict in the Amboseli ecosystem of southern Kenya. In this study, we learned that a large majority of Ilkisonko Maasai pastoralists in the region see lost livestock as a problem in their communities because they occur frequently and are often the victims of attacks by large carnivores. Study participants were split on whether numbers are increasing, but there was broad agreement that poor herding practices are the main cause of lost livestock and that these practices are worsening over time as more children attend school and adults devote less time to mentoring and herding.

This leads eventually to a lack of well-trained mature herders, including those available to be hired by families lacking in-family herders. These paid herders present a challenge in that their skills as well as dedication to the family and the livestock are difficult to assess and often lacking. In anticipation of this, paid herders are typically underappreciated and poorly paid. Many suggested that better pay and other rewards for paid herders, which would aid in revalorizing the profession, would go a long way toward remedying the problem of lost livestock, but families appear to be caught in a dilemma in this regard.

Although some livestock will be lost and killed by carnivores even under the best circumstances, a strong traditional herding culture appears to be the best way to minimize conflict while maintaining the extensive land tenure system that allows for sustained coexistence with diverse wildlife (Hobbs et al., 2008; Groom and Western, 2013). Indeed, we find that each herder and herder-mentor best practice synergistically prevents lost livestock, improves pasture management, and maximizes livestock productivity.

This is a key point—attentive, thoughtful, and well-planned herding manages livestock such that they *simultaneously* find good forage, address collective management goals, and avoid wildlife conflict (**Figure 4**). These outcomes are inseparable from one another and from the traditional Maasai culture that both supports and is supported by herding. The alternatives, including land subdivision, sedentarization, and market-based commercial ranching, irrevocably sever these dependencies. In fact, we suggest that Western livestock sustainability efforts largely consist of attempts to stitch these multiple elements back together; good herding achieves this as a matter of course.

Lion Guardians, led by their Ilkisonko Maasai staff, is now implementing these findings within their collaborative, community-based model. The overarching goal of this work is to support a best practice herding culture on the group ranches in the Amboseli ecosystem. Key subgoals include improving the perception of herding and livestock among the youth, increasing the supply of verifiably skilled and dedicated paid herders, and creating opportunities for herders, elders, and others to discuss herding practices. Ultimately, the success of this effort will be found in the continuity of the dynamic cosmoecological balance that traditional Maasai culture strikes among people, livestock, and wildlife—which is to say, in the maintenance of resilience in the face of change.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Colorado State University IRB. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

All authors contributed to the conception and design of the study. KJ and JM collected and analyzed the data. KJ wrote the first draft of the manuscript and all authors contributed to manuscript revision, as well as read and approved the submitted version.

FUNDING

This work was funded by a team fellowship from the Center for Collaborative Conservation at Colorado State University.

ACKNOWLEDGMENTS

We thank the government of Kenya and leadership of the group ranches for permission to undertake this work. Numerous Lion Guardians staff members, especially Luke Maamai and Philip Briggs, supported and advised in ways large and small. Jeremy Goss, Nikki Best, and other staff of the Big Life Foundation shared data and expertise. Jasmine Bruno and Hailey Wilmer provided comments that substantially improved the manuscript and Linda Nagel provided crucial early support. Two reviewers provided helpful suggestions. Most of all, we are grateful to the Maasai people and communities of the Eselenkei, Mbrikani, and Olgulului–Ololarashi Group Ranches for their generosity in sharing their time, knowledge, and hospitality. We hope this work helps to repay our debt of gratitude.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Sustainable Food Systems

REVIEW
published: 16 September 2020
doi: 10.3389/fsufs.2020.00141

Do Differences in Livestock Management Practices Influence Environmental Impacts?

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Herbivore-carnivore interactions are fundamental to grassland ecosystem functionality and to the human cultures that have long depended on these ecosystems for their nutrition. However, a large literature has developed during the past century indicating that animal agriculture is responsible for numerous negative environmental impacts. In this paper, I review literature on some of the environmental impacts of two different livestock management approaches, industrial-conventional (IC) management and regenerative-multi-paddock (RM) management. I consider the null hypothesis that the environmental impacts of ruminant livestock production are independent of the approach used to manage animals and grazing lands. It evident in the literature that managed grazing ecosystems are complex, and for certain system attributes, such as forage quality and plant community structure, the better management system is difficult to discern. In other areas definitive differences in impacts appear clearly management dependent. For instance, the soils of RM grasslands exhibit higher microbial biomass and diversity, and higher fungal: bacterial ratios than IC soils. Several impacts associated with livestock production appear to have less to do with grazing, *per se*, and more to do with support factors, such as feed production and manure management. The compilation of data from numerous sources suggests that RM management may reduce blue withdrawals and GHG emissions by >50%, relative to IC management. Accumulating data also suggest that a significant portion of anthropogenic CO_2-eq emissions can be removed from the atmosphere and stored in the soil by applying RM management practices. Finally, it is suggested that while research design may affect the outcomes of some studies, the quality and quantity of the science may not resolve many discrepancies in the data. It is suggested that the viability and sustainability of animal agriculture may depend upon broadening the goals of practitioners to include both food production and the restoration and protection of agricultural ecosystem services.

Keywords: meat production, regenerative agriculture, multi-paddock livestock management, industrial agriculture, conventional livestock management, livestock impacts

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Specialty section:
This article was submitted to
Agroecology and Ecosystem Services,
a section of the journal
Frontiers in Sustainable Food Systems

Received: *26 March 2020*
Accepted: *05 August 2020*
Published: *16 September 2020*

Citation:
Kleppel GS (2020) Do Differences in
Livestock Management Practices
Influence Environmental Impacts?
Front. Sustain. Food Syst. 4:141.
doi: 10.3389/fsufs.2020.00141

INTRODUCTION

Research conducted over nearly a century identifies clear connections between animal agriculture and environmental disruption. Livestock grazing has long been associated with biodiversity loss in plant and wildlife communities, the dispersal of invasive species, degradation of soil structure, and desertification (Daubenmire, 1940; Savory, 1983; Allen et al., 1991; Savory and Butterworth, 1999; Drewry, 2006; Harrison and Bardgett, 2010; Wirsenius et al., 2010; Alkemade et al., 2013). Cattle grazing and livestock feed production are responsible for >65% of the deforestation that has taken place in Brazil and other tropical and subtropical regions (Vale et al., 2019). Animal agriculture is an important source of ammonia, greenhouse gas emissions (GHG) [Parris, 2011; USEPA (U.S. Environmental Protection Agency), 2017; Food Agriculture Organization, 2019] and blue water withdrawals [USGS (U.S. Geological Service), 2005; Rotz et al., 2019]. Runoff from livestock and feed production operations are significant non-point aquatic contamination sources [Agouridis et al., 2005; USEPA (U.S. Environmental Protection Agency), 2017].

These obviously negative impacts contrast markedly with the natural historical record documenting the roles of herd forming ungulates in maintaining the functionality of grass- and rangeland ecosystems and the human cultures that have depended on these systems for hundreds of millennia (Oksanen et al., 1981; Frank et al., 1998; Baltica and Boskovica, 2015). Large ungulates are keystone species in wild grassland ecosystems globally, supporting higher trophic transfer efficiencies than herbivores in most other kinds of terrestrial ecosystems (Stuart-Hill and Mentis, 1982; Frank et al., 1998). An estimated 168 million ruminants, including 50–60 million bison roamed the grasslands of pre-Colombian North America, supporting enormous soil fertility, and biodiversity in the plant communities they grazed (Frank et al., 1998; Skarpe and Hester, 2010). Greenhouse gas production, particularly methane production, by these ungulates was equivalent to that produced by modern livestock [Smith et al., 2016; USEPA (U.S. Environmental Protection Agency), 2020]. Massive ungulate herds also grazed and in some cases continue to graze the grasslands of Eurasia and Africa (Janis, 2010) and although the carbon and nitrogenous gas produced by these mammals once raised GHG levels in the atmosphere, they are not known to have significantly altered global climate (Smith et al., 2016). These wild, herd-forming ungulates did, however, represent critical nutritional and cultural resources to pre-agricultural human societies.

One must ask why large ruminants that have so profoundly contributed to the fertility and well-being of terrestrial ecosystems and the humans who inhabited them, have today become anathema to human and environmental health. Certainly, domestication has not changed the anatomies or physiologies of herbivores in meaningful ways. It is unlikely, then, that the negative impacts of animal agriculture are due to the species being produced. It seems more likely that livestock management practices determine impacts. It should, therefore, be possible to mitigate at least some impacts of animal agriculture by modifying production practices.

In this paper I address the null hypothesis that the environmental impacts of animal agriculture, particularly those associated with the production of ruminant species, are independent of management. I used data from the technical literature and popular media in this investigation. The focus of the paper is on livestock management practices in industrialized countries, including but not limited to the United States, the United Kingdom, Canada, Australia and the European Union, as well as certain developing countries, such as Brazil. Comparisons were made between two very different management models. One of these is generally associated with the industrial model of agriculture and based on pasture management practices that will be referred to as "conventional grazing." The other is consistent with the regenerative model of agriculture and a set of livestock management practices collectively referred to as "multi-paddock grazing" (MP). Throughout this paper I will use the abbreviation IC to refer to the industrial-conventional management collective and RM to refer to the regenerative-multi-paddock management collective. In many cases I will refer to a system by its collective management approach, i.e., IC or RM. However, there are times, particularly in the experimental literature, when the collective management approach is not specified but the grazing practice (e.g., conventional or MP) is. Furthermore, there are times when data from several grazing operations or experimental systems are considered together without specification of an overall or collective strategy. In these cases, I will confine my description to the grazing practice (conventional or MP) rather than collective approach (IC or RM). It is recognized that animal agriculture exists along a continuum of practices with many operations combining elements of both industrial and regenerative practice.

To be clear, a variety of "traditional" practices (as distinguished from conventional practices) are used to manage livestock on pastures and rangelands in both the developed and developing world. These vary along a continuum from relatively unmanaged seasonal grazing (e.g., traditional Scottish and Icelandic sheep farming) to carefully managed seasonal livestock migrations (e.g., African Maasai cattle herders; French mountain shepherds, see Meuret and Provenza, 2014). In this paper, I will not dwell on the many, often ancient, practices used by traditional herding cultures, particularly in the developing world. Many of these are under stress from anthropogenic (e.g., Mongolian herders) and environmental forces (e.g., Saami reindeer herders of Scandinavia; Changpa nomads of the Kashmiri high-ice deserts). They should become the focus of further research, as they contribute to both fertility and stress in agricultural landscapes. The focus of this paper, however, is on comparing conventional grazing within the context of the industrial agricultural model, and multi-paddock grazing as incorporated into the regenerative agricultural model.

INDUSTRIAL AGRICULTURE AND CONVENTIONAL LIVESTOCK PRODUCTION

Modern industrial agriculture originated in Europe and the United States during the mid-eighteenth century in parallel with the Industrial Revolution. All efforts in agriculture were focused on boosting production and efficiency to meet the growing demand for food created by the massive demographic shift from the countryside to emerging urban manufacturing centers (Pollard, 1981; Wiesner et al., 2015). After the first and second World Wars mechanization and the development of synthetic fertilizers approximately doubled crop production. Synthetic pesticides (e.g., DDT) permitted the creation of large-scale crop monocultures year after year (Kleppel, 2014; Bellis, 2018). During the second half of the twentieth century the Green Revolution brought selectively bred plant varieties, especially cereal grains, to the developing world (Borlaug, 1970, 2002), but possibly at an unsustainable cost in terms of fossil fuels use, synthetic fertilizer applications, and blue water withdrawals (Brown, 1970; Cribb, 2010; Shiva, 2016). Today, as genomics, artificial intelligence and other information technologies surge, a new revolution in industrial agriculture is underway. Its success will be measured by the role it plays in feeding an exploding human population in the face of climate change and resource decline.

Optimization of production is the focus of modern industrial animal agriculture. This is often accomplished by finishing livestock in confined animal feeding operations (CAFOs). While increasingly limited in Europe (Imhoff, 2010), CAFOs are widely used in the US. Typically, beef cattle are moved from grazing lands to the CAFO at ∼6-months of age and are ready for slaughter 3–5 months later. Dairy cattle and swine may be confined during much or all of their lives. The CAFO maintains livestock at high densities. Energy rich rations consisting of silage and/or pelletized grains, are typical feeds. Growth stimulants, including hormones, as well as certain antibiotics delivered at sub-medicinal levels that stimulate citric acid cycle activity, are widely used in the US (less so, outside of the US) to increase the rate of weight gain (Pollan, 2006; Kleppel, 2014). The US Food and Drug Administration [FDA (U.S. Food and Drug Administration), 2013; FDA (U.S. Food Drug Administration), 2019] has tightened control over (but not banned) the use of antibiotics in animal feeds due to their role in the production of antibiotic resistant, pathogenic bacteria [Feingold et al., 2012; FDA (U.S. Food and Drug Administration), 2013; FDA (U.S. Food Drug Administration), 2019]. Although beyond the scope of this paper, CAFO practices, which reduce finishing times by 30–50% relative to finishing on pasture, have been criticized as inhumane and unsafe (Schlosser, 2001; Pollan, 2006; Ebner, 2017). Nonetheless, the industrial model of livestock production is the globally dominant meat production system, accounting for more than 80% of the meat produced in the United States (Schlosser, 2001; Ikerd, 2008).

Conventional livestock management which, in this paper, refers to the on-farm portion of livestock production, prior to movement to the CAFO, dovetails with the industrial model in its focus on specialization and monoculture, in its extensive use of chemical and other inputs and its reliance on grain-based or grain supplemented nutrition for ruminants, even when animals are on pasture. Stock densities on pasture tend to be relatively low and stock rotation (i.e., movement to fresh pasture) tends to be relatively infrequent (weeks to seasons) if it occurs at all. Overgrazing is common in conventional grazing systems and may be compensated for by supplementing with hay, silage and/or pelletized grain.

REGENERATIVE AGRICULTURE AND MULTI-PADDOCK GRAZING

Regenerative agriculture focuses at least as strongly on the restoration and management of soil health and agro-ecosystem functionality as on production (Doran et al., 2002). Doran (2002) defines soil health as "… *the capacity of a living soil to function within natural or managed ecosystem boundaries, to sustain plant and animal productivity, maintain or enhance water and air quality, and promote plant and animal health*."

Regenerative agriculture has its roots in the early to mid-twentieth century, beginning with the work of Howard (1940, 1947), Balfour (1943) and the emergent organic and (what became) the holistic management and sustainable agriculture movements of the 1960s and beyond. The regenerative approach is a response to evidence that soil health, functionality and quality have been lost or have deteriorated to the extent that much of the earth's arable soils are incapable of producing nutrient dense food and have lost the capacity to support essential ecosystem services (Pimentel et al., 1987; Crosson et al., 1995; Lal, 2001, 2019; Pimentel and Burgess, 2013; Montgomery, 2017). As such, regenerative operations frequently employ organic or "nature-based" practices (Brown, 2018) with the co-equal goals of producing nutrient dense food while restoring and managing environmental quality (Bouma, 2002; Jackson, 2002).

Pasture-based livestock production is key to regenerative farming and ranching. Pasture-based producers feed ruminant livestock primarily on forages, hay, and/or haylage. Omnivorous, non-ruminant livestock, such as swine and poultry, usually receive some grain-based feed supplements. Stock densities of ruminants in this system are usually 2–4 times higher than in conventional grazing systems and rotation to fresh pasture generally occurs every 0.5–3 days (Flack, 2016). A rotational cycle through a subdivided pasture system, or multi-paddock system, should require at least 30 days, but rotational cycles of 60 to >100 days are not uncommon (Gerrish, 2004). Rotational cycles can be adjusted to accomplish ancillary goals, such as invasive plant management, or to respond to changing vegetation, weather patterns (e.g., drought) or other variables (see Kleppel et al., 2011; Girard Cartier and Kleppel, 2015; Bishopp, 2020). Several workers have described these methods in detail, using such terms as holistic planned grazing, management-intensive grazing and intensive rotational grazing (Savory, 1983; Savory and Butterworth, 1999, 2016; Gerrish, 2004; Flack, 2016; Salatin, 2019). Collectively, they are referred to as multi-paddock (MP), or adaptive multi-paddock (AMP) livestock management (Teague et al., 2011; Rowntree et al., 2019). Multi-paddock management attempts to mimic the evolved herding behaviors of wild, ungulates (Voisin, 1959; Acocks, 1966a,b). Protagonists of multi-paddock management claim that this approach enhances soil fertility and health, reduces overgrazing, and reduces disease and morbidity within the herd. In this paper, I will examine some of these claims.

Wild Ungulates and the Multi-Paddock Approach to Grazing

About 40% the Earth's land area is suitable for agriculture and about one-third of that can support large scale crop production (Revelle, 1976). The remainder will only support animal agriculture. Whether produced conventionally or by RM practices, most domesticated ruminants forage on pasture or rangeland during at least a portion of their lives. The way land is used, and the amount of land used for grazing differ with practice, as do the responses of the soil, vegetation and water supplies to the stocking rates and activities of the animals.

Observations of wild, herd forming ungulates inform RM practice. Studies in the African Serengeti and Yellowstone National Park, Wyoming, USA have demonstrated that grazers, particularly large herd-forming ungulates, migrate across landscapes in response to stimuli associated with the seasonal growing cycle of the plant community (McNaughton, 1985; Frank et al., 1998). "Green waves" of primary production during the rainy season in the Serengeti and the vernal thaw in Yellowstone, trigger these migrations. Herd trajectories are refined by gradients in macro-nutrient and mineral concentrations in the forage (McNaughton, 1990). Plant communities in the Serengeti are, not surprisingly, dominated by grazing-tolerant species (McNaughton, 1984; Archibald, 2008), which tend to grow close to the ground and to be shorter in height than the same species in un-grazed grasslands. Nonetheless, compensatory biomass production in grazed plant communities tends to be higher than in grasslands from which large grazers have been excluded (McNaughton, 1984, 1986). Furthermore, studies in both wild and agricultural landscapes suggest that plant community species richness tends to be higher in ecosystems grazed by herd-forming ungulates (unencumbered by human artifacts) than in un-grazed systems, exclosures, or un-grazed sections within a particular landscape (Frank, 2005; Marion et al., 2010; Girard Cartier, 2017).

The capacity of soil-plant-herbivore interactions to translate from wild to agricultural ecosystems predicts the nature and extent of impacts that livestock may have on soil, forage, and aquatic resources. These, I suggest, will be determined by the way the livestock is managed within the grazing ecosystem.

ENVIRONMENTAL IMPACTS OF ANIMAL AGRICULTURE

This paper compares IC and RM practice in four categories of environmental impacts associated with livestock agriculture. These are: (i) impacts to plant communities and soil health; (ii) impacts to water and soil-water interactions; (iii) impacts from agricultural ammonia (NH_3) emissions; and (iv) impacts associated with climate change.

Impacts to Plant Communities and Soil Health

That livestock activities, including grazing, egestion and excretion, and trampling affect the structure and functioning of grassland ecosystems has led some workers to suggest that grazing and animal agriculture are ecologically destructive (Belsky, 1987; Mligo, 2015). Logic, however, causes one to question that notion, and numerous studies, both empirical and model-based, have demonstrated that a multiplicity of geophysical, biological, behavioral, and natural historical factors, functioning over seasonal to evolutionary timescales influence the ways that wild and domesticated grazers affect grassland ecosystems (McNaughton, 1985; Milchunas et al., 1988; Milchunas and Lauenroth, 1993; Cingolani et al., 2005; Patra et al., 2005; Villalba and Provenza, 2009; Hilario et al., 2017). Plant community biomass and composition, as well as plant physiology are influenced by the timing and intensity of grazing (Hayes and Holl, 2003; Frank, 2005). For example, Daubenmire (1940), studying the effects of domesticated livestock grazing on plant communities in the bunchgrass prairie of Washington state, USA, reported that heavy grazing resulted in severe defoliation and changes in dominance patterns and other structural variables in the prairie grass community. Furthermore, he noted that heavy grazing sometimes created areas of bare ground and altered patch structure. The effects of cattle grazing on the bunchgrass prairie community varied with the temporal onset of grazing and its persistence.

Interestingly, the factors that determine grazing intensity are often vaguely described in the literature and vary from one study to the next. Research published more than a half century ago, however, provides guidance on what determines grazing intensity. Voisin (1959) noticed that wild ungulates move continuously across a landscape. More recently, Owen-Smith et al. (2010) suggested that herd movements tend to be continuous over a hierarchy of spatial scales. Conventionally managed livestock, however, may remain in a single pasture for an entire grazing season over multiple years. Acocks (1966a; 1966b, cf. Hoffman, 2003) observed that wild, herd forming ungulates aggregate at relatively high densities. For example, Venter et al. (2017) reported wildebeest herds of >20 tons ha^{-1} (>100 head ha^{-1}) in a 24 km^2 region of the Serengeti. Conversely, domesticated livestock are often stocked at much lower densities [e.g., 1.2–2.5 tons ha^{-1}; UMass (Sustainable UMass), 2020] on pasture and rangeland, and moved infrequently, if at all. At low stocking rates livestock graze selectively, ultimately overgrazing patches and creating bare ground that becomes susceptible to drying, capping and erosion (Savory and Butterworth, 1999). Soil structural integrity deteriorates rapidly under these conditions, and the capacity of the soil to retain water and carbon is lost (Savory and Butterworth, 1999, 2016; Gerrish, 2004; Lal, 2004, 2015). Even in pastures composed of monocultures or only a few plant species, continuous or near-continuous grazing will produce these same outcomes (Massy, 2018).

Following on the observations of Acocks and Voisin, workers hypothesized that by mimicking the aggregation and movement patterns of wild ungulates, livestock could be managed without damaging grassland ecosystems (Goodloe, 1969; Savory, 1978, 1983; Savory and Parsons, 1980; Savory and Butterworth, 1999, 2016; Teague et al., 2009). Among the principal findings of researchers and practitioners of MP management are that frequent rotation and relatively long periods of pasture rest are key to pastoral ecosystem functionality and livestock health (Gerrish, 2004; Flack, 2016; Savory and Butterworth, 2016). In a typical multi-paddock operation, the vegetation in a single paddock experiences intense grazing pressure for a short period of time. This is followed by a period of pasture rest that varies with vegetation growth rates, such that over the course of the season the grassland is only lightly impacted. Some pastoralists have suggested that the rest period afforded to a grassland, more than the stocking rate (which can vary widely, e.g., from 5 to 125 tons ha^{-1}), may be critical to determining the impacts of grazers in a landscape (Salatin, 2019). Badgery (2017) compared the effects of high rotation frequencies and long periods of pasture rest (57 d, 114 d, or flexible rest period) on forage biomass and beef cattle production with conventional (continuous) grazing. While the effects varied with plant species composition, overall plant biomass and ground cover were significantly higher in the multi-paddock than the conventionally grazed system. Production was statistically similar in both experimental grazing systems. Teague et al. (2013) have been critical of such studies, pointing to the difficulties of designing experiments in which one attempts to hold a suite of secondary variables constant while the single variable of interest (e.g., rest period) is manipulated.

Several studies suggest that livestock managed according to the multi-paddock model can increase plant species richness and the functionality of grassland ecosystems (Booysen and De, 1969; Howell, 2008; Brown, 2018). Teague et al. (2011) observed higher production of seral grasses, and lower incidences of bare ground in pastures in north central Texas that used AMP practices relative to conventionally grazed pastures. Similarly, Girard Cartier and Kleppel (2017), Teague and Barnes (2017), and Kleppel (2019) observed higher plant biodiversity, forage biomass or both in pastures in upstate New York and north central Texas managed by MP and RM practices relative to pastures managed conventionally. Cassidy and Kleppel (2017) reported that Savannah sparrow (*Passerunculus sandwichensis*) and Bobolink (*Dolichonyx oryzivorus)* abundances were 2–3 times higher in pastures managed by MP and RM practices than in conventionally managed pastures.

Not all comparisons of MP and conventional grazing support these observations. In fact, there is a lack of consensus on the benefits of MP and RM management to plant community structure or function relative to IC and conventional grazing practice (Gosnell et al., 2020 and references therein). Teague et al. (2013) suggested possible explanations for contradictory results, but disagreements remain about the efficacy of multi-paddock techniques relative to conventionally managed grazing (e.g., Barnes and Denny, 1991; McCollum et al., 1999; Briske et al., 2008; Hawkins et al., 2017; and others). These discrepancies may be due, in part, to differences in the ways managers respond to environmental variability (Voisin, 1959).

The effects of grazers on soil structure and composition vary with the timing of deployment, rotation frequency, and species, breeds, and stocking rates. For example, grazing during dry or wet periods can have significant effects on soil structure, which will vary depending upon soil type, slope and landscape roughness, and the nature of vegetative cover. Verchot et al. (2002) observed that nitrogen (N) mineralization and immobilization proceeded at rates nearly an order of magnitude higher in the wet bottomlands of Yellowstone National Park (YNP) than in dry uplands areas, independent of whether the landscape was grazed or not grazed by wild ungulates. Conversely, Frank et al. (2000) reported significant differences in soil N-dynamics in grazed and un-grazed portions of the northern winter range of YNP. In livestock grazing systems, relationships among variables may be management-dependent. Girard Cartier (2017), working with sheep, reported differences in soil N-dynamics in bottomland and upland sites in upstate New York, USA that were associated with both landscape attributes and management practices (MP vs. continuous grazing).

The intimate coupling that exists between the soil microbial community, the plant community, and the activities of ruminants is critical to the functioning of both wild grassland and pastoral ecosystems (Bardgett et al., 1997, 2001; Oates et al., 2018). Grazing has a strong influence on this functionality and on the way livestock management can influence the structure and stability of both forage and soil microbial communities. For example, heavy grazing often results in severe defoliation and the production of highly labile root exudates that favor the growth of bacteria in the rhizosphere. Conversely, light grazing results in production of less labile root exudates that support the growth of fungal species (Bardgett and Leemans, 1995; Bardgett et al., 1998). One would expect, therefore, that fungal:bacterial (F:B) ratios would be higher in MP soils than conventionally managed soils, if indeed, MP management represents a form of "light" grazing. This is important because, as a rule, higher F:B ratios reflect greater soil organic matter (SOM) stability and greater water holding capacity. Furthermore, diversity is key to the stability of soil microbial communities and therefore to the interdependent functioning of the soil-forage-grazer system. Few studies, however, have compared soil microbial community structures and compositions in differently managed grasslands. Teague et al. (2011) in north central Texas, and Kleppel (2019) in upstate New York independently observed higher F:B ratios and greater microbial diversity in the soils of pastures managed by MP practices than by conventional practices. Multivariate analyses (Kleppel, 2019) revealed that different variables may drive changes in microbial biomass in soils of differently managed pastures, even when the pastures are near each other. These findings support the hypothesis that grazing management practices can influence the structure and functioning of the soil microbiome and thereby the structure of the soil itself.

Impacts to Water and Soil-Water Interactions

Water Pollution and Soil Degradation

It is not news that agriculture contributes significantly to water pollution. Runoff linked to the management of livestock and manure, as well as feed production are key contributors to that signal (Parris, 2011). The impacts of animal agriculture vary with regional differences in soil type, topography, weather, climate, and vegetation. The effects of RM and IC practices on water quality differ over a variety of scales. On Texas ranches, switching from multi-paddock to heavy continuous grazing practices resulted in increased runoff and losses of sediment, inorganic nitrogen, and phosphorus on the order of 140–160% (Park et al., 2017). Switching from continuous to MP grazing practices resulted in comparable decreases in erosion and nutrient leaching.

While ultimately, soil type and water delivery rate are the overarching determinants of infiltration rate, livestock, and pasture management practices can alter this process (Laycock and Conrad, 1967; Savory and Butterworth, 1999; Franzluebbers et al., 2012). However, comparisons between the effects of livestock management practices on water infiltration and soil compaction (i.e., bulk density) are inconsistent. Abdel-Magid et al. (1987) observed no effect of rotational frequency or stock density on bulk density, but infiltration declined at higher stock densities in sandy loam soils of the high-plains grasslands near Cheyenne, Wyoming, USA. Thurow et al. (1986) reported that in semi-arid Texas grasslands, infiltration rates, and bulk densities were less severely impacted by multi-paddock grazing than by continuous grazing, though Warren et al. (1986a) noted that both stock density and vegetation type may affect soil compaction and infiltration. Warren et al. (1986b) also reported that water infiltration into soils devoid of vegetation decreased significantly under intensive rotations with impacts increasing as a function of simulated rainfall. Teague et al. (2020) expressed concern about the artificiality of the design of these experiments. Kleppel (2019) studying grasslands grazed by large and small ruminants, as well as un-grazed hayfields, observed no effect of management practice (MP v. conventional v. hayfields) on soil moisture or infiltration rates, but found significantly less compaction (lower bulk densities) of MP soils than of conventionally grazed or hayfield soils in the silty-clay loams (principally Angola, Burdette, and Tuller-Green) and hilly landscapes of upstate New York.

TABLE 1 | Farm-to-gate blue water requirements for traditional beef cattle breeds produced by industrial-conventional (IC) and regenerative-multi-paddock (RM) management.

Industrial-conventional[a]		**Regenerative-multi-paddock**[b]	
	Liters kg^{-1} CW		**Liters kg^{-1} CW**
Drinking	62.9	Drinking	62.9
Feed production	2032.1	Feed production – min	201.2
Total requirement	2095.1	Feed production – max	955.1
		Total requirement – min	264.1
		Total requirement – max	1018.0

[a] *Data from Rotz et al. (2019).*

[b] *To estimate minimum (min) and maximum (max) feed production requirements, i.e., use factors relating to production of grain feeds, as well as synthetic chemical inputs were removed from the use factor list (Rotz et al., 2019, their table, p. 3) to create a list of RM use factors. Then, the minimum water requirement for RM feed production = (Σ minimum values for RM use factors/ Σ minimum values for all use factors) × Feed production water requirement (2032.1 L kg^{-1} CW). The maximum water requirement for RM feed production was estimated by replacing minimum use factors by maximum use factors.*

Blue Water Withdrawals

Agriculture is water intensive. Between 30 and 40% of blue water withdrawals in the United States and $\sim$60–70% of blue water withdrawals worldwide are associated with agricultural activities (USGS (U.S. Geological Service), 2005; Schlosser et al., 2014). In the US, only about 7.5% of agricultural water use is directed toward livestock production and only 3% is consumed as drinking water by cattle (Rotz et al., 2019). Approximately 90% of all blue water withdrawals for agriculture are used for irrigation (91.7 TL) [USDA/ERS (U.S. Department of Agriculture/ Economic Research Service), 2019a]. About 60% of that is for production of livestock feed crops: corn (25%), forage (18%) and soybeans (14%) [USDA/ERS (U.S. Department of Agriculture/ Economic Research Service), 2019b].

Rotz et al. (2019) conducted an extensive and elegant analysis of the environmental footprint of beef production in the United States. The authors used an Integrated Farm System Model (IFSM; Rotz et al., 2016) to estimate energy use, greenhouse gas (GHG) emissions, reactive N releases and blue water withdrawals for production of both traditional beef breeds and culled dairy cattle. They reported a farm-to-gate blue water consumption of 23.2 TL for the US herd, or 2,095 L/kg of carcass weight (CW). Only 0.7 TL nationally, or 62.9 L/kg CW of total blue water withdrawal accrues from drinking and 6–11% of the water consumed by a steer is returned to the hydrological cycle by excretion (as urine and dung) and respiration (Nader et al., 1998). The fate of excreted water depends on practice. In pasture-based practice, water in urine and dung is returned to the soil where it may serve as a vehicle facilitating microbial contact for nutrient regeneration. In a CAFO, urine and dung are treated as contaminants and may be composted in sumps or other waste management systems.

Rotz et al. (2019) did not distinguish between IC and RM blue water withdrawals. However, using their **Table 1** (p. 3), which provides blue water use factors for feed production, it was possible to separate factors associated with IC and RM operations (**Table 1** in this paper). I used Rotz et al.'s blue water withdrawal estimates for IC practice, but because minimum and maximum values were provided for some feed production use factors, I preserved the range of estimates of water withdrawals associated with feed production in RM operations. The relative difference between blue water use for feed production by the two practices is substantial. IC practices require 53.1–90.1% more water than RM practices due to the lower dependence of RM practice on grain-based feeds. For a pasture-based RM operation between 251.2 and 955.1 liters of water will be used to produce the forage and hay-based products needed to generate one kg of red meat, reducing the blue water requirement from 2,095.0 L kg^{-1} CW to between 264.1 and 1,018.0 L kg^{-1} CW.

Impacts From Agricultural Ammonia (NH_3) Emissions

Ammonia emissions contribute to eutrophication and acidification in aquatic ecosystems, vegetation damage and alteration of plant community composition in terrestrial ecosystems, and human morbidity (Kelly et al., 2005). Agriculture is a significant ammonia source. For instance, $\sim$80–94% of all NH_3 emissions in Europe and the United States are thought to be contributed by agricultural activities (Webb et al., 2005; Herbert et al., 2020). Agricultural emissions in the United Kingdom were estimated to be 228 kt-N at the turn of the twenty-first century (Pain et al., 1998; Sutton et al., 2000). Animal agricultural emissions [1.67 mtons y^{-1} in the US (USEPA (U.S. Environmental Protection Agency), 2016)] are generated by animal housing and confinement practices, manure storage and slurry spreading, inorganic fertilizer use, and grazing. Together, housing and confinement practices, manure spreading, and fertilizer use account for about 75% of all emissions. The ammonia contribution associated with grazing is relatively minor, about 12% (Misselbrook, 2015).

I am not aware of studies comparing the magnitudes of ammonia emissions and impacts on farms employing RM practices with those produced by IC operations. It seems reasonable, however, to hypothesize that IC agriculture creates a substantially larger ammonia footprint than RM agriculture due to intensive confinement and other practices. Further research in this area seems warranted.

Impacts Associated With Climate Change

Agriculture is a significant source of greenhouse gas (GHG) emissions. Three factors determine the net agricultural contribution: (i) CO_2-eq emitted; (ii) CO_2-eq removed and (iii) CO_2-eq stored in the soil.

CO_2-eq Emitted

Farming, forestry, and land use change associated with agriculture contribute 24–31% of the 50.9 GT of annual global GHG emissions (IPCC, 2014). Nearly half of this is the result of rainforest destruction, much of it for livestock grazing and feed-grain production (IPCC, 2018). In aggregate, livestock production represents 14.5% (7.1 GT) of total GHG emissions globally (Olivier and Peters, 2018; Food Agriculture Organization, 2020). Feed production (including the soils used to grow feed crops), i.e., the cultivation of grains used for livestock feeds, usually in large monocultures produced with the use of synthetic fertilizers and pesticides, is the largest GHG contributor within animal agriculture. Feed production accounts for ∼45% (3.2 GT) of total GHG emissions within the category. This is followed by enteric (principally methane) production (39%), manure management (10%), and transportation and processing (6%).

In 2017, agriculture contributed ∼9.1% of the 6.5 GT of CO_2-eq emitted in the United States [USEPA (U.S. Environmental Protection Agency), 2016]. Crop production (including that required for livestock feeds) contributed about 58% (3.77 GT) of total US agricultural GHG emissions. Livestock production contributed 42% (2.73 GT). Rotz et al. (2019) provide a breakdown of the source-terms: Enteric GHG production, principally as methane, contributes 56% of livestock-based CO_2-eq; pasture, range and crop lands emit 24% of all CO_2-eq (mostly as N_2O). Manure contributes slightly <20% of CO_2-eq-—10% as CH_4 and <10% as N_20. Fertilizer, electricity, fuel production and other upstream sources contribute 13% and fuel combustion and lime decomposition contribute 4%.

The values presented above on do not distinguish among livestock management practices and would therefore be assumed to be skewed toward emissions arising from conventional grazing and IC practices that dominate animal agriculture. Given the growing interest in regenerative agriculture, however, it seems reasonable to attempt a comparison of GHG emissions from RM and IC livestock production practices (**Table 2**). By obviating the GHG emissions associated with feed-grain production, emissions are reduced by ∼59%. While enteric methane production by "grass-fed" cattle will be as much as 20% higher than by grain-fed animals, the use of frequent pasture rotations reduces enteric methane production by, on average, 22% (DeRamus et al., 2003). Although manure management practices vary widely in both IC and RM systems, a review of several sources (see notes below **Table 2**) suggests an average estimated difference of 56.3% (± standard deviation = 45.2) between IC and RM operations. Transportation and energy inputs (oil and fuel) were estimated to be 28% lower for RM animal agriculture than for IC agriculture (Pimentel et al., 2006). Applying these changes, RM management appears capable of reducing annual global GHG emissions from livestock production by ∼35.2%, to 4.6 GT CO_2-eq y^{-1}. Estimates by Havlik et al. (2014) suggest that changes from conventional to RM practices would lower GHG emissions by about 3.2 GT CO_2-eq y^{-1}, consistent with the estimate presented in **Table 2**. The effect of forage quality on GHG emissions is not captured in **Table 2**, but improvements in forage quality would be expected to lower enteric methane production further (Beauchemin et al., 2008; Herrero et al., 2013).

TABLE 2 | Greenhouse gas emissions (as GT CO_2-eq y^{-1}) associated with livestock production by industrial-conventional (IC) and regenerative-multi-paddock (RM) practices.

	GHG from management approach	
	IC CO_2-eq (GT y^{-1})	RM CO_2-eq (GT y^{-1})
Feed production	3.2	1.3[a]
Enteric processing	2.8	2.7[b]
Manure management	0.7	0.3[c]
Transportation and energy	0.4	0.3[d]
Total	7.1	4.6

Data for (globally dominant) IC practice are from Food Agriculture Organization (2019). Estimates for RM management reflect recalculation of emissions from each category based on studies comparing IC and RM (or organic) practices.

[a] *Reflects removal of grain production and production of synthetic inputs derived from the use factors of Rotz et al. (2019).*

[b] *Reflects a 20% increase in GHG emissions assuming a grass-based, rather than a grass-grain based diet, and a 22% decrease in GHG emissions from multi-paddock rotational practices (DeRamus et al., 2003).*

[c] *Based on the mean difference (56.3%) in CH_4 and N_2O emissions associated with manure management and distribution practices on conventional and regenerative (organic) farms. Sources: Chadwick (2011), Sneath et al. (2006), Weiske et al. (2006), and Yamulki (2006).*

[d] *Reflects a 28% reduction in GHG emissions by using RM (organic) practices (Pimentel et al., 2006).*

CO_2-eq Removed

Grasslands play a critical role in photosynthetic carbon sequestration (Derner and Schuman, 2007; Sacks et al., 2014). Net terrestrial primary productivity (NPP), on the order of 56.4–62.1 GT yr^{-1}, constitutes just over half of the annual global production (Foley, 1994; Field et al., 1998). Tropical rainforests (17.8 GT yr^{-1}) and savannahs + perennial grasslands (19.2 GT yr^{-1}) account for 60–65 percent of the total.

Stanley et al. (2018) used a life cycle assessment (LCA) to investigate the path of carbon through multi-paddock and conventional beef cattle finishing systems in the American mid-west. Their study revealed significantly higher net GHG production by MP than by conventional practices, due to a >2.5-fold higher enteric GHG emission rate from MP systems than from conventional, grain-based systems. Furthermore, over the life cycle of production, GHG emissions from MP systems were 1.6 times higher than that from conventional management when carbon flux into the soil (i.e., sequestration) was not considered. However, when sequestration was included in the assessment, the MP model significantly out-performed the conventional model, removing more than twice the CO_2-eq of conventional beef production. LCA studies by Pelletier et al. (2010) and Lupo et al. (2013) support these observations, suggesting a 24–30% reduction in net GHG production as a function of sequestration from grass-fed beef production. These observations are consistent with an LCA analysis by Wang et al. (2015) for beef production in Texas, and they track well with empirical observations (Teague et al., 2011; Dowhower et al., 2019; Rowntree et al., 2019). The importance of C-sequestration by grasslands is clearly critical to the efficacy of agriculture as a vehicle for GHG removal. As such, MP practices may prove to be a valuable tool for climate change mitigation. As Lal (2019) states,

> *"The technical potential of carbon sequestration in world soils may be 2 billion to 3 billion mt per year for the next 50 years. The potential of carbon sequestration in soils and vegetation together is equivalent to a draw-down of about 50 parts per million of atmospheric CO2 by 2100."*

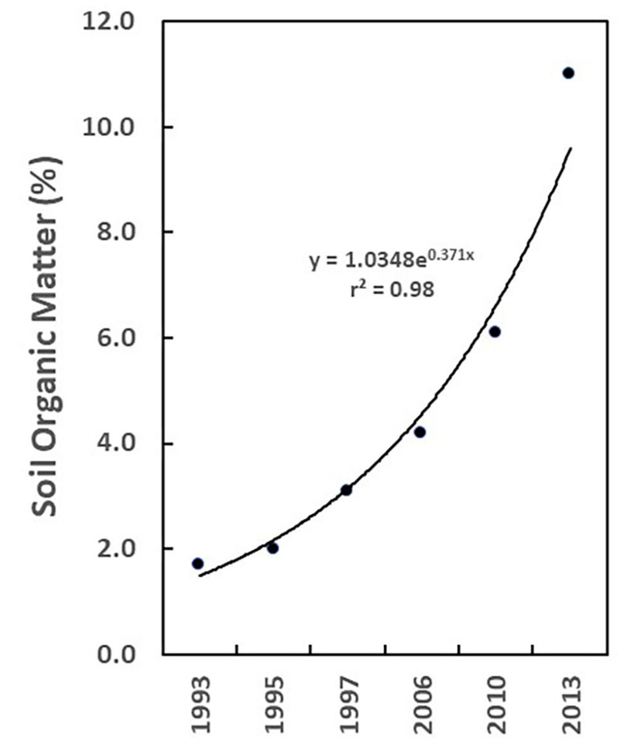

FIGURE 1 | Soil organic matter (SOM; %) at Brown Ranch, near Bismarck, North Dakota, USA, 1993–2013 (source of data: Brown, 2016).

CO_2-eq Stored in the Soil

Grassland and agricultural soils, which cover 53.6% of the earth's land area, store between 52 and 55% of the net terrestrial primary production (Sacks et al., 2014). Turnover of above-ground primary production by aerobic decomposition occurs on timescales of seasons. Herbivorous conversion of plant biomass to dung and urine increases turnover efficiency by 21% (Yoshitake et al., 2014), and facilitates development of soil microbial community structure, which in turn promotes the stabilization and storage of carbon in the soil (Merrill et al., 1994; Bardgett et al., 1998). Patchy deposition of dung, as occurs when livestock densities are low, is obviated by MP practices that manage at higher stock densities and rotation frequencies (Gerrish, 2004; Flack, 2016).

Integration of livestock and crop production may offer additional opportunities to mitigate GHG emissions (Liu H. et al., 2015; Lal, 2020). Conservation agriculture (CA), described by Lal (2004, 2015, 2019), focuses on increasing carbon storage in the soil during crop production. CA practice involves a commitment to minimal disruption of the soil surface (e.g., low-till or no-till planting), and to ensuring that the soil is always covered with forage, cover crops, or harvest tailings. CA also encourages diversification of vegetation and crop rotation (Farooq and Siddique, 2014). One can speculate that when overlaid on the CA framework, the integration of high frequency rotations of densely stocked ruminants through a rotational cycle that includes harvested crop fields, followed by prolonged rest, would enhance carbon sequestration and storage in croplands while improving fertility. In a case study described in the popular media, Brown (2016, 2018) tracked the deposition of carbon into the soil of his 2000 ha ranch near Bismarck, North Dakota, USA over 23 years. The ranch is managed by integrating RM livestock practices with the principles of conservation agriculture to produce beef cattle, sheep, chickens and a variety of crops. During the course of Brown's analysis, soil organic matter on his ranch increased more than 5-fold, from 1.7 to 11.0% (**Figure 1**).

To summarize, it would appear that MP and RM practices are capable of making significant contributions to climate change mitigation. GHG emissions can be reduced by more than 30%, C-sequestration can be increased by 24–30% (and possibly considerably more), and the time required to convert photosynthetically fixed carbon, i.e., plant biomass, into stable carbon in the soil can be reduced by 21% through grazing, relative to the time required for oxidative turnover. By applying the reduction in GHG emissions via C-sequestration to the estimated emissions from RM practices in **Table 2**, the net GHG contribution by animal agriculture would be 3.2–3.5 GT CO_2-eq y^{-1} or, conservatively, 45.1–49.3% (i.e., removal of more than half) of current emissions.

These estimates support the conclusion that agriculture has a critical role to play in the removal of carbon from the atmosphere and in the stabilization and storage of carbon in the soil (Food Agriculture Organization, 2019).

Sacks et al. (2014) go further, suggesting that well-managed grazing in arid and semi-arid regions, where severe soil degradation and desertification have occurred, can play a pivotal role in carbon sequestration and climate change mitigation:

> *This approach…Holistic Planned Grazing, the effectiveness of which has been demonstrated on over millions of hectares on four continents…has the potential to remove excess atmospheric carbon resulting from anthropogenic soil loss over the past 10,000 years and… all industrial-era greenhouse gas emissions. This sequestration potential…could, in theory, return 10 or more gigatons of…atmospheric carbon to the terrestrial sink annually and lower greenhouse gas concentrations to pre-industrial levels in a matter of decades…"*

Clearly, the possibility of a pasture-based approach to planetary carbon management is worthy of further consideration.

DISCUSSION

From this brief review, it is evident that significant differences exist between the impacts of IC and RM management with respect to key ecosystem attributes. Though the issue is far from resolved, RM practices appear in many respects to be environmentally benign relative to their IC counterparts. The environmental impacts considered here, and the differences between the management practices that create them may not be the direct result of livestock activities on pasture or rangeland. Often, they are due to differences in the resource intensities (e.g., water or fossil fuels) required to support IC or RM management.

Papers published between the 1980s and the present have repeatedly questioned the efficacy of various forms of MP management, particularly Savory and Butterworth's (1999, 2016) holistic approach (e.g., Holechek et al., 2000; Briske et al., 2008; Hawkins et al., 2017; and others). Some of the hypotheses and observations promoted by Savory, such as the ability of holistic management to mitigate desertification and climate change (Savory, 2013) have been particularly contentious (Briske et al., 2013). However, Teague et al. (2009, 2013), Wang et al. (2016), and others (e.g., see Teague, 2014) have pointed to the technical and scaling issues that may influence the interpretation of the reductionist approaches typical of traditional experimental comparisons of livestock performance and their environmental consequences under IC management. It has also been suggested that contradictory results may accrue, at least in part, from perceptual differences in the management and operational goals of RM and IC management by both researchers and graziers (Briske et al., 2011). The contentiousness of the debate may contribute to its apparent un-resolvability (Collins, 1981). Briske et al. (2011) suggest moving beyond the debate over whether one management approach is better than the other. They suggest that the focus should be on finding adaptive approaches to livestock production and pasture/rangeland management that respond to the realities of meat production. Sherren and Kent (2019) decry the "linear" (i.e., reductionist) thinking that dominates the issue. The capacity of scientists to deal effectively with complex systems has long been problematic (Capra, 2005). Grazing ecosystems and the outcomes of herbivore-plant-soil interactions, while seemingly simple, are actually functionally complex (Liu J. et al., 2015). Sherren and Kent (2019) and Wynne (1992) point out that frequently researchers exclude or simply miss the realities of livestock management as experienced by graziers. Briske et al. (2011) and Gosnell et al. (2020) suggest incorporating multi-dimensional, socio-ecological perspectives into efforts to understand livestock management dynamics and its outcomes.

Traditionally, livestock farming, and ranching have had an overriding purpose: production (Toombs and Roberts, 2009). The determination of how to produce the greatest weight gain in the shortest amount of time is of interest to all farmers, ranchers, and students of animal science. Comparisons of livestock weight gain in MP and conventional grazing systems have not been consistent, and more than likely depend upon interactions among stocking rates, forage compositions and any number of highly variable environmental forcing functions as well as the spatial scales at which observations are made (Derner and Hart, 2007; also see Teague et al., 2013 for more detailed treatment of this subject).

Notwithstanding the importance of production, the slow but persistent emergence of the organic, sustainable, and regenerative farming movements have made environmental stewardship an additional, and even principal goal of animal agriculture. The practitioner's approach toward livestock management broadens when the focus of one's work includes land stewardship. Livestock is no longer the sole product. In fact, livestock becomes a tool to be used in the regenerative process. The convergent goals—production and stewardship—are not necessarily complementary and achieving one goal may impede achievement of the other, at least temporarily. For example, cattle produced by RM management often require 3–6 months longer to finish than grain-supplemented, pastured, or feedlot-finished cattle. However, RM practice may provide positive outcomes by improving soil health and forage quality, and by mitigating a substantial portion of total global GHG emissions.

It is common knowledge among both farmers and researchers that soil loss and grassland degradation are at near crisis stage (Pimentel, 1997, 2006; Montgomery, 2017; Brown, 2018; J. Kempf, pers. comm. 2017). It is not simply appropriate, but necessary, to the future of agriculture, that some of our attention be focused on soil and ecosystem regeneration. When one manages for soil health, water quality, GHG mitigation, biodiversity, and the restoration of other essential ecosystem services, as well as for livestock production, even the most fundamental management decisions will likely differ from those made when production is the only focus of one's practice. Consistent with the advice of Briske et al. (2011) and Gosnell et al. (2020), we must recognize that complex issues have only partial solutions in science, and that fuller and more satisfying solutions accrue by integrating scientific and practical knowledge (Sherren and Kent, 2019).

CONCLUSION

It is worth remembering that agriculture provides 98% of the food that humans consume, and that meat is critical to the global food supply (White and Hall, 2017). Two thirds of the land on which food is produced can only be used for meat production. If nothing else, this review has supported the concern of many that agriculture is the cause of significant environmental pollution, ecosystem stress, habitat destruction and the loss of ecosystem services. This must change; meat production must and can become a vehicle for creating protein sufficiency, environment integrity and the restoration of ecosystem services, globally. It is the very definition of a non-sequitur that: while food is a critical part of our life support system, to produce food we must destroy our life support system.

The results of the present analysis suggest that producing livestock need not destroy our life support system. RM practices, with their focus on the restoration and enhancement of ecosystems and the critical services they provide, appear to have the potential to make meat production a more environmentally benign process. Clearly, much is unknown. Data gaps remain; improvements in practice are needed and, in some cases, forthcoming. Supply chain models to ensure the economic viability of RM livestock production at scale are, at best, in the early stages of development. Adoption by farmers and ranchers remains limited, and policies and educational programs that encourage greater participation in RM practice are often lacking or poorly advertised (Francis et al., 1986). Efforts to discourage regenerative meat production by special interests and naivete within certain sectors of the research community have slowed development of sustainable meat production practices (e.g., Willett et al., 2019). Yet, given that meat consumption is increasing worldwide (NAS, 2015), adoption of environmentally regenerative meat production practices seems crucial.

Although enough food is currently produced to provide a calorically sufficient daily ration to every human being on earth, we are rapidly approaching carrying capacity (Cribb, 2010; Tilman et al., 2011). Within the next 30 years, as the human population approaches 10 billion, as the climate becomes increasingly hostile, as water, soil, biodiversity, and other resources disappear, it will become increasingly difficult to feed ourselves (Larson et al., 1983; Pimentel et al., 1992; IPCC, 2019). Although regenerative production will not slow population growth and will never, in and of itself, provide the solution to world hunger, agriculture, including animal agriculture, can play an important role in GHG mitigation, soil-health restoration, and water and biodiversity conservation (Lal, 2004; Herrero and Thornton, 2013; Sacks et al., 2014; Cassidy and Kleppel, 2017; Montgomery, 2017; Stanley et al., 2018). The effectiveness of agriculture as a tool, not only for feeding ourselves but for meeting the challenges posed by human population growth, and in the process providing a sustainable income to farmers and ranchers has been suggested by research and demonstrated in practice (Food Agriculture Organization, 2013; Kleppel, 2014; Teague and Barnes, 2017; Brown, 2018; Massy, 2018; Amadu et al., 2020). Livestock production represents a tool, not only for providing calories and protein to our species over the next half century, but for ensuring the livability of our planet to humans and myriad other species well into the future.

AUTHOR'S NOTE

Ungulates are key to human nutrition and the functioning of Earth's ecosystems. Nonetheless, animal agriculture is a significant contributor to grassland degradation and soil destruction, water pollution and depletion, and global greenhouse gas emissions. It seems a non-sequitur that the production of food, part of our life support system, should be linked to degradation of the environment (i.e., our life support system). I reviewed the literature on two approaches to livestock management, one based on industrial agriculture, the other on regenerative agriculture, to ascertain whether one system is environmentally benign relative to the other. There is a lack of consensus on which approach is less destructive of plant communities or soil structure, though regenerative management appears to support larger, more diverse soil microbial communities. Furthermore, regenerative animal agriculture appears less likely to contribute to water pollution, to have lower water withdrawal requirements, and to be associated with lower greenhouse gas emissions and higher greenhouse gas removal rates than industrial management. By broadening the focus of animal agriculture to include both production and stewardship we can feed our species while reducing damage to the environment.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

FUNDING

Internal funding from the University at Albany, SUNY.

ACKNOWLEDGMENTS

I am grateful to F. D. Provenza for many useful conversations and for comments on an earlier draft of the manuscript.

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Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Sustainable Food Systems

REVIEW
published: 29 September 2020
doi: 10.3389/fsufs.2020.534187

Managing Grazing to Restore Soil Health, Ecosystem Function, and Ecosystem Services

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OPEN ACCESS

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Australian National University, Australia

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Specialty section:
This article was submitted to Agroecology and Ecosystem Services, a section of the journal Frontiers in Sustainable Food Systems

Received: 11 February 2020
Accepted: 19 August 2020
Published: 29 September 2020

Citation:
Teague R and Kreuter U (2020) Managing Grazing to Restore Soil Health, Ecosystem Function, and Ecosystem Services.
Front. Sustain. Food Syst. 4:534187.
doi: 10.3389/fsufs.2020.534187

Ruminants including domestic livestock, have been accused of causing damaging impacts on the global environment and human well-being. However, with appropriate management, ruminant livestock can play a significant role in efforts to reverse environmental damages caused by human mismanagement and neglect. Worldwide, at least one billion people living in grazing ecosystems depend on them for their livelihoods, usually through livestock production, and for other ecosystem services that affect human well-being. For long-term rangeland sustainability and ecological resilience, agricultural production policies are urgently needed globally to transform current damaging industrial inorganic input agricultural practices to resource conservation practices that enhance ecosystem function. This is supported by evidence that farmers and ranchers who apply regenerative management practices to restore ecosystem functionality create sustainable, resilient agroecosystems cost-effectively. With enhanced management of grazing resources, domesticated ruminants can be used to produce higher permanent soil cover of litter and plants, which are effective in reducing soil erosion and increasing net biophysical carbon accumulation. Incorporating forages and ruminants into regeneratively managed cropping systems can also elevate soil organic carbon and improve soil ecological function and reduce production costs by eliminating the use of annual tillage, inorganic fertilizers and biocides. Ecosystem services that are enhanced using regenerative land management include soil stabilization and formation, water infiltration, carbon sequestration, nutrient cycling and availability, biodiversity, and wildlife habitat, which cumulatively result in increased ecosystem and economic stability and resilience. Scientists partnering with farmers and ranchers around the world who have improved their land resource base and excel financially have documented how such land managers produce sound environmental, social, and economic outcomes. Many of these producers have used Adaptive Multi-Paddock (AMP) grazing management as a highly effective approach for managing their grazing lands sustainably. This approach uses short-duration grazing periods, long adaptively varied post-grazing plant recovery periods requiring multiple paddocks per herd to ensure adequate residual biomass, and adjustment of animal numbers as environmental and economic conditions change. Using this approach, farmers and ranchers have achieved superior ecosystem and profitability outcomes. This manuscript summarizes the use of AMP grazing as regenerative tool for grazed and rotationally cropped lands.

Keywords: ecosystem services, grazing management practices, regenerative agriculture, soil health, sustainable capitalism

INTRODUCTION

For the continued delivery of essential ecosystem services supporting the livelihoods of people living in grassland and savanna ecosystems, it is critical to maintain or enhance the productive capacity and resilience (Frank et al., 1998; Janzen, 2010). Such ecosystem services include the maintenance of stable and productive soils, the delivery of clean water, the sustenance of functional soil-biosphere hydrological cycles, and plants, animals and other organisms that support ecosystem function and human livelihoods and well-being. Agro-ecosystems that include grazing are more productive, stable and resilient when the soil is fully functional biologically, and they provide greater earnings and more abundant ecosystem services (Teague et al., 2013).

While developments in knowledge and technology have greatly increased agricultural productivity, inadequate attention has been given to long-term sustainability of natural resources and ecosystem services provided by agroecosystems. Through repeated soil tillage, artificial fertilizer application, and widespread biocide use, grazing and cropping agriculture is globally implicated in negative impacts on land resources and climate (MEA, 2005; Delgado et al., 2011). Carbon levels in most agricultural soils have declined in the last 100 years (Lal, 2004). In a global analysis, Sanderman et al. (2017) found that the largest SOC losses coincide with cropping regions but grazing, especially in arid and semiarid regions that are globally more extensive, was responsible for at least half of the total SOC loss. Biomes that are predominantly grasslands and savannas lost more SOC than the cropland and crop/natural vegetation categories, and the regions that have lost the most SOC relative to historic levels include the rangelands of Argentina, southern Africa and Australia. Such massive soil carbon losses have led to the degradation of soil structure, productivity and resilience as well as their capacity to infiltrate, filter and retain surface water, which collectively cool soils. These effects have led to impoverishment and loss of soil, disrupted hydrological and biogeochemical processes, contamination of water bodies by fertilizer and biocide runoff, loss of biodiversity, excessive water use and aquifer depletion, and increased greenhouse gas (GHG) emissions implicated in climate change as noted in the reviews by Lal (2003) and Janzen (2010).

Ecologically sensitive management of soil and appropriate inclusion of perennial forages and ruminants in mixed crop and grazing agro-ecosystems has been demonstrated to decrease the problems associated with current tillage and inorganic chemical input-based cropping and feedlot-based livestock production systems. Permanent cover of forage plants is critical for reducing soil erosion and, when ruminants consuming only grazed forages are included and managed appropriately, results in carbon sequestration that exceeds ruminant carbon emissions (Stanley et al., 2018). Regeneratively managed agro-ecosystems incorporating forages and ruminants minimizes the damage of tillage and inorganic fertilizers and biocides, elevates soil organic carbon, improves soil ecological function, and enhances biodiversity Janzen, 2010; Delgado et al., 2011; Gattinger et al., 2012; Aguilera et al., 2013). The innovative regenerative grazing management we refer to as adaptive multi-paddock grazing (AMP) has been operational for four decades in many parts of the world. Positive ecological and economic results have been achieved by AMP managers in various climatic areas ranging from mean annual precipitation of arid (200 mm) to humid (+2,000 mm) regions where grazing is practiced in North America, South America, Hawaii, central and southern Africa, Australia and New Zealand. This has been independently documented by Montgomery (2017) and Massy (2018). These are recent comprehensive global reviews on the subject.

In this paper we describe historical effects of herbivory on grasslands, characteristics of alternative grazing management approaches to restoring grassland health, biological drivers and causal mechanisms in grazing ecosystems, and limitations of past research. We emphasize the importance of collaborating with exemplary ranchers and farmers to understand grazing management strategies that lead to cost-effective restoration of ecological function and ecosystem services in agricultural systems which support sustainable income in a variable environment. Throughout we focus on how different strategies affect ecosystem functionality, productivity, and sustainability by modifying soil processes that underlie water and nutrient cycling and plant growth (Teague et al., 2013).

HISTORICAL HERBIVORY EFFECTS ON GRASSLANDS

Grasslands co-evolved with herbivores since the late Mesozoic Era as complex, dynamic ecosystems comprised of grasses, soil biota, grazers, and predators (Retallack, 2013). Spatial and temporal variation in the grazing landscapes caused large concentrated herds of grazing ungulates to move regularly to satisfy water and nutrient requirements and to avoid recently grazed and fouled areas, and in response to their social organization and the influences of fire, predation, hunting and herding (Bailey and Provenza, 2008; Provenza, 2008). Such periodic concentrated herbivory led to relatively short periods of heavy and uniform use of grass species as animals moved across the landscape. These periods of intense herbivory were generally followed by periods of herbivore absence during which defoliated plants regrew before the grazers returned to the area. Early hunter gatherers increasingly affected the landscape by deliberately burning areas to open them up, to drive wild animals toward hunting parties, and to attract wild grazers to recently burned areas (Pyne, 2001).

This resulted in grazed ecosystems that are complex and highly resilient and sustain considerably higher levels of herbivory and animal biomass than other terrestrial habitats (Stuart Hill and Mentis, 1982; Frank et al., 1998). The interaction of fluctuating climatic conditions, fire and grazing created the resilient and dynamic networks of organisms capable of responding to episodic biophysical events, and ecosystems that never reach a steady-state or climax seral stage but rather such periodic disturbances rejuvenated and transformed grasslands, including soil structure and nutrients, plant species composition, structure and biodiversity (Rice and Parenti, 1978; Pickett and White, 1985; Hulbert, 1988).

In the evolution of grassland and savanna ecosystems, synergistic interactions between soil fungi and microbes, plants, and various associated animal life forms resulted in the biosequestering of atmospheric carbon into stable soil carbon pools; these enhanced the productivity, resilience, hydrology and carbon capture capacity of these soils and the balance between carbon accumulation and oxidation rates (Frank and Groffman, 1998; Altieri, 1999; Van der Heijden et al., 2008; De Vries et al., 2012; Morriën et al., 2017). These high carbon soils have high water holding capacity, which can extend the longevity and area of green photosynthesizing leaves, and elevated evapotranspiration of water vapor and substantial latent heat fluxes that govern 95% of the earth's heat dynamics and hydrological cooling of earth and its climate (Veizer et al., 2000; Ferguson and Veizer, 2007; Pokorný et al., 2010). While these integrated biophysical systems (soils, hydrology, plants and animals) resulted in carbon sequestration rates that exceeded oxidation rates, human agricultural activities including repeated burning and tilling, burning and overgrazing have led to the reversal of the soil carbon dynamic and the depletion of accumulated soil carbon.

With the arrival of European settlers in North and South America, Africa and Australia, migratory free-ranging herds of large grazing ungulates and transhumance livestock herding were increasingly replaced by sedentary domestic livestock production, land was increasingly subdivided into fenced landholdings and predators were widely exterminated (Oesterheld et al., 1992; Provenza, 2008). Under private land tenure, grasslands were traditionally used for livestock production by allowing grazing animals to disperse freely within individual landholdings. This grazing management approach is generally referred to as season-long continuous grazing (CG) and generally leads to long-term concentration of grazers on preferred areas (especially lower lying, flatter areas with more palatable and easily accessible plants near water resources) and repeated use of preferred forage species (Fuls, 1992; Kellner and Bosch, 1992; Teague et al., 2004). Such long-lasting, selective herbivory on individual properties has led to localized overgrazing, proliferation of less palatable grass species and woody plants, increased bare areas and, ultimately, the decline in the ecological functionality of grazed landscapes (Briggs et al., 2005; Archer et al., 2017). Continuous concentrated grazing can also lead to collapse of soil aggregation and structure, lower surface water infiltration rates, less plant-available soil water, and increased surface water runoff, soil erosion, nutrient movement to downslope water bodies, and ultimately eutrophication and impairment of freshwater sources (Thurow, 1991; Burkart and Stoner, 2002; Babiker et al., 2004; Webber et al., 2010). In the last 70 years, increasingly industrialized grazing and cropping practices have greatly accelerated these effects by applying excessive grazing pressure under continuous grazing practices combined with the overuse of fire, tillage, inorganic fertilizers, biocides, and irrigation that collectively oxidize soil carbon (Delgado et al., 2011).

CHARACTERISTICS OF ALTERNATIVE GRAZING MANAGEMENT APPROACHES

Two alternative grazing management approaches to continuous grazing (*CG*) have been proposed to mitigate long-term overuse of preferred areas and grasses and to simulate the historic patterns of periodic concentration of grazing followed by post-grazing herbaceous recovery periods (**Figure 1**). The first approach is pyric herbivory *(PH)*, which combines rotational patch burning as the primary mechanism for concentrating grazing animals and moving their impact across the landscape, with constant continuous stocking over the entire management unit (Fuhlendorf et al., 2006). The second approach is adaptive multi-paddock *(AMP)* grazing, which uses multiple paddocks per herd with the goal of managing grazing resources to improve ecological function (Teague et al., 2013). This is achieved by adjusting animal numbers to match available forage, using short grazing periods, leaving sufficient post-herbivory plant residue for regrowth, and providing long recovery periods to adaptively accommodate intra- and inter-seasonal variation in herbaceous plant growth. It is important to emphasize that *AMP* grazing is not equivalent to rotational grazing, which is a generic term used for diverse grazing management approaches that subdivide the grazing area into any number of paddocks that are grazed sequentially using pre-determined grazing periods.

Periodic concentrated herbivory is likely to affect the whole management unit of a ranch in various ways depending on the periodicity of repeated herbivory. Under *CG*, long-term overutilization of preferred areas tends to lead to decrease in biodiversity, organic matter transfer to soils, nutrient cycling, ground cover and high-quality forage and therefore loss of topsoil and productivity. By contrast, it has been claimed that under *PH* and *AMP* grazing, periodic concentration of grazing animals followed by subsequent extended post-defoliation recovery

Grazing system characteristics	CONTINUOUS GRAZING (CG)	PYRIC HERBIVORY (PH)	ADAPTIVE MULTI-PADDOCK (AMP)
	Low density of animals that can roam freely across the ranch High area selectivity due to animal preferences Limited post-herbivory recovery period Low proportion of forage consumed Patchy soil cover due to area selection Dispersed fecal deposition across total area	High density of animals on recently burned areas, otherwise low density Minimal area selectivity on recent burns No immediate post-fire plant recovery period Moderate proportion of forage consumed Intermittent soil cover due to fire/grazing effect Dispersed fecal deposition except burned areas	High density of animals within paddocks representing a small portion of the ranch Minimal area selectivity – high grazer conc. Short grazing period/long post recovery period High proportion of forage consumed Consistently high soil cover Periodically high fecal density
1. Bio-diversity	Low arthropod and microbial biodiversity and biomass Low fungal to bacterial ratio	Temporally variable arthropod and microbial biodiversity and biomass Variable fungal to bacterial ratio	High arthropod and microbial biodiversity and biomass High fungal to bacterial ratio
2. Soil Health	Slow OM transfer to soil Spatially patchy soil aggregation & SOM Low soil fertility/soil water capacity High proportion bare ground on preferred areas	Spatially/temporally variable OM transfer to soil Spatially/temporally var. SOM & soil aggregation Fluctuating soil fertility & water holding capacity Increased bare ground on recently burned areas	Rapid OM transfer to soil High SOM & soil aggregation High soil fertility & water holding capacity Low proportion of bare areas
3. Eco-Services	Slow dung decomposition Slow nutrient turn over time Slow soil carbon storage Low water infiltration & fast runoff in bare areas Spatially highly variable forage quality	Spatially/temporally var. dung decomposition Spatially/temporally var. nutrient turn over time Spatially var. moderate carbon storage Spatially/temporally variable water infiltration Spatially variable forage quality	Rapid dung decomposition Rapid nutrient turn over time Rapid carbon storage Widespread high water infiltration Relatively uniform high forage quality
4. Ranch Economics	Low carrying capacity High supplemental feed needs Low profitability and resilience	Moderate carrying capacity Moderate supplemental feed needs Intermediate profitability and resilience	Elevated carrying capacity Low supplemental feed needs High profitability and resilience

FIGURE 1 | Postulated effects of alternative grazing management approaches on productivity and biodiversity, soil health, ecosystem services and ranch economics (Frank et al., 1998; Teague et al., 2013; Jakoby et al., 2015; Savory and Butterfield, 2016; Park et al., 2017; Stanley et al., 2018; Dowhower et al., 2019; Pecenka and Lundgren, 2019).

periods may lead to net ecosystem benefits including increased soil carbon, nutrient cycling, soil microbial function, above and below ground biodiversity, surface water infiltration, rooting depth, plant cover, herbaceous biomass, and ultimately ranch profitability (Jakoby et al., 2014, 2015; Martin et al., 2014). The primary difference between the two approaches is the double defoliation effect of fire followed by grazing in *PH* compared to defoliation by herbivores only with *AMP* grazing, leading to the intended outcomes of greater spatial heterogeneity across the landscape in *PH* grazing and more uniform forage utilization across the landscape in *AMP*. Therefore, the relative net benefits under these different management choices need to be determined at the spatial and temporal scales of managed landscapes and not simply in short-term plot treatments that do not reflect real world conditions with which farmers and ranchers have to contend (Teague et al., 2013).

Management decisions affect how grasslands sequester atmospheric carbon and provide other essential ecosystem services, including soil water retention, herbaceous biomass production, and, therefore, support ranch profitability. For long-term sustainability of rangelands livestock producers need to adopt grazing management practices that improve soil and ecosystem function and resilience (Havstad et al., 2007). To achieve this goal, they should aim to increase solar energy capture, water infiltration and retention, soil organic matter accumulation, nutrient cycling, and the above and below ground biodiversity needed for ecosystems to function properly (Teague et al., 2013). *PH* grazing has been shown to have periodic, patchy low ground cover with nutritious regrowth in burned areas, which herbivores preferentially graze, leading to heterogenous grass cover with underutilized, lower quality forage in unburned areas, and mixed biodiversity and structural diversity across the landscape (Fuhlendorf et al., 2006). By contrast, *AMP* grazing has the potential to reverse causal mechanisms of ecosystem degradation operating under *CG* by decreasing bare ground, increasing water infiltration rates and soil water storage capacity and reducing surface water runoff and therefore soil and nutrient losses, increasing fungal to bacterial ratios, and increasing soil carbon, and ultimately restoring productive herbaceous plant communities by reducing the ability of herbivores to select only the most nutritious grass species (Sovell et al., 2000; Webber et al., 2010; Delgado et al., 2011; Teague et al., 2011, 2013; Weltz et al., 2011).

BIOLOGICAL DRIVERS AND CAUSAL MECHANISMS IN GRAZING ECOSYSTEMS

Rangeland productivity and resilience to environmental variability are a function of soil health and microbial functional diversity (Plassart et al., 2008; Morriën et al., 2017). High soil microbial biomass contributes to improved soil aggregation, porosity, water infiltration rates and water holding capacity, and more rapid soil carbon and nutrient turnover (Coleman and Crossley, 1996; Six et al., 2004). In turn, soil health, which is a collective term for these factors, is a more reliable predictor of herbaceous productivity than land use history (De Vries et al., 2013) or clay mineralogy (Kallenbach et al., 2016). Microbial carbon plays a disproportionately large role in soil aggregate formation (Bardgett and McAlister, 1999; De Vries et al., 2013), which affects soil porosity, aeration, water infiltration rate and water holding capacity.

While the greatest limiting factor in grazing land ecosystems is the infiltration and retention of surface water in the soil (Thurow, 1991), optimal ecosystem function also requires efficient solar energy capture, soil organic matter accumulation, efficient nutrient cycling, and high levels of below and above ground biodiversity (Teague et al., 2013; Savory and Butterfield, 2016). Soil health is mediated by the interdependence of soil microbes, fungi, insects, plants and animals. Plants support microbial life by supplying carbohydrates, root exudates and detritus upon which microbes feed, while benefiting from nutrient release resulting from interactions among soil archaea, bacteria, fungi, and other microbial and eukaryotic species. Therefore, the way in which plants are managed and utilized in grazing can directly affect the associated ecosystems because the energy driving ecological functions is derived predominantly through the conversions of solar energy to carbohydrates by photosynthesizing plants.

The functions provided by the synergistic networks of soil organisms include: soil aggregation and stabilization (Van der Heijden et al., 2008); aeration and water holding capacity (Altieri, 1999); nutrient cycling, accumulation and retention (Green et al., 2008; Khidir et al., 2008); biotic and abiotic stress tolerance (De Vries et al., 2012) and buffering the impact of environmental factors on plants (Van der Heijden et al., 2008). Importantly, arbuscular mycorrhizal fungi (AMF) are keystone species in many terrestrial ecosystems, particularly grasslands, because they can enhance plant diversity, mediate interactions among plants and other microbes, and enhance plants' access to nutrients (Averill et al., 2014). Additionally, symbiosis between AMF, rhizobia and leguminous plants can enhance photosynthesis by 50% (Kashuk et al., 2009), and AMF contributes directly to the soil organic matter through secretion of soil glycoproteins that increases soil aggregate stability, thereby enhancing soil aeration and surface water infiltration (Rillig, 2004).

Improvement in grassland soil organismal composition enhances carbon cycling and nitrogen cycling to increase hydrological function and biological fertility (Altieri, 1999; Van der Heijden et al., 2008; De Vries et al., 2012). At high microbial densities and species biodiversity, symbiotic interactions among species can lead to enhanced biological outcomes via the phenomenon of quorum sensing (Nealson et al., 1970). Grazing management strategies aimed at restoring soil function tend to expand below ground microbial networks and increase the efficiency of nutrient cycling and carbon uptake by diversifying the composition and activities of fungi Ngumbi and Kloepper, 2016; Slade et al., 2016; Morriën et al., 2017. Other key biological drivers of ecosystem function that can be enhanced by adjusting grazing management to optimize benefits provided by arthropods, such as dung beetles, and earthworms. Such beneficial management can strongly benefit soil structure and ecological functions (Herrick and Lal, 1995; Richardson and Richardson, 2000; Wardle and Bardgett, 2004; Blouin et al., 2013; Pecenka and Lundgren, 2019).

Livestock production systems that use artificial inputs (e.g., inorganic fertilizers, pesticides and livestock medications) or grazing practices that result in inadequate post-herbivory ground cover, impair soil organisms, their interactions and their functions, diminish the ecological functions they perform, and reduce the delivery of ecosystem services (Iglesias et al., 2006; LaCanne and Lundgren, 2018). By contrast, under appropriate management, a grass-fed ruminant enterprise that avoids the use of damaging inputs can also be ecologically beneficial and regenerative by supporting the mechanisms that lead to increased soil health to provide the nutritional needs of plants and livestock.

LIMITATIONS OF PAST RESEARCH AND LEARNING FROM OUTSTANDING MANAGERS

To succeed in the short and long term, ranchers need to achieve high levels of soil and vegetation function, animal performance, and profit within the constraints of the inherent landscape heterogeneity of their unique properties. This requires monitoring the responses of the ecosystems they manage to their operational practices at diverse temporal scales. Critically, in dynamic climatic and economic environments, ranchers must also manage adaptively in order to achieve their desired outcomes, avoid management decisions that create negative impacts on their land, and maximize the positive soil-based interactions that enhance soil health. A primary reason why grazing management researchers have failed to achieve similar results to outstanding grazing managers using adaptive, regenerative *AMP* rotational grazing management practices (Briske et al., 2008) is that they have not adapted grazing treatments to achieve the best possible ecological and economic results (Teague et al., 2013; Teague, 2015).

The majority of earlier grazing studies found little difference between rotational grazing and lightly stocked continuous grazing (Briske et al., 2008, 2011). However, this conclusion is largely based on reductionist grazing experiments that were not adaptively managed to specifically achieve best outcomes under changing conditions and, therefore, they do not reflect the successes that have been achieved with *AMP* grazing on many commercial ranches (Teague et al., 2013). The potential of multi-paddock grazing can only be achieved in field studies if they are managed adaptively over multiple years based on protocols that have produced successful results in commercial ranch settings (Teague and Barnes, 2017). Long-term management of an area to improve soil and ecosystem function can produce entirely different results than an area that has been conventionally managed and has not enhanced ecosystem services. An experiment that does not take such factors into account will likely provide results that do not reflect potential improvements in long term management outcomes.

Most grazing research on rangelands has been too short-term and too small-scale to identify longer-term unintended consequences or the management implications of the experimental grazing treatments (Teague et al., 2013). For the sake of repeatability and scientific rigor and due to budgetary constraints, grazing studies have generally examined rigidly applied treatments at spatial and temporal scales that preclude the evaluation of adaptive management possibilities within the context of commercial-scale operations. Most studies have been conducted at small spatial scales that force animals to graze evenly and, therefore, prevent the heterogeneity of grazing that leads to long-term grassland degradation under continuous grazing at commercial scales (Teague and Barnes, 2017). As a result, much grazing systems research has shown that all forms of "rotational" grazing management ("systems") produce limited or no improvement in grazing resources compared to continuously grazed areas. The relatively few studies that have incorporated realistic context of scale and complexity, coupled with a well-planned adaptive application of treatment, have shown numerous benefits of AMP grazing over continuous grazing (Teague et al., 2013).

Most rangeland grazing research has been too short-term and small-scale to identify longer-term consequences or the management implications of the experimental grazing treatments (Teague et al., 2013). Generally, this research has been conducted over 2 to 3 years in small paddock trials that inhibit heterogeneous grazing patterns, which lead to long-term grassland degradation under continuous grazing at commercial ranch scales (Teague and Barnes, 2017). Additionally, short-term grazing experiments do not overcome the legacy effects of previous grazing management and, for the sake of repeatability and scientific rigor, such studies have generally examined a limited number of rigidly applied treatments that preclude the evaluation of adaptive management effects (Van der Ploeg et al., 2006). As a result, short-term, small-scale grazing systems research has not shown substantial environmental changes and led to the erroneous conclusion that all forms of "rotational" grazing management ("systems") produce limited or no improvement in grazing resources compared to continuously grazed areas (Briske et al., 2008). Grazing affects many ecosystem variables at different temporal and spatial scales; these variables include but are not limited to soils organic matter, soil microbes, arthropods, vegetation, and non-livestock herbivores. Differentially lagged grazing effects on such variables necessitates consistent application of grazing management treatments for 5 years, 10–15 years or decades in humid, mesic and dry environments, respectively, to capture diverse environmental changes at the landscape level (Franzluebbers and Stuedemann, 2010). The relatively few studies that have incorporated realistic contexts of scale and complexity, coupled with a well-planned adaptive application of treatment, have shown numerous benefits of AMP grazing over continuous grazing, even where the latter is practiced at low stocking rates (Earl and Jones, 1996; Murphy, 1998; Gerrish, 2004; Jacobo et al., 2006; Provenza, 2008; Ferguson et al., 2013; Teague et al., 2013; Flack, 2016; Rowntree et al., 2016; Wang et al., 2016; Dowhower et al., 2019).

To help livestock producers achieve superior grazing management results, integrative and multidisciplinary research is needed to understand how they can achieve desired ecological, economic, and social goals on their landscapes in changing environments. Research is also needed to test hypotheses of causal above- and below-ground biological mechanisms underpinning responses to different grazing management approaches (Teague, 2015). To understand these critical elements of superior grazing management requires conducting research with innovative land managers on real operations, applying adaptive treatments, and combining detailed field experimentation with embedded, small scale, reductionist experiments in the context of the management options being studied, and simulation modeling approaches (Teague et al., 2013; Jakoby et al., 2014, 2015; Martin et al., 2014; Müller et al., 2014; Wang et al., 2016; Park et al., 2017).

Collaborating with ranchers who have simultaneously improved the biophysical conditions of their environments as the basis for achieving superior economic returns in different ecological and cultural settings is fundamentally important to learn how to improve the three-part components of operational sustainability—ecological, economic, and social (Van der Ploeg et al., 2006). Not only have such producers developed improved management protocols, but they have effectively managed cash flows and learned how to avoid unintended consequences while transitioning from non-sustainable traditional to regenerative production systems that improve soil health on their land (Teague et al., 2013). Moreover, such producers achieve best management outcomes by combining goal directed adaptiveness with a deep understanding and observations of the response dynamics of biophysical processes on their land to alternative management interventions.

A lack of systems training precludes many agricultural and ecological researchers from being able to adequately manage research projects to demonstrate the best possible outcomes of innovative management options (Van der Ploeg et al., 2006). In contrast, ranchers are less constrained by strictures of conventional scientific research protocols and are more likely to apply adaptive learning principles to test different combinations of practices and approaches within realistic whole-ranch systems (Teague, 2015). Working with leading ranchers can facilitate development of more sustainable agricultural practices for several reasons (Van der Ploeg et al., 2006), including: (i) addressing questions at commercial ranch scale; (ii) using a whole-system framework to integrate component science elements; (iii) incorporating pro-active management to achieve desired goals under changing circumstances; and (iv) identifying emergent properties and unintended consequences; and (vi) extend the usefulness of information developed in research to land managers.

A tool that enhances understanding and provides a solid theoretical base for all scientific investigations is systems simulation modeling. This approach facilitates understanding biophysical processes and management hypotheses at the landscape scale and testing them against observed results (Díaz-Solís et al., 2009; Teague et al., 2009). However, it is essential to constantly check model outputs with data from field experiments from collaborating commercial ranching operations to ensure the models are well-grounded in quantified long-term treatment responses and that their outputs are not extrapolated beyond real-world outcomes.

MANAGING GRAZING TO RESTORE ECOLOGICAL FUNCTION AND ECOSYSTEM SERVICES

Using well-planned and adaptively managed multi-paddock grazing management protocols is the key to sustainable use of grazing lands and recovery from degradation and involves using short grazing periods, retaining sufficient litter and plant cover to protect the soil and allow rapid plant regrowth. Such management allows adequate time for grazed plants to regrow and adjusting stock numbers to match available forage biomass ensures available forage always provides for ecosystem function, adequate animal nutrition and avoids unnecessary costs (Earl and Jones, 1996; Jacobo et al., 2006; Provenza, 2008; Ferguson et al., 2013; Teague et al., 2013; Wang et al., 2016).

AMP grazing facilitates the adjustment of these elements to avoid soil loss, strengthen soil and ecological function, increase herbaceous plant biomass and minimize the increase in unproductive species composition, leading to the achievement of desired resource and financial outcomes. In grasslands and savannas, the application of regenerative high-density *AMP* grazing management has been shown globally to be capable of reversing degradation emanating from the long-term practice of continuous heavily-stocked grazing (Gerrish, 2004; Teague et al., 2011, 2013; Jakoby et al., 2014, 2015; Savory and Butterfield, 2016). Additionally, in semiarid areas where this regenerative grazing management has been practiced for decades, improvements have been observed in biodiversity including pollinators, plant productivity, litter cover, nitrogen-fixing legumes, re-perennialization of ephemeral streams and watershed function (National Research Council., 2002).

Where scientists have worked with ranchers practicing *AMP* grazing to regenerate soil health and ecosystem functionality, positive resource and economic outcomes have been reported (Teague et al., 2013; Savory and Butterfield, 2016; Teague and Barnes, 2017). Specifically, studies in Argentina, Australia, Germany, Southern Africa, and the USA have reported positive resource and economic results from regenerative ecological grazing when research incorporates the following four factors. The research, (i) was conducted at the scale of ranching operations; (ii) grazing resource utilization was adjusted proactively as growing conditions changed to achieve desired ecosystem and production goals; (iii) when grazing treatments had been applied for sufficiently long time periods to overcome biophysical response lags and to incorporate intra- and inter-seasonal variations in diverse environmental factors, and (iv) parameters indicating change in ecosystem function and not just production outputs were measured and acted upon (Earl and Jones, 1996; Murphy, 1998; Gerrish, 2004; Jacobo et al., 2006; Müller et al., 2007; Provenza, 2008; Teague et al., 2011, 2013; Jakoby et al., 2014, 2015; Martin et al., 2014; Müller et al., 2014; Flack, 2016; Wang et al., 2016).

AMP grazing protocols were specifically designed to emulate ecosystem processes that evolved in response to intense, periodic herbivory by large herds of ungulate grazers and they have been effective in reversing the damage caused by continuous grazing in a timely and cost-effective manner (Gerrish, 2004; Teague et al., 2011, 2013; Wang et al., 2016). The use of AMP grazing principles increases livestock carrying capacity over time while improving ecological function, as paddock number increases. However, this is not intensive grazing but intensive management of grazing (Dowhower et al., 2019) as it reverses the impacts of intensive grazing by specifically avoiding overstocking of, and overgrazing by, livestock in an adaptive manner in response to variable weather (Jakoby et al., 2014, 2015; Teague et al., 2015; Wang et al., 2018). In combination, these actions result in light to moderate grazing impact on herbaceous plants, the soil and the ecological functions they perform (Teague et al., 2013; Jakoby et al., 2014; Teague and Barnes, 2017; Dowhower et al., 2019).

While some have touted the advantages of *PH*, for enhancing the biodiversity of certain categories of species, notably grassland birds many of which have become substantially threatened and endangered (Fuhlendorf et al., 2006), from an ecosystem sustainability perspective, the temporal juxtaposition of fire and grazing can have negative outcomes. The reasons for this are that frequent fire decreases vegetation cover which leads to increased soil surface temperatures that, in turn, can lead to disruption of the hydrological cycle, soil compaction, nutrient losses via runoff, and volatilization and leaching (Wright and Bailey, 1982). Continuous livestock grazing reduces grass biomass and creates patchy vegetation interspersed with bare soil. With the patch burning and continuous grazing that characterize *PH* grazing, the newly burned patches each attract heavier use while relieving previously burned patches of defoliation to allow some recovery. However, heavy grazing by livestock on burned patches and underutilization of grasses in unburned areas can reduce overall biomass production and (by design) lead to patchy vegetation, which is interspersed with bare ground. In contrast, rotational grazing in general and *AMP* grazing in particular, provide longer more substantive, extended recovery time periods after burning and grazing. This results in less bare ground and more plant cover to lower soil surface temperatures, enhance soil carbon to maintain or improve healthy soil hydrological characteristics, while maintaining or enhancing productive herbaceous species composition on both burned and unburned areas (Teague et al., 2008, 2010).

One disadvantage of frequent burning in *PH* grazing is that, while burned vegetation and ground cover can recover within the year of burning in wetter areas, in semi-arid rangelands where droughts occur frequently it may take several years of average or above average rainfall for full soil function and herbaceous vegetation recovery. When drought conditions precede or follow the application of fire, bare ground, annual forbs and grasses, and even woody plants may increase at the expense of productive perennial grasses that may require 3–5 years or longer to recover after fire (Wright and Bailey, 1982; Teague et al., 2008). This is not the case in *AMP* grazing where burned areas are not immediately subject to grazing but are provided sufficient time to recover if fire is applied. In summary, *AMP* grazing offers substantial benefits over *CG* and *PH* for reducing weather-related production risks, especially after fire. It also facilitates the attainment of ranchers' goals to improve ecological function of their production base in order to enhance the delivery of ecosystem services, economic returns and long-term sustainability of their ranching operations.

MANAGING FOR MULTI-FUNCTIONALITY IN AGRICULTURAL SYSTEMS

How well-grassland and savanna ecosystems are managed to regenerate soil and ecosystem function governs our future. Carbon rich soils benefit all terrestrial ecosystems, and managing to increase soil carbon is fundamental to improving ecosystem services including water infiltration and retention; soil retention; soil nutrient cycling and retention; biodiversity enhancement including fungi, microbes, insects, plants, and animals; wildlife nutrition and habitat; livestock forage; all of which can help support ranch profits and resilience in changing climates. To achieve this, agriculture needs to change from traditional high-input cropping and grazing practices to low-input practices that increase atmospheric carbon sequestration via photosynthesis and increase soil microbes that enhance soil water and nutrient cycles and that minimize soil carbon release back into the atmosphere. This will require increasing the amount of land under perennial or opportunistic plant growth, increase seasonal longevity of plant photosynthesis associated with enhancing carbon sequestration, and the degree to which sequestered carbon is converted into stable soil organic carbon, and not oxidized back into CO_2 by burning or oxidation (Delgado et al., 2011).

While people have minimal capacity to control non-anthropogenic drivers of environmental change (Plimer, 2009), human impact on the environment caused by unsustainable agricultural practices can, in many cases where excessive soil loss has not occurred, be addressed by reversing the degradation of the landscapes by switching from extractive and environmentally harmful practices and inputs to regenerative grazing and cropping practices (Delgado et al., 2011; Teague et al., 2013). This will require using management practices that effectively and efficiently restore hydrological cycles, soil health and the delivery of critical ecosystem services.

The water cycle is the thermostat of global climate change governing massive energy changes required to melt polar ice, water evaporation and precipitation (Shaviv and Veizer, 2003), and the carbon cycle is affected by the water cycle (Plimer, 2009). Atmospheric water vapor and droplets are the most prevalent and potent GHG and the most limiting commodity for plant growth production that provides food for animals and people.

Practices that can be adopted to substantially enhance soil carbon include regenerative cropping, regenerative grazing in cropped areas and grasslands, restoration of shelter trees in grazing lands, and reduction of rangeland wildfires (Delgado et al., 2011; Teague et al., 2013). The key to optimizing ecological function and reversing degradation caused by previous mismanagement in both cropping and grazing systems is use of management practices that elevate soil health. Specifically, soil ecological function is maintained by minimizing bare ground by maintaining plant and litter cover throughout the year, using perennial rather than annual plants, using diverse species mixes and cover crops, managing grazing to promote the most productive plants, maximizing plant growth days each year, eliminating high impact tillage practices, using organic soil amendments, and minimizing artificial inorganic fertilizer and biocides use, (Delgado et al., 2011; Teague et al., 2011; Gattinger et al., 2012; Aguilera et al., 2013).

The water cycle and vegetation play a fundamental role in maintaining local climate through energy transfers in the process of evapotranspiration (ET); specifically, the interaction of water and plants dampen temperature maxima resulting from intense solar radiation (Pokorný et al., 2010). Given water vapor's potency as a heat absorber, evapotranspiration from plants transfers heat from the earth's surface into the atmosphere, thereby cooling the surface, and accounts for about 24 % of natural global hydrological cooling (Pokorný et al., 2010). Modification of landscapes by agriculture, overgrazing, deforestation, wetland drainage, and urbanization that remove transpiring vegetation diminishes the self-regulatory damping of solar radiation and temperatures by healthy ecosystems. For evapotranspiration to deliver substantial cooling requires extensive ground cover of actively growing plants to maintain a healthy hydrological cycle (Ferguson and Veizer, 2007). Elevation of soil carbon enhances both surface water infiltration, soil moisture holding capacity and soil fertility needed to support plant growth and high green leaf area that increase evapotranspiration and plant biomass.

Soil health, defined as the continued capacity of soil to function as a vital living ecosystem, determines the quantity and quality of ecosystem services delivered for the benefit of current and future generations. Paleo records provide evidence that management of grassland agroecosystems can create a large C sink (Retallack, 2013). Equally, changing management approaches in ruminant-based production chains can improve soil health and thereby create net C sinks (Wang et al., 2015; Rowntree et al., 2016; Stanley et al., 2018). Given that most agricultural producers have not used conservation practices outlined by Delgado et al. (2011), applying such practices more broadly could lead to substantial soil health improvements and, therefore, a significant increase in C sink (Conant and Elliott, 2001; Liebig et al., 2010; Teague et al., 2011; Machmuller et al., 2015; Dowhower et al., 2019; Hillenbrand et al., 2019). To determine what management changes will lead to soil carbon gains, it is necessary to include all production chain elements that affect the carbon footprint of the entire system under review (Teague et al., 2016), including the beneficial ecosystem services that well-managed grazing systems can provide.

Combining crop rotation with livestock grazing can enhance soil function and health (Delgado et al., 2011). Row crop rotations that include legumes, and cover and forage crops can produce permanent ground cover and increase soil carbon, water infiltration and fertility. Furthermore, grazing livestock can accelerate nutrient cycling through the decomposition of residual aboveground biomass (Teague et al., 2016). Including forage and grazing animals in cropping systems by sowing winter crops into permanent summer pastures significantly reduces the damaging effects of many current cultivation and management practices, including loss of soil and SOC, and GHG emissions. This management is particularly effective and necessary where soil erosion potential is moderate to high (Delgado et al., 2011). Similarly, using a grazing-cropping rotation with perennial pasture or rangeland on cropland vulnerable to degradation in the Australian ley farming systems is very effective in reducing the overall crop and livestock-associated carbon footprint (Carberry et al., 1996). Adoption of such low-cost management strategies promotes the restoration of perennial grasses without limiting crop production and is an economically viable strategy for regenerating degraded land (Millar and Badgery, 2009). Pasture-cropping, developed by Australian farmer Colin Seis, is a strategy that integrates livestock and *AMP* grazing to provide optimum levels of defoliation and plant recovery between grazing bouts, with direct seeding of annual crops into perennial grass communities during dormancy in a rotation that maintains or strengthens the perennial herbaceous base (Millar and Badgery, 2009; White, 2012). Ley and pasture-cropping facilitate year-round, actively growing groundcover and greatly extend plant growth days, improve soil structure, soil nutrients and soil organic carbon, reduce wind and water erosion and weed competition, and improve biodiversity and ecological resilience, even under drought stress.

While some studies claim that finishing beef cattle on grain-based feeds lowers GHG emissions per kilogram beef produced to give a lower carbon footprint compared to grass-finished beef such studies do not take into account the full carbon footprint of the different production chains (Teague et al., 2016; Stanley et al., 2018). Although grain finishing reduces overall production time to slaughter and lowers enteric fermentation during this time (Stackhouse-Lawson et al., 2012; Capper and Bauman, 2013) such calculations do not take into account the negative carbon footprint associated with the full grazing on perennial pastures in the production chain of grass-fed beef. Life cycle analyses that include all GHG emissions associated with the production of grain-based feeds, including the production and application of inorganic fertilizers and irrigation water to produce grain, show that the C footprint as well as soil erosion associated with grain-finished beef substantially exceeds the C footprint of grass-finished beef (Teague et al., 2016; Stanley et al., 2018). Additionally, C sequestered by plants grazed by cattle exceeds the enteric emissions of the grazing animals (Wang et al., 2015; Rowntree et al., 2016). The C footprint of the beef production chain can be substantially reduced when ruminants are finished on forages and grains produced using regenerative cropping practices that have a negative C footprint (Gattinger et al., 2012; Aguilera et al., 2013). If combined with regenerative *AMP* grazing, the whole production chain could result in substantive increases in soil carbon levels and associated ecological benefits.

MANAGING TO ACHIEVE SUSTAINABLE INCOME GOALS IN A VARIABLE ENVIRONMENT

For continuously grazed rangeland, to achieve sustainable goals it is extremely important to choose an appropriate business management goal structure (Teague et al., 2009). Earning capacity can be four times higher for rangeland in excellent condition than in poor condition (Teague et al., 2009), however, under continuous grazing, profit is maximized at stocking rates that are higher than those that would maintain or increase long-term range condition due to negative impacts on the land from patch overgrazing. To prevent overgrazing and long-term degradation of continuously grazed areas, using light stock rates has been identified as an essential management choice (Briske et al., 2008); however, this incurs an opportunity cost due to lower livestock production and, therefore, income generation. The spatial model of Jakoby et al. (2015) identified several viable low risk management choices are possible with continuous grazing or few paddocks per herd, but they require relatively low stocking rates that result in low productivity and economic returns. Periodic resting and rotational grazing (in particular *AMP* grazing) have been shown to have considerable potential for decreasing negative grazing impacts in environments where there is considerable area selective grazing and vegetation regrowth is relatively slow (Snyman, 1998; Teague et al., 2004; Müller et al., 2007).

Research incorporating protocols that have provided desired resource and economic improvements by conservation ranchers have substantiated the positive soil and ecosystem results reported by regenerative livestock producers. Jakoby et al. (2014) determined that grazing management that used a large number of paddocks per herd to ensure short grazing periods and adequate post-grazing plant recovery facilitated resource improvement and produced optimal economic results. However, economic risk decreased only with management adjustments that accounted for forage quality in each paddock and seasonality over the modeled landscape (Jakoby et al., 2015). Similarly, Teague et al. (2015) found that excessively long grazing or recovery periods resulted in poorer animal performance and plant recovery, which leads to negative economic consequences, as acknowledged by consultants working with ranchers (Walt Davis[1], Dave Pratt[2], Dr. Allen Williams[3] pers. com.).

The use of many paddocks per herd combined with adaptive stocking management is less sensitive to overstocking than constant stocking and with appropriate management increases ecological function (Jakoby et al., 2015; Teague et al., 2015). The advantage of AMP over continuous grazing is less critical at low stocking rates, it becomes increasingly essential as stock numbers increase, to improve net economic returns. Similarly, at the scale of commercial ranches, Wang et al. (2016) demonstrated that,

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[1] Walt Davis, Davis Consulting, Available online at: https://waltdavisranch.com/

[2] Dave Pratt, Ranch Management Consultants, Available online at: https://www.ranchmanagement.com/

[3] Dr. Allen Williams, Livestock Management Consultants, LLC, Available online at: https://joyce-farms.com/

AMP grazing with short periods of grazing and sufficiently long periods of post grazing recovery improved grass composition and productivity, and livestock dry matter consumption relative to continuous grazing, especially with heavier stocking rates and lower initial standing crop and forage composition. Conversely, the advantages of AMP grazing are less evident with favorable rainfall conditions, light stocking, low levels of undesirable plants, and when short post-grazing recovery periods are provided. Overall, these studies have found that under both low- and high-risk management strategies, AMP grazing using large paddock numbers improved resource condition, increased the likelihood of attaining a minimum income goal, lowered income variability, and produced superior economic returns on investment (Jakoby et al., 2015).

CONCLUSIONS

To ensure long-term sustainability and ecological resilience of agroecosystems, agricultural management decisions needs to be guided by policies that encourage cropping and grazing protocols that regenerate soil and ecosystem function in uncertain, variable, and rapidly changing climates. With appropriate management of grazing and cropping enterprises, soil ecological functions can be regenerated or enhanced to improve essential ecosystem services that support human well-being, while simultaneously reducing the use of costly and potentially damaging artificial inputs. Regenerating soil health and ecosystem function can be achieved using conservation agricultural practices to support ecologically healthy resilient agroecosystems, improve net profitability, and enhance watershed hydrological function.

Research conducted on managed landscapes shows that AMP grazing and regenerative forage-cropping strategies incorporating short periods of high-density grazing with long recovery periods, cropping rotations that include forages and grazing ruminants while eliminating or substantially reducing soil tillage, inorganic fertilizers and biocides can regenerate soil and ecosystem function on commercial-scale landscapes. Affected ecosystem services include solar energy capture, soil carbon accumulation, soil formation and stabilization, surface water infiltration, soil-biosphere cooling, nutrient cycling and retention, plant biomass production, biodiversity, and wildlife habitat. An increase in permanent cover of forage plants is highly effective in reducing soil erosion and increasing the infiltration of precipitation into the soil. Additionally, grass-fed livestock produced using well-managed AMP grazing can result in a net carbon sink. Similarly, incorporating forages with ruminants in rotational cropping systems can regenerate soil ecological functions in agro-ecosystems and elevate soil C. Using goal-oriented planning and monitoring protocols to reverse damages created by poor grazing, tillage, inorganic fertilizer, and biocide application practices, biodiversity and wildlife habitat can also be effectively facilitated when included in management goals.

To eliminate the damaging effects of current agricultural practices and to restore soil and ecosystem function and resilience it will be essential to change current unsustainable and costly and damaging high-input agricultural practices to low-input regenerative practices. A key to regenerating ecosystem services provided by grazing lands as the base to improve landowner incomes is to adopt well-planned and adaptively managed AMP grazing as it provides substantive advantages over CG as well as PH with continuous stocking. To promote continuous light grazing in the hope that it will minimize the negative historical impacts of poor grazing practices may, at best, sustain or perhaps slightly improve the degraded grazing land resource. However, *CG* or *PH* will not likely produce adequate economic returns to encourage managers to adopt land management practices that reverse soil degradation and will, therefore, not likely increase food production or profit potential. On the other hand, appropriately managed AMP grazing can not only support higher livestock production per hectare and secondary production efficiency, but also improve soil ecological function and, therefore, provision of ecosystem services and profits from grazing ecosystems (Jakoby et al., 2015).

To increase the scale of adoption of land management practices documented to improve soil health, scientists will need to collaborate with managers who have shown how to improve their natural resource base to prosper financially to identify management factors that lead to land improvement and to achieve sound environmental, economic and social benefits. In areas where cropping is not possible due to climate, edaphic or topographic constraints, grazing of livestock in a manner that enhances soil health will reduce agriculture's C footprint substantially. Ruminant livestock are an important tool not only for livelihoods of people living in such regions but also for achieving sustainable agriculture where cropping is feasible if appropriate regenerative grazing and cropping management is practiced. Doing so can increase atmospheric C sequestered and soil carbon capture to more than offset ruminant GHG emissions, and that improves ecosystem services that are essential for long-term human well-being.

AUTHOR CONTRIBUTIONS

RT was invited to write the paper, conceived the contents, and wrote the paper. UK co-wrote and edited the paper and contributed content to each section of the paper. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Sustainable Food Systems

REVIEW
published: 06 October 2020
doi: 10.3389/fsufs.2020.00128

Plant-Based Meats, Human Health, and Climate Change

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There is wide scale concern about the effects of red meat on human health and climate change. Plant-based meat alternatives, designed to mimic the sensory experience and nutritional value of red meat, have recently been introduced into consumer markets. Plant-based meats are marketed under the premise of environmental and human health benefits and are aimed appeal to a broad consumer base. Meat production is critiqued for its overuse of water supplies, landscape degradation, and greenhouse gas emission, and depending on production practices, environmental footprints may be lower with plant-based meat alternatives. Life-cycle analyses suggest that the novel plant-based meat alternatives have an environmental footprint that may be lower than beef finished in feedlots, but higher than beef raised on well-managed pastures. In this review, we discuss the nutritional and ecological impacts of eating plant-based meat alternatives vs. animal meats. Most humans fall on a spectrum of omnivory: they satisfy some nutrient requirements better from plant foods, while needs for other nutrients are met more readily from animal foods. Animal foods also facilitate the uptake of several plant-derived nutrients (zinc and iron), while plant nutrients can offer protection against potentially harmful compounds in cooked meat. Thus, plant and animal foods operate in symbiotic ways to improve human health. The mimicking of animal foods using isolated plant proteins, fats, vitamins, and minerals likely underestimates the true nutritional complexity of whole foods in their natural state, which contain hundreds to thousands of nutrients that impact human health. Novel plant-based meat alternatives should arguably be treated as meat alternatives in terms of sensory experience, but not as true meat replacements in terms of nutrition. If consumers wish to replace some of their meat with plant-based alternatives in the diet (a "flexitarian approach") this is unlikely to negatively impact their overall nutrient status, but this also depends on what other foods are in their diet and the life stage of the individual.

Keywords: plant-based meat, sustainability, meat, nutrition, diet, climate change, vegetarian and non-vegetarian diet

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Specialty section:
This article was submitted to
Agroecology and Ecosystem Services,
a section of the journal
Frontiers in Sustainable Food Systems

Received: *23 April 2020*
Accepted: *22 July 2020*
Published: *06 October 2020*

Citation:
van Vliet S, Kronberg SL and Provenza FD (2020) Plant-Based Meats, Human Health, and Climate Change.
Front. Sustain. Food Syst. 4:128.
doi: 10.3389/fsufs.2020.00128

INTRODUCTION

Novel plant-based meat alternatives such as the Impossible™ Burger and Beyond Burger® are becoming increasingly popular with consumers and have attracted considerable financial investments, media coverage, and research attention. Their success has led other food companies to produce their own versions of these products. The plant-based meat market is growing rapidly and is expected to be worth more than $30 billion by 2026 (Statista, 2020.[1]). Meat alternatives, formulated to mimic the taste and sensory experience of red meat, are marketed for their ecological and health benefits compared to red meat. While ingredients vary amongst plant-based meat products, the new generation of alternatives is formulated specifically to mimic the sensory experience and macronutrient content of meat by using plant proteins (e.g., soy, pea, potato, rice, wheat, and/or myocprotein), fats (e.g., canola, coconut, soybean, and/or sunflower oil), and other novel ingredients (e.g., soy leghemoglobin, red-colored vegetable extracts, and/or flavoring agents). Additionally, various vitamins and minerals that are naturally found in meat (e.g., zinc, iron, and B-vitamins) are increasingly added to plant-based meats (Curtain and Grafenauer, 2019). By doing so, novel plant-based meat alternatives are able to closely mimic the Nutrition Facts panels of meat (**Figure 1**). Plant-based meats may also reduce apprehensions regarding the effects of red meat on human health and climate change, and fit with recommendations for dietary transitions toward reduced meat consumption and increased plant-based diets, particularly in Western civilization (Godfray et al., 2018; Graça et al., 2019). Moreover, the novel meat alternatives are particularly targeted at flexitarians—omnivores who are looking to eat less animal foods. Given the close resemblance of novel plant-based meat alternatives to meat, we will discuss the nutritional and ecological impacts of eating plant-based meat alternatives vs. animal meats, while also providing a broader discussion of the ecological and health effects of replacing animal foods with plant foods.

NUTRIENTS IN PLANT-BASED MEATS AND MEAT

Omnivory or Optionality?

A core question in discussions of replacing animal foods with plant-based substitutes is whether plant-based substitutes can adequately satisfy nutrition requirements. As omnivores, humans tend to satisfy some nutrients more readily from plant sources while other nutrient requirements are generally better satisfied by consumption of animal foods. For example, our vitamin C and magnesium requirements are much more readily fulfilled by plant than animal foods. In addition, plant-based diets are often higher in folate, manganese, thiamin, potassium, and vitamin E (Davey et al., 2003). Plant foods also provide a wide array of phytochemicals that have important regulatory roles in human health (Briskin, 2000). The findings of extensive *in vitro* and *in vivo* experimental data, furthermore, suggest that plant compounds can antagonize some of the deleterious effects of compounds found in cooked red meat (e.g., heterocyclic amines, nitroso compounds, malondialdehyde, advanced glycation end products etc.) (Pierre et al., 2003; Vulcain et al., 2005; Gorelik et al., 2008; Hur et al., 2009; Li et al., 2010; Van Hecke et al., 2017a).

These findings may represent a mechanistic explanation—but certainly not the only one—for why high quality omnivorous diets (also rich in plants) do not show the typical associations between red meat consumption and negative health outcomes (Key et al., 2003; Schulze et al., 2003; Kappeler et al., 2013; Lee et al., 2013; Roussell et al., 2014; Wright et al., 2018; Deoula et al., 2019) that are often observed in population studies of individuals consuming a typical Standard American/Western Diet (Wang and Beydoun, 2009; Chan et al., 2011; Pan et al., 2011; Micha et al., 2012; Abete et al., 2014), though more work is needed to firmly establish this hypothesis.

On the other hand, vitamins A (retinol), B_{12} (adenosyl- and hydroxocobalamin), D (cholecalciferol), K_2 (menaquinone-4), minerals such as iron and zinc, and long-chain polyunsaturated fatty acid (PUFAs) (e.g., docosahexaenoic acid [DHA] and eicosapentaenoic acid [EPA]) are more readily, or exclusively, obtained from animal sources as opposed to plant sources. These nutrients play essential roles in tissue development and regeneration (Georgieff, 2007; van Vliet et al., 2018). While plant foods often contain precursors to these nutrients, considerable portions of the population experience a poor *in vivo* enzymatic conversion of plant-precursors into forms usable by the human body (Brenna, 2002; Burdge, 2006; Tang, 2010). For example, the conversion of carotenoids (provitamin A) to retinol (vitamin A) is in the range of ∼3.5 to 28%, depending on the genetic variability between individuals, and highlights that "poor converters" are unable to obtain sufficient retinol when relying on plant foods only. Retinol deficiency is especially prevalent in the developing world, particularly in young children and women of childbearing age, who largely depend on the consumption of provitamin A (primarily β-carotene) in vegetables and fruit to satisfy their vitamin A needs, with many failing to do so (Sommer and Vyas, 2012).

Of course, individual genetic differences related to nutrient metabolism (Brenna, 2002; Burdge, 2006; Stover and Caudill, 2008; Tang, 2010), at the same time, also explain why some individuals can thrive on plant-based diets, while others following a vegan/vegetarian diet report health problems associated with nutrient deficiencies. For example, there are five times more former vegans/vegetarians than current vegans/vegetarians in the US, of which 53% reported that they followed the diet <12 months (Faunalytics, 2015). While many factors contribute to the difficulties in adhering to plant-based diets (including social factors and food options), intra-individual differences in nutrient metabolism (Brenna, 2002; Burdge, 2006; Stover and Caudill, 2008; Tang, 2010; van Vliet et al., 2015) make it highly unlikely that everyone can thrive on a plant-based diet. The same is likely true for those on "carnivorous" diets (mostly or exclusively animal foods) (Mcclellan and Du Bois, 1930), though more work is needed to confirm this hypothesis.

While human omnivory should arguably not be interpreted as true optionality for either plant or animal foods, concerns regarding the negative effects of animal foods on human and environmental health have led to widespread suggestions to replace traditional animal foods with plant-based foods to meet the vast majority of our nutritional needs (Godfray et al., 2018; Willett et al., 2019). The shift toward replacing animal foods with plant substitutes is, furthermore, enabled by modern food technologies that allow for the production of plant-sourced

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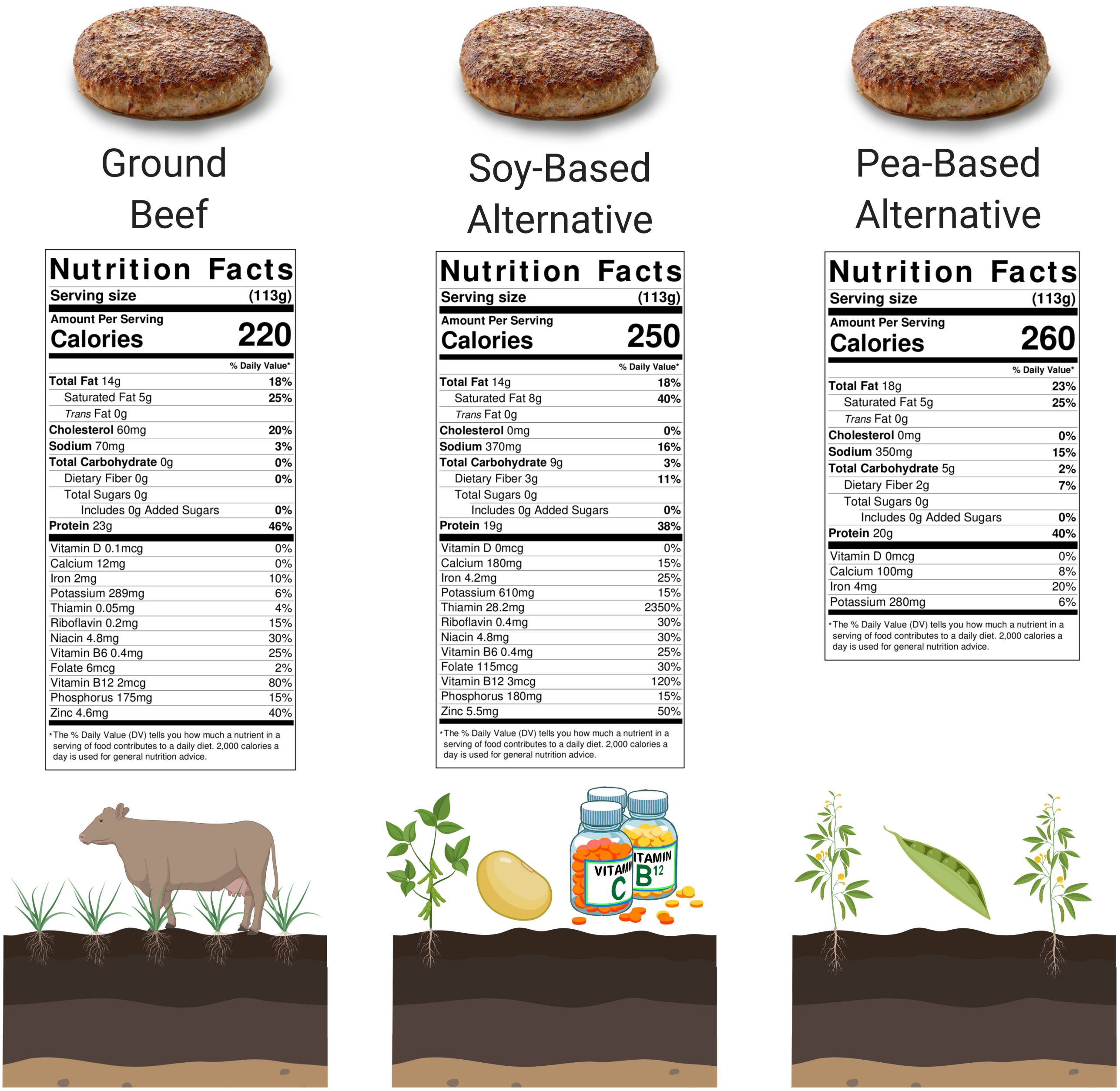
[1] Statista (2020). https://www.statista.com/.



Nutrition Facts	
Serving size	**(113g)**
Amount Per Serving **Calories**	**220**
	% Daily Value*
Total Fat 14g	**18%**
Saturated Fat 5g	**25%**
Trans Fat 0g	
Cholesterol 60mg	**20%**
Sodium 70mg	**3%**
Total Carbohydrate 0g	**0%**
Dietary Fiber 0g	**0%**
Total Sugars 0g	
Includes 0g Added Sugars	**0%**
Protein 23g	**46%**
Vitamin D 0.1mcg	0%
Calcium 12mg	0%
Iron 2mg	10%
Potassium 289mg	6%
Thiamin 0.05mg	4%
Riboflavin 0.2mg	15%
Niacin 4.8mg	30%
Vitamin B6 0.4mg	25%
Folate 6mcg	2%
Vitamin B12 2mcg	80%
Phosphorus 175mg	15%
Zinc 4.6mg	40%

*The % Daily Value (DV) tells you how much a nutrient in a serving of food contributes to a daily diet. 2,000 calories a day is used for general nutrition advice.

Nutrition Facts	
Serving size	**(113g)**
Amount Per Serving **Calories**	**250**
	% Daily Value*
Total Fat 14g	**18%**
Saturated Fat 8g	**40%**
Trans Fat 0g	
Cholesterol 0mg	**0%**
Sodium 370mg	**16%**
Total Carbohydrate 9g	**3%**
Dietary Fiber 3g	**11%**
Total Sugars 0g	
Includes 0g Added Sugars	**0%**
Protein 19g	**38%**
Vitamin D 0mcg	0%
Calcium 180mg	15%
Iron 4.2mg	25%
Potassium 610mg	15%
Thiamin 28.2mg	2350%
Riboflavin 0.4mg	30%
Niacin 4.8mg	30%
Vitamin B6 0.4mg	25%
Folate 115mcg	30%
Vitamin B12 3mcg	120%
Phosphorus 180mg	15%
Zinc 5.5mg	50%

*The % Daily Value (DV) tells you how much a nutrient in a serving of food contributes to a daily diet. 2,000 calories a day is used for general nutrition advice.

Nutrition Facts	
Serving size	**(113g)**
Amount Per Serving **Calories**	**260**
	% Daily Value*
Total Fat 18g	**23%**
Saturated Fat 5g	**25%**
Trans Fat 0g	
Cholesterol 0mg	**0%**
Sodium 350mg	**15%**
Total Carbohydrate 5g	**2%**
Dietary Fiber 2g	**7%**
Total Sugars 0g	
Includes 0g Added Sugars	**0%**
Protein 20g	**40%**
Vitamin D 0mcg	0%
Calcium 100mg	8%
Iron 4mg	20%
Potassium 280mg	6%

*The % Daily Value (DV) tells you how much a nutrient in a serving of food contributes to a daily diet. 2,000 calories a day is used for general nutrition advice.

FIGURE 1 | Nutrition Facts panels of 4 oz. (113 grams) of novel plant-based meat alternatives and ground beef. Food sources in their natural state contain thousands of compounds that are capably of impacting human health, the vast majority not appearing on consumer Nutrition Facts panels (Barabási et al., 2019). Despite comparable Nutrition Facts panels, important nutritional differences are expected between beef and the plant-based meats due to differences in their predominant originating source (bovine vs. soy vs. pea-derived). At present, novel plant-based meat alternatives should arguably be treated as meat alternatives in terms of sensory experience, but not *per se* as true nutritional replacement for meat. It is expected that both beef and plant-based meats will have a have a significant role to play in our future food supply (Godfray, 2019). *A popular soy-based alternative is fortified with iron (from soy leghemoglobin), riboflavin, niacin, vitamin B_6, vitamin B_{12}, and zinc, while a popular pea-based alternative is not fortified. Created with BioRender.com.

foods that are able to match the macronutrient, vitamin and mineral content of animal foods by using isolated plant proteins, bioengineered ingredients, and/or synthetic vitamins and minerals (**Figure 1**).

Moreover, a potential reason why the novel plant-based meats that look, feel, and taste like meat are of interest to consumers is that they may be able to better satisfy the "intrinsic desire" that humans have for eating meat (Piazza et al., 2015). For example, despite an aversion in vegetarians toward animal foods at the subjective level, the intrinsic motivational salience (desire for meat) was preserved on the neural level similar to that of omnivores (Giraldo et al., 2019). Noteworthy, is that this "subconscious motivation for eating meat" was observed already after a single overnight fast, which is far from a starvation-like state. Given the close resemblance of novel plant-based meat alternatives to meat, in the following section we address the following question: Can plant-based alternatives meet the nutritional requirements traditionally fulfilled by eating animal foods?

Protein

The recommended dietary allowance (RDA) for protein in adults is 0.8 g protein/kg bodyweight per day (∼56 g for a 70 kg individual) (Institute of Medicine, 2005). However, this amount should be viewed as the minimum to prevent deficiency in young adulthood rather that an amount that promotes optimal health (Wolfe and Miller, 2008; Phillips et al., 2016). Furthermore, the protein RDA is considered too low for middle-aged and older adults (>50 y) (Bauer et al., 2013; Deutz et al., 2014), and for adults who seek to maximize cellular adaptations from regular physical activity/exercise (Kato et al., 2016; Morton et al., 2018).

Animal foods such as meat are often recommended to meet protein needs because they provide dietary protein at a modest caloric load, and are considered of higher protein quality when compared to plant sources (FAO/WHO/UNI, 2011). The protein digestibility-corrected amino acid score (PDCAAS) and digestible indispensable amino acid score (DIAAS) are the two major standards used to evaluate the quality of dietary protein sources. Plant proteins often have lower scores (ranging from 0.4 to 0.9) than animal proteins (> 0.9). The lower PDCAAS/DIAAS of plant sources is, in part, due to their reduced digestibility as a result of the presence of "anti-nutrients"—phytates and trypsin inhibitors that interfere with digestion and absorption of protein (Sarwar Gilani et al., 2012). The advantage of novel meat alternatives is that they use concentrates and/or isolates of soy, pea, and other plant proteins. These purified protein sources are lower in anti-nutritional factors and, therefore, have comparable PDCAAS/DIAAS to most animal proteins including meat (Rutherfurd et al., 2014; Hodgkinson et al., 2018).

Based on their respective PDCAAS/DIAAS, one could expect that isolated plant proteins would result in a similar anabolic response when compared to animal sources. However, a number of studies have demonstrated that purified plant proteins have a lower skeletal muscle anabolic response when compared to isonitrogenous amounts of animal proteins with similar PDCAAS/DIAAS (Wilkinson et al., 2007; Tang et al., 2009; Phillips, 2012; Yang et al., 2012; Gorissen et al., 2016). Plant proteins tend to be particularly low in either lysine or methionine as well as leucine, which are essential amino acids that cannot be synthesized *in vivo* and need to be obtained through the diet (van Vliet et al., 2015). For instance, both soy and pea protein, the most commonly used protein sources in novel plant-based alternatives, are particularly low in methionine when compared to beef, in addition to being slightly lower in lysine as well (**Figure 2**).

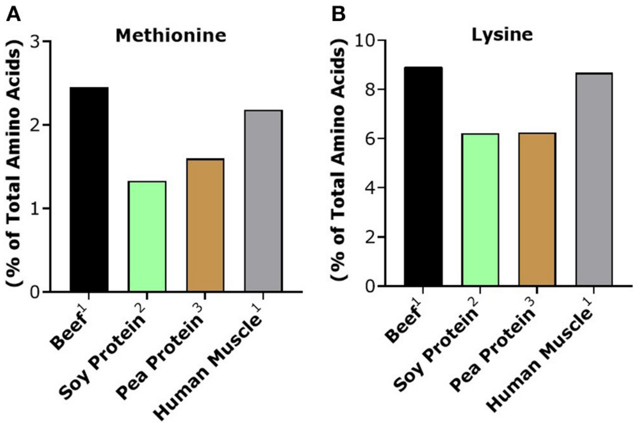


FIGURE 2 | Methionine **(A)** and lysine **(B)** content of beef and plant proteins commonly used in plant-based meat alternatives. Human muscle is provided as a reference standard. ^{1}From Burd et al. (2012). ^{2}From Tang et al. (2009). ^{3}From Khattab et al. (2009).

The issue of an unbalanced amino acid profile can be solved by combining isolated plant proteins that are lower in lysine yet higher in methionine (e.g., wheat, rice, hemp, and maize) with plant proteins that are higher in lysine yet lower in methionine (e.g., soy, potato, and pea) in a single product or by adding crystalline amino acids to the product (van Vliet et al., 2015). While a popular pea-based alternative contains some isolated rice protein, which is complementary to pea protein, it is unlikely (based on the listed order of ingredients) that the amount is sufficient to increase the methionine content of the product. Similarly, a popular soy-based alternative has a limited amount of potato protein (<2% of total ingredients), but potato, like soy, is low in methionine and high in lysine. While we have previously theorized that blending different complementary plant sources is a promising strategy to improve the skeletal muscle anabolic response to ingested plant protein (van Vliet et al., 2015), no studies have yet determined if this brings the muscle anabolic response from plant sources up to the level of animal proteins. Of note is recent work that showed that consumption of complementary plant proteins still resulted in 30–40% lower circulating essential amino acid availability when compared to a leucine-matched amount of whey protein (Brennan et al., 2019). These data suggest that, despite the blending of plant-based sources to make a complete amino acid profile, the anabolic potential may still be reduced when compared to animal-based protein.

A potential alternative strategy to overcome the lower anabolic effects of plant vs. animal proteins is to simply eat more plant proteins. Consuming 40 g of soy protein results in a similar muscle anabolic response as 20 g of whey protein (Yang et al., 2012). Adding a high dose of rice protein (48 g) to an omnivorous diet is also as effective as a protein-matched amount of whey protein in augmenting resistance-exercise induced gains in muscle mass. This is in contrast to studies that show a superior training-induced skeletal muscle gains after consuming lower doses of animal vs. plant proteins (ranging from 17.5 to 25 g) (Hartman et al., 2007; Volek et al., 2013). Nonetheless, it may reasonably be expected that the consumption of plant-based meat alternatives as part of an omnivorous diet is unlikely to negatively impact skeletal muscle mass or affect protein requirements.

Vitamin B_{12}

The cobalamins (vitamin B12) are the best-known members of the group of compounds collectively known as corrinoids. Cobalamin (vitamin B_{12}) is an essential nutrient that plays a role in DNA synthesis, myelin formation, red blood cell production, and maintenance of central nervous system function (Yamada, 2013). Humans must obtain vitamin B_{12} from the foods they eat or via supplementation. While gut bacteria in our large intestine still produce some corrinoids, including small amounts of active forms of cobalamin (Kirmiz et al., 2020), evolutionary pressures likely resulted in preferential absorption of B_{12} in the small intestine as a result of regular animal consumption (Seetharam and Alpers, 1982). This has resulted in a dependence on exogenous B_{12} that has likely persisted for at least 1.5 Ma (Dominguez-Rodrigo et al., 2012). Indeed, the receptors necessary for absorbing B_{12} are found only in the small intestine in modern-day humans, upstream of the site of bacterial corrinoid production (Seetharam and Alpers, 1982).

Biologically active B_{12} is found predominantly as adenosyl cobalamin in animal flesh (Czerwonka et al., 2014) and as hydroxocobalamin in eggs and dairy (Matte et al., 2012). These active forms of vitamin B_{12} bioaccumulate in animal products predominantly through microbial synthesis in the gut of ruminants, through consumption of soil and feces in non-ruminant herbivores, and through phytoplankton consumption in aquatic animals (Watanabe and Bito, 2018). A common misperception is that the majority of cattle receive supplemental B_{12} and that humans are essentially consuming B_{12} supplements via a "middle-man." While there is some evidence that high-producing dairy cows need more B_{12} than their microbes produce (Girard and Matte, 2005; Akins et al., 2013), the reality is that B_{12} is seldom fed to cattle, which is likely due to its high cost and limited benefits for production (Akins et al., 2013).

Although limited amounts of B_{12} are also found in some plant foods, such as mushrooms and fermented vegetables, the majority of B_{12} in plants are biologically inactive corrinoids (i.e., B_{12} analogs) (Stupperich and Nexø, 1991) that may compete with transport of biologically active B12, thus potentially aggravating a B_{12} deficiency (Dagnelie et al., 1991). Several plant-based foods, particularly those meant to replace animal foods—cereals, non-dairy milks, vegan spreads, and plant-based meat replacements—are often fortified with supplemental B_{12} to counteract deficiency. The common supplemental form of B_{12} used in these products is cyanocobalamin which is relatively inexpensive to produce and has stability to heat exposure (Goldstein and Duca, 1982).

Cyanocobalamin is a man-made form of Vitamin B_{12} that normally occurs only in trace amounts in human tissue, particularly in smokers (Paul and Brady, 2017). While all forms of vitamin B_{12}—naturally occurring adenosylcobalamin and hydroxycobalamin and the man-made form cyanocobalamin—are absorbed with similar efficiency (Paul and Brady, 2017), a potential concern with meeting B_{12} requirements through cyanocobalamin is that its tissue retention rates, and subsequent metabolic activity, are reduced compared to naturally occurring forms of B_{12} (Glass et al., 1961; Hertz et al., 1964; Okuda et al., 1973; Paul and Brady, 2017). Additionally, the B_{12} found in animal foods is protein-bound and therefore partially protected from light degradation (Linnell and Matthews, 1984). Nonetheless, eating cyanocobalamin-fortified foods or ingesting cyanocobalamin supplements can improve vitamin B_{12} status in adults (Tucker et al., 2000, 2004; Damayanti et al., 2018) and children (Sheng et al., 2019), which is also why fortifying meat alternatives with B_{12} is encouraged. This is especially important for vegans and vegetarians, and the elderly (even omnivores) who often have low B_{12} status (Herrmann et al., 2003a,b; Andrès et al., 2004), and rely on food fortification and/or supplementation to meet B_{12} needs. It is important to highlight that only less than a quarter of plant-based meat substitutes are fortified with B_{12} (Curtain and Grafenauer, 2019).

Iron

Dietary iron is found as heme iron in animal foods, particularly in red meat, and as non-heme iron in plant foods, particularly in pulses, grains, green leafy vegetables, and certain fruits. Heme iron is 5-10-fold more bioavailable than non-heme iron (Hurrell and Egli, 2010), and explains why omnivores often have higher serum ferritin levels (a marker of iron status) (Haider et al., 2018). The uptake of iron, particularly non-heme iron, is limited by several plant compounds such as phytates, polyphenols, and calcium, present in both plants and dairy (Hurrell and Egli, 2010).

In contrast to most plant foods, which predominantly contain non-heme iron as part of their natural food matrix, the iron in a market leading soy-based alternative is heme iron purified from yeast that is genetically engineered to express the leghemoglobin protein normally found in the root nodules of soy plants (i.e., soy leghemoglobin) (Fraser et al., 2018). While the amino acid sequence of leghemoglobin is vastly different from animal heme counterparts, iron uptake of leghemoglobin had similar bioavailability as bovine hemoglobin in a human epithelial cell culture model (Proulx and Reddy, 2006). Importantly, initial studies regarding safety of yeast-derived soy leghemoglobin show little concern for genotoxicity and immunogenicity in *in vitro* and short-term (28-day) *in vivo* animal studies (Fraser et al., 2018; Jin et al., 2018). Future work should confirm the bioavailability and long-term safety of yeast-derived soy leghemoglobin consumption *in vivo* in humans, and particularly in children where soy allergy is more common (Savage et al., 2010). While some concern exists with consumers regarding the use of genetically modified ingredients in food products (Scott et al., 2018), a recent consumer survey suggests that the presence of soy leghemoglobin in a popular soy-based meat alternative does not appear to be a barrier to consumption or perceived healthfulness of the product (International Food Information Council, 2020).

A market leading pea-based meat alternative contains non-heme iron naturally present in peas (**Figure 1**). While the bioavailability of non-heme iron is reduced compared to heme, non-heme iron can still represent an important dietary source of iron (Young et al., 2018). Vitamin C, and ironically meat, are main enhancers of non-heme iron absorption (Hurrell and Egli, 2010), which is why adding meat to plant-based meals improves uptake of non-heme iron from plants (Bjorn-Rasmussen and Hallberg, 1979; Kristensen et al., 2005). Vitamin C also enhances iron uptake by acting as a chelator in the gut

(Conrad and Umbreit, 1993). Important to note is that a market leading soy-based meat alternative is supplemented with sodium ascorbate (vitamin C), which presumably counteracts some of the inhibitory effects of the phytates, found in soy protein, on iron absorption (Hurrell et al., 1992).

Despite increased awareness, iron deficiency remains one of the most common nutrient deficiencies in both developed and developing countries, and population groups such as children, adolescent females, and older individuals are particularly at risk for deficiency (Patel, 2008; Beck et al., 2014; Gibson et al., 2014). On the other hand, excessive heme iron intake is increasingly linked to the promotion of cardiovascular disease (CVD) (Fang et al., 2015). The association of heme iron intake and CVD is particularly prevalent in US cohorts, but is inconsistent in cohorts outside of the US (Fang et al., 2015). Interestingly, even in the US the association between high heme iron intake and risk of CVD was absent in the first cohort of NHANES, which was studied during the 1970s (Liao et al., 1994) when red meat intake was higher compared to present day (Daniel et al., 2011). This heterogeneity between studies likely suggests that the background diet in which red meat is consumed may be an important modulating factor. In particular, the deleterious effects of red meat consumption may be perpetuated when meat is consumed as part of the Standard American Diet, rich in processed foods and inadequately counterbalanced with whole food plant sources. For example, polyphenols, phytates, calcium, and fibers inhibit heme iron absorption (Hurrell and Egli, 2010; Ma et al., 2010), and this may explain why some epidemiolocal studies find that risk of heme iron intake and CVD disappears with extensive adjustment for diet quality (i.e., diets also high in whole plant foods) (Galan et al., 2009; de Oliveira Otto et al., 2012; Kaluza et al., 2014).

Zinc

Similar to iron, zinc deficiency can be a concern in both developed and developing countries (Alloway, 2008), and those who restrict animal foods often have lower zinc status (Foster et al., 2013; Foster and Samman, 2015). Uptake of zinc from plant sources can be lower as a result of the presence of anti-nutrients such as phytates, lectins, and certain fibers (Harland and Oberleas, 1987; Welch, 1993). Similar to iron, zinc uptake from plants can be improved when consumed in conjunction with animal foods (Sandström et al., 1989). While soy protein contains limited amounts of zinc, a popular soy-based alternative is fortified with zinc gluconate to bring its level up to that of beef (**Figure 1**). Nevertheless, zinc absorption from fortified plant foods, at equal zinc content of beef, is lower than that for beef (Zheng et al., 1993; Etcheverry et al., 2006). We note that a well-planned vegan diet rich in legumes, nuts, seeds, and other zinc-rich plant foods can potentially provide adequate amounts of zinc (Eshel et al., 2019). Of further consideration when meeting zinc (and iron) requirements with supplementation is that this practice may reduce the absorption of other minerals such as copper (Yadrick et al., 1989), thus increasing their dietary requirements. The latter can be mitigated by consuming copper-rich (plant) foods (e.g., nuts, seeds, and leafy greens).

Essential Fatty Acids

The ω-6 fatty acid linoleic acid (C18:2, LNA) and the ω-3 fatty acid alpha-linolenic acid (C18:3, ALA) are essential fatty acids that cannot be synthesized *in vivo* by humans and must be obtained from dietary sources (Barcelo-Coblijn and Murphy, 2009). ALA is the parent precursor to the long-chain polyunsaturated fatty acids (LCPUFA) eicosapentaenoic acid (C20:5 n-3, EPA) and docosahexaenoic acid (C22:6 n-3, DHA). ALA and LNA are commonly found in plant foods but can also be found in limited quantities in animal foods, while DHA and EPA are found exclusively in animal foods and certain algae.

While ALA can be converted to DHA and EPA through a series of elongation and desaturation steps, this conversion is poor and often <1% (Su et al., 1999; Brenna, 2002; Pawlosky et al., 2003). Moreover, this conversion efficiency also depends on the presence of co-factors such as selenium, zinc, iron and vitamin B_6 (Brenner, 1981), which are less bioavailable from plant foods. For these reasons, vegetarians can have lower levels of DHA and EPA when compared to omnivores (Rosell et al., 2005).

DHA and EPA have been studied extensively for their importance in cardiovascular function, immunomodulation, vision, and cognitive function (Swanson et al., 2012). DHA is a major constituent of the brain phospholipid membrane (30–40% of total fatty acids), and low circulating levels are associated with accelerated brain aging (Tan et al., 2012; Otsuka et al., 2014). Nonetheless, as studies suggest that the human brain only requires 5 mg of DHA per day (Rapoport et al., 2007; Umhau et al., 2009), it is estimated that 1,200 mg of ALA can provide these minimum requirements (Barcelo-Coblijn and Murphy, 2009), though this minimum amount is not considered optimal for health. While no official daily recommended intakes exist for DHA and EPA, numerous studies demonstrate that combined intakes of DHA and EPA ranging from 250 to 1000 mg/day improve cognitive function and other health parameters (Yurko-Mauro et al., 2015; Derbyshire, 2018), and such amounts are therefore often recommended by various health organizations (WHO, 2008; EFSA, 2012).

The ω-3 fatty acid ALA is found in substantial amounts in certain vegetable oils, such as flax seed oil (53 % ALA), chia seed oil (64% ALA), perilla oil (60% ALA), and camelina oil (38% ALA), though consumption of the latter two oils is generally restricted to Asian and Nordic countries, respectively (Barcelo-Coblijn and Murphy, 2009). While the amount of ALA necessary to ensure minimum DHA requirements in the human body can be obtained with modest intake of these oils, the majority of vegetable oils consumed in industrialized countries is in the form of ω-6 LNA-rich seed oils such as soybean, corn, sunflower, and canola oil, which contain <10% ALA. For instance, sunflower oil and canola oil—the main oils in the novel plant-based meat alternatives—contain only 1% (sunflower oil) and 10% (canola oil) ALA. Given the already low conversion rates of ALA to EPA and DHA, respectively, plant-based meat alternatives in their current state likely will not provide meaningful amounts of very long-chain PUFAs in the diet.

Another potential issue is that the ω-6 fatty acids such as LNA directly compete with ALA for enzymes involved in elongation and desaturation, which further diminishes the ability to obtain DHA and EPA from ALA (Sprecher et al., 1999). This is particularly problematic when one considers that the increased consumption of high LNA seed oils in the modern Western Diet has resulted in an ω-6-to-ω-3 fatty acid ratio of 16:1 (Simopoulos, 2002), whereas historical intakes puts this ratio closer to 1:1 (Eaton et al., 1998; Simopoulos, 2002). This high ω-6-to-ω-3 fatty acid ratio is considered an important underlying cause for the increasing incidence of metabolic disease and all-cause mortality in Western countries (Das, 2006; Zhuang et al., 2019). Experimentally substituting ω-6-rich LNA oils with ω-3-rich ALA oils reduces inflammation (Rallidis et al., 2003; Bemelmans et al., 2004), which represent a mechanistic explanation for why consuming ω-3-rich ALA oils may be cardioprotective. Thus, a suitable improvement to the novel plant-based meat alternatives could be to consider the use of high ALA oils, rich in ω-3, instead of high LNA oils rich in ω-6 fatty acids. An important consideration is that high ALA oils are more prone to lipid oxidation (and perhaps represents a reason why high LNA oils are typically used in meat substitutes); however, the addition of natural anti-oxidants (Wang et al., 2018; Lu et al., 2020) as well as entrapment of high ALA oils with isolated plant proteins (Karaca et al., 2013; Bajaj et al., 2015) represent worthwhile opportunities to explore for producers of plant-based meat substitutes that consider the use of high ALA oils in their products, which potentially increases their healthfulness.

It is often stated that ω-3 fatty acids are present in such modest amounts in land animal-sourced foods, such as beef, that they do not represent a valuable dietary source of these essential fatty acids. However, this notion fails to take into account the abundance of the ω-3 fatty acid docosapentaenoic acid (C22:5, DPA) in beef, particularly pasture-raised beef, which raises platelet EPA and DHA levels as a result of *in vivo* conversion (McAfee et al., 2011). While DHA can also be directly obtained in substantial amounts from offal cuts of meat—for instance, 100 g of grass-fed beef liver provides 80 mg of DHA (Enser et al., 1998)—the consumption of organ meat is not as common anymore in Western diets and marine sources account for the majority of dietary intake of the ω-3 fatty acids DHA and EPA (Bauch et al., 2006; Papanikolaou et al., 2014).

Secondary Nutrients

While we have highlighted several important individual nutrients thus far, foods in their natural state are considerably more complex than their essential fatty acid, amino acid, vitamin, and mineral content would suggest. Food sources contain hundreds-to-thousands of biochemicals that are important to human metabolism (Barabási et al., 2019). While many of these nutrients are considered non-essential or conditionally-essential based on life-stages, and are often less appreciated in discussions of human nutritional requirements, their ability to impact human metabolism should not be ignored.

For example, creatine has been studied extensively for its ability to enhance athletic performance (Cooper et al., 2012), but creatine also plays an important role in cognition (Avgerinos et al., 2018). As creatine is found only in animal foods, vegans and vegetarians often have lower bodily stores (Burke et al., 2003), and vegetarians provided with supplemental creatine showed substantial improvements in memory tasks (Benton and Donohoe, 2011). Similarly, the antioxidants anserine, carnosine, and taurine are found (almost) exclusively in animal foods (Hou et al., 2019). Increased anserine and carnosine intake provide neurocognitive protection in humans (Szczesniak et al., 2014; Rokicki et al., 2015).

Taurine is an amino acid found almost exclusively in animal foods and though small amounts may be found in some plant foods such as cereals, legumes, and grains (a thousand times less when compared to animals foods) (Pasantes et al., 1989), these amounts are insufficient to meet human requirements (Laidlaw et al., 1990). It is often stated that since taurine can be synthesized *in vivo* from methionine and cysteine via cysteinesulfinic acid decarboxylase (CSD), taurine requirements can be met by consumption of plant proteins that are rich in methionine and cysteine, which can be found in adequate amounts in several legumes and grains (van Vliet et al., 2015). However, CSD levels in the human body, which allows for the conversion of taurine from methionine and cysteine, are insufficient to maintain tissue concentrations over time (Ripps and Shen, 2012). Taurine impacts nearly every vital organ in the body and plays vital roles in eye health (Froger et al., 2014), brain function (Kilb and Fukuda, 2017), mitochondrial functions (Suzuki et al., 2002), skeletal muscle cell differentiation (Miyazaki et al., 2013), and cardiovascular health (Waldron et al., 2018). Future studies are needed to better understand how these differences in secondary nutrients between plant-based meat alternatives and meat impacts short- and long-term health.

Fortifying Foods to Mimic the Natural Food Source

A recurring concern is that natural whole foods are extremely complex and the reductionist approach of trying to "mimic" whole food sources (whether it be meat or other foods) by combining several isolated nutrients likely underestimates the true complexity and health benefits of eating whole foods (Lichtenstein and Russell, 2005; Jacobs and Tapsell, 2007). In particular, fortification of a low-meat diet with zinc and other minerals found in meat did not result in similar zinc status as when these minerals were provided in the diet as part of the natural matrix of meat (Hunt et al., 1995). Moreover, adequate intakes of zinc, copper, and vitamins A and D were associated with decreased risk of cardiovascular disease and all-cause mortality when obtained from foods, but not from supplements, in a recent large population-based study (Chen et al., 2019). Similarly, carotenoid-containing foods are associated with a decreased risk of various cancers (van Poppel and Goldbohm, 1995), retinopathies (Goldberg et al., 1988; Seddon et al., 1994), and cardiovascular disease (Kritchevsky, 1999). However, the results of interventional and epidemiological studies suggest that carotenoid and/or vitamin A supplements do not decrease the risk of cancer or cardiovascular disease, and might even raise the risk for some sub-populations (The Alpha-Tocopherol Beta Carotene Cancer Prevention Study Group, 1994; Omenn et al., 1996; Druesne-Pecollo et al., 2010; Bjelakovic et al., 2012). Similar findings have been made in studies of calcium that show a potential for increased cardiovascular disease risk with supplementation (Bolland et al., 2011; Li et al., 2012), but not when calcium is obtained from food (Xiao et al., 2013). Finally, similar findings have been made for vitamin C and selenium supplements that show no benefits on mortality in a systematic review of RCTs comprised of nearly 300,000 individuals (Bjelakovic et al., 2012). Thus, it appears that simply ingesting these nutrients outside of their natural food matrices may not be an optimal solution for promoting health. Thus, obtaining nutrients from whole food sources as opposed to supplemental forms is emphasized regardless of the individual's diet (Jacobs and Tapsell, 2007; van Vliet et al., 2018).

THE ECOLOGICAL IMPACTS OF PLANT-BASED MEAT VS. MEAT CONSUMPTION

The plant vs. meat controversy takes on other dimensions when assessing environmental degradation and climate change, both of which adversely affect human health and are crucial considerations when making recommendations on diets for livestock and humans. Meeting requirements of nutrients with plant foods (e.g., folate, manganese, thiamin, copper, and β-carotene) may come at a lower environmental footprint (i.e., less greenhouse gas emissions) than when these nutrients are met with animal foods (Eshel et al., 2019). Nonetheless, it has been suggested that similar amounts of protein, iron, and vitamin A can be obtained from carefully selected plant-based diet at a lower carbon footprint when compared to omnivorous diets/animal foods (González et al., 2011; Eshel et al., 2019); however, such comparisons do not take into account the reduced bioaccessibility and bioavailability of plant sources for these nutrients (Stover and Caudill, 2008; Tang, 2010; van Vliet et al., 2015). Moreover, when footprints—land use for production and as greenhouse gas emissions (GHGE)—are calculated to consider amino acid content and nutrient density (e.g., iron, vitamin B_{12}, zinc, retinol, and amino acids), the footprint of animal foods may be more similar to plant foods (Drewnowski et al., 2015; Tessari et al., 2016) because animal foods can more readily meet our needs for these specific nutrients.

The lower carbon footprint of plant-based meat alternatives is touted as a main reason for choosing plant alternatives over beef. Recent life-cycle analysis (LCA) of the Beyond Burger® and the Impossible™ Burger demonstrates a smaller carbon footprint (+3.2 and 3.5 kg CO2-eq emissions/per kg product, respectively) compared to US beef finished on total-mixed rations in feedlots (Heller and Keoleian, 2018; Quantis International, 2019a), which ranges from +10.2 to +48.5 kg CO_2-eq per kg product, depending on the model used, the geographical location where the cattle are raised, and the inclusion of GHGE potential of retail, distribution, restaurant or at home use, and end-of-life stages (Heller and Keoleian, 2018; Stanley et al., 2018; Asem-Hiablie et al., 2019; Rotz et al., 2019) (**Figure 3**).

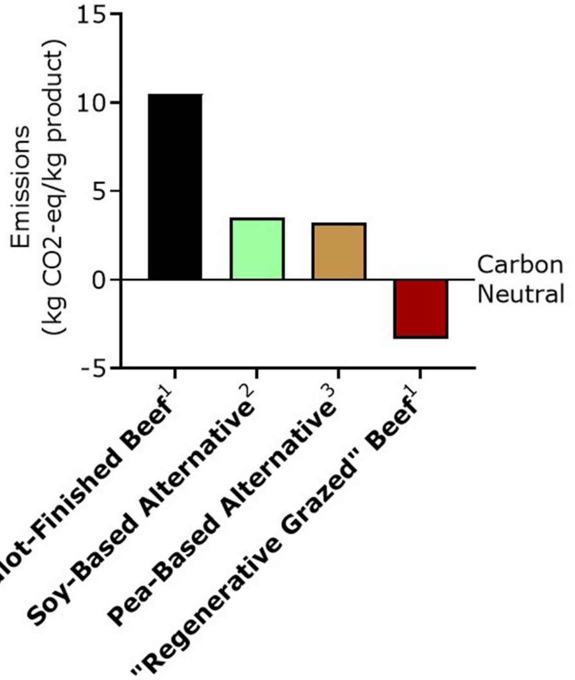


FIGURE 3 | Comparison of possible greenhouse gas emissions impacts of various beef production systems and meat alternatives. All values include cradle-to-distribution LCA, but excludes GHGE potential of retail, restaurant or at home use, and end-of-life stages. [1]From Stanley et al. (2018) assuming an edible yield of 60 and 55% carcass weight for feedlot-finished and "regenerative grazed" (adaptive multi-paddock grazed) beef, respectively with an addition of +0.3 CO_2-eq per kg product as published in Asem-Hiablie et al. (2019) to account for the lack of inclusion of GHGE potential of packing, which is taken into account in the LCA of the meat alternatives. [2]From Quantis International (2019b). [3]From Heller and Keoleian (2018). CO_2-eq, Carbon dioxide equivalent; GHGE, Greenhouse gas emissions; LCA, Lifecycle analysis.

While meat alternatives may have a lower environmental impact when compared to feedlot-finished beef, well-managed pasture-based livestock systems fix at a minimum all the GHG they emit (and sometimes more) even when taking into account all aspects of the production process (Allard et al., 2007; Teague et al., 2016; Stanley et al., 2018). Pastured beef systems that use land management practices such as rotational grazing—where lands are allowed to properly recover after a grazing period—and/or cover crop grazing suggest that the amounts of carbon sequestered in the soil more than offsets the ruminants' GHGE, resulting in a net negative carbon footprint (Allard et al., 2007; Teague et al., 2016; Stanley et al., 2018). By having livestock participate in carbon cycling by spending their lives on well-managed pastures—grooming and fertilizing vegetation and soil (Reeder and Schuman, 2002)—such production systems have the potential to help mitigate climate change (or in the very least not exacerbate it further) while ensuring a degree of food security (Teague et al., 2016).

Well-managed grasslands, especially in more mesic areas, can act as carbon sinks in a variety of geographical locations worldwide and depending on geographical locations, may be more reliable carbon sinks than forest (Dass et al., 2018; Viglizzo et al., 2019). It must be noted that the two (forests and livestock) are not mutually exclusive to begin with, as demonstrated by successful implementation of silvopastoralism—a type of agroforestry integrating trees, forage, and livestock—in forested areas across the globe as a strategy to enhance carbon sequestration, soil health, and food security for those inhabiting such areas (Kumar and Nair, 2011). Thus, considerations regarding livestock-production systems should be tailored to fit the geophysical landscape instead of attempting—often at great expense—to change the environment to fit the production system. For example, it would be suitable to practice silvopasture techniques with locally adapted animals in landscapes such as the Amazon rather than attempting to convert its forests to pasturelands (Nair et al., 2011).

It must be noted though that not all pasture-based (grass-fed) operations are *per se* regenerative or neutral, and depending on management practices, grass-fed beef systems can have a higher carbon footprint than some feedlot systems (Pierrehumbert and Eshel, 2015; Lynch, 2019). It is also important to highlight that the amount of carbon sequestered with well-managed grazing of livestock on carbon-depleted soils is initially more rapid and diminishes over time as soil health is restored (Godde et al., 2020), which is not surprising once equilibrium of ecological systems are reached. This notion should be considered in the discussions below.

By performing an ISO-compliant partial LCA of pasture-raised (grass-fed) beef in the Midwest US, Stanley et al. (2018) found a net negative carbon footprint of ∼−3.5 CO2-eq/per kg beef (assuming a 55% edible yield of hot carcass weight). We note that the value from the pasture-finished beef LCA assessment excludes the GHGE of getting the product case-ready, which is included in the plant-based meat LCAs. This is expected to add +0.3 kg CO2-eq/kg product (Asem-Hiablie et al., 2019) which would put the LCA analysis from so-called regenerative, grass-fed beef at −3.2 CO2-eq/per kg beef (**Figure 3**). This means that over the lifecycle of the animal more carbon was sequestered than emitted.

Notably, the same company (Quantis International) that demonstrated a +3.5 CO2-eq emissions/per kg product in the LCA analysis of the Impossible Burger$^{\mathrm{TM}}$ (Quantis International, 2019b) also demonstrated a −3.5 CO2-eq/per kg beef produced using regenerative livestock grazing practices (Quantis International, 2019a). While these reports are not peer-reviewed, it is encouraging that the values reported by Quantis International are close to those reported in peer reviewed work on so-called regenerative beef (Stanley et al., 2018) and the work performed on plant-based meat alternatives by academic scientists (Heller and Keoleian, 2018).

Nonetheless, the LCAs performed on meat alternatives and pasture-finished beef both exclude GHGE potentials of retail, and restaurant or at home preparation, end-of-life stages, and other localized or indirect impacts. Acknowledging the difficulty in assessing all aspect of environmental footprints, future work should confirm these LCA analysis with full accounting for all GHGE to provide for even-handed assessments (Halpern et al., 2019).

Greenhouse gasses are often lumped together under the umbrella of CO_2-eq, which equates different GHGs to carbon dioxide (CO_2) (Allen et al., 2018). However, different gasses have different global warming potentials (GWP) and their exact values depend on the CO_2-eq metrics and the timescale (e.g., 20 or 100 years) that is used to express its GHGE contribution (Lynch, 2019). While livestock production also includes significant emissions of CH_4 (methane), plant based-meat emissions mostly consist of CO_2 from energy generation (Heller and Keoleian, 2018). Livestock add 14.5% to GHGE globally (Gerber et al., 2013). Of that, 9.5% is producing feed for livestock, processing, and transportation, while the remaining 5% is methane from rumen (enteric) fermentation and manure. While methane is a potent GHG, it is also temporary one; it lasts a decade before it breaks down into CO_2 that can be sequestered in soil. With a stable or slightly decreasing population of cattle in the US, though not globally, the methane belched from cattle is not likely to add new carbon to the atmosphere (Lynch, 2019). On the other hand, once we put carbon dioxide in the atmosphere from burning fossil fuel—whether from transportation or food production—it persists for thousands of years. These nuances are important to recognize in discussions on carbon footprints of different foods and dietary patterns.

The carbon footprint of meat alternatives is likely lower than the majority of beef consumed in the US, because that beef is produced primarily from feedlots that rely on fossil fuel-intensive methods (Poore and Nemecek, 2018) (∼96% of all beef in the US is finished in feedlots). Some suggest that with increased conversion to pasture-based beef production systems in the US, domestic beef consumption will have to be reduced by about 40% due to unavailability of land-provided roughage feed is used to supplement cattle on pasture (Hayek and Garrett, 2018). These estimations do not take into account the potential for increased carrying capacity from multi-species grazing with little dietary overlap, for instance mixing cattle with sheep or goats, which improves productivity of both animals and vegetation when compared to grazing of either animal alone (Walker, 1994; Celaya et al., 2008; Anderson et al., 2012; Ferreira et al., 2013). Moreover, properly management multi-species grazing can also maintain plant diversity and thus improve ecological resiliency and pasture health (Anderson et al., 2012). This would obviously mean that we would have to diversify our meat and milk intake to include products from other livestock, including sheep, goats and perhaps smaller mammals such as ducks and rabbits.

Another opportunity to further increase the carrying capacity of a pasture-based livestock, which is often not taken into account in discussions on the carrying capacity of pasture-based production systems, is to strategically supplement livestock on pasture with edible by-products (Sunvold et al., 1991; Macdonald et al., 2007). Ruminants have the unique capacity to upcycle by-products from industrial and agricultural production (Mottet et al., 2017). For example, when corn is used to make ethanol, only the starch portion is used and its by-product (the outer shell, oil, and germ) can be made into a high-fat, high-protein cake fed to cattle. Crop residues such as straws, stover, and sugar-cane tops as well as phytochemically-rich byproducts of fruit and vegetable processing such as leaves, pomace, peels, rinds, pulp, seeds, stems etc. to livestock (Sruamsiri, 2007; Wadhwa and Bakshi, 2013; Nwafor et al., 2017) provide similar opportunities to upcycle these nutrients. Offering these byproducts to cattle on pasture can potentially mitigate some nutritional deficits, enhance use of unpalatable vegetation, reduce the risk of overgrazing, and mitigate issues of reduced land availability (Provenza et al., 2003).

Offering by-products on pasture, as opposed to feeding them to cattle in feedlots, would also mitigate some of the animal welfare issues associated with feedlots such as unfamiliar environments, inability to self-select their diet, and the ability to express natural behavior (Atwood et al., 2001; Villalba and Manteca, 2019). Offering by-products to cattle on pasture may represent a worthwhile opportunity for the livestock industry to improve consumer perception while maintaining the ability to upcycle by-products to meet customer demand. It will be important to use only industrial by-products that would have been produced anyway, rather than growing feed with the specific intent of giving it to livestock.

Recent studies also show that the mixture of forages animals eat on pasture influences how long it takes them to reach slaughter weight. Compared with grazing a monoculture of grass, cattle eating diverse mixtures of plants, some of which contain tannins, gain weight more efficiently and can reach finish body condition nearly as quickly as animals in feedlots—and they do so with less GHGE (Villalba et al., 2019). Providing ruminants with forages that contain secondary compounds such as tannins and terpenes also decreases nitrogen in urine and increases nitrogen in tannin-rich manure that builds soil organic matter (Villalba et al., 2019).

Finally, discussions on whether pasture-based productions systems can sustain meat consumption revolve around the ability of pasture-based systems to support the consumption of popular retail cuts (i.e., steaks, roasts, beef). For instance, Hayek and Garrett (2018) assume a 60% edible yield in their calculations on the carrying capacity of pasture-based beef production systems to support US consumption. While this number is justifiable, another 20% of the animal is entirely suitable for human consumption and includes organs, bones, and tallow (USDA, 2015). For example, increased consumption of organ meats—often much denser in vitamins and minerals (e.g., 10–1000 fold higher in retinol, iron, copper and vitamins B_6, B_{12}, and K_2) than muscle meat (USDA, 2016)—was recently found to reduce meat intake-associated GHGE by 14% (Xue et al., 2019).

While not a panacea for saving the planet from climate change, agricultural practices that integrate regenerative livestock grazing practices with plant farming are an important step in the right direction to reduce the carbon footprint and land use of animal agriculture. Of 80 ways to mitigate climate change evaluated in Project Drawdown, regenerative practices—farmland restoration, conservation agriculture, agroforestry, silvopastoralism, and managed grazing—jointly rank number one as a way to sequester GHG (Hawken, 2017). Furthermore, by integrating livestock grazing with plant farming, one can also improve crop yield and soil fertility (Maughan et al., 2009; Bell et al., 2014). The symbiotic relationship between plants and herbivores, which each system strengthening the other, are important to appreciate in discussions on whether we displace livestock production.

When the projected increase to nearly ten billion people is combined with an increase of 32 percent in per-person-emissions from global shifts to ultra-processed diets by 2050, the net effect is an estimated 80 percent increase in GHGE (Tilman and Clark, 2014). Alternatively, GHGE may not increase if diets were vegetarian, pescatarian, or Mediterranean that include whole food sources of fruit, vegetables, seafood, grains, eggs, dairy, as well as limited amounts of beef, lamb, and poultry (Tilman and Clark, 2014). For example, the high carbon footprints in an urban Japanese population was largely explained by confectionary consumption, dining out, and alcohol consumption, whereas consumption of meat and vegetables contributed much less to the footprint—meat only contributed to 9% of the difference between low and high dietary carbon footprints (Kanemoto et al., 2019). Findings along similar lines were made recently in an Australian cohort, where "discretionary foods" (sugar-sweetened beverages, alcohol, confectionary, and other ultra-processed foods) made up the largest share of the environmental footprint (Ridoutt et al., 2020). Future studies should confirm this hypothesis in European and American households, but similar results can reasonably be expected due the prevalent consumption of the Standard Western/American diet.

Moreover, biophysical simulation of various diet patterns suggests that a healthy omnivorous diet—rich in whole-food plant and animal sources—has the greatest carrying capacity for feeding populations in diverse regions throughout the world (Peters et al., 2016). Vegan and vegetarian diets have a greater carrying capacity than the Standard Western Diet—high in processed foods (Peters et al., 2016). On this basis, some make a case for adoption of a plant-based diet, but a diet that contains only plant foods does not integrate farming and grazing to improve the fertility of soil—which synergistically strengthens both plant (Maughan et al., 2009; Bell et al., 2014) and livestock farming systems (Teague et al., 2016)—nor does it efficiently use land that could otherwise feed more people (Peters et al., 2016; Van Zanten et al., 2016). The latter point is significant because two-thirds of earth's land mass, which is unsuitable for crop production (FAO, 2020), is home to billions of people who depend on managed livestock grazing for their livelihood. In discussions of dietary transitions towards plant-based substitutes it is, therefore, crucial that no policies are set into place that threaten the health and livelihood of the world's poorest.

Another important point to consider is that most crops are grown in monocultures where life below and aboveground is sacrificed by chemical and/or mechanical means. While eating roots of carrots, seeds from almonds, or plant-based meat alternatives from peas or soy does not directly involve killing animals, indirectly it does. The habitats of other plants and animals are destroyed. One large and visible example is grassland birds who have lost more than 50% of their populations in North America in the last 50 years due to large-scale farming practices be it plant or animal farming (Rosenberg et al., 2019). Another clear example is found in the Southern Peninsula of

Malaysia and Borneo where replacing native forests with oil palm plantations has contributed to a reduction in the total number bird and butterfly species by ∼80% (Koh and Wilcove, 2008) and Orangutans by ∼85% (Ancrenaz et al., 2016).

There is considerable difficulty in estimating the number of animals killed as part of "collateral damage" in agriculture (i.e., animals not killed for consumption) (Fischer and Lamey, 2018); however, conservative yearly estimates in the US put this number in the tens of millions and includes mammals, fish, reptiles, and other amphibious creatures. In particular, Fischer and Lamey (2018) put this number at roughly 127.5 million field deaths per year in the US with a lower bound of 63.75 million per year, though it must be noted that considerable uncertainty exists regarding this number due to absence of systematic data collection on field deaths. For perspective, 40 million cattle and 120 million pigs are estimated to be slaughtered for consumption each year in the US (Fischer and Lamey, 2018). Whether intended deaths (through animal consumption) are morally equivalent to "unintended" deaths (through plant agriculture including those for human consumption and animal feed) is beyond this review [see Fischer and Lamey (2018) for a further discussion]. It serves the point that in food systems, life consumes life to live. Nonetheless, that improvements must be made in plant farming and livestock production methods in ways that enhance the welfare of livestock and wildlife is something arguably most agree on (meat and plant-eaters alike).

The ecological impacts of human diets are not as simple as plant vs. meat discussions might suggest. The global food system is far too diverse and contingent on unique environmental and socioeconomic circumstances to allow for one-size-fits-all policy recommendations. As the latest IPCC Report points out, mixed plant farming-livestock grazing systems can heal damage done by years of continuous arable cropping reliant on mechanical and chemical inputs (IPCC, 2019). In the process, we may increase the number of animals grazing phytochemically rich landscapes that nuture animals, soil, plants, and people, and provide food that is biochemically richer and arguably more nourishing for *Homo sapiens* and the planet.

CONCLUSION

Humans satisfy requirements for certain nutrients much better from plant foods, while needs for other nutrients are met more readily from animal foods. Plant nutrients (i.e., phytochemicals) often protect against potentially harmful compounds in cooked animal foods (Van Hecke et al., 2017b), while animal foods also facilitate the uptake of several plant nutrients (e.g., zinc and non-heme iron) (Sandström et al., 1989; Hurrell and Egli, 2010). Thus, plant and animal foods interact in symbiotic ways to improve human health.

While plant-based diets are being promoted for human and environmental health reasons (Eshel et al., 2019; Willett et al., 2019), this may put large portions of the population at greater risk for nutrient deficiencies and accompanying health issues (Payne et al., 2016). This may especially be the case for vulnerable populations such as children, elderly, and nursing mothers who are at increased risk for nutritional deficiencies. Some suggest that in order to meet requirements for several key nutrients with plant foods (vitamins A, $B_{3,6,12}$, choline, zinc, iron, and selenium), more plants should be ingested to overcome their reduced bioavailability and supplements should be taken if deficiencies arise (vitamin B_{12} would have to be supplemented regardless). However, intra-individual differences in nutrient metabolism (Brenna, 2002; Burdge, 2006; Stover and Caudill, 2008; Tang, 2010) may preclude portions of the population to thrive on vegan/vegetarian diets, regardless of how well the plant-based food or diet may be "designed."

Many scientists are concerned about the reductionist approach of simply adding isolated forms protein, vitamins, and minerals to foods, or diets in general, and designating them as nutritionally adequate (Lichtenstein and Russell, 2005; Jacobs and Tapsell, 2007). As whole foods contain hundreds-to-thousands of compounds that act synergistically to impact human health (Barabási et al., 2019), adding synthetic nutrients to food sources often does not confer similar benefits compared to when these nutrients are ingested as phytochemically and biochemically-rich whole foods—whether it be plant or animal foods (Lichtenstein and Russell, 2005; Jacobs and Tapsell, 2007).

Scientists who operate in the realms of nutrition and ecology, those in companies that produce plant-based meat alternatives, and the general public arguably share similar concerns about the influence of agriculture on climate change. Where groups differ is in their solution to the challenge. There are many whole-foods dietary options that could substantially improve human and ecological health (Tilman and Clark, 2014)—whether they be vegetarian, pescatarian, or omnivorous. We contend that an omnivorous diet rich in whole foods, produced using sustainable agricultural practices that integrates plants and animals in agroecological ways (i.e., in harmony with natural systems), is most likely to benefit human and ecological health.

At present, novel plant-based meat alternatives should arguably be treated as meat alternatives in terms of sensory experience, but not *per se* as true nutritional replacement for meat. If consumers wish to replace some meat in their diet with plant-based alternatives (a "flexitarian approach"), this is unlikely to negatively impact their overall nutrient status; however, this also depends on what other foods are routinely consumed and the life stage of the individual (e.g., infancy, pregnancy, or advancing age). That said, it is important for future work to compare human health outcomes in response plant-based vs. animal meat consumption. Such studies can ensure, and potentially improve, the healthfulness of plant-based meat alternatives and meat itself, as it is likely that both will have a have a significant role to play in our future food supply.

AUTHOR CONTRIBUTIONS

SV and FP wrote the first draft of the manuscript. SK critically revised the text and made substantial contributions to the manuscript. All authors approved the final version of the manuscript.

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Conflict of Interest: SV reports a grant from the North Dakota Beef Association to study the impact of diet quality on the relationship between red meat and human health and has not accepted personal honoraria from any organization to prevent undue influence in the eye of the public. FP reports receiving honoraria for his talks about behavior-based management of livestock.

The remaining author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Sustainable Food Systems

ORIGINAL RESEARCH
published: 04 December 2020
doi: 10.3389/fsufs.2020.544984

Ecosystem Impacts and Productive Capacity of a Multi-Species Pastured Livestock System

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Regenerative agriculture is a newly codified approach to agriculture that emphasizes reducing reliance on exogeneous inputs, as well as restoring and enhancing ecosystem services such as soil carbon (C) sequestration. These regenerative agriculture principles suggest that modern livestock systems can be redesigned to better capitalize on animals' ecological niche as biological up cyclers and may be necessary to fully regenerate some landscapes. One example is a multispecies pasture rotation (MSPR) system, which symbiotically stacks multiple animal production enterprises (i.e., chickens, cattle, sheep, and pigs) on one landscape. We conducted a whole-farm life cycle assessment (LCA) of an MSPR in the southeastern United States that was originally converted from degraded cropland. We compared the production outputs, greenhouse gas (GHG) emissions, land footprints, and soil health outcomes to a conventional, commodity (COM) production system of each respective species. Our 20-year MSPR chronosequence of soil C and other soil health indicators shows dramatic improvement since establishment, sequestering an average of 2.29 Mg C ha^{-1} yr^{-1}. Incorporation of soil C sequestration into the LCA reduced net GHG emissions of the MSPR by 80%, resulting in a footprint 66% lower than COM. However, when comparing required land between the two systems for food production, MSPR required 2.5 times more land when compared to COM. Thus, while our model indicates that MSPR can simultaneously produce protein while regenerating land, a considerably greater land area is needed when compared to COM. Our results present an important yet paradoxical conclusion on land and food production balance. Should society prioritize an input-intensive, COM system that produces more food from a smaller yet degrading land base? Or, alternatively, should systems such as MSPR that produce less food on a larger, but more ecologically functional landscape be more highly prioritized? These complexities must be considered in the global debate of agricultural practice and land. Our results indicate MSPRs are a useful model for alternative livestock production systems with improved environmental outcomes, but in this study may present considerable land-use tradeoffs.

Keywords: regenerative agriculture, soil carbon (C) sequestration, life cycle (impact) assessment, multi-species grazing, holistic planned grazing^{TM}

Edited by:
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Specialty section:
This article was submitted to Agroecology and Ecosystem Services, a section of the journal Frontiers in Sustainable Food Systems

Received: 23 March 2020
Accepted: 22 October 2020
Published: 04 December 2020

Citation:
Rowntree JE, Stanley PL, Maciel ICF, Thorbecke M, Rosenzweig ST, Hancock DW, Guzman A and Raven MR (2020) Ecosystem Impacts and Productive Capacity of a Multi-Species Pastured Livestock System.
Front. Sustain. Food Syst. 4:544984.
doi: 10.3389/fsufs.2020.544984

INTRODUCTION

Livestock are often considered agriculture's key greenhouse gas (GHG) emitter, contributing more than one-third of agricultural emissions (EPA, 2019). Typically, livestock production in the United States is highly specialized and intensified and is often cited as having both lower GHG [on a per carcass weight (CW) basis] and land-use footprints than pasture-based livestock systems. Alternatively, pasture-based systems often have less GHG intensity from a land use basis (Cardoso et al., 2016). However, current studies neither robustly consider complexity in diversified pasture-based livestock systems, nor consider the role of soil carbon (C) in GHG flux as well as land-use tradeoffs. This study aimed to contribute to this gap, in part, by quantifying GHG emissions, soil C sequestration, soil health, and land footprint of a farm using a diversified, multispecies pasture rotation (MSPR) in Clay County, Georgia, USA. We then compared emissions and land use to conventional, commodity (COM) production systems for beef, pork, and poultry.

Diversified farms supply 60 and 75% of the world's meat and dairy, respectively (Herrero et al., 2010; FAO, 2014). Expanding the use of diversified farming methods for animal production (including integrated crop-livestock systems, carefully managed grazing, and MSPRs) can lead to improved environmental outcomes and beneficial ecosystem services (e.g., wildlife and pollinator habitat, improved nutrient cycling) in addition to food production (Russelle et al., 2007; Kremen et al., 2012; Rivera-Ferre et al., 2016; Kremen and Merenlender, 2018; Kumar et al., 2019). Importantly, MSPRs take advantage of an "agromutualism" that builds symbiotic relationships between enterprises that lead to ecological and economic benefits. These production systems differ from industrial methods in focusing on biodiversity and mimicking natural ecological mechanisms (e.g., enhancing soil C sequestration through rotational grazing on rangelands and improving water and nutrient cycling through improved soil health), rather than specialization and intensification, albeit with considerably less overall production. However, few studies have explored such diversified livestock production systems in the United States, instead focusing mostly on very extensively (e.g., pastoralism) and intensively (e.g., feedlot) managed systems.

Livestock GHG footprints are calculated using life cycle assessment (LCA), which is an accounting approach that reports emissions resulting from all inputs and outputs of a production system on a per kg of CW of meat produced (kg CO_2-e kg CW^{-1}). LCA methodologies are often based on generally accepted Intergovernmental Panel on Climate Change (IPCC) calculations to estimate system GHG fluxes for processes such as enteric fermentation (enteric CH_4), manure management, and feed production. These calculations rely on metadata accumulated over time and often from scientific literature. While these accounting principles and approaches are useful, supported by scientific literature, and give broad-based estimations on the impact of a system, they often do not account for the complexity of on-farm management and commonly trade-off regional specificity for global or national generalizations. Further, very complex diversified livestock systems are scientifically underrepresented in the literature compared to simplified animal production systems, and scientific studies of extensive systems often reduce complexity to regimented management practices designed to reduce the very complexity that farmers and ranchers face daily (Teague et al., 2013).

Recent studies show that livestock-induced soil C changes can have large impacts on the GHG balance of these production systems (Beauchemin et al., 2011; Teague et al., 2016; Stanley et al., 2018). Grazing lands are one of the most significant reservoirs of soil organic carbon (SOC) (Conant et al., 2017), containing more than 30% of total global SOC (Follett et al., 2000; Lal, 2002; Schuman et al., 2002; Derner and Schuman, 2007). Livestock are the primary users of this extensive land base and are an important management tool for mediating increased soil C sequestration (Liebig et al., 2010; Teague et al., 2011; McSherry and Ritchie, 2013; Machmuller et al., 2015; Wang et al., 2015; Griscom et al., 2017). Although our knowledge of management impacts on soil C sequestration is expanding, LCAs consistently omit it from GHG analysis (Rotz et al., 2019). Soil C has been historically excluded from LCA for a number of reasons, including lack of data on soil C sequestration, to provide conservative GHG estimates (Rotz et al., 2019), and an assumption that soils, without additional carbon inputs, are in long-term equilibrium. However, globally grass and cropland soils are highly degraded and thus have a long-term sequestration potential (Cotrufo et al., 2019; Yang et al., 2019; Lavallee et al., 2020). Some studies have shown that when including soil C changes to LCA parameters, the overall CO_2-e can decrease considerably (Pelletier et al., 2010b; Stanley et al., 2018). Thus, changes in soil C could possibly be the greatest opportunity for reducing beef's carbon footprint.

In addition to GHG emissions and soil C sequestration, land use is a key evaluation metric of livestock systems. A growing global population and per-capita meat demand have increased the impetus for more efficient, and thus higher intensity, meat production. However, there are tradeoffs to extensive vs. intensive livestock production systems. For example, although overall land use is often lower in intensive systems, they often use a higher percentage of arable cropland suitable for other uses than extensive systems, which rely primarily on marginal lands. The MSPR examined in this study is an interesting case that is neither extensive nor intensive. Rather, it is a stacked-enterprise system in which animal stock density and rotational management are characteristically "intensive," but taking place on an "extensive," low-input, pasture-based landscape. We examined the total land-use tradeoffs for this system compared to conventional production systems for each animal species.

We hope to, in part, fill these gaps in the literature through this study in two ways: (1) by conducting a comparative analysis of an MSPR and a conventional US animal production system, thereby addressing the extensive–intensive dichotomy, and (2) using soil C sequestration and land-use trade-offs as additional comparative metrics in addition to GHG emissions.

METHODS

Site Description

The USDA-certified organic farm, White Oak Pastures (WOP), is in Clay County, GA, and spans 1,214 ha of land. The prevailing soil types are Faceville, Marlboro, and Greenville fine sandy loam. Average annual rain is 1,342 mm yr^{-1}, and mean high and low annual temperatures are 26 and 12°C, respectively (University of GA Environmental Monitoring Network 1957–2016).

Clay County, GA, was a historical scrubland/oak savanna, but agriculture has been and is currently the predominant land use (River Valley Regional Commission, 2014). Agriculture in the region most commonly employs a general crop rotation of cereal grains, corn, soybeans, cotton, and peanuts. Alternatively, WOP produces five red meat and five poultry species (including eggs)—totaling 142,935 animals annually—which are managed together on the same landscape. WOP acquires degraded croplands and converts them to MSPRs with a 3-year regeneration strategy. In years 1–3, cow–calf pairs are placed on the land at daily stock densities of 23–46 Mg ha^{-1} and fed hay throughout the winter (mean daily intake: 10 kg per animal). This supplies additional manure and organic matter (OM) from unconsumed hay to the soil, which is incorporated into the soil via animal impact. Bahiagrass (*Paspalum notatum*) is then aerial seeded and allowed to germinate. WOP is certified USDA Organic and thus does not apply chemical fertilizer or herbicides. However, residual chemicals from the transitioning degraded cropland pose a challenge to the farm. This transition process is illustrated in **Figure 1**.

A combination of fertility practices is used to provide additional nutrients to the soil, including 1-cm compost application (produced and sourced on farm), and the addition of pastured layers or broiler chickens supplemented with feed. As conditions improve and forage quantity increases (years 4 and beyond), compost application is ceased, and cattle are then grazed using holistic planned grazing methodology (Savory and Butterfield, 2016). Holistic planned grazing (HPG) is a grazing process that entails high animal stock densities, division of the land into temporary small subunits (paddocks), and carefully planned herd movements that act in concert with forage availability and seasonality. Land managers use HPG with varying degrees of paddock "rest and recovery" periods to meet goals such as land improvement, increased livestock productivity, and maintenance of seasonal wildlife habitats. The manager at WOP uses livestock to defoliate plants at high stock densities (25–50 Mg ha^{-1} daily) and then quickly moves them off the grazed paddock daily to allow the grazed plants to enter full recovery. All beef cattle are in one single herd as opposed to the conventional practice of grouping animals by cow–calf, yearlings, and bulls. The final MSPR includes cattle, small ruminants (sheep and goats), poultry species (laying hens, guinea fowl, turkeys, ducks, and geese), swine, and rabbits, which are moved together in various herd combinations across the farm.

Clovers, forbs, and nut (primarily pecan) bearing trees are also introduced into the farm landscape to increase native plant diversity and to replicate historic oak-savanna silvopastoral conditions. These silvopastoral landscapes are also used for on-farm hog production, which is one of several other enterprises including USDA-certified organic produce, agritourism, and an on-farm restaurant.

Life Cycle Assessment

All emissions were calculated using a deterministic environmental impact model created in MS Excel with standard IPCC GHG inventory methodologies (IPCC, 2006). Face-to-face meetings, farm records, and a semistructured in-person interview with the farmer yielded model inputs and outputs. Questions included farm size and management practices (both spatial and temporal), number of animal units for each livestock category, exogenous input amounts and sources, production indicators, packing plant throughput, and quantification of animals not grown on-farm, but harvested at the on-farm USDA-inspected abattoir. Subsequent composting methods and application data were also collected. All major GHGs [methane (CH_4), carbon dioxide (CO_2), and nitrous oxide (N_2O)] from direct and indirect sources were calculated using either Tier 1 (soil CH_4 and N_2O) or 2 (enteric CH_4, $Ym = 6.0$) (IPCC, 2006) methodologies. Other emissions including feed production and transport, on-farm and abattoir energy use, and compost production were calculated (EPA, 2020). Emissions from energy used for equipment manufacture were excluded based on their minor contribution ($< \sim 3\%$) (Lupo et al., 2013). All gasses were converted to CO_2 equivalents (CO_2-e) using current 100-year global warming potentials ($CO_2 = 1$, $CH_4 = 30.5$, $N_2O = 265$). We defined the functional unit for this model as kg of CO_2-e per kg of meat on a CW basis (kg CO_2-e kg CW^{-1}).

Soil Sampling and Analyses

To estimate soil C sequestration rate and changes in other soil health indicators, soils were sampled along a 20-year degraded cropland to MSPR chronosequence. The chronosequence consisted of a currently cultivated cropland (year 0) and fields converted from cropland to pasture 1, 3, 5, 8, 13, and 20 years ago. Year 0 represents land that has been continuously farmed for a minimum of a decade with rotations of corn (*Zea mays*), peanuts (*Arachis hypogaea*), wheat (*Triticum*), and soybeans (*Glycine max*). The land was routinely tilled, and chemical fertilizer and herbicides were applied annually. Initial land transformation began in year 1 when off-farm hay was applied across the degraded land and then fed to cattle grouped in relatively high stock densities (25–50 Mg ha^{-1} daily). This helps to both break up capped soil and more evenly disperse nutrients back into the soil from manure, urine, and residual hay. The following spring, grass was aerial seeded onto the land. In years 1–3, these fields are minimally grazed and receive 1 cm of compost ha^{-1} yr^{-1}. After year 3, exogenous inputs (hay and compost) were ceased, and the regeneration strategy shifted toward an animal-only approach, whereby animals were the primary mechanism of improving the land. This was done by increasing grazing exposure, introducing multiple livestock species including pastured poultry into the MSPR, and continually rotating animals across the land using HPG. Year 20 represents a grassland site that did not receive compost or poultry impact, only planned beef cattle grazing.

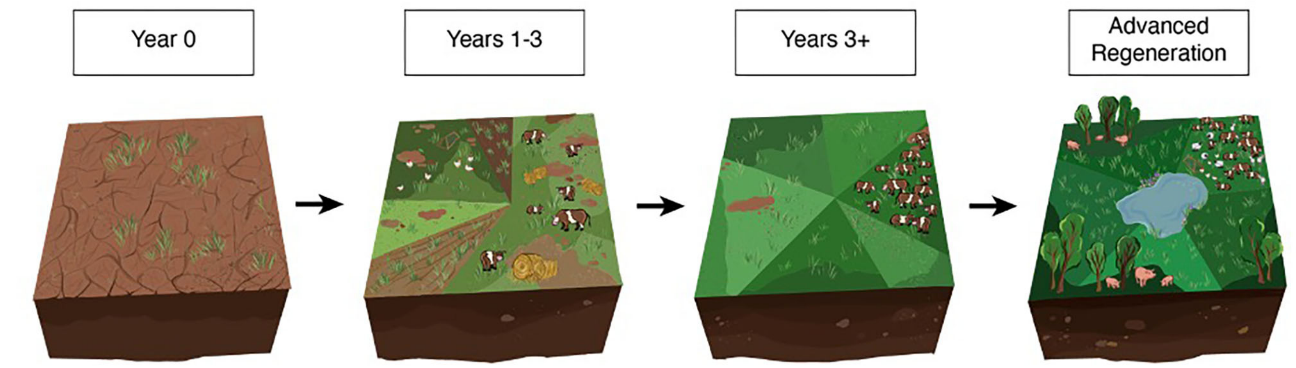

FIGURE 1 | The regeneration process employed by White Oak Pastures. Year 0: Degraded cropland is acquired; Years 1–3: Hay is fed to cattle grouped in moderate densities, compost is applied, grass is seeded, and cattle and poultry are grazed at low stock densities; Years 3+: Animal stock densities are increased (25 to 50 Mg ha^{-1} daily), and holistic planned grazing (HPG) is implemented, where animals are rotated often and land is rested between grazing events; Advanced Regeneration: Represents a regenerative landscape (no seedings, added hay or compost since year 3) including rotations of diverse animal species with improved soil health and water cycling.

In the spring of 2018, soil samples were collected from each field. Our objective was to find a site that had no animal impact for the year 0 chronosequence site. However, this location had received one instance of animal impact via hay feeding at the time of sampling. Therefore, we chose to resample at a newly acquired location that had received no animal impact and was more indicative of a true year 0. We then chose to use data from the newly acquired site as year 0, and the data from the originally sampled site as year 1. We set out to collect a minimum of four soil cores at intervals spaced 10 m apart along set transects. However, because of dry conditions, we were able to collect only one intact soil core from the year 0 site. Although there was very little difference in soil C stock between year 0 and year 1, we elected to include this in the model as a true year 0 site. We also experienced dry, difficult sampling conditions in year 13, enabling collection of two intact soil cores.

Each field was sampled within the dominant soil type according to Web Soil Survey, which was either a Faceville, Marlboro, or Greenville sandy loam in each location. At each sampling location, four 1-m soil cores were sampled (although soil conditions prevented all four samples at the 50- to 100-cm depth from being collected at some sites) using a 5.7-cm diameter Giddings probe (Windsor, CO) for soil C analysis, and eight 10-cm soil cores were collected using a 3.2-cm-diameter hand probe for soil health analysis. Meter-deep intact soil cores were separated into 0- to 10-, 10- to 30-, 30- to 50-, and 50- to 100-cm depths and sieved to 8 mm. Samples from each location were analyzed by depth for bulk density (20-g subsamples were weighed, dried at 105°C, and reweighed to determine the mass of dry soil per unit volume) and soil C [soils were ground on a ball mill and analyzed using a CN analyzer (LECO CHN-2000 autoanalyzer)], and later averaged to obtain field-level means. We used the minimum equivalent mass (Lee et al., 2009) to convert C concentrations to C stocks (Mg C ha^{-1}).

Hand cores (10-cm depth) were placed on ice the evening of collection and delivered overnight to Cornell University. Samples were analyzed by sampling location for the Comprehensive Assessment of Soil Health, which is a suite of soil tests including texture by hydrometer, pH, wet aggregate stability, permanganate oxidizable (active) C (POXC), microbial respiration via 4-day incubation, autoclave citrate-extractable (ACE) soil protein, and available water-holding capacity (AWC); (Moebius-Clune et al., 2016). Soil health analyses were not performed on the year 0 site.

Soil clay contents ranged from 5 to 20%. Least-squares means of equivalent mass carbon stocks, wet aggregate stability, active C, ACE soil protein, and microbial respiration were calculated to account for clay content as a covariate where clay was significant ($\alpha = 0.05$). Clay was not a significant covariate for water-holding capacity. Soil C sequestration rate was calculated using linear regression on least-squares means of carbon stocks. All statistical analyses were completed using RStudio Team 2019 with the package lsmeans (Boston, MA).

Comparison to COM Animal Production

To understand the relative emissions and land use of the MSPR examined in this analysis, we compared beef, pork, and poultry results of this LCA to COM agricultural production of beef (Rotz et al., 2019), pork, and poultry (Gerber et al., 2013).

We retrospectively determined land needed to grow feed (for pork, poultry, and feedlot beef) or graze and grass-finish beef cattle based on the CW output of the WOP MSPR and the Georgia crop and hay production averages (USDA NASS, 2018). For the non-ruminant diets, we used an 80% corn, 20% soybean meal diet per COM standard production. Importantly, pork and poultry finishing diets are more variable than our standard ration and can include dried distiller's grains and synthetic amino acids among other feedstuffs. Because of the difficulty of accounting for these differences across a large geographical context, we chose a standard baseline for diet comparison.

For the beef cattle land comparison, we first used the number of cow–calf pairs necessary to produce the annual beef output (268,777 kg yr^{-1}) at WOP for 1 year (n = 992). Stocking

TABLE 1 | Overall market animal production and carcass output.

Animal	*N*	Mean carcass weight (kg)	Total carcass weight (kg)	% of farm production	Productivity (kg ha^{-1})
Cattle	990	271	268,777	42	221
Swine	597	109	65,049	10	54
All Poultry	141,348	2	275,472	43	227
Eggs*	–	–	22,106	3.5	18
Sheep	267	20	11,481	0.8	4
Goats	82	14	2,542	0.2	1
Rabbits	88	2	140	<0.01	0.1
Total	143,372	–	645,567	100	525

**A 49.61 g egg^{-1} was used as a conversion factor.*

rate for the system was calculated based on existing Georgia recommendations (0.81 ha per cow; D. Hancock, personal communication, 2019). Total land needed for grazing and hay was calculated at 0.66 ha per grass-finished steer in the MSPR. Because beef grown in feedlots are considerably heavier and require less land for feed, we used beef CWs and land use data from Stanley et al. (2018) to adjust cows and land needed for feed production. We also calculated the additional hay needed for supplementation in the COM system using the Stanley et al. (2018) feedlot diets and then divided by the mean hay production per acre in Georgia (USDA NASS, 2018).

RESULTS

Meat Production and Emissions

Overall animal productivity and GHG emissions of the MSPR system are reported in **Tables 1**, **2**. Beef, poultry, and swine comprise 96% of the overall production on a CW basis. Each year, the MSPR at WOP (including all animals) harvests 143,372 animals, totaling 637,910 kg of total CW. Summing all animals in the MSPR, the farm produces 525 kg CW ha^{-1}. Thus, the overall productivity of the total MSPR is substantially higher when compared to grass-finished beef only (221 kg CW ha^{-1}).

While beef cattle comprise 42% of overall CW production, their emission on a CO_2-e kg CW basis is higher than in other systems. Cattle contribute 33.55 kg CO_2-e kg CW^{-1}, whereas swine and all poultry contribute 15.15 and 9.69 kg CO_2-e kg CW^{-1}, respectively. The beef cattle contribute 68% of total farm emissions, totaling 9,018,105 kg CO_2-e. Poultry was the second greatest contributor to overall emissions at 20%, while contributing 43% to the overall farm production. Emissions from swine production align evenly with productivity, totaling 7% of the farm GHG footprint and 10% of farm production. Eggs and all other species, primarily sheep and goats, contribute <1% of the overall farm GHG footprint.

Total farm emissions categorized by animal production, feed, land, and slaughter vary by species. Beef cattle account for about 95% of animal and 52% of land emissions. Poultry production, the second largest contributor to on-farm productivity, is responsible for 63% of total feed emissions and 68% of total slaughter emissions. The MSPR total carbon footprint was 13,225,972 kg CO_2-e, with animals as the greatest emissions category (58%), followed by land (20%) and feed (19%).

Soil Parameters

We observed substantial increases across a suite of soil health indicators over the 20-year chronosequence (**Table 3**). Wet aggregate stability increased from 0 to 53% over the chronosequence, with a 5-fold increase between years 3 and 20 ($p = 0.02$). Microbial respiration increased from 0 to 0.56 mg CO_2 day^{-1} by year 3 and 1.16 mg CO_2 day^{-1} by year 20 ($p = 0.03$), whereas POXC increased 10-fold across the chronosequence ($p < 0.01$). ACE protein, which estimates the amount of mineralizable organic *N*, increased from 0 to 23 mg g^{-1} over the chronosequence, with a 4-fold increase from year 3 to year 20 ($p < 0.01$). There was no observable increase in AWC.

Soil Carbon Sequestration

In addition to soil health indicators, we also measured SOC stock from year 0, prior to MSPR initiation, to year 20. Initially, SOC stocks were ~10 Mg C ha^{-1} and increased to 50 Mg C ha^{-1} in year 20, a 5-fold increase across 20 years of management. The highest measured soil C stock was in year 13, measuring 65 Mg C ha^{-1}. Importantly, the year 20 site received no compost applications or poultry disturbance and reflected only the impact of grazing and perennial conversion from annual cropland. Soil carbon stocks at equivalent minimum mass increased linearly at a rate of 2.29 Mg C ha^{-1} yr^{-1} ($p = 0.04$, $R^2 = 0.60$; **Figure 2**). Field-level standard errors for each soil depth is given in Supplemental Info (**Supplementary Table 1**). Soil OM (SOM; **Table 3**) concentration reflected comparable increases at the surface from 1 to 5% in years 0 and 20, respectively. Overall, the transition from a conventional row crop model to MSPR improved soil physical and biological attributes and consequently significantly improved soil C stocks.

The overall MSPR beef footprint totaled 33.55 kg CO_2-e kg CW^{-1} and was 36.5% greater compared to the COM beef GHG footprint (21.3 kg CO_2-e kg CW^{-1}). The greatest emission disparity between production methods was observed in pork, where MSPR pork was 3-fold greater compared to a COM production footprint (15.15 vs. 4.6 kg CO_2-e kg CW^{-1} for MSPR and COM pork, respectively). The MSPR poultry was over twice that of COM poultry but in each production system represented the least emission intensity of all species analyzed in the model (**Figure 3**).

We next totaled all emissions in each species production category and present the overall net emission for the MSPR as compared to COM. The overall MSPR carbon footprint for poultry, pork, and beef produced on farm totaled 20.8 kg CO_2-e kg CW^{-1}, 44% greater than COM, which totaled 11.9 kg CO_2-e kg CW^{-1} for all livestock species produced.

We integrated measured soil C sequestration (**Figure 2**) into the net emissions from MSPR and COM. We used mean soil C sequestration of 2.29 Mg C ha^{-1} yr^{-1} for MSPR and considered COM to be in a soil C dynamic equilibrium. Incorporation of soil C sequestration as a GHG sink in the MSPR system reduced emissions from 20.8 to 4.1 kg CO_2-e kg CW^{-1} representing an

TABLE 2 | Overall farm emissions by animal species.

Animal	Animal emission (kg CO_2-e)	Feed emission (kg CO_2-e)	Land emission (kg CO_2-e)	Slaughter emission (kg CO_2-e)	Total emission (CO_2-e kg CW^{-1})	Carbon footprint (kg CO_2-e)
Cattle	7,310,521	262,571	1,399,275	45,738	33.55	9,018,105
Swine	45,750	683,675	230,106	26,140	15.15	985,671
All Poultry	5,950	1,618,693	849,684	194,481	9.69	2,668,808
Eggs*	–	848	428	10,456	0.53	11,732
Sheep	213,500	636	141,047	7,842	69.65	363,025
Goats	106,750	212	68,762	2,614	154.54	178,338
Rabbits	–	21	11	261	2.09	293
Total	7,682,471	2,566,656	2,689,313	287,532	285.2	13,225,972

**Indicates A 49.61 g egg-1 was used as a conversion factor.*

TABLE 3 | Soil indicators.

	Year							Equation	*p*-value	R^2
	0	1	3	5	8	13	20			
Water-stable aggregation (%)	–	0*	11	7	47	47	53	$y = 2.9 + 2.9x$	0.02	0.76
Microbial respiration (mg CO_2 day^{-1})	–	0*	0.56	0.54	0.94	1.16	1.16	$y = 0.07 + 0.01x$	0.03	0.75
Active C (ppm)	–	80	325	380	522	884	844	$y = 167 + 41x$	< 0.01	0.85
Water holding capacity (g water g $soil^{-1}$)	–	0.19	0.20	0.15	0.15	0.28	0.21	–	0.44	–
ACE soil protein (mg g^{-1})	–	0*	5	3	15	22	23	$y = 0.2 + 1.3x$	< 0.01	0.86
Soil organic matter (%)	–	1.1	2.0	2.8	2.6	3.5	5.2	$y = 1.1 + 0.22x$	< 0.01	0.93

**Indicates Negative least-squared means were adjusted to 0.*

~5-fold drop in emission intensity. The resulting 4.1 kg CO_2-e kg CW^{-1} of net MSPR emissions then become 7.8 kg CO_2-e kg CW^{-1} lower than COM. These results point to the dramatic changes that can occur in animal protein LCA when accounting for changes in soil C stocks over time. Importantly, if we were to attribute the soil C sequestration across the chronosequence to only cattle, MSPR beef produced in this system would be a net sink of −4.4 kg CO_2-e kg CW^{-1} annually.

Finally, in **Figure 4**, we calculated the land required to produce all proteins in the COM and MSPR models. The required land to graze beef and supply feed for each species (poultry, pork, and beef) is considerably greater for the MSPR system than COM. The MSPR required 2.5 times more land when compared to COM to produce the same amount of CW. Thus, while our model indicates that MSPR can simultaneously produce protein while increasing soil health indicators and soil C stock, a considerably greater land area is needed when compared to COM.

DISCUSSION

Meat Production and Emissions

We report animal production and resulting emission metrics of an MSPR production system whose owner's primary goal is to farm regeneratively. Gosnell et al. (2019) define regenerative agriculture as an "alternative" form of food and fiber production oriented toward enhancing resilience and ecological health.

With respect to on-farm production, 42% of the overall farm CW was produced from cattle, where the mean grass-finished beef CW was 271 kg hd^{-1}. Most beef LCAs measure productivity on an animal performance basis vs. actually indicating a CW (Pelletier et al., 2010b; Lupo et al., 2013) or determine the amount of animals necessary to produce a certain amount of beef (Capper, 2012). However, we were only able to collect CWs from the packing facility, making comparisons back to a live weight productivity difficult. However, our reported MSPR finished beef CW closely aligns with Stanley et al. (2018), who reported a 280 kg hd^{-1} in an adaptive multipaddock (AMP) grazing system—a similar management strategy, but using beef cattle only. Importantly, these results show that grass-finished CWs are ~33% lower than existing grain-finishing beef LCAs (Pelletier et al., 2010b; Lupo et al., 2013; Stanley et al., 2018).

The interview with the owner of WOP indicated that the average age of slaughtered beef cattle was between 20 and 22 months of age (data not shown). This is considerably less than a recent study by Heflin et al. (2019), who modeled a grass finishing system in the lower Southern Plains and indicated a time to slaughter of 30 months with an average CW 40 kg greater than our MSPR system. However, that the WOP MSPR system reached similar CWs 10 months sooner, comparatively, than other grass-finished beef systems is an important improvement

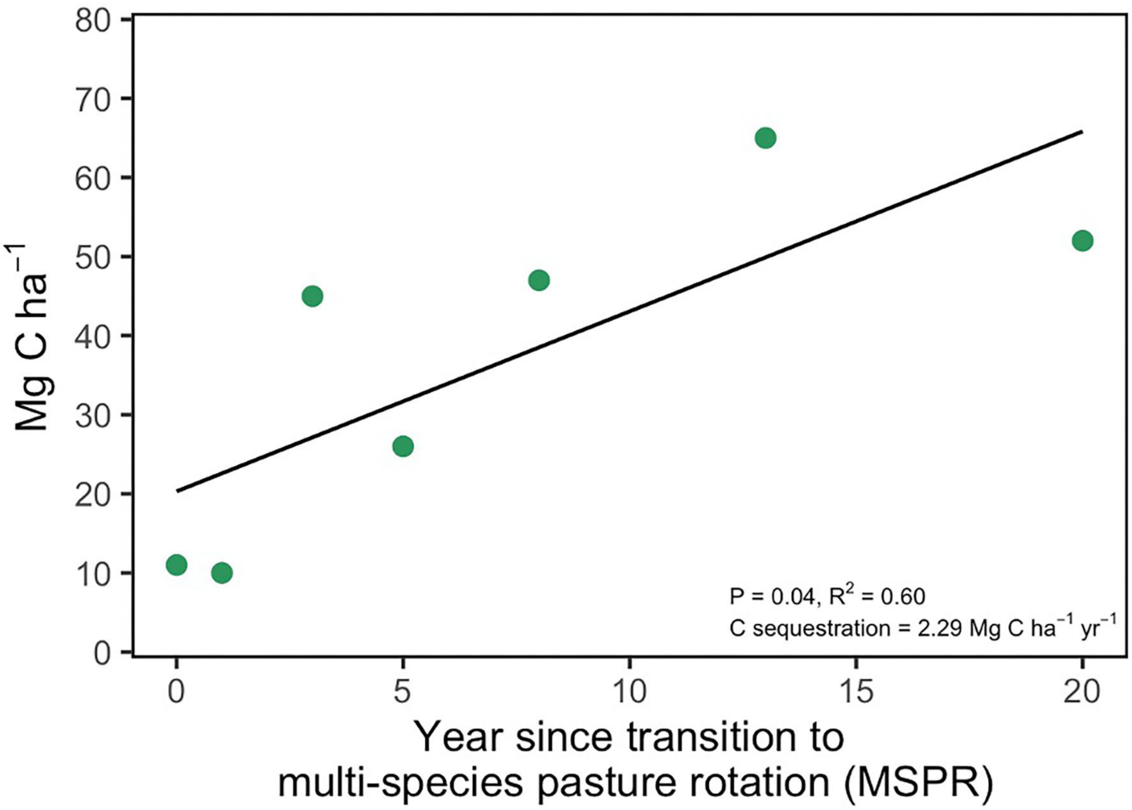

FIGURE 2 | Soil carbon stock at equivalent soil mass of 9,900 Mg/ha. Points represent least-squared means adjusted for soil clay content generated from 4 in-field replicate soil samples.

that both reduced GHG emissions over a shorter lifetime while simultaneously producing other food animal proteins.

Life cycle emissions for beef cattle in the MSPR were 33.55 kg CO_2-e kg CW^{-1}. This is 30% higher than the most current models evaluating business-as-usual beef cattle production systems (with grain finishing) in the United States (Rotz et al., 2019). This is due to the widely accepted fact that grass-finished cattle have a higher enteric CH_4 footprint than those finished on grain because of differences in feed digestibility. In our study, 81% of beef cattle footprint is attributed to enteric CH_4. However, the proportional trade-offs of specific GHGs in each production system are also important to consider. For example, while enteric CH_4 in the MSPR was proportionately high, CH_4 is a short-lived climate pollutant where C is contained in existing biomass and cycled quickly through the atmosphere, lasting on average 10 years before being oxidized (Lynch et al., 2020; Thompson, 2020). Alternatively, although overall emissions in grain-finished beef systems are lower, the portion of fossil-fuel derived emissions is higher, including CO_2 and N_2O (lasting 1,000 and 100 years on average, respectively) arising from fertilizer production and application for fodder crops and fossil fuel–derived energy use (Picasso et al., 2014). Pierrehumbert and Eshel (2015) also report less overall climate impact of pastured-beef systems with no or minimal fertilization, despite greater enteric CH_4 emissions compared to feedlot systems. Recent IPCC estimates show that global CO_2 and N_2O concentrations have been rising more rapidly than CH_4, which has been plateauing (IPCC, 2014). The shorter life span of CH_4 in the atmosphere, however, also makes it an attractive target for near-term GHG mitigation.

The beef cattle in the MSPR represent the largest emission source in the production system for three reasons: they make up the largest group of animals in the system, they produce high CWs, and they contribute more CO_2-e per kg of CW compared with other livestock categories. Studies have demonstrated that intensive feeding and management of beef cattle in grain-fed system result in higher CW and lowest overall CO_2-e kg^{-1} emission (Heflin et al., 2019; Kamilaris et al., 2020). However, they generally lack a systems perspective to net GHG fluxes, thereby omitting soil carbon sequestration, which has great potential to mitigate GHG emissions for grass-fed systems (Liebig et al., 2010; Pelletier et al., 2010a). Inclusion of field-measured soil C sequestration (as a CO_2-e sink) has been shown to completely mitigate the C footprint of intensively managed grass-finished cattle in some specific cases (Stanley et al., 2018) and drastically lower (but not neutralize it) in others (Machmuller et al., 2015; Wang et al., 2015; Hillenbrand et al., 2019). Although few exist, these cases present a unique nexus that (a) alleviates the pressure

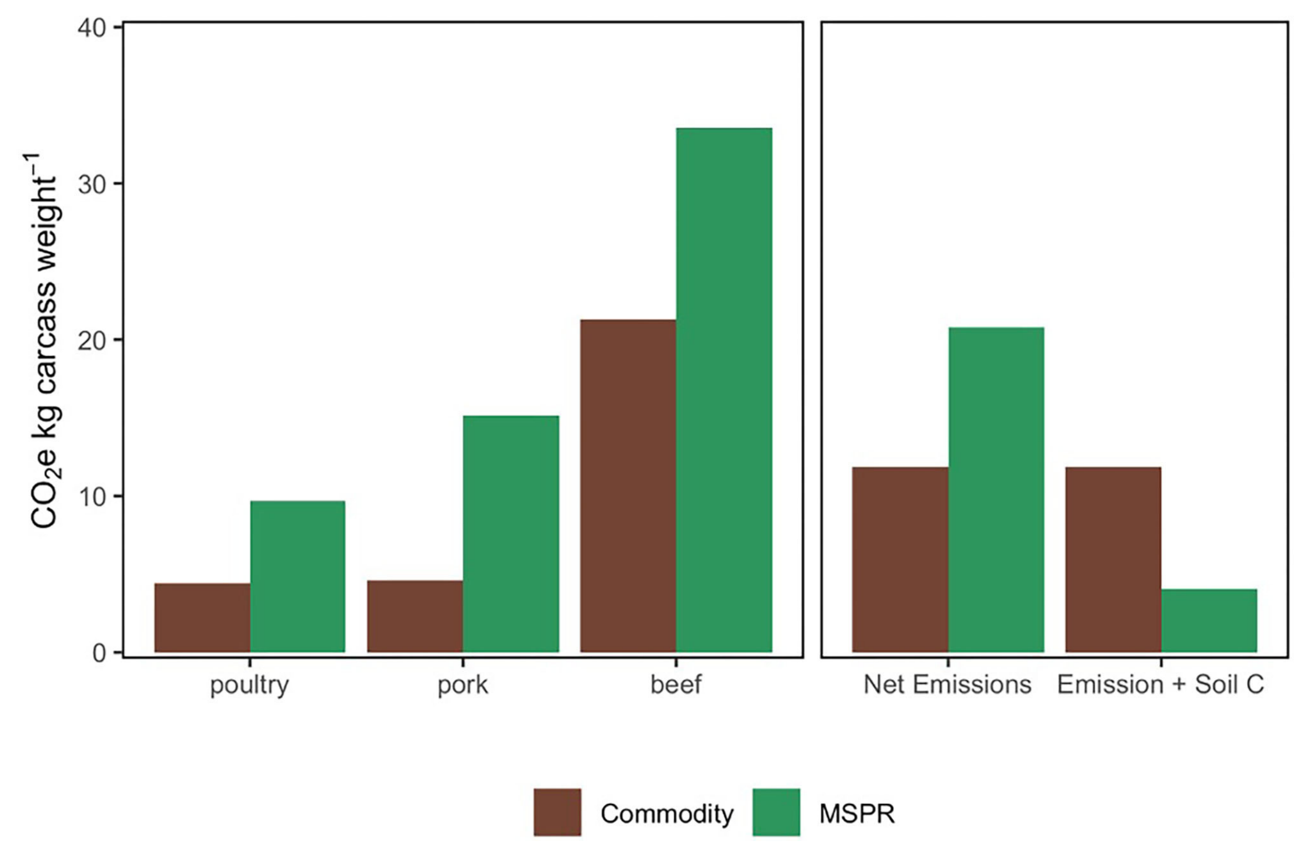

FIGURE 3 | Comparison of a Commodity and Multi-Species Pasture Rotation (MSPR) CO_2-e on a kg CW basis by specie (left) and then aggregated for the mean overall net farm emission with and without soil C sequestration (right).

to use input and fossil-fuel intensive production systems to maximize cattle gains and lower per-kg CO_2-e and (b) maximizes biological ecosystem functions to reduce net GHG emissions while maintaining productivity.

Less dichotomy exists in comparing the MSPR pork and poultry outputs to generally accepted COM pork and poultry outputs. More difficulty arises when comparing pastured poultry models in the literature. For pastured broiler only models, recommendations range from 500 to as much as 1,000 broilers 0.40 ha^{-1}, with almost all nutrients coming from cropland derived feed instead of pasture (Meeh et al., 2014). At WOP, 445,182 eggs were produced using the MSPR, weighing an average of 49.6 g (data not shown) totaling 22,106 kg of eggs.

Although poultry production, including eggs, represents 46.5% of the total carcass weight in this system, they contribute only 20% of total carbon footprint. Feed production for poultry was the largest impact category (Tongpool et al., 2012; MacLeod et al., 2013), mainly comprising energy- and protein-rich ingredients (more than 60%). In our system, emissions from feed totaled 60.6% of the total poultry carbon footprint. For eggs, however, emissions associated with slaughter (processing and transport) outpaced those from feed production, contributing 89 and 7%, respectively. Poultry-meat produces a greater emissions footprint than eggs partly because rations for broiler chickens, on average, include a higher share of soybean products, which are sourced from areas where land-use change is taking place (MacLeod et al., 2013).

Feed production was proportionally the greatest emission source for both poultry and swine, whose diets consisted of primarily corn (80%) and soybean (20%) products. These results are generally consistent across the literature, although COM swine production systems often have larger GHG footprints associated with facilities (Pelletier et al., 2010a; Eshel et al., 2014; Kebreab et al., 2016; Tallaksen et al., 2020).

Soil Parameters

We observed large increases across the suite of soil health indicators examined in the MSPR chronosequence, indicating improvements in soil function as a result of perennial establishment and regenerative MSPR management at WOP. SOM is related to nearly every soil-related ecosystem service including water and nutrient cycling, habitat for biodiversity, and erosion control (Wall et al., 2012). Observed increases in SOM were likely mediated by greater aggregation, as aggregation is one of the primary mechanisms of SOM stabilization via physical protection and microbial habitat (Tisdall and Oades, 1982; Gupta and Germida, 2015), and we

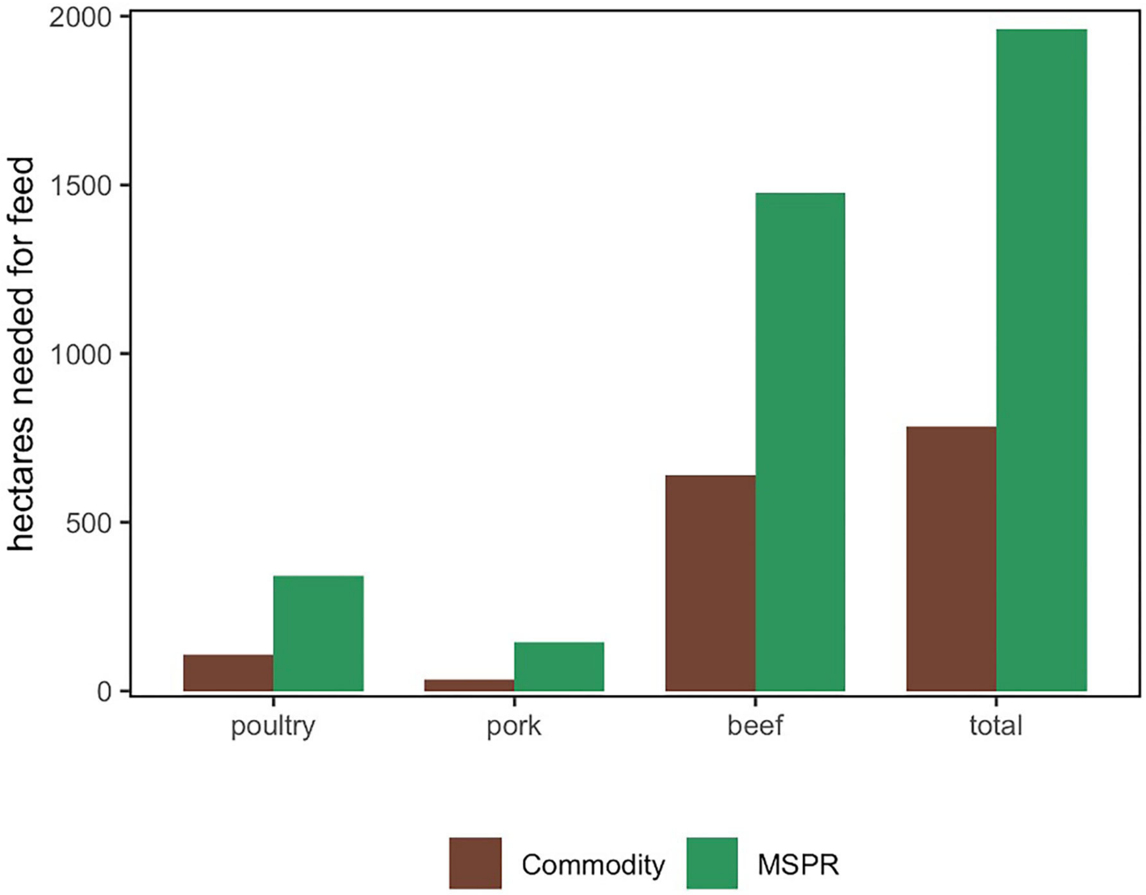

FIGURE 4 | Comparison of a Commodity and Multi-Species Pasture Rotation (MSPR) for land needed to graze beef and supply feed for poultry (275,242 kg), pork (65,049 kg) and beef (268,777 kg) similar to outputs of monitored MSPR farm.

observed a 5-fold increase in both SOM and wet aggregate stability over the chronosequence. Additionally, higher wet aggregate stability indicates an improved ability to maintain soil structural integrity in the face of events such as extreme precipitation, leading to greater water infiltration and reduced erosion (Franzluebbers, 2002). We expected these increases in aggregation and SOM to translate to greater AWC. However, we did not observe an increase in AWC across the chronosequence, further adding to literature suggesting the link between SOM and AWC is not as pronounced as previously thought (Minasny and Mcbratney, 2017).

Rapid responses in microbial respiration (2-fold increase), ACE protein (5-fold increase), and active C (10-fold increase) during the chronosequence indicate the enhancement of soil C and N cycling with MSPR. Microbial activity in annual cropland soils is often limited by C availability (Schimel, 1986), and the increase in active C and microbial respiration observed within the first several years of the chronosequence reflects the alleviation of C limitation via greater C inputs in the perennial MSPR system. Additionally, increased ACE protein reflects a growing pool of readily mineralizable organic N as a result of greater plant inputs, animal manures, and additions of other organic materials such as compost. Large reservoirs of organic N coupled with an active microbial community are critical for efficiently meeting plant N needs in agroecosystems, as organic N released slowly through mineralization is more efficiently utilized than pulse additions of inorganic N via synthetic fertilizer (Gardner and Drinkwater, 2009). Together, the improvements across the suite of soil health properties measured here indicate that the building blocks for a growing microbial community in soils under MSPR management were met, ultimately contributing to the increased soil C pool and more efficient N cycling.

Soil Carbon Sequestration

Over the 20-year chronosequence, the MSPR system at WOP sequestered an average of 2.29 Mg C ha^{-1} yr^{-1} (**Figure 2**). However, the oldest location in the chronosequence received grazing only rather than all management practices applied to younger sites (e.g., compost). Thus, the average C sequestration rate may have been higher if this site were more representative of the entire chronosequence.

Compared to other literature, our estimated soil C sequestration rate lies toward the higher end—both above (Wang et al., 2015; Conant et al., 2017) and below (Stanley et al., 2018) reported values from others. It is important to note that each system is unique and that resulting soil C sequestration with the application of a management system like the MSPR employed by WOP will differ based on land use history (e.g., conversion from cropland or overgrazed pasture), time since adoption (discussed more in detail below), and changing weather conditions (e.g., drought) among other factors. For example, Stanley et al. (2018) reported average SOC sequestration after five-year conversion from continuous haying and grazing to AMP grazing (analogous to the HPG system used at WOP, but with cattle grazing only). Our system reflects a longer transition, over 20 years, which may explain the lower average sequestration rate, comparatively. Alternatively, the MSPR system in this study was employed after conversion from degraded cropland, was combined with compost application, and was conducted in a non-arid ecosystem. These practices explain the higher relative sequestration rates compared to some others (Wang et al., 2015; Conant et al., 2017).

In this study, SOC sequestration is estimated via a space-for-time substitution rather than directly measuring SOC change over time. While it has limitations, without baseline SOC data for each field, the chronosequence approach is the best alternative for measuring temporal SOC changes with differing management when compared within soil types and has been used widely throughout the ecological sciences (Walker et al., 2010).

Our estimated SOC sequestration rate (2.29 Mg C ha^{-1} yr^{-1}) is an average over 20 years. To better assess temporal dynamics of SOC sequestration, we can also analyze how the sequestration rate changes over time. It is commonly assumed that there is a finite capacity of soils to store C and that sequestration rates will slow over time as soils come closer to a "saturation" point. Our results indicate a sharp increase in SOC stocks from years 1 to 3, with slower increases from years 5 to 13. Soil C stock at the oldest MSPR site (at 20 years) indicated a slightly lower soil C stock than the 13-year site, which may suggest a peak soil C accumulation at ~13 years since establishment of the MSPR. However, we do not believe this is indicative of a declining sequestration rate due to proximity to saturation. Rather, we posit that this is an artifact of management differences between the sites, as the 20-year site received grazing only, rather than the entire suite of management interventions (i.e., compost, poultry manure) that were applied to all other MSPR sites across the farm.

Further, carbon stock alone does not allow us to make conclusions about soil C storage capacity, which can be better informed by the relative distribution of soil C between mineral-associated OM (MAOM) and particulate OM (POM) (Cotrufo et al., 2019). These authors also showed that soil C in grasslands is contained mostly in the MAOM fraction, which is often microbially processed and high in N, making it highly persistent and stable in soils (Lavallee et al., 2020). MAOM also saturates in soils because of the finite availability of mineral surfaces to sorb OM. However, the authors also suggest that POM can be indefinitely accrued in soils irrespective of MAOM saturation and, further, that most grassland soils are unlikely to be "saturated" with respect to MAOM-C. We did not fractionate SOM into MAOM and POM pools in this analysis; however, given the large increases in soil aggregation, it is likely that POM is increasing with MSPR adoption in this system, because POM persistence is largely dependent on aggregation. Further, results presented by Cotrufo et al. (2019) and others (West and Six, 2007; Jagadamma et al., 2014; Nicoloso et al., 2018) lead us to question the certainty of soil C saturation in grassland soils.

The results of other soil parameters in addition to the SOC sequestration in this study allow us to infer management drivers as well as functional changes in the soil. In general, soil C stock can be increased by (a) increasing C inputs to the soil or (b) reducing the relative rate of loss (as CO_2) via decomposition or stabilization, which reduces emissions to the atmosphere that would otherwise occur (Conant et al., 2017). In our MSPR system, C inputs were increased in three ways, by the increase of native and perennial plant diversity under MSPR as clovers, forbs, and nut bearing trees; by the addition of compost and manure from livestock; and via exogeneous poultry feed. Further, the short-duration, high-intensity grazing (otherwise termed HPG; as well as rotation with other animals) used in this system has been shown to maximize plant residue left in the pasture and improve below-ground soil C allocation via plant roots (Teague et al., 2011).

Soil C sequestration is a vital ecosystem function to mitigate climate change. Here, we demonstrate that land restoration using MSPR is an important regenerative agricultural tool to support this effort.

Net GHG Footprint and Land Use

While the GHG footprint of the MSPR is considerably greater than corresponding COM estimates (**Figure 3**), the reverse is true after incorporation of the on-farm soil C sequestration as a GHG sink. When considering only standard LCA boundaries on a kg CO_2-e kg CW^{-1}, animals in the COM system are more efficient—gaining more weight in less time and thus contributing 43% fewer GHGs (MSPR: 20.8 kg CO_2-e kg CW^{-1} vs. COM: 11.9 kg CO_2-e kg CW^{-1}). However, our on-farm analysis of soil C accrual at WOP revealed a sequestration rate of 2.29 Mg C ha^{-1} yr^{-1}, on average, over 20 years of MSPR adoption. After incorporating this into our LCA boundaries, this reduced the GHG footprint of the MSPR system by 80% (from 20.8 to 4.1 kg CO_2-e kg CW^{-1}), ultimately finishing at 66% lower than comparative COM production.

However, when comparing required land between the two food production systems, MSPR required 2.5 times more land than COM production. Thus, while our model indicates that MSPR can simultaneously produce protein while regenerating land and can contribute other ecosystem services, a considerably greater land area is needed when compared to COM. However, MSPR is well-suited for more marginal lands while requiring fewer exogenous inputs such as feed stocks. Consequently, increased implementation of MSPR on marginal lands, including degraded cropland, could free up more productive land for production of higher value and more nutrient dense crops. Theoretically, this trade-off in land use could also, to an extent, partially mitigate the greater land area needed for MSPR livestock production vs. COM.

Our results present an important yet paradoxical conclusion on land and food production balance in the face of climate change. Should society prioritize an input-intensive, COM system that produces more food from a smaller, yet degrading land base with externalized societal costs? Or, alternatively, should systems such as MSPR that produce less food on a larger, but more ecologically functional and diverse landscape be more highly valued? These complexities must be considered in the global debate of agricultural practice and land, as land-management strategies that prioritize soil health to regenerate agroecosystems are increasingly needed to meet the needs of a growing population.

Regardless of the starting point on any farm or ranch, we hope to emphasize the importance of diversifying as a process to provide and enhance ecosystem services that are becoming increasingly important in addition to food production, such as resiliency and adaptive capacity to extreme weather, nutrient cycling, water retention, and climate change mitigation. Teague et al. (2016) provides a cadre of tools to improve ecosystem services in both cropping and grazing systems, which can be implemented by farms and ranches of all production types. For example, reducing and eliminating tillage, maintaining soil cover with cover crops, increasing biodiversity and nutrient cycling via integrated crop-livestock systems, and maximizing rest periods in grazing-only systems are all tangible actions for regenerating agroecosystems (Brewer and Gaudin, 2020). The WOP MSPR examined in this study exemplifies a farm using a highly evolved production system at the far end of the diversification spectrum.

Lastly, although we highlight the need for more research on diversified livestock production systems, the benefits of diversified agroecological production systems for the provisioning of ecosystem services are well-established. The results of this research point us to other important and timely questions of farmer practice adoption, payment for ecosystem services (PES), and other incentivization mechanisms (Gosnell et al., 2020). Currently, underdeveloped PES and carbon markets present major challenges to the adoption of regenerative agricultural practices in the United States. As it becomes increasingly clear that deployment of carbon capture and storage (CCS) technologies (potentially via PES), in addition to GHG mitigation measures, will be necessary to meeting our climate goals, regenerative agriculture is arising as a practice with clear CCS potential. Thus, we recommend that federal monetization strategies be developed to increase adoption of regenerative agricultural practices simultaneously to ongoing research, rather than sequentially.

CONCLUSIONS AND IMPLICATIONS

Diversified livestock production systems are highly underrepresented in scientific literature, despite evidence of widespread global use (Robinson et al., 2011). We present, to our knowledge, the most robust analysis of an MSPR system in the scientific literature comprising beef, pork, and poultry. In addition to business-as-usual LCA methodology, we also incorporated measured on-farm soil health parameters, including soil C sequestration. Most often, animal production LCAs are generated for one species of livestock and likewise are analyzed with broad-based formulas generated from empirical models across large geographical contexts. Our study provides unique model parameters for an actual farm in the United States, populated with on-farm generated vs. literature derived production metrics with actual soil C and subsequent soil health data across time and space.

This study provides interesting new context to current agricultural debates, including those surrounding land-sharing vs. land-sparing, sustainable intensification, and the use of regenerative agriculture to sequester soil C. WOP is a USDA Organic MSPR employing principles of regenerative agriculture through holistic management. As defined by Gosnell et al. (2019), regenerative agriculture "focuses on enhancing and restoring holistic, regenerative, resilient systems supported by functional ecosystem processes and healthy, organic soils capable of producing a full suite of ecosystem services, among them soil carbon sequestration and improved soil water retention." Our results indicate that this system does, in fact, regenerate ecological function including soil health, resilience, GHG mitigation, and biodiversity. It accomplishes this by managing animals intensively (not to be confused with input-intensity) in an otherwise extensive system (no chemical fertilizers, biocides, tillage, etc.). When comparing this approach to a business-as-usual COM-based approach, and including soil C sequestration, the overall emission footprint of the regenerative agriculture approach was 3-fold less. Adoption of practices such as the MSPR investigated in this study should be incentivized at a greater scale while concomitantly investigating technologies and approaches that can reduce the necessary land needed to produce the regenerative proteins.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

JR led overall project management, data analysis, and writing. PS contributed in project conception, data management, and writing. IM oversaw dataset management for production and emissions of all livestock in the White Oak Pastures production system and also assisted with writing. MT oversaw life cycle assessment model development, and assisted with writing. SR oversaw all soil data collection, laboratory analysis, and statistical analysis of data and assisted with writing. DH assisted with chronsequence development, provided overall guidance on the farm site, and assisted with writing. AG developed and created the figures. MR aided in project conception and assisted with writing. All authors contributed to the article and approved the submitted version.

FUNDING

General Mills Inc funded the project in entirety.

ACKNOWLEDGMENTS

The authors would like to thank the WOP Farm: Will Harris, Jenni Harris and Jodi Harris Benoit and the all staff who provided information for this study. Secondly Jeff Hanratty and Jerry

Lynch with General Mills Inc. were instrumental in funding this project. Equally supportive, Jon Dettling from Quantis provided important input and guidance for the project. Finally, Taylor Collins and Katie Forrest from Epic Provisions were instrumental in advocating and supporting this project.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2020.544984/full#supplementary-material

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Conflict of Interest: The authors declare receiving funding from General Mills Inc. The funders had the following involvement in the study: funding for the project design, soil and data collection, soil analysis and overall life cycle assessment.

This project began under the auspices of collecting data solely for the internal use of General Mills Inc. After data collection and analysis, General Mills Inc. gave the authors permission to publish the project results in manuscript form.

SR was an employee of General Mills Inc. MT was an employee of Quantis International at the time of study completion.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Sustainable Food Systems

REVIEW
published: 19 March 2021
doi: 10.3389/fsufs.2021.566338

Non-fiber Carbohydrates in Forages and Their Influence on Beef Production Systems

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Forages can provide a complete diet for ruminant animals, increasing the sustainability of beef production systems worldwide while reducing competition with humans for agricultural land or grain crops. Much of the emphasis on the nutritional characteristics of forages has been on the fiber, sugars, starch, and protein they supply to the rumen, despite the fact that other less-explored constituents, i.e., neutral detergent soluble fiber (NDSF) and other non-structural or non-fiber carbohydrates (**NFC**) also play a key role in the nutrition of ruminants. This paper explores the less investigated potential of temperate legumes to accumulate levels of NFC comparable to corn silage or beet pulp in cool, dry environments under irrigation, and its implications for forage-based beef production systems. We conclude that genetic or managerial interventions (i.e., breeding programs, defoliation frequency) or ecological conditions (i.e., climate, elevation) that increase concentrations of NFC in legumes can enhance beef production, meat quality, and the efficiency of nitrogen utilization by ruminants while reducing environmental impacts.

Keywords: neutral detergent soluble fiber, legumes, carbohydrates, beef production systems, cattle

OPEN ACCESS

Edited by:
Urs Feller,
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René Baumont,
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Specialty section:
This article was submitted to Agroecology and Ecosystem Services, a section of the journal Frontiers in Sustainable Food Systems

Received: 27 May 2020
Accepted: 19 February 2021
Published: 19 March 2021

Citation:
Villalba JJ, Ates S and MacAdam JW (2021) Non-fiber Carbohydrates in Forages and Their Influence on Beef Production Systems. Front. Sustain. Food Syst. 5:566338. doi: 10.3389/fsufs.2021.566338

INTRODUCTION

The most productive cultivated forages such as grasses, legumes, and forbs provide a complete diet for the ruminants—primarily cattle and sheep—with which they co-evolved (Grove and Rackham, 2001; Diamond, 2002). Most cultivated forages used in temperate climates originated in the Mediterranean regions of southern Europe and North Africa (Zeder and Hesse, 2000; Wilkinson et al., 2004). Unlike grain crops, the entire shoot biomass of forages is grazed or harvested and fed to ruminants as hay or silage. Plant tissues are composed of cell with walls of varying thicknesses composed primarily of cellulose (Gilbert, 2010; Cosgrove, 2012), which can be digested by rumen microbes (Allen and Mertens, 1988; Weimer, 1992). Forage biomass is often characterized by the relative proportions of fiber, which refers to the dry mass of plant cell walls, and cell contents, which refers to the dry mass of lipids, sugars, proteins, nucleic acids, and nutrient ions in the protoplasm of plant cells (**Figure 1**) (Van Soest, 1994).

When the nutritive value of grasses and legumes cultivated in temperate climates is compared, the concentraton of fiber is greater in grasses (e.g., 65% of dry mass) than in legumes (e.g., 50% of dry mass), while the concentration of protein is greater by a similar proportion in legumes, largely because the leaves of legumes are low in fiber and because legumes create sufficient nitrogen fertilizer for their own needs internally, in association with soil bacteria (Van Soest, 1994; Franche et al., 2009; Garg, 2009). Feed consumed by cattle is digested by microbes including bacteria,

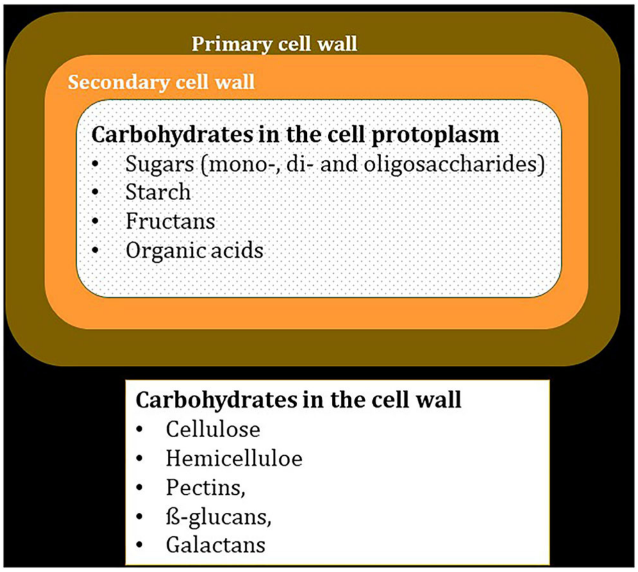

FIGURE 1 | A simple schematic to illustrate the carbohydrates located in plant cell walls or in the protoplasm, enclosed by the cell membrane.

TABLE 1 | Structural (cell wall) and non-structural (cell contents) carbohydrate components of forages.

Plant carbohydrates		Analytical fractions			Digestible by mammalian enzyme	Common sources
Structural or Cell Wall Carbohydrates	Cellulose	ADF	NDF		No	C_3 and C_4 grasses and legumes
	Hemicellulose				No	C_3 and C_4 grasses and legumes
	Pectic substances	NDSF	NFC		No	Legumes, forbs, citrus pulp, sugar beet pulp
	Galactans				Partially*	Legumes, Lupinus seeds
	β-glucans				No	Small grains
Cytoplasmic or Cell Contents Carbohydrates	Fructans			Water-soluble carbohydrates	No	Temperate cool season grasses
	Sugars				Yes	Corn, small grain products, bakery waste, potatoes
	Organic acids				Yes	Molasses, sugar beet pulp, citrus pulp
	Starch				Yes	Silage, additives, whey

**Mammalian enzymes partially digest some galactans (Hall et al., 1999).*
ADF, acid detergent fiber; NDF, neutral detergent fiber; NDSF, neutral detergent soluble fiber; NFC, non-fiber carbohydrates. The NDSF fraction is solubilized when dried, milled plant material is boiled for 30 min in neutral detergent solution while the NDF fraction is not. Neutral and acid detergent solutions and analytical procedures for other plant carbohydrate components are described by Hall (2000).

archaea, protozoa, and fungi in a large forestomach, the reticulorumen. As is the case for other microbial systems, the balance of available proteins and carbohydrates in the rumen dictates the rate of microbial colonization of organic matter (Hall et al., 1999; Hall and Herejk, 2001). This is similar to soil microbial systems, where sufficient nitrogen must be present for microbes to mineralize roots or the plant litter that accumulates on the soil surface (Rigby et al., 2016), and it is also important in the rumen, where forage biomass is digested by microbes that are in turn digested by the ruminant (Nocek, 1988; Archimède et al., 1997; Owens et al., 2014). This paper focuses on the importance of the nutritive value of grasses and legumes for beef production systems, with emphasis on the less investigated potential of temperate legumes to accumulate significant levels of readily digestible carbohydrates in their shoots when grown under irrigation in semi-arid temperate climates.

PLANT CARBOHYDRATES

The structural or cell wall fraction of forages is a biologically complex entity representing the incompletely digestible fraction of forages, comprising the carbohydrates cellulose, hemicellulose, pectic substances, galactans, and ß-glucans (**Table 1**), plus the phenolic macromolecule lignin. The hemicellulose-lignin-cellulose, or neutral detergent fiber fraction (**NDF**) of cell walls, is insoluble in neutral detergent solution, and the lignin-cellulose, or acid detergent fiber (**ADF**) fraction is insoluble in acid detergent solution, chemicals commonly used for *in vitro* analysis of forages (Van Soest, 1994). In contrast, the non-structural or cell contents fraction of plant material comprises the carbohydrates starch, sugars (water soluble carbohydrates; **WSC**), organic acids (**OA**) and fructans (**Table 1**), plus lipids, proteins and nucleic acids, and is soluble in neutral detergent solution (Van Soest, 1994; Hall et al., 1999). Pectins, galactans and ß glucans are located in the cell wall and are considered structural carbohydrates but are soluble in neutral detergent solution and readily digestible by rumen microbes. They are therefore included in non-fiber carbohydrates (**NFC**) along with starch, WSC, OA, and fructans (**Table 1**). The components of the neutral detergent-soluble or NFC fraction of forages are the basis for another important nutritive value characteristic of feeds, total digestible nutrients (TDN), a metric that summarizes the energy value of ruminant feeds required for the production of milk and meat (Van Soest, 1994). High-quality forages grazed by cattle often have excessive protein but insufficient energy. When this occurs, amino acids are deaminated and used for energy, resulting in significant N losses to the environment (Satter and Roffler, 1975; Haynes and Williams, 1993). Therefore, identifying growth conditions that increase the energy value of forages and balance the ratio of energy to protein in forages will allow greater efficiencies and ruminant productivity while reducing the environmental impacts of livestock production systems without adding costly inputs.

NON-FIBER CARBOHYDRATES AND RUMINANT NUTRITION

The diverse group of carbohydrates accumulated in the shoots of forage plants are chemically and nutritionally complex (Hall et al., 1999). We will distinguish the readily digestible NFC carbohydrates from slowly digestible cellulose and hemicellulose, or NDF. Some authors refer to NFC by the more technical term neutral detergent-soluble carbohydrates (**NDSC**) (Hall et al., 1999). We will refer to the subset of NFC found in the cell wall (galactans, pectins and ß glucans) as neutral detergent-soluble fiber or **NDSF** (**Table 1**) (Hall et al., 1999).

In grains, the NFC fraction is dominated by starch (e.g., 70%), with levels of NDSF as low as 6–10%, whereas NDSF predominates in soybean hulls, beet pulp, citrus pulp, and pasture forbs including legumes (Hall, 2000). While the concentration of pectin in alfalfa cell walls is reported to range from 100 to 200 g kg^{-1} in stems and from 250 to 300 g kg^{-1} in leaves (Hatfield and Weimer, 1995), the pectin concentrations of grasses is typically only 10 g kg^{-1} DM (Hatfield et al., 1999). Pectins are complex polysaccharides that include galacturonic acid, arabinose, galactose, xylose, rhamnose, glucuronic acid, and fucose (Van Soest, 1994) and are a dominant fraction of NDSF. Preliminary analyses suggest that the pectin component of NFC varies in response to growth environment (MacAdam, 2019). Compared with the NFC totals of 42% in leaves and 13% in stems of New York-grown alfalfa (Hall et al., 1999), the total NFC concentrations in the leaves and stems of alfalfa grown in the Mountain West were 42 and 37%, respectively, with as much as 20% of the dry matter (**DM**) of both leaves and stems estimated to be pectins (MacAdam, 2019).

Few studies of forages report NFC concentrations, but focus instead on the concentration of starch and WSC, which ferment rapidly to lactic acid in the rumen, lowering the pH (Strobel and Russell, 1986; Ben-Ghedalia et al., 1989). In contrast, the fermentation of pectin, a dominant component of the NDSF fraction of dried citrus and beet pulps, results in a high ratio of acetate to propionate plus little or no lactate, and thus pectin fermentation does not lower rumen pH (Hall et al., 1998; Hall, 2000). Fermentation of the NFC fraction of forages begins rapidly and proceeds at greater rates than the fermentation of the NDF fraction (Titgemeyer et al., 1992; Hall et al., 1998; Arthington et al., 2002) with the added benefit that increments in the concentration of NFC in legumes promotes a glucogenic fermentation and enhances microbial N synthesis in the rumen (Berthiaume et al., 2010).

Non-fiber carbohydrates are ∼98% digestible (Van Soest, 1967), but components vary in their fermentation and digestion characteristics and thus in the profile of metabolizable nutrients that they provide (Leiva et al., 2000). For instance, ruminal fermentation of NDSF such as pectic substances is extensive (Titgemeyer et al., 1992) and rapid (Hatfield and Weimer, 1995) although fermentation of pectin slows if rumen pH decreases, while fermentation of starch and sucrose continues, lowering rumen pH even further (Strobel and Russell, 1986). The metabolizable nutrients produced in the rumen by sugars and starch are enriched in propionate, which is converted to glucose in the liver, whereas those produced by NDSF are enriched in acetate, which is lipogenic (Hall, 2000). Pectin ferments more rapidly in the rumen than starch, so pectin-rich diets result in less microbial production per unit of carbohydrate digested than starch-rich diets. Dairy diets enriched in pectins resulted in greater milk fat while diets enriched in starch resulted in greater milk protein, either because pectin is digested more rapidly than starch, thereby yielding less microbial protein, or because a greater proportion of absorbed protein is utilized for glucose production in pectin-rich diets (Leiva et al., 2000).

Neutral detergent-soluble fiber can represent a key source of energy in beef and sheep finishing diets as well as in dairy cow diets (Leiva et al., 2000; Caparra et al., 2007; Favarola et al., 2016), with fewer negative effects on rumen fermentation (e.g., reduction of ruminal pH) than starch-rich diets (Bampidis and Robinson, 2006). Nevertheless, diets with high NDSF may yield less metabolizable protein than those containing greater amounts of starch (Rosendo et al., 1999), although other studies have observed improved microbial synthesis (Zhao et al., 2013) and flow of microbial crude protein (CP) to the small intestine (Huhtanen, 1988), with reductions in urinary N excretion (Gressley and Armentano, 2005) and improved animal performance (Kim et al., 2007) in response to supplemental NDSF. Legume forages are enriched in protein, so diets with elevated NDSF from legumes would contain sufficient metabolizable protein to complement the energy supplied by the NDSF fraction. While NDSF is almost entirely digestible by rumen microbes, the rumen digestibility of the NDF in feeds varies enormously, ranging from 13% for peanut hulls to 78% for soybean meal (Varga and Hoover, 1983). Almost all the information available on NDSF is derived from studies that use products rich in this fraction (such as beet pulp) added to feedlot rations.

A significant gap in knowledge exists regarding the influence of NDSF on the nutrition of grazing livestock or the agroecological variables that impact the concentration of this fraction in forages, despite the fact that increasing the use of legumes with elevated NDSF and reducing the use of starch-rich concentrates would enhance the sustainability of forage-based livestock production systems. A particular benefit of NFC in forages over grain is reduced competition for grain in beef production systems. Such a benefit is already being recognized in dairy systems; Münnich et al. (2018) calculated that substituting beet pulp (a source of NDSF) for maize grain in one-third of a Simmental dairy cow diet on a dry matter (DM) basis reduced human-edible food use by about 37% while increasing fiber digestibility.

Effect of Neutral Detergent-Soluble Carbohydrates on Performance of Beef Cattle

While it is known that the amount and composition of NFC fractions of ruminant diets serve a different function from structural carbohydrates, study of the NFC fraction of forages has largely been limited to WSC or starch and not on the effects of other fractions such as NDSF on rumen function. However, it has been demonstrated that differences in dietary starch and pectin result in differences in protein and fat production in ruminants. It has also been demonstrated that digestion of NDF decreases when forage diets are supplemented with either starch or pectin at high levels, likely due to a decrease in pH below 6.2 and competition for N between NFC- and NDF-digesting microorganisms (Cameron et al., 1991; Grant and Mertens, 1992).

Newly developed grass cultivars, such as high-sugar ryegrass varieties, have been bred for greater contents of WSC to increase the supply of energy to the rumen and the synchrony of energy with CP to increase the efficiency of N use in pasture-based systems (Edwards et al., 2007). When the effects of different levels of the water-soluble carbohydrate component of NFC in perennial ryegrass (*Lolium perenne* L.) on rumen metabolism and N absorption were investigated with grazing Hereford × Friesian steers, Lee et al. (2002) reported that DM intake increased for cattle grazing high-sugar perennial ryegrass, contributing to higher flows of non-ammonia N to the duodenum, and increased the absorption of amino acids from the small intestine. Conversely, in a study conducted with ruminally cannulated Holstein–Friesian steers, the addition of sucrose to diets based on grass silage at 90 g/kg DM only tended to increase OM digestion in the rumen, but did not affect intake or digestion of NDF organic matter (Owens et al., 2008).

The majority of the work that investigated the effects of NFC on the digestion efficiency and performance of beef cattle was performed by direct supplementation with carbohydrates rather than by employing forages containing varying types and concentrations of NFC. Feeding supplemental NFC, in particular at high rates, without providing additional rumen-degradable protein in diets, may potentially hinder forage fiber digestion (Arroquy et al., 2004). Most studies suggest that the efficiency of NFC supplementation may be optimized by providing supplemental rumen-degradable protein in conjuction with NFC in diets (Heldt et al., 1999).

Overall, increases in the concentration of NFC to levels commonly used in total mixed rations positively affects animal performance. For instance, Ramos-Aviña et al. (2018) reported higher average daily gain of Holstein steers fed diets containing high concentrations of NFC in an indoor feeding study, without affecting DM intake. Nevertheless, there is a paucity of information on the effect of the NDSF fraction of forages on animal performance and in particular, on meat quality. The majority of the studies that investigated the effects of NDSF used either citrus pulp or beet pulp as the main source, while only a few studies compared forages containing different amounts of these carbohydrates. Use of citrus pulp, a byproduct with high contents of NDSF, has been associated with positive effects on ruminal fermentation (Pinzon and Wing, 1976), fiber digestion (Miron et al., 2002), and microbial protein synthesis (Ariza et al., 2001). Supplementation of beef cattle that were fed a tropical grass-based diet (*Cynodon nlemfuensis* Vanderyst) with increasing amounts of pelleted citrus pulp had a positive effect on digestibility of total diet dry matter and organic matter owing to greater NDSF content (predominantly pectins) (Villarreal et al., 2006). Huhtanen (1988) also reported greater rumen and total track digestibility of NDF when cannulated cattle were fed beet pulp-containing diets as compared to barley-based (high starch) diets. In a study that compared the effects of starch from cereals with isoenergetic diets containing soluble fiber from beet pulp as 50% of the diet DM on the fattening characteristics of Belgian Blue, Limousin and Aberdeen Angus cattle, no diet effect was found on animal performance, DM intake, or meat quality (Cuvelier et al., 2006). In a comparison of the digestion of isonitrogenous diets in sheep supplemented with either pectin or starch, Ben-Ghedalia et al. (1989) found that rumen pH was significantly greater (6.42 vs. 6.18) and rumen ammonia concentration was significantly less (17 vs. 24 mg/100 mL) for pectin- vs. starch-supplemented sheep.

Effect of Non-fiber Carbohydrates on Meat Quality

MacAdam and Villalba (2015) reported that beef cattle grazing the perennial legume birdsfoot trefoil (*Lotus corniculatus* L.), with an NFC concentration of 40% of dry mass, had nearly twice the gain during finishing compared with beef cattle grazing grass pastures. Consumer sensory panels rated steaks from these high-NFC legume-finished cattle comparable to grain-finished cattle for tenderness and juiciness due to greater deposition of intramuscular fat, and steaks from both legume- and grain-finished cattle were preferred over steaks from grass-finished cattle (Chail et al., 2016). When the NFC concentrations of the grain and legume pasture diets in this study were compared, their concentrations were both about 40%, twice that of the grass pasture diet. When the NFC concentration of hay made from alfalfa and other perennial legumes grown in the Mountain West was measured, it ranged from 36 to 40% (Stewart et al., 2019) and 42 to 48% for the same legumes sampled in pastures (MacAdam, 2019). Therefore, NFC losses during field curing are ∼5% of dry mass, and perennial legume hay has an NFC concentration more similar to corn silage or beet pulp (36 and 38%, respectively) than to conventional alfalfa hay (26%), based on numerous samples from commercial dairy farms located in the Central Valley of California (Getachew et al., 2004).

Acetate and propionate from rumen fermentation can both be directed to fat deposition in cattle, but propionate must first be converted to glucose in the liver, which is an energy-consuming process (Smith and Johnson, 2014). In young cattle, glucose is used preferentially for intramuscular fat accumulation (marbling), while acetate is used preferentially for subcutaneous (back) fat deposition (Smith and Crouse, 1984). However, as cattle mature, the use of acetate in marbling increases and the use of glucose decreases (Choi et al., 2014). Eight-month-old Angus steers on high-energy (70% ground corn) diets or lower-energy (corn silage) diets had similar DM intake, marbling, and *Longissimus thoracis et lumborum* cross-sectional area. However, the steers fed ground corn carried 30% more backfat at 18 months than the corn silage-fed steers (Smith and Crouse, 1984). Intramuscular fat deposition depends on a sufficient supply of energy, whether in the form of glucose or acetate, and excess energy will be accumulated as backfat, at least in Angus cattle (Smith and Johnson, 2014). These data suggest that increasing NFC in the form of pectins is more desirable than by increasing starch.

Corn grain is estimated to contain 6–10% NDSF, 0–5% sugars, and 70% starch; in contrast, citrus pulp and beet pulp typically contain about 30% NDSF, 10% sugars, and 1% starch on a dry matter basis (Hall, 2000). The perennial

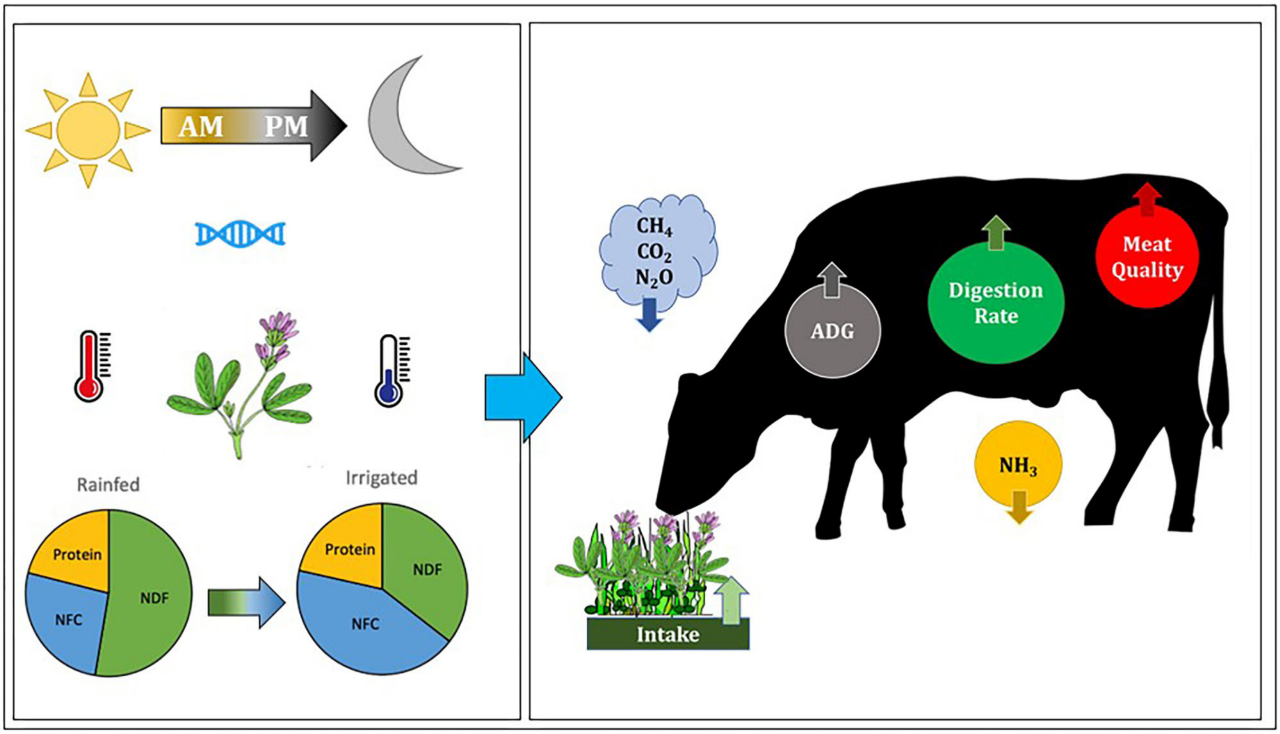

FIGURE 2 | Factors that increase the NFC of alfalfa and other perennial legumes include harvesting in the afternoon rather than the morning, breeding for greater pectin concentration, and greater photosynthesis combined with reduced aerobic respiration. Relatively dry climates in which forages are grown under irrigation are exposed to long hot sunny days with more solar radiation and therefore produce more photosynthate than more humid environments, and lower relative humidity results in cool nighttime temperatures that reduce aerobic respiration. The reduced fiber and increased NFC concentration of these forages result in more rapid digestion and emptying of the rumen, leading to greater intake, and increased ruminant production of meat and milk. Increased NFC also results in better protein utilization, increased nitrogen retention, less nitrogen excretion, and reduced enteric emissions of methane and carbon dioxide.

forage legumes cultivated under irrigation in the western US contain NFC concentrations similar to corn silage (35–45%), but starch and WSC concentrations were not elevated (MacAdam, 2019) and OA concentrations tend not to vary greatly, so elevated NFC in perennial legumes is thought to be due to greater pectin concentrations. In ruminant studies where dietary starch was replaced by beet pulp or citrus pulp, both rich in NDSF, the resulting blood glucose of dairy cows (Belibasakis and Tsirgogianni, 1996; Münnich et al., 2018) and lambs (Bhattacharya and Harb, 1973; Sharif et al., 2018) was unaffected.

ENVIRONMENTAL BENEFITS OF NON-FIBER CARBOHYDRATES

In addition to reducing the use of grain in ruminant diets, the use of forages with elevated NFC, such as perennial legumes cultivated in the Mountain West, will benefit the environment by increasing ruminant production efficiency relative to cattle fed forages with lower NFC concentrations (**Figure 2**). In a study of ewes (Barrios-Urdaneta et al., 2003) where 85% of the diet dry matter consisted of barley grain or dried citrus pulp, the citrus pulp diet significantly reduced excretion of nitrogen in the urine, but feces nitrogen excretion was unchanged. Forages are typically high in rumen-degradable protein but low in non-structural carbohydrates, causing rumen microbes to use protein as an energy source and resulting in excess rumen ammonia (NH_3^+)-nitrogen (Satter and Roffler, 1975) and excretion of increased amounts of urea, the predominant nitrogen-containing compound in the urine. Excretion of excess nitrogen results in both a metabolic cost to the animal (Lobley and Milano, 1997) and increased environmental pollution. Urea is rapidly hydrolyzed to ammonia that is converted to nitrate (NO_3^-) in the soil (Haynes and Williams, 1993), where it can be leached to groundwater and waterways (Leip et al., 2015). Large losses of NH_3^+ also occur by volatilization after urination, as well as losses of nitrous oxide during the denitrification process (Lee et al., 2014). Thus, providing feeds sufficiently high in NFC to match rumen-degradable protein concentration has been proposed as a potential management approach for reducing nitrogen losses (Dalley et al., 2017).

In pasture-based production systems, feeding grass varieties containing elevated WSC, a subset of NFC, reduced nitrogen excretion in urine and feces by providing sufficient readily available (and synchronous) energy for microbial capture of digested grass protein to increase microbial protein synthesis (Miller et al., 2001; Ellis et al., 2012). High-sugar ryegrass, chicory, and plantain varieties have also been used in pasture systems to achieve such goal (Totty et al., 2013; Bryant et al., 2020; Wilson et al., 2020). The digestibility and composition of forages with greater NFC concentrations have a substantial impact on methane (CH_4) production from ruminants through more rapid ruminal fermentation and passage rates per unit of feed (**Figure 2**) (Hindrichsen et al., 2005). Knapp et al. (2014) reported that a 5% increase in apparent total-tract NDF digestibility led to a 5% decrease in CH_4 methane production per unit of energy-corrected milk due to greater yield of volatile fatty acids relative to increases in CH_4, and increased milk yield.

FACTORS AFFECTING THE CONCENTRATION OF NFC IN FORAGES

Maturity

Plant maturity at the time of harvest is one of the primary factors decreasing nutritive value of forages in both grazed and conserved forage/livestock production systems, at least in humid environments. The nutritive value of forages declines with increasing plant maturity due to accummulation of structural carbohydrates (NDF) and an increasing stem-to-leaf ratio. In general, as alfalfa matures, the proportions of fiber, and lignin increase and the proportions of protein and NFC decrease (Martin et al., 2004). It should be noted that Martin et al. (2004), working in Wisconsin, report that "exceptional quality" alfalfa hay is expected to have an NFC concentration of 31.5%, while NFC concentrations of Mountain West alfalfa hay are routinely 36–39% (MacAdam and Yost, 2020). Yu et al. (2003), working in Saskatchewan, reported that the changes in carbohydrate fractions as plant maturity advanced were slight in alfalfa, and there were no changes in timothy grass (*Phleum pratense* L.). Similarly, alfalfa cultivated in the northern Mountain West maintained a constant NFC concentration of about 40% as it matured from the vegetative to the early bloom stage (MacAdam, 2020).

Defoliation

Harvest management of forages, in particular the defoliation time, frequency and intensity, affects plant regrowth, persistence, morphological structure, and chemical composition. Under frequent defoliation, either in the form of grazing or mechanical harvesting, pasture grasses produce smaller tillers but at higher density (Matthew et al., 1996). Therefore, non-structural carbohydrates of both harvested forage material and remaining stubble may be depleted by recurrent defoliation because the NFC stored in the stubble of plants provides energy for regrowth (Donaghy et al., 2008; Alderman et al., 2011). Overall, the water-soluble carbohydrate component of NFC is reduced in grasses as defoliation severity increases (Lee et al., 2008). Conversely, as defoliation interval increases, the nutritive value of grasses declines along with digestibility, but at varying rates depending on the grass species (Turner et al., 2006).

A number of studies reported substantial changes in chemical composition of winter annual small grains in relation to grazing and defoliation when used as supplementary off-season grazing as well as grain crops. Defoliation of such forages in early vegetative stages may have a positive effect on the nutritive value of the regrown forage material (Jacobs et al., 2009; Keles et al., 2013). Cazzato et al. (2012) reported that mechanical harvest of vegetative triticale in winter resulted in an increase in NDF but a decrease in lignin at the heading stage. Similarly, Jacobs et al. (2009) reported varying rates of increase in metabolizable energy and WSC concentrations of oat and barley varieties at silage harvest following two spring grazings at the tillering and stem elongation stages in a dual purpose management system. Ates et al. (2017) also reported that straw of spring-defoliated triticale, wheat and rye had less NDF and acid detergent fiber (ADF) but greater CP, NFC, and metabolizable energy concentrations than straw from undefoliated crops. However, Francia et al. (2006) reported no substantial changes in the nutritive value of oat or barley regrowths in relation to spring defoliation or grazing management in the Mediterranean region.

Breeding Programs

Extensive work has been devoted to improving the fiber digestibility of forage species to improve ruminant productivity. A number of breeding studies focused on increasing the NFC concentrations of forage grasses and legumes to develop varieties with high digestibility. In particular, increasing pectin concentration as the major component of NDSF in alfalfa (*Medicago sativa* L.) has been the focus of several breeding programs (Tecle et al., 2006), one resulting in a patent application for High Pectin Alfalfa (Hatfield et al., 2006). The patent application reported that the improved alfalfa had a pectin concentration consistently 2–3% greater than the control which resulted in an estimated increase of between 90 and 900 kg of milk per acre of alfalfa.

Sound

A recent study reported that plants increase nectar sugar concentration in response to pollinator sounds (Veits et al., 2019). Although no information was provided on NFC concentrations in the leaves of these plants, further studies may investigate effects of pollinator sounds on NFC concentrations in both grazed and conserved forages.

Photosynthesis

The NFC concentration of plants is affected by a wide range of environmental factors such as light and temperature. Photosynthesis responds to diurnal fluctuations in solar radiation, and affects the non-structural carbohydrate concentration of plants through accumulation of starch in leaves during the day that provides the energy for plant growth and maintenance processes. Consequently, greater concentrations of NFC in afternoon compared with morning harvests have been reported in pasture grasses and legumes. As the day progresses, the rate of carbon fixation progressively exceeds carbon export from leaves, and the benefit of greater concentrations of NFC in forages is therefore demonstrated by feeding alfalfa harvested in the afternoon compared with alfalfa harvested in the morning. Elevated NFC in afternoon-cut forage resulted in greater DMI and milk yield (Brito et al., 2008), nitrogen use efficiency (Berthiaume et al., 2010), and rumen bacterial protein synthesis

(Brito et al., 2009). Feeding alfalfa genotypes with elevated NFC during continuous culture rumen fermentation likewise resulted in significant increments (+14%) in the synthesis of bacterial protein (Berthiaume et al., 2010). Thus, greater concentrations of readily accessible carbohydrates in the form of NDSF can enhance DM intake and rumen fermentable energy, which in turn improves ruminant performance and nitrogen utilization in beef cattle while reducing urinary nitrogen outputs (**Figure 2**).

Harvesting the grass timothy (*Phleum pratense* L.) in the afternoon as compared to the morning resulted in higher NFC, mainly sucrose concentrations, and decreased ADF and NDF concentrations (Bertrand et al., 2008). Similar results were obtained with a number of grass and legume species from a range of functional and structurual groups (Fisher et al., 1999, 2002; Griggs et al., 2005; Yari et al., 2014) that were harvested in the afternoon compared with the morning. Concentrations of non-structural carbohydrates, the cell contents subset of NFC, also vary depending on forage species and growth period (Pelletier et al., 2010). For instance, Owens et al. (1999) reported that starch accounted for most of the daily change in non-structural carbohydrates in fresh alfalfa, whereas in red clover (*Trifolium pratense* L.), quantitative increases in sugar and starch had an equal impact on non-structural carbohydrate concentration.

Management practices have been developed to take advantage of higher non-structural carbohydrates concentrations of pasture species in the afternoon. For instance, having a sufficiently high non-structural carbohydrates concentration is critical for successfully ensiling forages and the resultant silage quality, in particular for forages that are difficult to ensile such as alfalfa and red clover (Owens et al., 2002). Harvesting forages in the afternoon may improve the ensiling process by providing additional non-structural carbohydrates for the rapid growth of lactic acid-producing bacteria. This would in turn reduce DM losses, improve aerobic stability and reduce clostridial spoilage that occurs when lactic acid production occurs too slowly.

Livestock are able detect the difference in non-structural carbohydrates concentrations of plant species, and exhibit preference for forages harvested in the afternoon (Fisher et al., 1999). Similarly, allocating new pasture strips in the afternoon rather than morning has been reported to increase the milk yield of dairy cows (Orr et al., 2001) and liveweight gains of beef heifers (Gregorini et al., 2008).

Temperature and Altitude

Temperature has a strong influence on plant growth, development and chemical composition (Jung, 1989; Buxton, 1996). The increased lignification of individual plant cells and in particular reduced fiber digestibility at higher temperatures in both tropical and temperate forage species was consistently reported with the effect being less profound in tropical species in a number of studies (Akin et al., 1987; Wilson et al., 1991; Buxton and Fales, 1994). Extrapolating the research data from replicated studies, the negative effect of temperature on forage quality was also highlighted in a few recent review papers that forecasted decreasing forage digestibility due to rising global temperatures (Dumont et al., 2015; Lee et al., 2017; Ghahramani et al., 2019). Physiologically, lignin synthetic enzyme activities increase in plants as a reponse to increasing temperatures (Buxton and Fales, 1994), while higher proportions of non-structural carbohydrates are metabolized into structural carbohydrates (Deinum and Knoppers, 1979). Overall, lignification was reported to be more extensive in stem than leaf tissues (Wilson, 1983a) and plants generally produced smaller leaves at increasing temperatures, leading to reduced leaf-to-stem ratios, an increased cell wall fraction, and lower dry matter digestibility (Wilson and Minson, 1983). Ultimately, non-structural carbohydrate concentrations of forages even at comparable plant maturity stages were lower at high temperatures (Xu and Huang, 2000).

The nutritive value of forages grown at higher altitudes is understood to be superior to forages grown at lower altitudes (Old et al., 2018). However, the apparent effects of altitude are more likely related to cooler growing-season temperatures at high elevations. Plant aerobic respiration uses the carbohydrates synthesized by photosynthesis for plant growth and maintenance (MacAdam and Nelson, 2017) and aerobic respiration decreases with temperature, increasing the accumulation NFC. It would be challenging to design a study to separate the effects of altitude and temperature on irrigated, field-grown legumes. However, irrigated alfalfa grown in Utah at 1,200, 1,500, 1,800, and 2,100 m a.s.l. did not differ in NDF, NFC, or TDN, which averaged 31, 37, and 69%, respectively (MacAdam and Yost, 2020). Early lines of low-lignin lines of alfalfa grown at an altitude of 15 m. a.s.l. at Davis, CA averaged NDF, NFC or TDN concentrations of 29, 39, and 71%, respectively (Putnam et al., 2017). While dissimilar in altitude, the common element of climate in these locations is the 20°C difference in mid-summer day-night temperatures. Under irrigation, alfalfa thrives at in daytime temperatures above 30°C. while night time temperatures in the range of 10–15°C result in a reduction in root and shoot respiration (Atkin and Tjoelker, 2003) with no deleterious effect on alfalfa.

Water Availability

In general, the nutritive value of perennial forages growing under moderate water deficits tends to be greater than for forages grown under full irrigation (Wilson, 1982, 1983a,b), provided that the deficit was not severe and was initiated early in herbage growth (Buxton, 1996; Reddy et al., 2003). In contrast, long or extreme droughts inhibit tillering and branching, accelerate the death of tillers and senescence of leaves, and relocate protein, nitrogen, and NFC from leaves to roots, reducing the nutritive value of the forage (Buxton, 1996; Durand et al., 2010; Liu et al., 2018).

Under well-watered conditions, the nutritive value of alfalfa declines with maturation (Kalu and Fick, 1981), but mean maturity stage decreases with increasing water stress (Van Soest, 1994). Water deficits may directly reduce the rate of plant maturation (Wilson and Ng, 1975; Wilson, 1982; Buxton, 1996). However, Halim et al. (1989) demonstrated that increments in stem protein concentration and reductions in cellulose concentration in alfalfa stems and leaves under water stress were not fully accounted for by differences in plant maturity. These authors attributed improvements in forage quality to greater leaf-to-stem ratio in water-stressed plants, given that water stress has the greatest effect on reducing stem growth (Halim et al., 1989). Under moderate water restrictions, *in vitro* dry matter digestibility of alfalfa is greater and concentration of NDF is less under prolonged water deficits that reduce plant water potential than in control plants grown without a water deficit (Halim et al., 1989; Peterson et al., 1992). Research with other legumes like birdsfoot trefoil, sainfoin (*Onobrychis viciifolia* L.), red clover (*Trifolium pratense* L.) and cicer milkvetch (*Astragalus cicer* L.) show similar patterns in response to water stress to those described for alfalfa (Peterson et al., 1992; Küchenmeister et al., 2013), although alfalfa yields tend to be less affected by drought than other species. When these alternative legumes were droughted, they produced biomass with lower concentrations of ADF, NDF, and lignin than alfalfa, with birdsfoot trefoil and cicer milkvetch producing the highest quality forage (Peterson et al., 1992). Nevertheless, because of its superior yield and persistence under drought, it was concluded that alfalfa would produce more nutrients per unit of area than the alternative legumes (Peterson et al., 1992).

It has been hypothesized that cell wall development during relatively severe water stress may be inhibited because more carbon in labile forms, like the sugars fixed by photosynthesis, is needed for osmoregulatory purposes (Wilson, 1982). In support of this idea, the concentration of glucose in cell walls tends to decline whereas the concentration of structural sugars tends to increase in forages during dry compared with wet years (Albrecht et al., 1987), and the concentration of cell wall monosaccharides is more sensitive to plant environment than other cell wall components (Buxton et al., 1987).

This has been confirmed by more recent controlled environment studies showing increments in the concentration of WSC due to water stress in forages like birdsfoot trefoil, sainfoin, white clover and perennial ryegrass (Küchenmeister et al., 2013). An increase in the concentration of WSC in plants will reduce the water potential and maintain uptake of soil water under drought stress (Morgan, 1984; Nakayama et al., 2007), an osmotic adjustment mechanism triggered in response to drought (Da Costa and Huang, 2006). Crude protein concentration in legumes tends to increase with water deficit in stems, but it decreases in leaves (Halim et al., 1989). Increased leaf senescence with water stress and translocation of amino acids to other plant parts (including stems) could explain this pattern (Halim et al., 1989). As a result, however, the ratio of CP to WSC decreases in forages under drought (Liu et al., 2018), resulting in greater N retention and less urinary excretion by ruminants (Moorby et al., 2006). Greater WSC concentrations and lower cell wall concentrations also result in greater forage digestibility, leading to increased intake.

Labile forms of carbon for osmoregulatory purposes may not only include increments of WSC, which are just a fraction of the non-structural carbohydrates present in forages, but also increments in OA, starch, and/or the NDSF fraction. Despite these benefits, no critical research has been conducted to explore the influence of water deficit on NFC, and in particular on NDSF, a significant component of legumes cultivated in cooler, drier environments. Moderate water deficits increase the concentrations of NFC in legumes and in grass-legume mixes, leading to enhancements in digestibility, animal performance and product quality, while improving the balance between NH_3-nitrogen and energy supply to the rumen. The latter increases nitrogen retention and reduces the excretion of urinary nitrogen to the environment (**Figure 2**).

CONCLUDING REMARKS AND FUTURE DIRECTIONS

Despite the aforementioned ability of forage legume shoots to accumulate NFC to levels comparable to corn silage or citrus pulp in dry, cool environments, and the potential benefits to ruminant meat and milk productivity, very little critical research has been conducted to explore the breeding potential or to define critical management practices and ecological conditions (i.e., climate, elevation, soil water status) that result in elevated concentrations of NFC in forages. There is particular value in studying the accumulation of pectins in legumes and non-leguminous forbs as a source of energy for rumen microbes equivalent to starch but without the risk of lowering rumen pH. We hypothesize that moderate water deficits and other conditions that increase the concentrations of NFC in legumes and in grass-legume mixes will enhance the kinetics of rumen fermentation and increase the digestibility of forages by improving the synchrony of energy and protein supply, with concomitant increased nitrogen retention, improved feed conversion efficiencies, reduced greenhouse gas emissions, and improved performance of ruminants (**Figure 2**). Defoliation in the afternoon rather than in the morning may contribute to increments in the concentration of NFC in all forages, and likely to increased pectin concentrations in legumes. Alfalfa has been successfully selected for greater pectin concentrations but no high-pectin cultivars have been released. Elevated photosynthetic rates combined with reduced aerobic respiration under irrigation in dry climates with long hot sunny days (maximizing solar radiation) results in the accumulation of more photosynthate than under humid environments, with the corollary of a better balance between the energy to protein ratio supplied to the rumen. Lower relative humidity typical of high altitudes results in cool nighttime temperatures that reduce aerobic respiration resulting in greater residual shoot NFC concentration and proportionally reduced fiber in legumes. Ecoregions with such characteristics should be identified so forage and ruminant producers can exploit these locations for the production and marketing of forages that enhance the productivity and sustainability of livestock production systems. Ruminal NH_3-nitrogen concentration typically decreases as dietary NFC concentration increases (Lee et al., 2002) and increased availability of fermentable energy in the rumen stimulates microbial growth (Brito et al., 2009), which improves animal performance. We have demonstrated that forage NFC concentrations can be significantly increased, resulting in improvements in ruminant performance and reduced carbon and nitrogen footprints, particularly when grazing nitrogen-rich legumes (Lagrange et al., 2020), representing a win-win situation for ruminant production systems.

AUTHOR CONTRIBUTIONS

JV, SA, and JM drafted the manuscript and wrote the review. All authors contributed to the article and approved the submitted version.

ACKNOWLEDGMENTS

This research was supported by the Utah Agricultural Experiment Station, Utah State University, and approved as journal paper number 9449.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Sustainable Food Systems

ORIGINAL RESEARCH
published: 20 April 2021
doi: 10.3389/fsufs.2021.500437

The Contribution of Mobile Pastoral Herds to Soil Fertility Maintenance in Sedentary Mixed Crop-Livestock Systems at Farm and Territory Scales—Part of Mutually Reinforcing Social and Ecological Relationships Supporting Sustainability

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Specialty section:
This article was submitted to Agroecology and Ecosystem Services, a section of the journal Frontiers in Sustainable Food Systems

Received: *25 September 2019*
Accepted: *04 March 2021*
Published: *20 April 2021*

Citation:
Alary V, Aboul-Naga A, Osman MA, Daoud I and Vayssières J (2021) The Contribution of Mobile Pastoral Herds to Soil Fertility Maintenance in Sedentary Mixed Crop-Livestock Systems at Farm and Territory Scales—Part of Mutually Reinforcing Social and Ecological Relationships Supporting Sustainability. Front. Sustain. Food Syst. 5:500437. doi: 10.3389/fsufs.2021.500437

Agricultural development through settlement schemes on desert lands has always raised acute debates, especially over environmental issues due to cultivation based on intensive additions of water and fertilizers. However, nutrient cycling approaches at the farm level are generally based on apparent N flows, i.e., purchased inputs and sold products, without considering nutrient flows driven by mobile herds crossing the arable lands of sedentary farmers. Through a territory level approach, the present study aimed to assess the contribution of mobile pastoral herds located in the newly reclaimed land on the western desert edge of the Nile Delta on the supply of the manure for local sedentary farms. Based on a survey of 175 farmers, we calculated the partial farm nitrogen balances. Supplemental interviews were conducted with the pastoral community to assess the additional manure coming from grazing practices in the research area. The results show that the sedentary mixed crop-livestock systems based on the planting of *Trifolium alexandrinum* and a manure supply make a useful contribution toward converting poor, marginal soil into fertile soil. Moreover, grazing of crop residue by pastoral herds on the reclaimed land contributes to social sustainability by maintaining social links between the first occupants, the Bedouins, and the new settlers. Grazing accounts for 9% to 34% of farm-level N input and 25% to 64% of farm-level N output depending on the village and the cropping system. This contribution calls for different rural policies that consider the complementarity between pastoral herders and sedentary farmers that supports both systems' social and environmental sustainability.

Keywords: crop-livestock systems, nitrogen balance, manure input, pastoral system, social interactions, reclaimed lands, Egypt

INTRODUCTION

Recent studies highlight the multiple benefits of integrated crop-livestock production systems in terms of the diversification of farm activities and the creation of a safety net that decreases farm household vulnerability (Barrett et al., 2001; Alary et al., 2011), and also in terms of efficiency and sustainability, partly due to the contribution of livestock to nutrient cycling (Powell et al., 1996; Herrero et al., 2010; Powell and Rotz, 2015). Nutrient balance and use efficiency are widely used as indicators to assess the dynamics of nutrient cycling and soil fertility (Stoorvogel and Smaling, 1990; Tittonell et al., 2005). The plot and the farm (or the household) are usually the reference points for estimating these indicators. However, farm-level approaches generally underestimate the nutrient flows driven by mobile livestock within a territory as pastoral herders traverse a wider area. Moreover, most social and ecological studies on the new cultivated zones in harsh environments shared by mobile herders and sedentary farmers highlight the conflictual and recurrent resource ownership problems and access (Bassett, 1988; Thebaud and Butterbury, 2001; Galvin, 2009). In this context, Powell et al. (1996) illustrated how land use and tenure policies inhibit livestock mobility. These rules reduce the farmer's access to manure from pastoral herds, increasing the need for other external nutrient inputs, such as mineral fertilizers, to prevent a decline in soil fertility and crop yields. This phenomenon is particularly acute in desert reclaimed lands that require significant nutrient additions before being cultivated and productive. Simultaneously, their settlement is largely criticized for displacing indigenous people, including pastoralists, which potentially strains the relationship between the two groups. Few studies integrate manure management's social and environmental dimensions at the territory level [as mentioned by Schlecht et al. (2004) and Vayssières et al. (2017)]. The present study aimed to assess mobile pastoral herds' environmental and social contributions at the territory level by focusing on nutrient flows and the consequent social interactions between pastoral herders and farmers.

The study area was the newly reclaimed arid lands (NRLs) at the West of the Nile Delta in Egypt. Generally, the location of these reclaimed lands, which are on sandy soils and supplied with pressurized irrigation water by sprinklers or drippers, make them suitable for the development of modern agriculture centered on cash crops. However, productivity in the NRLs has consistently remained low compared to the Nile Valley's older lands (Enien et al., 2000). The conversion of new desert soils to economically sustainable systems is a significant challenge in agricultural development. Crop fertilization and soil fertility management have been identified as crucial issues for farm intensification and diversification to realize the full agronomic and economic return of the newly reclaimed desert land (El Nahrawy, 2011). Under arid conditions and on sandy soils, manure increases biological activity in the soil and enhances soil properties. However, large amounts of N can be lost by leaching depending on the cropping system and water management (Cameron et al., 2013). These losses can reach 40–60% in the case of overuse of mineral fertilizers and over-irrigation, threatening social and ecosystem health in Egypt (Monem et al., 1997). In the context of newly reclaimed lands in Egypt, it is essential to improve soil properties without compromising the nitrogen balance. Manure is an important source of N, and it can enhance the physical structure of soils, subsequently improving stability and productivity (Hauck, 1978).

The reclaimed arid lands in the western part of the Nile Delta represent ∼40% of total Egypt's NRL, spawning from a national agricultural policy started in the 1960s to achieve different goals. Among them, we can cite the objectives of food security, rural employment, and increases in the export of crop products via the agriculture sector's modernization (Meyer, 1998). In the 70s, under Al Sadat's presidency, the preference for land attribution was given to agricultural high school or University graduates who were seen as promising individuals for new agricultural development (Mansour and Ismail, 1993). In the 80s, with the Mubarak National Resettlement Scheme for Graduates (MRS), land distribution was extended to all graduates from all types of high school programs and University faculties (Meyer, 1998). From the mid-90s, the National Resettlement Scheme has been extended to many beneficiaries, e.g., early retirees from the public sector, evicted land tenants, or female heads of households. Thus, the newly reclaimed land in Egypt has a variety of beneficiaries, which explains the range of farming systems (Alary et al., 2018) and complexifies these territories' social context.

Our objective was to assess mobile pastoral herds' contribution, which are located in the NRLs, to the supply of manure to local farms. Specifically, the study focused on the N supply from manure used by various crop-livestock systems. At the farm level, the N flow analysis allowed us to estimate the N contribution of livestock to the total N input. Comparing results to N exportation through livestock and crop products, we calculated the N balance. The N input and output are computed from a farm survey in the NRLs of the West Nile Delta. Supplemental interviews were conducted with the pastoral community to assess the additional manure coming from grazing practices in the research area. One of the leading hypotheses tested herein was that grazing livestock activities and herd mobility constitute a pillar of environmental and social sustainability in the Mediterranean rural zone. Moreover, their role is essential at different scales, i.e., both at the farm level (soil fertility and structure, forage supply, and household livelihoods) and at the territory level (relationships between herders and farmers, and N flows).

MATERIALS AND METHODS

Case Study and Materials

In the NRLs, various fertilization practices are embedded in the diversity of new settlers and cropping systems implemented on the newly reclaimed farmland. Thus, five zones in the NRLs were chosen according to a chronological gradient of land reclamation: Nahda in the reclaimed land settled in the 1960s (called Old NRLs), Sukhar el-Bangar (also called Bangar) primarily reclaimed in the 1980s, and Hammam in the 1990s, and Tiba and Bustan extension (New NRLs), settled at the end of the 90s (**Figure 1**) (Alary et al., 2018). Three villages

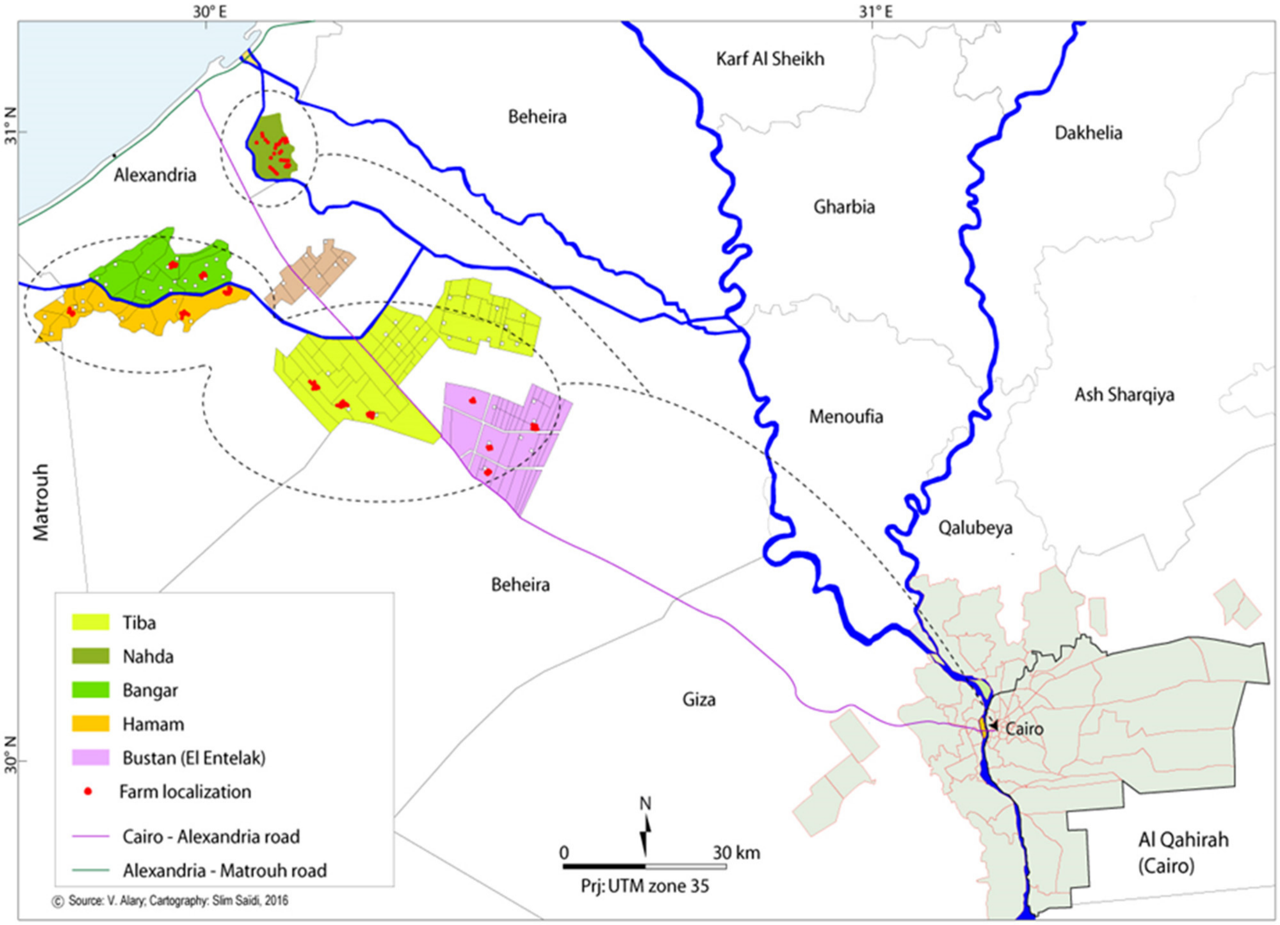

FIGURE 1 | The geographical location of the selected zones in the New reclaimed lands of the western part of Nile Delta (Egypt) (extracted from Alary et al., 2016, http://agritrop.cirad.fr/584660/).

were selected in each zone to reflect the diversity of land beneficiaries in each zone. Using snowball sampling (Goodman, 1961), we identified and surveyed 10 farmers per village. The target population was small and medium farms (from < 1 to < 2 ha). A total of 160 farmers, from small to medium farms, were surveyed in 2013 and 2014. Additionally, 15 farmers representing large farms were interviewed in 2014 to consider the diversity of farming systems. The final sample included 175 farmers (Juanes et al., 2020).

We developed and applied a semi-open-ended questionnaire for use at the farm level (Juanes et al., 2020). We explored three components in the farm survey: (1) family and house descriptions to assess family living conditions, (2) descriptions of the land and cropping systems used, including use of organic and mineral fertilizers, and (3) livestock structure and management, i.e., feeding system, animal movements (entries and exits), and animal performances.

For this paper, we selected the small and medium farms and removed two farms with incomplete datasets for crop management practices. In total, our final sample was 158 farms. Our sample was reduced to 154 farms for the calculation of agronomic indicators due to a lack of data on manuring practices on four farms.

Additionally, we conducted complementary interviews with Bedouin pastoralists around Tiba to understand the herds' contribution to manure provision and N supply for sedentary farms in the area (see **Supplemental Material c**). This fieldwork involved open-ended interviews with 10 Bedouin herders operating in the Tiba area. Each interview was composed of three parts: (1) history of the farmers and their family in the zone, (2) herd composition and the calendar of grazing per month over the previous year, and (3) arrangements and grazing costs. This research revealed the social and environmental links between the settled farms and Bedouin livestock systems by analyzing grazing practices and contracts at a territory level. Consequently, these practices were examined in conjunction with the diversity of farming systems in the Tiba zone.

Diversity of Settled Crop-Livestock Farming Systems

Considering the diversity of farming systems in the NRLs due to the gradient of settlement and the settlers' differential background (Alary et al., 2018), we used a multiple factorial analysis (MFA) to identify and characterize the prevailing farming systems. The variables in the MFA were: (1) the livelihood assets representing "family" characteristics (family structure, education level, family workers), "land" access (land tenure, cultivated land), and "livestock" asset (animal stock, livestock composition per species), and (2) farm management related to "labor" (contribution of family members and occasional workers), the "cropping system" (land use), and "livestock" system (animal management and performance). In these mixed crop-livestock systems, "dairy activity" reflects the degree of intensification regarding livestock activity and its position in the farming system. In total, we chose 37 variables classified into six thematic groups to understand the diversity of structure and functioning of the farm systems (**Table 1**). The variables of land tenure and district were projected as supplemental variables. The MFA approach allow us to calculate a series of scores that expressed similarities and differences between families. These scores were used to construct a hierarchy of partitions through agglomerative hierarchical classification (AHC) (Manly, 1994). All calculations were performed using the ADE4 package (Thioulouse et al., 1997) in R software (R Core Team, 2014) and resulted in clusters that characterize the prevailing farming systems in the entire zone.

TABLE 1 | Active variables classified into six thematic groups to represent the diversity of family farming systems in the newly reclaimed lands (Egypt).

Themes	Variables	Main hypothesis
Family	Education of the family head Age of the family head Family size; % schooled children; Number of children working on the farm; Number of potential male workers in the family; Number of potential female workers in the family; Number of family members working outside the farm; The number of family members who can work out of the farm.	Human asset, especially family composition and educational level, explain farm practices;
Labor	% of the salaried workforce in the total farm workforce; number of salaried agriculture worker; number of family farmworkers; total of farm employment (including family and salaried workers).	Labor management is a major factor to explain crop choices
Land	First land access in the zone; Total area owned by the family; The total cropped area by year; % rent land of total cultivated land; Purchased land area; Land accessed within the settlement program.	Land access and land tenure condition the land security and, consequently, the farm activities.
Crop system	% area cultivated with fodders; % area with food crops; % area with cash-crops; trees' area; % maize area; % wheat area.	Crop pattern
Livestock	Number of Total Livestock Unit (TLU); Number of fattening animals; Number of dairy animals; % dairy crossbred (/total dairy animals); % dairy buffaloes (/total dairy animals); Number of small ruminants. The number of fowls.	Livestock management
Dairy activity	Animal product in EGP (Egyptian pounds); % dairy product; Milk yield per head; Dairy product in EGP/total fodder area; Total TLU per fodder areas.	Dairy specialization

Nitrogen Balances of Sedentary Farms With and Without Interactions With Mobile Pastoral Herds

In the present research, the environmental analysis is on the nitrogen dynamics and the quantification of nitrogen flows more precisely. Two environmental indicators were calculated at the farm level: the N balance and the N use efficiency. The apparent N farm-gate balances (Simon and Le Corre, 1992; Nevens et al., 2006; Vayssières et al., 2011) corresponds to the farm N surplus (NS) (in kg N ha^{-1} year^{-1}), i.e., a positive and high N balance corresponds to a soil fertility increase, but also with a risk of N leaching. It was calculated as follows:

$$NS = (N_{\text{in}} - N_{\text{out}})/UAA \tag{1}$$

The farm N-use efficiency (NE) corresponds to the farm's ability to use N resources (like manure or feeds) to produce N (edible products). A higher efficiency corresponds to a more efficient and sustainable farm. It was defined as the dimensionless ratio:

$$NE = N_{\text{out}}/N_{\text{in}} \tag{2}$$

Where UAA is the total Agricultural Arable Land (in ha), N_{in} (in kg N year^{-1}) is the sum of N in imported biomass: concentrate feeds, forages, animals, mineral fertilizers, and manure. N_{out} (in kg N year^{-1}) is the total amount of N in exported biomasses: animals, milk, and crop products.

N inputs to crops comprise on-farm produced manure, off-farm purchased cattle and chicken manure, and mineral fertilizers. In our case study, the on-farm produced manure was mainly from cattle or buffalo. The quantity was estimated from the seasonal amounts of the overall manure spread on the land, the size of the area concerned, and the type of manure (fresh or dry with straw). We estimated an average density of 750 kg fresh matter per cube meter for bovine manure. The amount of purchased chicken and bovine manure (mainly to large dairy companies in the zone) was estimated from the total number of carts purchased by the farmers, using the average amount of manure per cart.

The N contents of the different biomass types were calculated based on previous research (FAO, 1978, 2005). We used technical coefficients to convert the quantity of manure into kilograms of nitrogen (N). For purchased mineral fertilizers, we used their composition. Estimating the N input for purchased feed and the

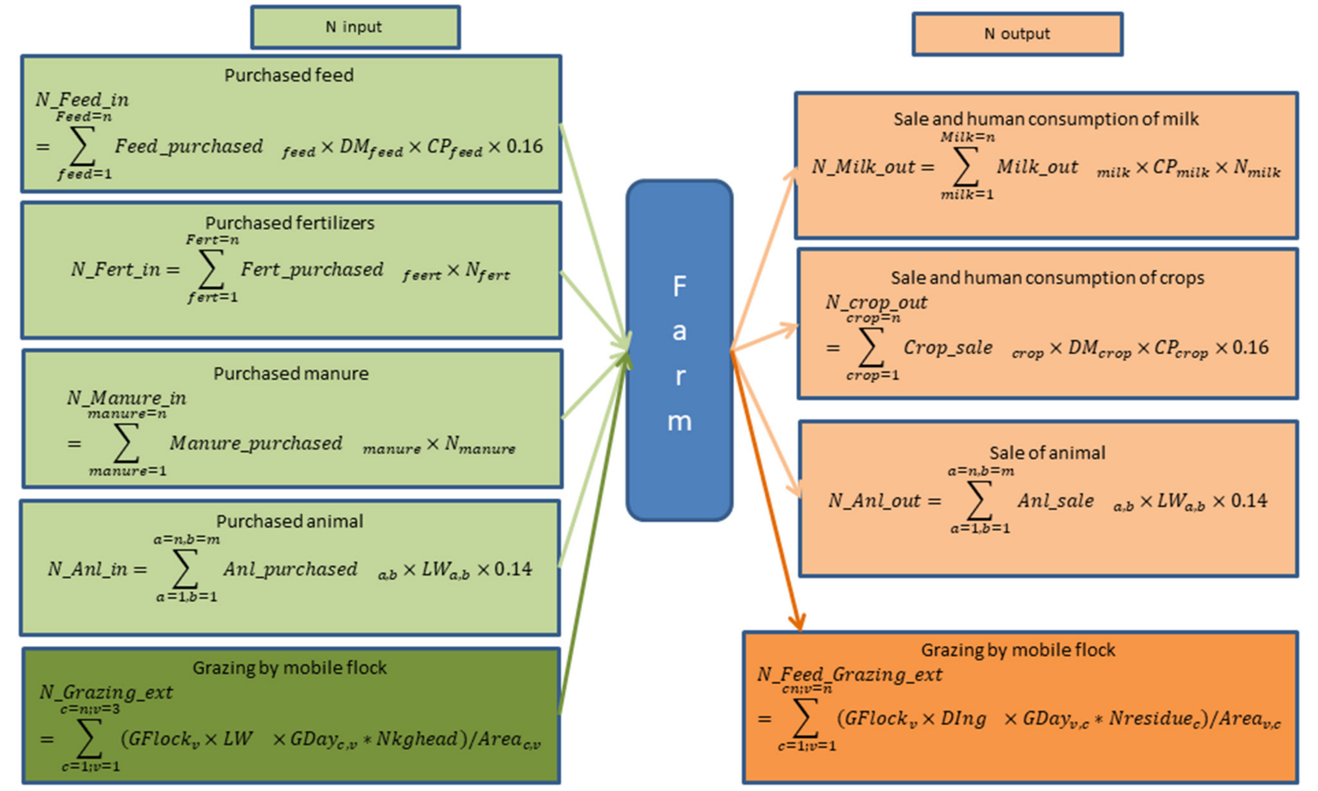

FIGURE 2 | Calculation of Nitrogen farm balance without (light color) and with (light and dark colors) taking account N flows due to grazing of mobile flocks. Feed: category of feed; Feed_purchased: quantity of feed purchased (kg yr l); DM: Dry matter intake; CP: crude protein content per kg; Fert: category of mineral fertilizer; Fert_purchased: quantity of purchased fertilizer per year; N: nitrogen content per kg; manure: type of manure (origin; mode of spreading); manure purchased: quantity of manure purchased per type; a: category of ruminant (buffalo; cattle; sheep; goat); b: category of age; An l_purchased: number of animal purchased; LW: live weight per head; Milk: category of milk product (by specie; by product: fresh, butter cheese); Milk_out: quantity of milk use; Crop_out: quantity of crop sold or consumed; crop: type of crop; Anl sale: number of head of animal sold; v: village for territorial nitrogen balance; c: residues crops; GFlock: grazing flock (in number); Gday: number of grazing days; Nkgh: eat nitrogen produced by head of the mobile flock; N residue: N content (kg yr^{-1}) of crop residual; Area: grazed crop area.

N output for the selling or self-consumption of crop products and residues required the use of a multitude of sources due to the diversity of crops and feeds at the different farms, such as Nijhof (1987a,b,c) and USDA (2015). The coefficients by crop products used in this study are in the **Supplemental Material a,b**. We estimated that 1kg of animal contained ∼0.5 kg of muscle with 28% protein for livestock. **Figure 2** represents the categories of input and uptake taken into consideration to estimate the N balance at the farm level.

In parallel, we assessed grazing contribution to fertilization levels based on the interviews with Bedouin herders in the Tiba area. We identified three grazing zones for three herder groups determined by their tribal memberships and their internal arrangements from the qualitative interviews. According to the cropland allocation in these zones, the herd size, and time spent in the zone, we estimated the quantity of organic manure provided by sheep and goats grazing in the Tiba zone. From the average amount of manure produced per head of sheep and goats, we estimated the N supply using coefficients from experimental trials on the quantity of defecation per day for each animal species and the estimation of nitrogen content (see Richard et al., 1989). For a sheep weighing an average of 32 kg live weight (LW), the daily ingestion of dry matter (DM) would be ∼460–780 g DM/day. With a digestibility of roughly 55.1%, the total defecated matter was estimated at 206–350 g DM. Assuming DM is one-third fresh matter, the average quantity of fresh matter of produced manure per head was 850 g/day per animal with a nitrogen content of 0.8%. For each zone (corresponding to one or two villages), we multiplied this coefficient by the number of animals and the number of grazing days described by the Bedouin herders to estimate the total N input in each grazing zone for 1year. Following the same method, we evaluated the N intake from crop residues based on a daily intake of 620 g DM/day/head.

RESULTS

Overview of the Diversity of Farming Systems in the NRL

The description of farming system diversity resulted from the MFA and clustering analysis to identify farm types from the farm survey database. The first analysis of variance shows a well-structured configuration based on the first two axes,

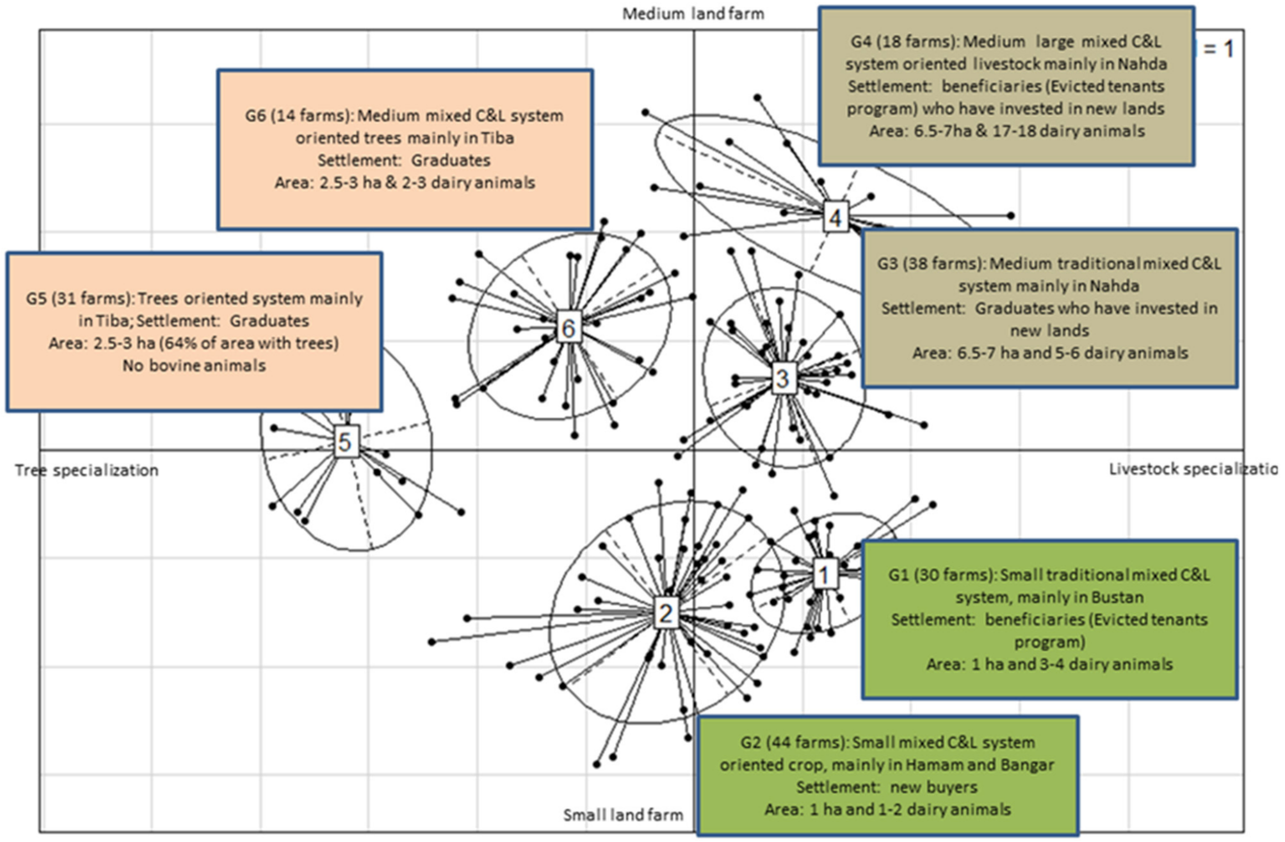

FIGURE 3 | Representation of the six family farming systems and their main characteristics in the first factorial plan (F1*F2). (1) C&L for integrated Crop and Livestock systems; (2) Each circle represents the confidence interval at 95% and the lines are the distance between each individuals and the center of gravity of each cluster.

representing 70% of the total variance (**Figure 3**). We observed a clear differentiation of the family farming systems according to land access on the first axis (37% of the Eigenvalue) and the tree *vs.* livestock orientated systems on the second axis (33.8% of the Eigenvalue). The agglomerative hierarchical classification allowed us to identify six clusters of family farm systems that were projected on the first factorial plan (F1*F2) in **Figure 3**.

Four of the six farm systems are considered as mixed crop-livestock systems from the Old NRLs (Groups G3 & G4 in **Figure 3**) and New NRLs (groups G1&G2, **Figure 3**). The medium and medium-large farm systems (Groups G3 & G4) started their activities in the 1970s and 1980s; most of these farm systems are located in the oldest land that was reclaimed in the 1960s (Nahda). The medium-sized farm systems (G3) are ∼2.5 ha in size and have 6 to 7 bovine animals, mainly consisting of crossbred cows for milk production. The large farms in Nahda (G4) have an average land area of 6.7 ha and ∼18 dairy animals, primarily consisting of 60% crossbred cows. The small-scale farms (G1) are located in the recently reclaimed lands from the 1980s (Hammam and Bustan). Another group comprises the non-graduate beneficiaries that obtained 1 ha within the Mubarack settlement program for evicted tenants. The other group (G2) includes new buyers who bought the land from other beneficiaries. For groups G1 to G4, the cropping system is based on a rotation of wheat and berseem (*Trifolium alexandrinum*) in winter with maize and various vegetables in the summer. Berseem and maize are mainly used for animal feed. Groups G5 and G6 (**Figure 3**) are tree-oriented farmers that recently obtained land in the New NRL, mostly in the Tiba zone and, to a lesser extent, in the Bustan zone. The majority of these farmers are University graduates who obtained 2 ha of land by auction at their arrival. Generally, these farmers opted for tree crops that would allow for more market opportunities. Group 5 is the most tree-specialized system.

Contribution of Livestock Activities to Crop Fertilization at the Farm Level

At this stage, we estimated the nitrogen flows entering cultivated plots for each farm type. The objective was to understand the relative contribution of livestock, through on-farm produced and off-farm purchased manure, to crop fertilization at the farm level without considering the manure from grazing by mobile herders. **Table 2** shows the relative contribution of produced and purchased bovine manure for each farming system. First, manure, including chicken and bovine manure, contributed up to 51% of the N supply in tree-oriented systems (G5), compared to the average 40% for the total farming systems. The lowest

TABLE 2 | Fertilization management at the farm level, without inputs from leased grazing (154 farms).

Farm types	G1	G2	G3	G4	G5	G6	Average
Sample	30	43	29	11	12	29	154
N input from bovine manure as a % of all the N used to fertilize crops from manure, including chicken manure	47%	46%	53%	54%	56%	49%	49%
N input from manure as a % of the total N used to fertilize crops, including mineral fertilizers.	40%	43%	35%	38%	51%	34%	40%
Farmers purchasing off-farm manure (% of farmers who purchased manure in the whole farmer population)	33%	47%	38%	18%	25%	38%	37%
The proportion of off-farm purchased bovine manure (% of the total used bovine manure, only for farmers who purchased bovine manure)	76%	80%	95%	100%	100%	70%	82%
N input (kg N/ha/crop cycle)	451	388	455	337	288	271	379
Cost of mineral fertilizer for food crops (US$/ha/crop cycle)	467	396	504	518	608	371	450
Cost of mineral fertilizer for fodder crops (US$/ha/crop cycle)	145	89	127	100	24	105	106

organic manure users were medium and large mixed crop-livestock systems in the Old NRL (G3 and G4 in the Nahda zone), suggesting that farmers settled in Nahda have already constituted their soil substratum over the 6 last decades of cultivation.

The origin of manure varied according to the zone and the farming systems. However, the proportion of bovine manure was approximately half of the manure input in the whole studied zone. About 37% of farmers purchased bovine manure (mainly from large dairy companies); among these farmers, the proportion of off-farm purchased bovine manure represented more than 70% of the bovine manure used on lands. In the tree-oriented farms (G5) and the large mixed farming systems (G4), <25% of the farmers purchased bovine manure. In general, most farmers are reluctant to buy bovine manure due to their fear of the dissemination of infectious diseases.

The N plot level inputs reached ∼379 kg N per ha and per crop cycle. This rate is extremely high. This desert environment is characterized by low organic matter in the soils, and this explained the manure's role as an organic matter amendment to the soil. The N input rate is the weakest for tree-oriented farms (G5 and G6), where farmers regulate fertilization according to perennial crops' N needs over the year. These results show the different roles of organic manure in this environment. The increasing gradient of manure use from the Old NRLs to New NRLs reflects the importance of organic manure in the first decades of desert land cultivation to build the soil organic matter capital in an arid desert with sandy soil (Enien et al., 2000; Malm and Esmailian, 2012).

The bovine manure purchase price was similar among the five zones, with a range of ∼11–13 US dollars per m^3 (**Table 3**). The chicken manure purchase price was the highest in Hammam, where the villages were distant from poultry farms. For mineral fertilizers, farmers in the Bustan zone paid the highest price per unit, mainly for ammonium nitrate and urea. In this zone, most farmers were obliged to cover their needs with mineral fertilizers from the market, which are more expensive than mineral fertilizers distributed through the cooperative. Some farmers in this zone preferred continued purchase of mineral fertilizers from their village of origin in the Nile Delta (Alary et al., 2018). In the other zones, the majority of the fertilizer input came from the local agricultural cooperative.

According to the interviewed farmers, the supply of bovine or chicken manure did not raise any problems due to the proximity of large specialized dairy farms or even multinational dairy farms with more than two thousand dairy cows. Only the limited supply capacity for mineral fertilizers by the agricultural cooperatives was systematically mentioned as a critical issue, knowing that the price doubled from that of the agricultural cooperative to that of the market for ammonium nitrate and urea.

Table 4 represents the nitrogen input and output at the farm level without considering grazing by mobile livestock. Mineral fertilizers and manure are the main N inputs (on average 84.1 and 12.6% of total farm N input, respectively), while crop products are the main output (on average 91.7% of total farm N output). The N input as mineral fertilizers and manure (both used to fertilize crops) exceed 2 to 3 times the N output from crop products, resulting in a positive N balance at the farm level that ranges from 221 to 488 kg N/ha/year. The farm N balances per ha are greater for mixed crop-livestock systems (G1, G2, and G3) than tree-oriented or specialized systems (G5 and G6, respectively); these higher N balances correspond to the higher purchase of mineral fertilizers for annual crops and feeds for livestock. N-use efficiencies range from 0.2 to 0.5. Efficiencies are higher for tree-specialized systems (G5) than livestock-oriented systems (G1, G3, and G4), which align with trees' capacities to uptake N from the atmosphere and soil.

Territory Level-Approach of N Flows and the Consequent Social Interactions Between Pastoral Herders and Farmers

Open interviews conducted with Bedouin herders in the Tiba area allowed us to understand the current tensions between pastoralists and farmers in the zone. In this territory, the majority of Bedouin herders originated from Wadi El Natrun. Their ancestors used to travel to the Tiba zone for rangeland when it primarily consisted of herbaceous and shrub vegetation until it was reclaimed for cropping. Thus, the Tiba zone is still perceived

TABLE 3 | Unit purchased price of organic and mineral fertilizers (in US$).

Zones	Bustan	Tiba	Hammam	Bangar	Nahda	Average
Bovine manure (US$/m^3)	13.5	10.6	12.6	12.9	11.2	12.1
Chicken manure (US$/m^3)	24.1	24.7	32.5	25.9	22.0	25.8
Ammonium Nitrate (US$/kg)	0.43	0.39	0.34	0.39	0.34	0.38
Sulfate ammonium (US$/kg)	0.23	0.23	0.22	0.29	0.44	0.28
Superphosphate (US$/kg)	0.18	0.14	0.15	0.14	0.13	0.15
Urea (US$/kg)	0.52	0.32	0.37	0.39	0.36	0.39

TABLE 4 | Nitrogen (N) flows, N balance, and N use efficiency at the farm level (154 farms), without inputs from leased grazing.

Variables	G1	G2	G3	G4	G5	G6	Average
Sample by farming type	30	43	29	11	12	29	-
N input (kg N) at the farm level							
Feed and forage purchases	46	20	28	29	1	14	23
Animal purchases	11	4	20	21	2	4	10
Mineral fertilizers	578	595	1099	971	541	788	844
Purchased manure	87	113	186	145	130	108	126
Total N inputs	722	733	1333	1167	673	914	1003
N outputs (kg N) at the farm level							
Animal sales	21	20	41	57	6	23	27
Animal product sales (e.g., milk)	7	4	11	23	0	6	8
Crop products	234	238	474	508	156	332	386
Total N outputs	262	261	525	589	163	361	421
N balance as input-output (kg year^{-1})	461	471	808	578	510	553	582
N use efficiency at farm level (outputs/inputs) (Dmnl*)	0.4	0.4	0.4	0.5	0.2	0.4	0.4
N balance per hectare of arable land (kg N ha^{-1} year^{-1})	442	488	422	263	257	221	367
N balance in kg per ha and per crop cycle (kg ha^{-1} year^{-1})	215	175	213	132	134	108	165

**Dmnl, dimensionless.*

and considered by the Bedouin herders as their tribal territory. Three main tribes are always present in the zone: *Gwabis*, mainly located in the southeast of Tiba, and *Ali Ahmar* and *Snena* in the northeast (**Figure 4**). These three Bedouin groups lived in tents until the end of the 1990s and the establishment of the canal in the Tiba zone. In 2014, most Bedouin herders were obliged to settle in blockhouses at the borders of the Tiba zone, but they were not given access to a water supply, electricity at home, and social infrastructure (no school or health care center). Since settlers' arrival on the NRLs, Bedouin herders have followed the agricultural calendar for grazing land (**Table 5**). In most cases, herders and landowners orally negotiate the terms of grazing, specifying the duration of grazing and the total cost. The charge for grazing paid by the herders varies from 39 US dollar/ha for sugar beets up to 91 US dollar/ha for peanuts in 2014, knowing that a flock contains ∼360–400 head (**Table 5**). As the grazing fee is negotiated for each plot and between the herder and the landowner, this cost is similar throughout the zone depending primarily on the available grazing resources (on pastureland) in the Wadi Natrou (i.e., the surrounding pastureland around the settlement). Some herders arrange for extra land in other neighboring villages. However, they previously grazed mainly in two villages in the area.

In the Tiba zone, mobile pastoral herds grazed on crop residues from March to October, starting with sugar beets in March–April, wheat in May, bean in June–July, and peanuts from September–October (**Table 5**). During the winter season, they moved to open pastureland along the international Cairo-Alexandria Road (see **Figure 3**), and feed was complemented with concentrates. Some herders store crop residues for the winter to complete the animal diets from November to December.

We estimated the grazing effect by mobile herds in terms of nitrogen flows entering and exiting cultivated plots (**Table 6**). The calculation of these N flows used the data from grazing management (herd size, duration), as described by Bedouin herders, and the average quantity of ingested forages and produced manure per grazing animal. These flows represented from 9 to 34% of farm-level N input and from 25 to 64% of farm-level N output depending on the village, the cropping system, and the tree plantation stage. In our case study, due to the recent tree plantations that are not yet producing, N output level appears very important. So, N feed intake by mobile herds is higher than N manure excreted on the fields, resulting in a negative N balance (estimated from the difference between N manure excreted and N feed intake), ranging from −9 to −42 kg

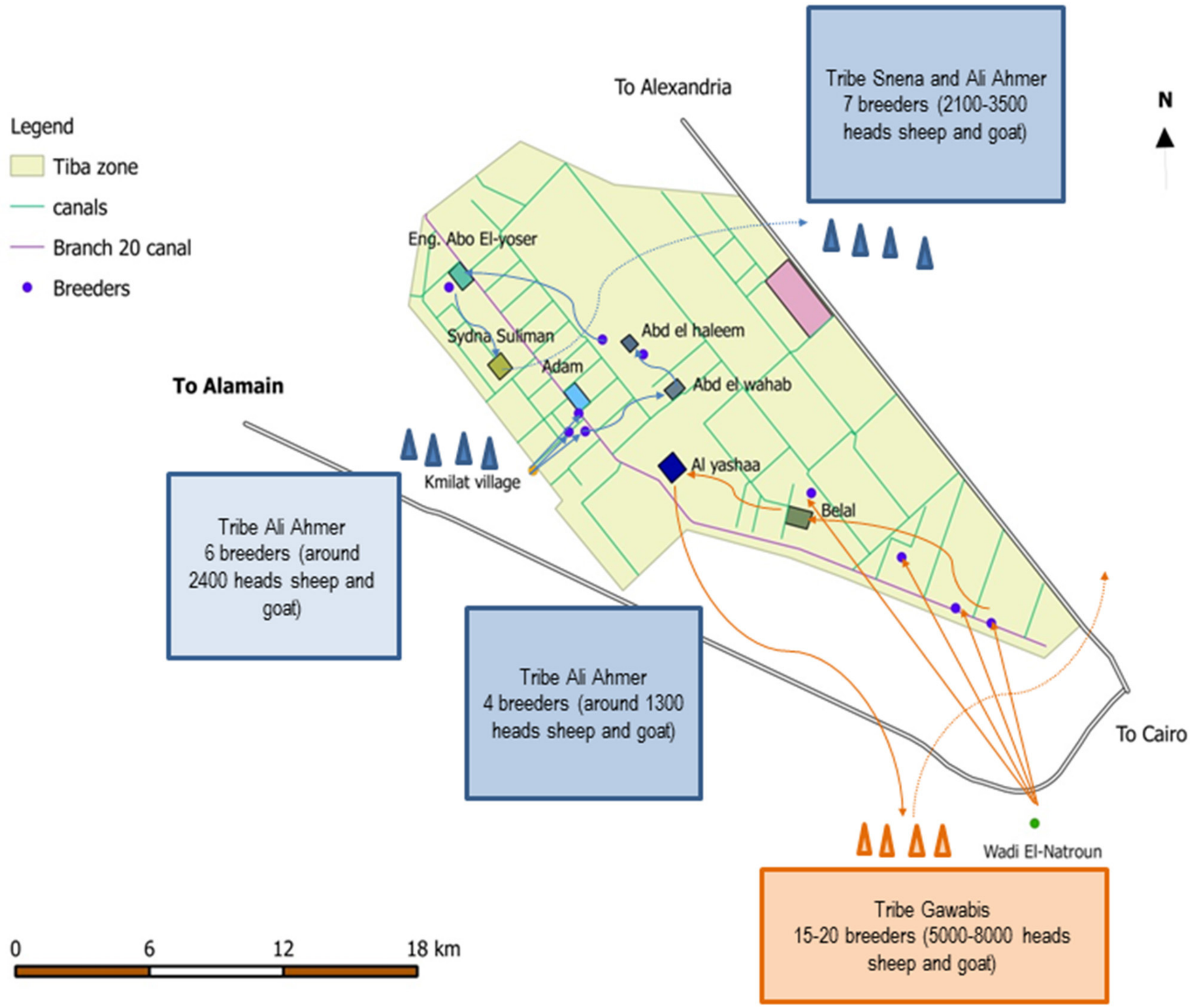

FIGURE 4 | Herd grazing circuits for the three Bedouins tribes in the Tiba zone (based on interviews).

TABLE 5 | Calendar of grazing period and total head manuring per season.

Months	First feed source	Range of cost payed by the herder (US$/ha per flock)	Grazing period (days per ha)	Number of sheep (head/ha/day)	Total manure input (kg N ha^{-1})	Unit feed cost (US$ per head and per day)
January to February	Rangeland	0				
March to April	Sugar beet	39–58	13.1	364	32.4	0.059
May	Wheat	73	3.0	562	18.2	0.187
June to July	Beans	72–86	6.6	805	45.6	0.084
August to October	Peanuts	60–91	22.1	419	52.2	0.088
November to December	Concentrates	-				

TABLE 6 | N flows due to grazing and N balance at the territory level taking account grazing practices.

Village	Adam village	Belal+Yashaa	Soliman
Descriptive characteristics of each sub-locations (grazing lands in ha and the animal stock)			
Mobile herds (Sheep and goats heads)	1,300	6,000	2,400
Surgarbeet (ha)	83	123	25
Bean (ha)	0	74	8
Wheat (ha)	53	364	204
Peanuts (ha)	34	235	60
Feed intake (in kg DM/ha/year)			
From sugarbeet	582	1,820	3,603
From Bean	0	3,002	11,188
From Wheat	461	306	219
From Peanuts	2,106	1,423	2,230
Tot ingested N by grazing flocks (kg N/ha/year)	43.2	91.0	231.4
% N farm outputs through grazing	25%	41%	64%
Manure supply (in kg FM/ha/year)			
To sugarbeet	797	2,495	4,939
To Bean	0	4,116	15,338
To Wheat	631	420	300
To Peanuts	2,888	1,952	3,057
Tot N supply by grazing flocks (kg N/ha/year)	34.5	71.9	189.1
% N farm inputs through grazing	9%	17%	34%
Grazing balance (kg N/ha/year)	−8.6	−19.1	−42.3
N balance at territorial level (kg N/ha/year)	223	213	190

1) the descriptive data gives the total land allocation by crops and the sheep and goat flock for each sub-location; 2) Feed intake in kg of dry matter per year is estimated from the total daily ingestion per the entire flock multiplied by the number of grazing days and divided by the grazing area; Total ingested N by grazing flocks is calculated based on the N content by kg DM of feed and the % N farm outputs and reported to the total N export per ha (composed of the N farm exit calculated in part 3.2); 3) The manure supply from the grazing flock is estimated by the total flock multiplied by the daily manure production divided by the number of grazing-days on the plots; Based on the N content by kg of fresh matter of manure, it is estimated the total N supply by the grazing flock per ha, and this is reported to the total N farm inputs estimated in this location;4) the grazing balance is the difference between the N supply and N exit from the grazing activity although the N balance at the territorial level is the difference between the total N input and output based on the farm and grazing practices.

N/ha/year. This N balance explains why the N balance at the territory level (ranging from 190 to 223 kg N/ha/year depending on the village) is lower than the N balance at the farm level (ranging from 221 to 257 kg N/ha/year depending on the farm type); the crop area in the current database corresponded to the cropping system in 2013–2014. With the rapid extension of tree plantations in the Tiba zone and the start of production of the plantations, crop residues grazing should be more restricted in the coming years by the landowners who will seek to protect their plantations. However, these preliminary results show how farmers can benefit from direct N-fluxed measurement to enhance N management.

According to the Bedouin interviewees, the main roles attributed by landowners to grazing herds were to clear the land and provide a supplementary income. On average, land leasing for grazing represented ∼200–220 US dollars/farm/year in 2015. The main reluctance of landowners is the risk of disease dissemination due to manure use, especially following the outbreak of foot and mouth disease in the area. However, farmers' mentioned benefits were that allowing herding keeps the land safe and, above all, prevents trouble or "looting" or "racketeering" with the Bedouin community. The majority of landowners said they feared trouble, land damage or racketeering caused by the mobile herders. Some of the farmers felt that one way to avoid social conflicts with Bedouins was to allow for grazing, consequently keeping the land safe.

DISCUSSION AND CONCLUSIONS

In African countries, manure represents a pivotal contributor to the fertilization of crops and reduced depletion of soil fertility (Rufino et al., 2007), and improving soil stability and its macro-structure (Bayu et al., 2005). Overall, nutrient cycling between livestock and crops through manure management and crop residue-based feeding systems are key-drivers to improve efficiency and sustainability of smallholder systems (Smith et al., 2009; Powell et al., 2010; Vayssières and Rufino, 2012; Alvarez et al., 2014). In the Mediterranean area, the intensification of cropping systems favoring tree plantations or cash crops along the coastline can favor the abandonment of livestock on farms and the relocation of livestock activities to the hinterland of either the mountains or non-irrigated plains. This farm specialization casts doubt on environmental sustainability, and it leads us to consider ways to strengthen relationships at the territory level between sedentary farms and mobile livestock systems (Alary et al., 2019). Therefore, studying the contribution of pastoral farming to agricultural systems at the territory scale allows us to better understand the possible synergies between these two systems through supporting sustainability-building social and ecological relationships.

Results reveal the critical role and contribution of livestock activity to crop fertilization and soil fertility maintenance, especially over the first decade of cultivation of the newly reclaimed desert land where manure is a significant source of N and organic matter. However, we observed a differential gradient of manure use according to the date of land settlement. In this new socio-economic environment, fertilization management varies according to the degree of integration of crop and livestock activities at the farm level based on the past experience (mainly knowledge and practices inherited from ancestors) of the new settlers coming from various agro-ecological regions of Egypt. At the territory level, the results reveal the multiple ecological and social services provided by diverse livestock systems to agriculture in Egypt's newly reclaimed desert land. Significantly, mobile herders' presence on the cultivated lands is as important in terms of support for social safety in the zone as it is in terms of valorizing residues. Moreover, the manure spread by animals contributes to soil structure maintenance. However, the input or output fluxes of nitrogen modify the final nitrogen balance at the farm level. This effect merits further attention from local or national agencies, especially those in charge of fertilization recommendations in the zone.

The system-gate approach based on the quantification of apparent N flows through farmers interviews gives a first calculation of the farm-gate N balance. These calculations highlight positive and high N balances in all farming systems (with an average N balance of ∼+367 kg/ha), that we can also observe in other parts of the world where farming systems use high levels of inputs as mineral fertilizers or concentrate feeds (Vayssières et al., 2009; Conijn et al., 2011). These high balances correspond to high N surplus and low N use efficiencies, resulting in a high risk of N losses to the environment, especially on sandy soils where N leaching can be substantial (Cameron et al., 2013). Soil N content measurements should confirm these potential risks. N flows quantification under real conditions, including soil N leaching and N gaseous emissions, would be valuable to confirm environmental risks and enhance soil fertility dynamics through manure management practices.

Finally, this study calls for socio-technical support to better understand nutrient and organic matter supplies and dynamics, especially the use of mineral fertilizers combined with manure, in accordance with soil management practices and social practices around livestock management social organization in the zone. Nutrient management is not only a matter for agronomists. Soil fertility maintenance as a livestock function involves a new way of thinking about the whole system, integrating territory-level dynamics, and calling for a renewal of livestock policy development that focuses on food and income production and supports good social and environmental relationships and opportunities for synergy.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Materials**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

VA contributions to the conception or design of the work/field work, drafting the work or revising it critically for important intellectual content, and write the paper. AA-N contributions to the conception or design of the work and provide approval for publication of the content. MO contributions to the conception or design of the work and contribution to farm data analysis. ID contributions to the conception or design of the work for approaching pastoral systems. JV Agree to be accountable for all aspects of the work related to the approach of nitrogen balance at the farm and local level, and co-write the paper. All authors contributed to the article and approved the submitted version.

ACKNOWLEDGMENTS

The material presented here has been collected in the framework of two collaborative research projects named CLIMED on The future of Mediterranean Livestock Farming Systems: Opportunity and efficiency of Crops–Livestock Integration, within the research program ARIMnet (2012–2016) and NARS on Collective action and agricultural productivity in Egypt's New Lands (Nasr canal command area), within the AIRD (Agence inter-établissements de recherche pour le développement) research program in Egypt. These two projects associated CIRAD (Center International de Recherche Agronomique pour le Developpement), ICARDA (International Center for Agricultural Research in the Dry Areas), and Animal Production Research Institute, Egypt (APRI). We especially thank all the researchers from CIRAD and APRI for their active participation in data collection and management and all the farmers and stakeholders in the studied areas. The current research paper has been done within the CGIAR Research program. The authors wish also to thank all donors and organizations who globally support the CGIAR Research Program's work through their contributions to the CGIAR system.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2021.500437/full#supplementary-material

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