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Health-Promoting Phytonutrients Are Higher in Grass-Fed Meat and Milk

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While commission reports and nutritional guidelines raise concerns about the effects of consuming red meat on human health, the impacts of how livestock are raised and finished on consumer health are generally ignored. Meat and milk, irrespective of rearing practices, provide many essential nutrients including bioavailable protein, zinc, iron, selenium, calcium, and/or B_{12}. Emerging data indicate that when livestock are eating a diverse array of plants on pasture, additional health-promoting phytonutrients—terpenoids, phenols, carotenoids, and anti-oxidants—become concentrated in their meat and milk. Several phytochemicals found in grass-fed meat and milk are in quantities comparable to those found in plant foods known to have anti-inflammatory, anti-carcinogenic, and cardioprotective effects. As meat and milk are often not considered as sources of phytochemicals, their presence has remained largely underappreciated in discussions of nutritional differences between feedlot-fed (grain-fed) and pasture-finished (grass-fed) meat and dairy, which have predominantly centered around the ω-3 fatty acids and conjugated linoleic acid. Grazing livestock on plant-species diverse pastures concentrates a wider variety and higher amounts of phytochemicals in meat and milk compared to grazing monoculture pastures, while phytochemicals are further reduced or absent in meat and milk of grain-fed animals. The co-evolution of plants and herbivores has led to plants/crops being more productive when grazed in accordance with agroecological principles. The increased phytochemical richness of productive vegetation has potential to improve the health of animals and upscale these nutrients to also benefit human health. Several studies have found increased anti-oxidant activity in meat and milk of grass-fed vs. grain-fed animals. Only a handful of studies have investigated the effects of grass-fed meat and dairy consumption on human health and show potential for anti-inflammatory effects and improved lipoprotein profiles. However, current knowledge does not allow for direct linking of livestock production practices to human health. Future research should systematically assess linkages between the phytochemical richness of livestock diets, the nutrient density of animal foods, and subsequent effects on human metabolic health. This is important given current societal concerns about red meat consumption and human health. Addressing this research gap will require greater collaborative efforts from the fields of agriculture and medicine.

Keywords: meat, milk, phytochemicals, organic, grass-fed, health, sustainability, nutrition

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INTRODUCTION

Navigating discussions on red meat and human and environmental health are challenging. On the one hand, reports such as those by the EAT-Lancet Commission asks consumers to embrace near plant-exclusive diets to reduce our impacts on planetary health (Willett et al., 2019). On the other hand, reports such as those by the United Nations Intergovernmental Panel on Climate Change (IPCC, 2019) suggest a critical role for sustainable livestock production systems in climate change mitigation by integrating tree, crop, and livestock production systems, while ensuring global food security and nutrient adequacy via consumption of moderate amounts of animal foods.

Meanwhile in the field of human nutrition, a wealth of epidemiological data associate animal food consumption, particularly red meat, with increased risk of cancer (Chan et al., 2011), cardiovascular disease (Zhong et al., 2020), obesity (Wang and Beydoun, 2009), and diabetes (Micha et al., 2012). This has led to widescale public health recommendations by the American Heart Association (Arnett et al., 2019), the World Health Organization (Bouvard et al., 2015), and the Dietary Guidelines for Americans (USDA, 2015) to reduce red meat consumption in an effort to halt metabolic disease. However, these recommendations have been challenged by the NutriRECS consortium, as scrutinizing the data with the GRADE (Grading of Recommendations, Assessment, Development, and Evaluations) system resulted in considerable uncertainty regarding the robustness of evidence associating consumption of red meat with increased risk of metabolic disease (Johnston et al., 2019).

While public health experts and climate scientists argue about whether we should rely on livestock production systems to meet the nutritional demands of a growing global population while tackling climate change, those who produce our food—the "average" farmer—are struggling financially (Wiggins et al., 2010). To make a decent living, farmers must balance trade-offs between land ecology, animal welfare, and profitability, which in modern-day farming practices are not necessarily in agreement with each other. High costs for inputs, but low income from farming, has created depression and suicide rates well-above national averages amongst farmers in the US, New Zealand, Australia, and Europe (Klingelschmidt et al., 2018).

Yet some farmers have costs of production much less than the national average and are able to cut costs, and thereby increase the profitability of their operations (Provenza, 2008). Increased consumer demand for (local) grass-fed meat and milk have encouraged a number of producers to implement farming practices many describe as regenerative agriculture (i.e., farming in harmony with agroecological principles). As some farmers have learned, they are able to cut costs and increase profits by focusing on reducing inputs such as water, fertilizer, concentrate feeds, and herbicides; by raising multiple species of livestock on diverse assemblages of cover crops and/or perennial plants; and by selling their meat and milk directly to consumers (Massey, 2017; Brown, 2018).

Pasture-based grazing systems, when managed in ways that mimic natural ecosystems, can improve plant diversity (Teague, 2018), soil carbon levels (Allard et al., 2007; Stanley et al., 2018), ecosystem function (Krausman et al., 2009; Teague and Kreuter, 2020), and water retention and quality of fresh water systems (Park et al., 2017). As the IPCC (2019) notes, Earth's health depends upon plant diversity and abundance, which can be improved by managing the grazing behavior of livestock when done in concert with agroecological principles (i.e., that mimic natural processes). That should come as no surprise in the light of plant-herbivore coevolution, which have evolved to form complex reciprocal relationships over millions of years.

The constant "arms race" between plants and herbivores has resulted in an extraordinary diversity of phytochemicals produced by plants (Burkepile and Parker, 2017). In turn, many of these plant phytochemicals are concentrated in the meat and milk of livestock grazing these plants (Børge et al., 2016; Delgadillo-Puga et al., 2019; Prache et al., 2020); their presence may act synergistically to enhance human health (Barabási et al., 2020). Importantly, the presence of these phytochemicals in pasture-raised animal products remains largely underappreciated in discussions of nutritional differences between grain-fed and pasture-raised (grass-fed) meat and dairy, which have predominantly been centered around the ω-3 fatty acids and CLA (Provenza et al., 2019). In this review, we discuss the information currently available on the wide range on phytochemicals found in grass-fed meat and dairy products and evaluate their potential health effects.

WHY BECOMING LOCALLY ADAPTED MATTERS

Natural landscapes are diverse mixtures of plants that occur in patches reflecting history of use in concert with particular soil, precipitation, and temperature regimes. Plants are nutrition centers and pharmacies with vast arrays of primary (e.g., protein, fiber, carbohydrates, fats, vitamins, and minerals) and secondary compounds (e.g., phenols, terpenoids, anti-oxidants, organic acids, and other phytochemicals) useful in both animal (Craig, 1999; Poutaraud et al., 2017) and human health (Kris-Etherton et al., 2002; Chadwick et al., 2013; Kim, 2016).

Of roughly 200,000 species of wild plants on earth, only a few thousand are eaten by humans, just a few hundred of these have been domesticated, and only a dozen account for over 80% of the current annual production of all crops (FAO, 2010). By focusing on a few species, people transformed the diverse world of plants into a manageable domain that generally met needs for nutrients, mainly energy, while limiting over-ingestion of toxins (Johns, 1994). In so doing, however, we narrowed the genetic basis of crop production to just a few plants, relatively productive in a broad range of environments, rather than broadening the range of plants that are valuable in local environments (Shelef et al., 2017). We have also discovered only a fraction of the plant mixtures useful in nutrition and health (Etkin, 2000) and we have simplified agricultural systems in ways that are having alarming consequences on the health of people and the planet (Provenza, 2018). Though often successful in the short term, "simplifying" ecosystems can lead to ruinous long-term impacts, as shown in marine, forest, and rangeland systems (Gunderson et al., 1995). By maximizing the output of one component of a system, we inevitably hasten the demise of ecosystems.

The United Nations Commission on Genetic Resources for Food and Agriculture has declared the loss of biodiversity as one of the major threats to the productivity and resilience of food production systems (Pilling et al., 2020). Biodiversity amongst soil microorganisms, plants, and animals, which have co-evolved to form complex symbiotic relationships over millions of years, are essential to maintain soil health and sustainable agroecosystems (Coleman and Whitman, 2005; De Faccio Carvalho et al., 2010). The structural and functional diversity inherent in natural systems increases productivity of plant and animal species, and enhances system resilience. Studies of natural systems highlight the benefits of plant and animal biodiversity for reducing inter-annual variability in production and minimizing risk of large-scale catastrophic events, such as wildfire and outbreaks of diseases and pests (Gunderson et al., 1995; Provenza et al., 2007). Diversity in terms of nutrition also increases the range of options available for both animals and humans to nourish themselves and medicate prophylactically.

Along with reductions in per capita meat consumption in industrialized nations (Godfray et al., 2018), meat consumption will arguably need to increase in developing nations to meet basic needs for protein, essential fatty acids, and micronutrients (Adesogan et al., 2019). It was recently estimated that animal-sourced food consumption at $^{1}/_{3}$ of total energy intake (i.e., a 1:2 energy intake ratio of animal to plant foods) will provide nutritionally adequate diets for most of the global population (Nordhagen et al., 2020), a target currently not met in the majority of low-to-middle income countries (FAO, 2020). By including complementary nutrient-dense plant foods (Eshel et al., 2019), and depending on intra-individual differences in nutrient metabolism (Brenna, 2002; Stover and Caudill, 2008; Tang, 2010; Engelken et al., 2014), even lower amounts of animal sources foods may be sufficient to achieve nutrient adequacy in certain individuals within the population. That is more feasible in high-income than low-income countries as a result of food availability (FAO, 2020).

Beyond meeting basic nutrient requirements, people in low-income countries often depend on livestock rearing not just for food, but for their entire livelihood; at the household level, livestock contribute 68% of income in low- to middle-income households (FAO, 2009). For the poorest, grazing livestock is an effective way to reduce poverty (Omamo et al., 2006) from the sale of excess foodstuff, fiber, and waste products, especially when livestock are managed in ways that sustain the natural resource base (e.g., increase soil organic carbon content, reduce soil erosion, and integrate crop-livestock systems) (IPCC, 2019). Importantly, 3.4 billion hectares (70% of current agricultural land) of land will support livestock and wild animals, but not crop production (FAOSTAT, 2020). That is significant because the majority of those lands are in developing nations and are home to billions of people who depend on livestock grazing for their livelihood.

As ecological, economic, and human health concerns mount—soil, water, and climate change; animal welfare; and red meat consumption and human health—demand for livestock reared on pasture will further increase in both developing and developed nations. For example, the US grass-fed beef market increased from $17 million in retail sales in 2012 to $480 million in 2019, and this trend is expected to continue in the years ahead (Nielsen, 2020). Moreover, the organic dairy market is expected to register a compound annual growth rate of 10% in the next 5 years (Kumar and Deshmukh, 2019). The challenges and opportunities are to create grazing-based livestock-production systems based on phytochemically diverse forages for specific ecoregions at temporal and spatial scales that enhance livestock production, ecological services, and animal and human health (Gregorini et al., 2017; Provenza et al., 2019).

While understanding animal adaptations to landscapes has always been an important aspect of nutritional ecology (Demment and Van Soest, 1985), until recently land managers have not attempted to put these ideas into practice on a wide-scale. We often consider cattle to be grass eaters and sheep to be forb eaters; however, they can thrive under a wide range of conditions, including shrub-dominated areas in the arid southwest US (Provenza and Balph, 1990), high-altitude pastures in the Alps (Verrier et al., 2005), and the Amazon rainforest (Loker, 1994), provided they have been selected anatomically, physiologically, and behaviorally to survive on their own in the landscapes they inhabit, and are compatible with wildlife inhabiting these environments (Provenza, 2008).

Offering locally-adapted animals choices on pastures and rangelands also allows each individual to meet its needs for nutrients and to regulate its intake of secondary compounds by mixing foods in ways that work for that individual (Provenza et al., 2003). Cattle, sheep, and goats eat more and perform better when they are offered a wide variety of plants that contain secondary compounds (Provenza et al., 2007). Variety is so important that bodies have built-in mechanisms to ensure animals eat a variety of foods and forage in different locations to satiate and meet nutritional requirements (Bailey et al., 1996; Provenza, 1996). Thus, variety not only enables individuality, it also greatly increases the likelihood of providing cells with the vast arrays of primary and secondary compounds essential for their nutrition and health. While we often do not think of animals as intelligent beings; animals, unlike humans, do not have to be told what to eat and nurture themselves prophylactically—to prevent disease—and medicinally—to treat disease (Provenza, 2008).

Livestock are intelligent beings (Marino and Allen, 2017); they possess most of the mental, emotional, and behavioral traits we identify in humans, and by nurturing livestock we can nurture ourselves (Provenza et al., 2019). During the Green Revolution (1950-60s), agricultural systems largely moved away from integrated multi-species livestock-crop systems toward farming systems where livestock are separated from plant farming, and finished (cattle and sheep) or raised almost exclusively (poultry and pigs) in concentrated operations where animals are fed total mixed rations. Depending on practices, confined feeding systems can thwart the animals' ability to self-select their own diet and express natural behavior, which can adversely affect their welfare and health.

For example, Carrillo et al. (2016) found increased blood glucose and cortisol levels in feedlot-finished vs. pasture-raised cattle, which indicates impaired metabolic health and increased stress in the feedlot-fed animals. Metabolomic and gene expression analyses also revealed mitochondrial dysfunction and impaired oxidative phosphorylation in muscle tissue of feedlot-finished cattle. These findings were corroborated by a recent report demonstrating that meat of grass-fed animals displays a phenotype of improved oxidative metabolism compared to meat from feedlot-finished animals (Apaoblaza et al., 2020). This is consistent with studies of lambs, who display similar elevations in blood cortisol and behavioral changes indicative of stress and fear when fed total-mixed rations, formulated for the "average lamb," compared to having a broader dietary choice (Catanese et al., 2013).

Importantly, the metabolic phenotype of the feedlot-finished animals described in the work by Carrillo et al. (2016) and Apaoblaza et al. (2020) shows similarity with the human phenotype of metabolic disease, which is also characterized by muscle mitochondrial dysfunction (Nisoli et al., 2007), increased oxidative stress (Whaley-Connell et al., 2011), and elevated blood glucose (Grundy et al., 2004) and cortisol (Rosmond, 2005). In contrast, the greater mitochondrial oxidative enzyme content in pasture-raised animals (Apaoblaza et al., 2020) can be considered that of a healthy athletic phenotype. Certainly, animal health issues can also arise in ill-managed pasture-based systems. While causality cannot be inferred from these data, the link between consuming meat and dairy products from animals—that display varying degrees of metabolic health—and the subsequent effects on human metabolic health requires further examination.

LINKING LIVESTOCK SYSTEMS TO HUMAN HEALTH

Several studies associate red meat, and to a lesser extent dairy, with an increased risk of cardiovascular disease (Kaluza et al., 2012; Ding et al., 2019), cancer (Ganmaa et al., 2002; Chan et al., 2011; Fraser et al., 2020), type II diabetes (Pan et al., 2011), and early mortality (Schwingshackl et al., 2017b; Zheng et al., 2019). However, associations between red meat and increased disease risk are not supported by several other studies, especially when dietary quality is high (i.e., diets rich in fruits/vegetables and low in ultra-processed foods) (Schulze et al., 2003; Kappeler et al., 2013; Grosso et al., 2017; Maximova et al., 2020). In the case of dairy, higher intakes are often also found to be neutral or even protective (Aune et al., 2012; Guo et al., 2017; Schwingshackl et al., 2017a). Regardless of the directionality of associations and potential nuances of residual confounding in associative data, currently available epidemiological data do not differentiate among ways that livestock are raised and finished (on pasture or feedlots) nor do epidemiological studies often discriminate different types of red meat (e.g., beef, pork, or lamb) and dairy (e.g., cow, goat, or sheep) that people consume (Provenza et al., 2019).

To determine whether livestock rearing practices modulate health associations, we encourage epidemiological studies to include questions regarding sourcing of meat and dairy (e.g., grass-fed, pasture-raised, organic, "conventional" [no designation on package] etc.) on self-reported dietary recalls and Food Frequency Questionnaires. A potential caveat is that those who buy more pasture-raised meat and dairy are more health-conscious to begin with (Ziehl et al., 2005), highlighting a need to account for both lifestyles and individual diets in studies comparing health associations with meat consumption from different livestock production systems (e.g., pasture-raised, grass-fed vs. grain-fed).

Meat and milk consumption, irrespective of rearing practices, substantially contribute to many essential nutrients in the human diet including protein, zinc, selenium, iron, phosphorus, calcium, and vitamins B_{12} and D (Phillips et al., 2015; De Gavelle et al., 2018). While little difference exists in total protein content between pasture-raised and feedlot-finished meat and dairy (Duckett et al., 2009; Schönfeldt et al., 2012), differences do exist in vitamins and trace minerals. For example, Duckett et al. (2009) compared riboflavin and thiamine in grass-finished vs. grain-finished beef, and found nearly 2-fold higher riboflavin concentrations and 3-fold higher thiamine concentrations in grass-finished beef. Pasture-raised meat and dairy also have more favorable fatty acid compositions compared to their feedlot-fed counterparts (Daley et al., 2010; Benbrook et al., 2018). Pasture-raised meat and dairy is generally lower in saturated fat and cholesterol, and contains more conjugated linoleic acid (CLA) and ω-3 fatty acids compared to feedlot-finished counterparts (Bergamo et al., 2003; Daley et al., 2010; Villeneuve et al., 2013; Coppa et al., 2019). It is often stated that ω-3 fatty acids are present in such modest amounts in pasture-raised beef that any difference between pasture-raised vs. feedlot-fed beef is not of biological relevance. This is arguably the case for the ω-3 fatty acids docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), which have been studied extensively for their ability to lower metabolic disease risk (Kris-Etherton et al., 2003; Calder, 2010). This notion, however, fails to take into account the abundance of the ω-3 fatty acid docosapentaenoic acid (DPA) in pasture-raised beef, which can effectively be converted to EPA *in vivo* in humans (Miller et al., 2013), and may exert anti-inflammatory effects on its own (Dalli et al., 2013). Eating pasture-raised beef increased blood levels of DPA and EPA concentrations of humans, while no such effects were observed with feedlot-finished beef (McAfee et al., 2011).

Dairy and meat from pasture-raised ruminants are also rich sources of conjugated linoleic acids (CLA). CLA refers to a family of geometric and positional isomers of 18-carbon linoleic acids that are produced by bacterial biohydrogenation of forage in the rumen or through subsequent δ-9-desaturase enzymatic conversion of trans-vaccenic acid (TVA) in the mammary gland and/or adipose tissue (Jahreis et al., 1997). While humans can also produce certain isomers of CLA *in vivo* through δ-9-desaturase conversion of TVA (Kuhnt et al., 2006), this conversion is so low that meat and milk represent the main sources of CLA for humans (Adlof et al., 2000).

CLA is predominantly studied for its anti-carcinogenic and anti-adipogenic properties. For instance, consumption of CLA-rich butter reduced cancer proliferation in animal models of breast cancer (Ip et al., 1999). In addition, dietary intake of CLA and serum concentrations of CLA are inversely related to risk of breast cancer and colorectal cancer in some (Aro et al., 2000; Larsson et al., 2005), but not all (Norris et al., 2009), population-based studies. Several studies find that the CLA content is 1.5 and 3 times times higher in pasture-raised meat and dairy, respectively, than grain-fed products (Dhiman et al., 1999; Daley et al., 2010; Benbrook et al., 2018), an outcome believed to be due to a more favorable rumen pH as a result of forage- as opposed to grain-feeding (Bessa et al., 2000). Unsurprisingly, consuming pasture-raised animal products elevates serum CLA concentrations in humans compared to grain-fed animals (Ritzenthaler et al., 2005; Brown et al., 2011).

While improved fatty acid ratios (ω-3: ω-6) and CLA have been the predominant focus in comparisons of pasture-raised, grass-fed vs. grain-fed meat and milk, emerging data indicate that when livestock are eating a diverse array of plants on pasture, many plant phytochemicals are also concentrated in their meat and milk (Prache et al., 2005; Carrillo et al., 2016). This is noteworthy as phytochemicals are often considered to occur only in plant foods.

PHYTOCHEMICALS IN MEAT AND MILK

Terpenoids

Terpenoids—monoterpenes, diterpenes, and sesquiterpenes—are a large and diverse class of phytochemicals studied extensively for their anti-inflammatory, anti-oxidant, anti-viral, and anti-carcinogenic properties (Zhang et al., 2005; Merfort, 2011; Chadwick et al., 2013). The presence of terpenoids in animal foods is directly related to the terpenoid composition of the animal's diet (Vialloninsta et al., 2000; Bugaud et al., 2001; Priolo et al., 2003). Animals grazing more botanically diverse pastures accumulate both higher amounts and a wider variety of terpenoids (and other phytochemicals) in their meat and milk compared to animals grazing non-diverse (i.e., monoculture) pastures, while concentrations of phytochemicals are further reduced—and often remain undetected—in the meat and milk of animals fed grain-based diets in feedlots (**Figure 1**).

Milk obtained from cattle grazing diversified forages contained 6 to 23 times more monoterpenes (α-thujene, camphene, o-cymene) and sesquiterpenes (α-copaene, ß-caryophyllene) than milk obtained from animals fed concentrates (Martin et al., 2005). Similarly, Agabriel et al. (2007) found that terpenes—such as α-copaene (anti-oxidant), β-bourbonene (anti-tumor, apoptosis inducer), β-pinene (anti-inflammatory, anti-oxidant, anti-tumor), β-Elemene (anti-inflammatory, anti-tumor), and sabinene (anti-inflammatory, anti-oxidant)—were higher in milk from pasture-raised animals with access to more forage diversity compared to animals fed grain-based diets. Likewise, Børge et al. (2016) found that δ-3 Carene, α + β-pinene, α-thujene, ß-citronellene, and sabinene concentrations (anti-inflammatory, anti-bacterial, anti-oxidant, and/or anti-carcinogenic) were collectively 5-fold higher in cream produced from animals raised on diversified pasture compared to cream from animals fed concentrates.

Amongst pasture-based systems, greater botanical diversity of forage generally results in higher terpenoid concentrations in meat and milk. For example, goats grazing a wide variety grasses, legumes, and forbs concentrated 5-fold more terpenoids in their milk compared to goats consuming a limited number of grasses (alfalfa, perennial rye grass, and orchard grass) (Fedele et al., 2007). Similar findings were made by Martin et al. (2005) who found that milk samples from cattle grazing diversified mountain pastures were enriched in terpenoids compared to cattle grazing a ryegrass monoculture. While the presence of terpenoids have predominantly been studied in dairy systems, higher concentrations of terpenoids have also been found in the meat of grass-fed cattle (Larick et al., 1987) and lambs (Priolo et al., 2003) compared to their grain-finished counterparts (**Table 1**).

Besides differences in pasture diversity, seasonality also impacts the terpenoid content of milk with highest concentrations observed during the summer, compared to the fall and spring, while concentrations are lowest during the winter (Agabriel et al., 2007; Chion et al., 2010; Valdivielso et al., 2017). These findings can be ascribed to the differences in cattle diets (fresh pasture vs. hay) (Valdivielso et al., 2017) and/or seasonal differences in terpenoid content of grazed plants (Mariaca et al., 1997). These differences can be substantial, as demonstrated by Valdivielso et al. (2017), who found that terpenoids were 5-fold higher in the summer compared to the winter, and 2-fold higher in the summer compared to the spring. Even during winter, when terpenoids concentrations in pasture-fed milk were lowest, concentrations remained 2-fold higher for pasture-fed compared to grain-fed animals, which obviously experience little seasonality due to largely standardized total-mixed ration feeding throughout the year (Agabriel et al., 2007).

Phenols

Phenols in plants exert strong *in vivo* anti-oxidative and anti-inflammatory effects in both animals (Poutaraud et al., 2017) and humans (Zhang and Tsao, 2016). Phenols consist of one (phenolic acids) or more (polyphenols) aromatic rings with attached hydroxyl groups as part of their structures (Lewandowska et al., 2013). Therapeutic benefits of phenols include protection again various cancers (Kampa et al., 2007; Zhou et al., 2016), hepatic disorders (Saha et al., 2019), cardiovascular disease (Khurana et al., 2013), neurodegenerative diseases (Vauzour, 2012), type 2 diabetes (Guasch-Ferré et al., 2017), obesity (Wang et al., 2014), improved immune function (Ding et al., 2018), and gut microbial composition (Cardona et al., 2013).

Similar to terpenoids, the presence of phenols in milk is directly related to the phenolic composition in the diet (De Feo et al., 2006; Besle et al., 2010; Di Trana et al., 2015), with higher concentrations observed during summer compared to winter (Cabiddu et al., 2019), and higher concentrations in meat and milk from animals fed a botanically diverse diet on pasture compared to animals raised on monoculture

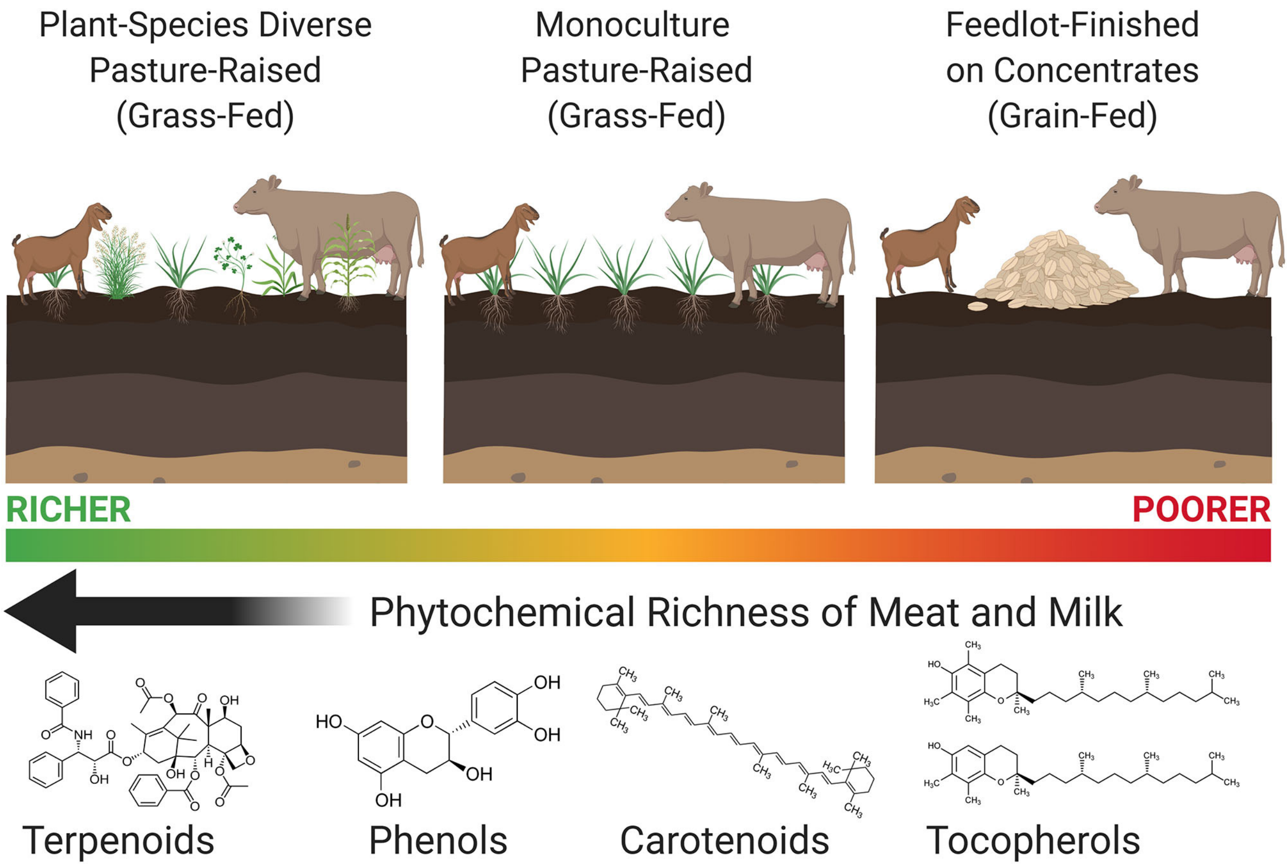

FIGURE 1 | The effects of livestock production systems on the phytochemical richness—terpenoids, phenols, carotenoids, and tocopherols—of meat and milk. Grazing livestock on plant-species diverse pastures concentrates a wider variety of phytochemicals in their meat and milk compared to animals grazing non-diverse pastures, while phytochemicals are further reduced and often remain absent in meat and milk from animals fed grain-based concentrates in feedlots. Created with BioRender.com.

pastures, with lowest concentrations found in animals fed grain-based concentrates (**Table 1**). For example, flavonoid and caffeoylquinic acid content is 6-fold higher in milk from cattle raised on botanically-diverse mountain pastures compared to cattle raised on monoculture grasses, and is largely undetected in milk from animals fed concentrates in confinement (Besle et al., 2004, 2010). In these studies, concentrations of phenols showed a clear stepwise increase as botanical diversity of forage increased (grassland pasture > grassland hay > ryegrass hay > ryegrass silage > concentrates). Likewise, Delgadillo-Puga et al. (2019) found that catechin, chlorogenic acid, gallic acid, and ferulic acid were present only in the milk of goats grazed on pasture and were undetectable when goats were fed concentrates in confinement. Finally, concentrations of equol, formononetin (both isoflavones), and enterolactone (a lignan) are higher in milk from cattle grazed on pasture than in milk from feedlots (Hoikkala et al., 2007; Adler et al., 2015). Higher equol and/or enterolactone intakes are associated with a reduced risk of osteoporosis, prostate, and breast cancer, as well as lower circulating levels of low-density lipoprotein cholesterol and C-reactive protein (Jackson et al., 2011; Rodríguez-García et al., 2019).

Pasteurization is another factor impacting the polyphenol content of dairy. For example, Cuchillo-Hilario et al. (2009) found that the polyphenol content in pasture-raised goat cheese was 3-fold higher in raw milk cheese than when the milk was pasteurized prior to making cheese. While pasteurization is the norm in the US, consumption of raw dairy is more accepted in other parts of the world, including several European and African countries (Mattiello et al., 2018; Baars, 2019; Meunier-Goddik and Waite-Cusic, 2019). For example, in the Netherlands, Gouda farmhouse cheeses are required by law to conform to traditional production methods, which prohibit pasteurization (Fischer Boel, 2009). Similarly, French artisanal cheeses are often made from raw milk and are considered superior to pasteurized cheeses. Besides enhancing health, phytochemicals also enhance flavor (Clarke et al., 2020), which can become compromised with heat treatment. Proper animal husbandry and hygiene practices on farms would enable farmers to obtain raw milk of high microbiological quality (D'Amico and Donnelly, 2010; Janštová et al., 2011; Giacometti et al., 2013; Baars, 2019). Nevertheless,

TABLE 1 | Impact of livestock diets on phytochemicals in meat and dairy.

Study	Foodstuff; Treatments	Compounds measured in meat and dairy (potential health effects)	Differences in meat and milk as a result of diet
Terpenoids			
Larick et al. (1987)	Beef fat; Monoculture pasture—fescue vs. brome vs. orchard grass— vs. concentrates	Azulene (anti-inflammatory), 1,2-Phetene (anti-inflammatory, anti-oxidant), Phytane (anti-inflammatory), Phytol (anti-oxidant), and three more terpenes	↑5-fold in fescue pasture vs. concentrates; ↑2.5-fold in brome or orchard grass vs. concentrates
Martin et al. (2005)	Cow milk; Diversified mountain pasture vs. ryegrass monoculture vs. concentrates	α-Copaene (anti-oxidant), α-Thujene (anti-inflammatory), Camphene (anti-bacterial), o-Cymene (anti-inflammatory, anti-viral), and eight more terpenes	↑6- to 23-fold in diverse pasture vs. ryegrass vs. concentrates.
Priolo et al. (2003)	Lamb fat; Diversified pasture vs. concentrates	β-Caryophyllene (anti-inflammatory), α+ β-Cubebene (anti-viral, anti-carcinogenic), zonarene (anti-microbrial), and five more terpenes	↑6-fold in diverse pasture vs. concentrates
Agabriel et al. (2007)	Cow milk; Diversified mountain pasture vs. temporary pasture + hay vs. temporary pasture + concentrates	β-Elemene (anti-inflammatory, anti-tumor) β-Pinene (anti-inflammatory, anti-oxidant, anti-tumor) Sabinene (anti-inflammatory, anti-oxidant), and fourteen more terpenoids	↑2-fold in diverse pasture vs. temporary pasture + concentrates; ↑1.5-fold in temporary pasture + hay vs. temporary pasture + concentrates
Fedele et al. (2007)	Goat milk; Diversified shrubland vs. mixed hay (alfalfa, rye grass and orchard grass)	Δ-3 Carene, 4- and α + γ-Terpineol, β-Cedrene, β-Farnesene, Isolongifolene, and Longifolene (collectively—anti-inflammatory, anti-bacterial, anti-oxidant and/or anti-carcinogenic)	↑5-fold diverse pasture vs. mixed hay
Børge et al. (2016)	Cow cultured cream; Diversified mountain pasture vs. concentrates	Δ-3 Carene, α + β-Pinene, α-Thujene, β-Citronellene, Sabinene and four more terpenoids (collectively—anti-inflammatory, anti-bacterial, anti-oxidant and/or anti-carcinogenic)	↑5-fold in diverse pasture vs. concentrates
Coppa et al. (2019)	Cow milk; Pasture (mix of diverse and non-diverse) vs. concentrates	α-Thujene, α-Pinene, β-Citronellene, Caparratriene α+ β-Caryophyllene, and five more terpenoids (collectively—anti-inflammatory, anti-bacterial, anti-oxidant and/or anti-carcinogenic)	↑2-fold pasture (mix of diverse and non-diverse) vs. concentrates
Polyphenols			
Besle et al. (2004)	Cow milk; Diversified mountain pasture vs. ryegrass monoculture vs. concentrates	Total phenol content	↑3-fold in diverse pasture vs. concentrates; ↑2-fold in ryegrass pasture vs. concentrates
Cuchillo-Hilario et al. (2009)	Goat cheese; Diversified shrubland vs. concentrates + hay	Caffeic acid (anti-inflammatory, anti-oxidant, anti-carcinogenic), Quercetin (anti-inflammatory, anti-bacterial, anti-oxidant, anti-carcinogenic), and total polyphenol content	↑13-fold in diverse pasture vs. concentrates
Adler et al. (2015)	Cow milk; Diversified pasture vs. concentrates	Isoflavones: Daidzein, Formononetin, Genistein, Equol Lignans: Enterolactone, Secoisolariciresinol (collectively—anti-inflammatory, anti-carcinogenic, anti-osteoporotic, and/or neuroprotective)	↑3-fold in diverse pasture vs. concentrates
Chen et al. (2015)	Yak meat; Diverse pasture vs. concentrates	Total phenol content	↑1.5-fold in non-diverse pasture vs. concentrates
Cabiddu et al. (2019)	Goat milk; Diversified shrubland vs. concentrates	Total phenol content	↑1.2 (winter) to 5-fold (summer) in pasture vs. concentrates
Coppa et al. (2019)	Cow milk; Pasture (mix of diverse and non-diverse) vs. concentrates	3,4-Dimethylphenol, 2,6-Quinolinediol, and eight more phenolic compounds (collectively—anti-inflammatory, anti-oxidant, and/or anti-carcinogenic)	↔pasture vs. concentrates
Delgadillo-Puga et al. (2019)	Goat milk; Diversified shrubland vs. concentrates + 30% *Acacia farnesiana* (AF) vs. concentrates	Catechin, Chlorogenic acid, Gallic acid, and Ferulic acid (collectively—anti-inflammatory, anti-oxidant, anti-carcinogenic, and/or neuroprotective)	↑2-fold in pasture vs. concentrates + 30% AF; undetectable in concentrates

(Continued)

TABLE 1 | Continued

Study	Foodstuff; Treatments	Compounds measured in meat and dairy (potential health effects)	Differences in meat and milk as a result of diet
Carotenoids and Tocopherols			
Prache et al. (2003)	Lamb fat; Diversified pasture vs. concentrates + hay	Lutein (anti-inflammatory, anti-oxidant, macular degeneration protective)	↑2.8-fold diverse pasture vs. concentrates + hay
Gatellier et al. (2004)	Beef meat; Pasture (unspecified) vs. concentrates	Total tocopherol content	↑1- to 1.3-fold pasture vs. concentrates
Havemose et al. (2004)	Cow milk; Grass-based forage vs. corn-based forage	$\alpha+\delta+\gamma$-Tocopherol, β-Carotene, Lutein, and Zeaxanthin (collectively—anti-inflammatory, anti-oxidant, anti-carcinogenic, and/or neuroprotective)	↑3-fold grass-based vs. corn-based
Descalzo et al. (2005)	Beef; Pasture (unspecified) vs. concentrates	α-Tocopherol and β-Carotene	↑2- to 7.5-fold pasture vs. concentrates
Agabriel et al. (2007)	Cow milk; Diversified mountain pasture vs. temporary pasture + hay vs. concentrates	β-Carotene and Lutein	↔ pasture vs. temporary pasture + hay vs. concentrates
Butler et al. (2008)	Cow milk; Pasture (unspecified) vs. concentrates	α-Tocopherol, β-Carotene, Lutein, and Zeaxanthin	↑1.4- to 1.8-fold pasture vs. concentrates
Röhrle et al. (2011)	Beef fat; Non-diverse pasture vs. concentrates	Lutein and β-Carotene	↑3.3- to 6-fold pasture vs. concentrates
Coppa et al. (2019)	Cow milk; Grass-based forage vs. corn-based forage	β-Carotene	↑1.2-fold in grass-based

however small the risk of pathogenic presence may be—<0.3% in aforementioned studies, generally limited to single farms—zero-risk is not possible and consuming raw milk can have serious adverse health effects (O'Callaghan et al., 2019). Whether such small risks are acceptable in food systems and whether the consumption of raw dairy from pasture-based systems (milk from concentrated feeding operations is generally not sold raw) should be left to individual choice is beyond the discussion of our work (for a nuanced discussion of the topic, see Baars, 2019). Cooking meat also reduces polyphenol and terpenoid contents by 25–60% (King et al., 1993, 1995; Kozová et al., 2009; Dadáková et al., 2011), with higher heat preparations (e.g., grilling and roasting) resulting in higher reductions compared to lower heat preparations (e.g., stewing and "sous vide") (Kozová et al., 2009; Dadáková et al., 2011).

The contribution of phytochemicals from pasture-raised meat and milk to overall dietary intake should not be underestimated. While total phenolic levels (expressed as gallic acid equivalents) in fruits and vegetables (Deng et al., 2013) are generally 5 to 20-fold higher compared to pasture-raised meat and milk (López-Andrés et al., 2013; Chen et al., 2015; Cabiddu et al., 2019; Delgadillo-Puga et al., 2019), various individual phytochemicals are abundant in pasture-raised meat and milk. For example, the amount of chlorogenic acid (12.3 mg/100 g) in pasture-raised milk (Delgadillo-Puga et al., 2019) may be on par or higher than several vegetables and fruits such broccoli (5.5 mg/100 g), cowpea (0.7 mg/100 g), and tomatoes (8 mg/100 g) (Deng et al., 2013; Arnaud, 2016). Furthermore, López-Andrés et al. (2013) found total phenolic levels in pasture-fed lamb liver to be 6.6 mg GAE/g product, which is comparable to values found in several fruits and vegetables including eggplant (6.7 mg GAE/g) and turnip (6.0 GAE/g), squash (5.0 mg GAE/g) and snap bean (5.9 mg GAE/g). Muscle meat is about 4-fold lower in phenolics compared to liver yet can still contributes meaningful amounts of phytochemicals in the human diet (Chen et al., 2015). Most commonly known for their presence in green tea, the flavonoids catechin, gallic acid, and chlorogenic acid have been extensively studied for their anti-oxidant, anti-inflammatory, and anti-carcinogenic effects (Kroes et al., 1992; Khan and Mukhtar, 2007; Verma et al., 2013). Importantly, the quantity of gallic acid (1.3 mg/100 g) and catechin (4.3 mg catechin/100 g) in diverse pasture-raised milk (Delgadillo-Puga et al., 2019) is comparable to average quantities found in some green teas (1.2 mg gallic acid/100 g; 4.3 mg catechin/100 g, respectively) (Henning et al., 2003). Similarly, the presence of quercetin and caffeic acid, which are anti-oxidants best known for their presence in onions (McAnlis et al., 1999) and coffee (Nardini et al., 2002) have also been readily detected in cheese from goats grazing botanically diverse shrubs and grasses (De Feo et al., 2006; Cuchillo-Hilario et al., 2009), albeit at 30-fold lower concentrations than what is found in onions, but similar to levels in cabbage, celery, potatoes, and several other fruits and vegetables (USDA, 2016b). We stress that these examples should not be interpreted as a meat vs. plant foods discussion nor as "evidence" that animal foods negate a need for obtaining phytochemicals from plant foods. Plant and animal foods arguably improve human health in synergistic ways (Barabási et al., 2020; Van Vliet et al., 2020). Rather these examples serve to illustrate that pasture-raised animal foods can contribute substantially to phytonutrient intake in the human diet. Whether the potential beneficial effects of consuming phytochemically-rich meat and dairy are analogous to, but distinct from, benefits attained by eating phytochemically-rich herbs, fruits, and vegetables should be assessed in future studies. Importantly, by consuming phytochemically-rich meat and milk we ingest a broad spectrum of phytonutrients from classes of plants (e.g., a wide variety of *Monocotyledoneae* and *Dicotyledoneae)* otherwise not readily consumed by humans.

Carotenoids and Tocopherols

Carotenoids are a class tetraterpenoids found abundantly in plants and fruits. β-carotene is the main isomer found in plants, however other carotenoids such as α-carotene and the xanthophylls lutein and zeaxanthin are also widely found in plants (Khoo et al., 2011; Eisenhauer et al., 2017). Carotenoids are fat soluble with β-carotene being quantitatively most abundant and responsible for the yellow tint of the fat in grass-fed beef and cow's milk (goats and sheep do not accumulate β-carotene, hence their milk is whiter) (Nozière et al., 2006; Dunne et al., 2009). Carotenoids can serve as precursors of vitamin A in humans (Haskell, 2012), and their intake is associated with a wide variety of health benefits including improved cognitive function (Grodstein et al., 2007), reduced risk of metabolic diseases such as cancer (Nishino et al., 2009), cardiovascular disease (Voutilainen et al., 2006), and diabetes (Sluijs et al., 2015), protection from age-related macular degeneration (Seddon et al., 1994), as well as more broadly being defined as having anti-oxidative and anti-inflammatory effects (Ciccone et al., 2013).

Tocopherols are a class of phenolic compounds, with vitamin E activity, best known for their anti-oxidative effects. Tocopherols exist as four structural isomers (α, β, γ, and δ) with α-tocopherol being the predominant form in both livestock (Nozière et al., 2006) and humans (Kinsella, 2007). Similar to carotenoids, tocopherols protect against cardiovascular disease (Huang et al., 2019), certain cancers (Helzlsouer et al., 2000; Das Gupta and Suh, 2016), neurocognitive decline (Mangialasche et al., 2012), and age-related macular degeneration (Delcourt et al., 1999).

Similar to terpenoids and phenols, the nature of forage also impacts carotenoid and tocopherol levels in meat and milk. Highest concentrations are found in animal grazing diverse pastures, with lower concentrations found in meat and milk from animals grazing monoculture pastures or fed dried hay (due to ultraviolet-light degradation of carotenoids after harvesting), while animals fed concentrates have the lowest concentrations of carotenoids and tocopherols (Nozière et al., 2006; Dunne et al., 2009) (**Table 1**). Positive curvilinear relationships were found between carotenoid intake and milk content of cows (Calderón et al., 2007) and the fat content of sheep (Dian et al., 2007). Others also found that, as the ratio of forage-to-total-mixed-rations increases, α-tocopherol, β-carotene, lutein, and/or retinol concentrations increase in a curvilinear fashion in milk (Pizzoferrato et al., 2007; La Terra et al., 2010; Salado et al., 2018).

Similar to other phytochemicals, seasonality affects carotenoid and tocopherol content in meat and milk from pasture-based systems, with higher amounts observed during the spring compared to the summer, fall, and winter (Nozière et al., 2006; Marino et al., 2012; Jain et al., 2020). For example, Nozière et al. (2006) found that β-carotene is highest in pasture-fed cow's milk during the summer, declines 1.5-fold during the fall, is 2-fold lower during the winter, and climbs back up during the spring. Similarly, Jain et al. (2020) found ∼10% lower β-carotene and α-tocopherol in US grass-finished beef during the fall compared to the spring, in addition to slightly lower iron and zinc concentrations. Carotenoid content of meat experiences less seasonal variation compared to milk. That is because the transfer of phytochemicals from forage into milk occurs within days (Vialloninsta et al., 2000; Calderón et al., 2007), while the phytochemical accumulation in meat occurs slowly over the lifetime of the animal (Prache et al., 2003).

While tocopherols and carotenoids are several-fold more abundant in plant foods compared to animal foods, their presence is noteworthy as they can protect meat and milk from protein and lipid oxidation (Realini et al., 2004; Pizzoferrato et al., 2007; Gonzalez-Calvo et al., 2015), which may improve protein digestibility and amino acid availability (Lund et al., 2011), lower the formation of pro-inflammatory compounds such as aldehydes generated by cooking (Lynch et al., 2001), and increase shelf life (McDowell et al., 1996). Moreover, eating pasture-raised beef raised circulating α-tocopherol and β-carotene to 1.2 and 1.5 times higher concentrations compared to feedlot-finished beef (Tartaglione et al., 2017).

Anti-oxidant Capacity of Pasture-Raised Meat and Dairy

Oxidative stress—characterized by excessive concentrations of reactive oxygen species (ROS)—can damage proteins, DNA and RNA, and plays a major role in the development of chronic ailments such as cardiovascular (Dhalla et al., 2000) and neurodegenerative diseases (Kim et al., 2015), cancer (Reuter et al., 2010), arthritis (Quiñonez-Flores et al., 2016), diabetes (Giacco and Brownlee, 2010), and other chronic diseases (Pena-Oyarzun et al., 2018). Antioxidants act as ROS "scavengers" by preventing and repairing damage caused by ROS, thus strengthening the immune system and offering protection against developing chronic diseases (Lushchak, 2014).

The increased phytochemical richness of the diets of animals grazing botanically diverse pastures results in higher anti-oxidant capacity in meat and milk. Anti-oxidant capacity is reduced when animals forage on monocultures of grass and the lowest anti-oxidant capacity occurs in meat and milk produced from animals fed concentrates in confinement (Descalzo et al., 2005; Cuchillo-Hilario et al., 2009; Kuhnen et al., 2014; Delgadillo-Puga et al., 2019) (**Table 2**). For example, Delgadillo-Puga et al. (2019) found that antioxidant capacity of pasture-raised goat's milk, assessed by its ferric ion antioxidant power (FRAP) (Huang et al., 2005), was 1.5- to 2.5-fold higher than milk from goats fed concentrates. Importantly, they found that anti-oxidant capacity of the milk was strongly correlated with the presence of phenols.

Descalzo et al. (2007) found that grass-fed beef also had a 1.5-fold higher FRAP capacity than beef from grain-fed animals. Additionally, compared to grain-fed beef, grass-fed beef had a higher glutathione content and redox potential (glutathione is one of the most potent intracellular antioxidants), and superoxide dismutase activity (an enzyme providing cellular defense against ROS) (**Table 2**). No differences were observed for other measures of anti-oxidant status such as Trolox equivalent antioxidant capacity (TEAC), catalase (CAT), and glutathione peroxidase (GPx). In contrast, Gatellier et al. (2004) found

TABLE 2 | Impact of livestock diet selection on anti-oxidant activity in meat and dairy.

Study	Foodstuff; treatments	Anti-oxidant activity of pasture vs. concentrate-finished meat and dairy (↑,↔, or↓); assay type
Anti-oxidant status		
Gatellier et al. (2004)	Beef meat; Pasture (unspecified) vs. Concentrate	↔ABTS, 1.1-fold ↓OH-Benzoate, 4-fold ↑SOD, ↔CAT, and 2.5-fold ↓GPx
Descalzo et al. (2005)	Beef meat; Pasture (unspecified) vs. concentrate	↔ABTS, 1.5-fold ↑FRAP, 1.8-fold ↑Glutathione, 1.1-fold ↑Glutathione redox potential, 1.4-fold ↑SOD, ↔CAT, and ↔GPx
López-Andrés et al. (2013)	Lamb liver; Monoculture pasture (ryegrass) vs. concentrate	1.3-fold ↑FRAP and 1.2-fold ↑Folin–Ciocalteu
Cuchillo-Hilario et al. (2009)	Goat cheese; Diversified shrubland vs. concentrates + hay	2-fold ↑ABTS and 1.6-fold ↑DPPH
Chen et al. (2015)	Yak meat; Diversified pasture vs. concentrate	1.4-fold ↑ABTS and 1.1-fold ↑FRAP
Delgadillo-Puga et al. (2019)	Goat milk; Diversified shrubland vs. concentrate	1.5-fold ↑DPPH, ↔FRAP, and 2.5-fold ↑ORAC
Luo et al. (2019)	Lamb fat; Diversified pasture vs. concentrate	1.5-fold ↑ABTS, 1.1-fold ↑CUPRAC, ↔ SOD, 1.6-fold ↑CAT, and 1.7-fold ↑GPX

ABTS, 2,2′-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid); CAT, catalase; CUPRAC, cupric ion reducing antioxidant capacity; DPPH, 2,2-diphenyl-1-picrylhydrazyl; FRAP, ferric ion antioxidant power; GPx, glutathione peroxidase; ORAC; oxygen radical absorbance capacity.

higher CAT and GPx activity for animals fed concentrates indoors compared to pasture-grazed animals, whereas the reverse was found for SOD activity. While the reasons for these divergent findings are unclear, a potential explanation is that the concentrate-fed animals were finished on private farms for only 3 months during the winter, which may not represent "typical" feedlot environments where animals are finished on concentrates for an average of 5 months (Drouillard, 2018). As the authors point out, the findings of their study may indicate a "production system effect" rather than a diet effect. Contrary to the feedlot-finished animals, pasture-finished animals can more freely engage in natural behaviors, which could further positively impact their anti-oxidant status (Gatellier et al., 2004). Finally, López-Andrés et al. (2013) found higher anti-oxidant activity (assessed by FRAP and Folin–Ciocalteu assays) in the liver of lambs raised on pasture compared to lambs fed concentrates in confinement.

Taken together, these data suggest that pasture-raising and finishing is beneficial for both the health of the animal and its meat and milk products. It is perhaps no surprise that the two are connected: a healthier animal provides healthier meat and milk. While the phytochemical richness and anti-oxidant capacity is enhanced in grass-fed meat and dairy, especially when raised on nutrient-rich species-diverse pastures, compared to animals that fed grain-based concentrates in confinement (e.g., feedlots), the question remains: Does the increased phytochemical richness of grass-fed meat and dairy have an appreciable effect on improving human health?

THE EFFECTS OF ANIMAL PRODUCTION SYSTEMS ON HUMAN METABOLIC HEALTH

The metabolic effects of consuming grass-fed meat and dairy vs. feedlot-finished counterparts have predominantly been studied for their ability to modulate inflammation and lipoprotein profiles (e.g., cholesterol and triglycerides). Low-grade systemic inflammation—characterized by elevated levels of the cytokines interleukin-6 (IL-6), tumor necrosis factor-alpha (TNF-α), and/or C-reactive protein (CRP)—participates in the development of metabolic diseases such as heart disease, cancer, type II diabetes, and arthritis (Libby, 2007). Importantly, cytokines are modulated in response to single meals (Holmer-Jensen et al., 2011), with compounding effects on the progression of metabolic disease when single meals that raise inflammation become dietary habits (Esposito and Giugliano, 2006). Modulating the inflammatory milieu by dietary choices, therefore, represents an important strategy to prevent or treat metabolic disease.

In a randomized cross-over design, Arya et al. (2010) found that eating kangaroo meat, obtained from animals foraging on native pastures, attenuated the postprandial rise in IL-6, TNF-α, and CRP compared to feedlot-finished (grain-fed) beef. A limitation of the study is that, despite all of the fat being cut off of both the beef and kangaroo steak, the kangaroo was presumably still leaner than the beef, which could have confounded the results. Another study found that daily consumption of pecorino cheese—made from sheep who foraged on diverse pastures in Tuscany, Italy—for 10 weeks reduced circulating levels of pro-inflammatory cytokines and improved erythrocyte deformability, which is indicative of improved red blood cell function (Sofi et al., 2010). Werner et al. (2013) showed similar decreases in CRP over 12-weeks with daily consumption of 39 g of butter from either mountain-raised or feedlot-fed cattle, despite a lower SFA content and improved ω-3-to-ω-6 ratio in pasture-raised butter. Total daily saturated and polyunsaturated fat intake was similar between groups, which could have washed-out any effects of the butter *per se*. No effect of either intervention was observed for lipid profiles, insulin sensitivity, or glucose tolerance.

Gilmore et al. (2011) found that consumption of 113g of beef, 5 times per week for 5-weeks, from cattle raised on non-diverse pasture (coastal Bermuda grass) or grain-finished in feedlots does not differentially impact inflammatory profiles (Gilmore et al., 2011). As highlighted in **Tables 1** and **2**, the phytochemical richness and anti-oxidant capacity is reduced in meat from animals raised on monoculture pastures compared to meat from animals with access to more forage diversity, and that could be a reason for the lack of changes in inflammatory biomarkers in this work. However, future clinical trials comparing inflammatory responses to botanically diverse diets vs. monoculture grass-fed diets vs. grain-fed meat (and dairy) are needed to test this hypothesis.

In the work of Gilmore et al. (2011), eating grain-fed beef patties also resulted in higher circulating levels of total high-density lipoprotein cholesterol (HDL-C) and triglycerides (Adams et al., 2010; Gilmore et al., 2011), but that was not observed when the group ate pasture-raised beef patties. When considering HDL-C differences by particle size, no differences were observed in large and medium HDL particle size between interventions. Levels of large HDL particles show the strongest inverse relationship with cardiovascular risk compared to other HDL particle sizes in population-based studies (Mora et al., 2007; Van Der Steeg et al., 2008). In contrast, Brown et al. (2011) found that consuming dairy and meat from pasture-fed cattle for 8 weeks did not alter lipoproteins profiles, body composition, or glucose tolerance compared to a diet comprised of products from grain-fed cattle. Fatty acid profiles were similar for SFA, MUFA, and PUFA, only CLA was higher in the group that consumed pasture-fed meat and milk. Unfortunately, no information was provided on the diet fed to pasture-raised and grain-fed cattle. Taken together, these data suggest the lipid content of animal products may affect lipoprotein profiles of consumers, and that pasture-raised meat and milk may have greater anti-inflammatory properties compared to feedlot-finished animals. However, evidence is too sparse to make definitive claims and further clinical nutrition trials are needed.

SUITABILITY AND SCALABILITY OF PASTURE-BASED LIVESTOCK SYSTEMS

Grass-fed beef represents 4% of the US beef market (Cheung and McMahon, 2017) and organic milk represent 5.5% of the US dairy market (Gerdes, 2019). Organic milk that is truly from pasture-raised cattle may represent only 0.5%, though that market is growing rapidly and achieved a 58% increase in sales in 2018 (Gerdes, 2019). While concentrated animal feeding operations (CAFOs) are the predominant model in the US, in countries such as New Zealand, Australia as well as some European, South-American, and African nations the finishing model may be increasingly pasture-based. Especially in the US and Western countries the issue is complicated by confusion over the many labels—such as "organic," "grass-fed," "pasture-raised," and "free-range"—that consumers generally associate with healthier products. For example, organic does not necessarily mean animals were raised and finished on pasture. According to the USDA, the requirement is for cattle to have free access to certified-organic pasture for the entire grazing season (at least 120 days), while only 30% of the cattle's diet needs to come from pasture (USDA, 2016a). In the recent past, US farmers could make a good living by switching to organic production, but organic dairying is becoming a victim of its own success. A handful of large scale "organic" dairies—which now feed thousands of cows a diet of organic grain and stored forages with limited access to pasture—produce more milk than all organic, grass-fed dairy farms in Wisconsin combined (Whoriskey, 2017). To further complicate the matter, grass-fed also does not necessarily mean animals were raised on pasture without confinement (Provenza et al., 2019). Even the term "grass-fed" can mean animals were fed grass pellets in a feedlot-type production model or were grazing monoculture grasses. As we have described, this does not result in similar phytochemical richness and favorable fatty acid profiles compared to animals raised on pasture with access to a wide variety of different grasses, forbs, and shrubs. The uncertainty about product quality may be the result of a change in the USDA Agricultural Marketing Service (AMS) regulation of standards for "grass-fed." While the claim "grass-fed" can still be made through the USDA, AMS discontinued the verification of the applicant's programs to the Standard in 2016. To truly know whether animals were raised on pasture, consumers would have to rely on third-party verification (e.g., "100% Pasture-Raised," "Global Animal Partnership 5-Step® Animal Welfare Rating," "Regenerative Organic Certified™" etc.), establish contact with local farmers, and/or use Internet resources to gain insight into production practices of farmers.

With increased conversion to pasture-based beef production systems in the US, some suggest that domestic beef consumption will have to be reduced by about 40% due to lack of land (Hayek and Garrett, 2018). This estimate includes feeding roughage on pasture and is based on the current status quo of continuous grazing practices. To help meet needs, most people in high-income countries, such as the US and Europe, can reduce red meat consumption with no harm to their health, and likely even improve their health when diet quality would increase as a result (Fogelholm et al., 2015; Grosso et al., 2017; Guasch-Ferré et al., 2019). However, there are several opportunities by which improved management practices can increase the carrying capacity of livestock in pasture-based models, while enhancing ecosystem function. For example, grazing management practices that use ecological principles can increase the carrying capacity of livestock by 50–70% compared to continuous (largely unmanaged) grazing (Jacobo et al., 2006; Jakoby et al., 2015; Wang et al., 2016; Teague and Kreuter, 2020). This is a key point in discussions on whether pasture-based systems can support demand and productivity (Gerrish, 2004). Managed grazing positively influences plant-soil interactions, including plant root exudation and mycorrhiza (Gianinazzi et al., 2010), by recycling nutrients in feces and urine back into the soil through the actions of microorganism and small soil animals (e.g., earthworms and dung beetles) (Holter, 1983; Nichols et al., 2008; Menta and Remelli, 2020), which improves soil health and ecosystem function. Moreover, nutrient-rich soils and plant biomass have potential to improve the health of animals and humans by increasing the phytonutrient density (e.g., terpenoids, phenols, and other anti-oxidants) of pasture-raised meat and milk. In support of the soil-plant-animal-human health connection is that grazing nutrient-rich soils can positively impact the mineral content of grass-fed beef (Leheska et al., 2008). Additional long-term ecosystem benefits from agroecological grazing systems include increased plant and animal biodiversity, carbon sequestration, wildlife habitat, water infiltration and retention, and last but not least, improved resiliency and profitability for farmers through reduction of input cost (Gerrish, 2004; Meuret and Provenza, 2015; Teague and Kreuter, 2020). For a further discussion on soil health and ecosystem function in the context of agroecological grazing systems we refer the reader to the recent work of Teague and Kreuter (2020).

There is also potential for increased carrying capacity from multi-species grazing with little dietary overlap. For instance, integrating cattle with sheep, goats, and pigs and/or potentially other feed-conversion-efficient herbivores such as ducks, geese, and rabbits can improve animal productivity compared to grazing single species (Dumont et al., 2020; Martin et al., 2020) This synergy is achieved because different species exploit different ecological niches and one species can increase resource availability for another species (Walker, 1994; Anderson et al., 2012; Dumont et al., 2020). This would mean that we would have to diversify our meat and milk intake to include products from other livestock such as goats, sheep, bison, duck, geese, and rabbits to name a few. It is noteworthy that consumption of products from many of these livestock is already common practice on other parts of the world or are increasing rapidly in the US (e.g., bison consumption).

Greater diversification of livestock can allow for more efficient use of the resources provided by a particular ecosystem. For example, goats and sheep readily eat species of forbs, shrubs and trees that large herbivores like cattle and bison often avoid, while larger herbivores can better utilize lower quality forage compared to small herbivores such as sheep and goats (Steuter and Hidinger, 1999; Fraser et al., 2014; Cuchillo-Hilario et al., 2018; Martin et al., 2020). These examples illustrate that selection of animals that most effectively use, and more importantly, conserve the natural resource base in a given geographical location should be a key consideration to improve the efficiency and scalability of pasture-based livestock systems. For example, in the US, 53% of all red meat consumed is from beef, 46% is from pork, while <1% comes from other herbivores (STATISTA, 2019). Limiting consumption to only two to three species conflicts with herbivore diversity found in natural ecosystems, and arguably the level of diversity that is desired in agroecologically appropriate livestock systems.

Differences in phytochemicals and fatty acids between animal species further illustrates the importance of livestock diversification—different species provide different nutrients in the human diet. For example, β-carotene and lutein is lower in the meat and milk of goats and sheep compared to bovines (Yang et al., 1992; Lucas et al., 2008). On the other hand, retinol (vitamin A) concentrations are 2-fold higher in milk and meat of ovines compared to bovines (Martin et al., 2004; Darwish et al., 2016), owing to a higher efficiency of converting carotenoids into retinol in ovines (Yang and Tume, 1993). The ω-3 fatty acid content of milk and meat from goats is also 1- to 2-fold higher compared to cow's milk and meat, while cow's milk contains 1.5- to 2-fold higher concentrations of CLA compared to goat's milk (Yang et al., 1992; Lucas et al., 2008). Finally, lamb meat contains 1.5- to 2-fold higher concentrations of CLA compared to beef (Schmid et al., 2006).

Strategic supplementation of livestock on pasture with industrial by-products, inedible to humans (Sunvold et al., 1991; Macdonald et al., 2007), also has potential to increase the carrying capacity of pasture-based grazing systems and mitigate potential welfare issues associated with feedlots, such as reduced ability to express natural behavior and self-selection of diets (Atwood et al., 2001; Villalba and Manteca, 2019). For example, feeding limited amounts of phytochemically-rich fruit and vegetable by-products such as leaves, pomace, peels, rinds, pulp, seeds, and stems (Sruamsiri, 2007; Wadhwa and Bakshi, 2013; Salami et al., 2019) to livestock on pasture can potentially mitigate some nutritional deficits, decrease environmental impacts, and reduce the of risk of overgrazing and land unavailability, while enhancing the phytochemical richness of meat and milk (Provenza et al., 2003, 2019; Salami et al., 2019).

To improve the health and fertility of soils, many farmers in North and South America, Europe, and elsewhere are adding cover crops into rotations with cash crops such as wheat, corn, and soybeans on millions of hectares of land. Cover crops can be grasses or broadleaf plants—ideally mixtures of both—and are often rich in phytochemicals. They can be grown in the fall after cash crops are harvested or grown through the entire growing season. However, there are seed and seeding costs for growing cover crops, and a good way for farmers to reclaim these expenses is to graze them with livestock (Bergtold et al., 2019). Grazing not only helps justify the costs of growing cover crops, but cover crops increase carrying capacity by providing feedstuffs to livestock and reducing negative environmental externalities such as soil erosion and chemical runoff associated with both crop and livestock farming (Fisher et al., 2012; Bergtold et al., 2019). These ecosystem services are achieved by nutrient recycling, reduced need for pesticide application, and by strengthening soil-plant-herbivory interactions to achieve synergy between agricultural production and environmental quality (Lemaire et al., 2014). Therefore, cover crop grazing provides further potential to increase land and forage available to pasture-based livestock production systems, while providing important agroecological benefits.

Strategies that integrate multi-species grazing, mixed crop-livestock systems, and/or phytochemically rich by-product feeding should not be viewed as "silver bullet" approaches to climate change or to meet an ever-growing demand for red meat. However, practices that promote good land stewardship and effective use of resources should be incentivized to sustain and improve the natural resource base upon which agriculture depends—in turn, benefiting the presence of health-promoting compounds in meat and milk from productive soils and vegetation.

We do not expect one paradigm (pasture-based grazing systems) to simply replace the other (feedlot-fed systems). That is not how shifts occurred historically. However, as paradigms gain momentum based on mounting evidence in their favor (e.g., the potential of managed grazing to increase the health of soils, plants, animals, and humans), new combinations of practices emerge. Eventually those practices come to better suit the ideas and the interests of various stakeholders (e.g., consumers, farmers, institutions, and industry). Given the environmental and human health concerns regarding the high-input feedlot model, the livestock industry will arguably have to shift toward an increasingly regenerative hybrid in the future. Even within pasture-based systems, there will be a need for a paradigm shift from conventional (e.g., unmanaged systems that risk overgrazing and land degradation) to agroecological practices that mimic processes of natural ecosystems (e.g., adaptive grazing, integrated crop-livestock systems, multi-species grazing, silvopasture systems etc.). If changes are not taken on an industry wide-scale, the livestock industry may be at risk from increasing societal and institutional pressures to adopt policies that will eventually force change (e.g., through loss of market shares and taxation). Concerns about climate change and associations of red meat and dairy with metabolic disease risk have led to rapid expansion of substitutes, which are touted as better than traditional meat and dairy for environmental and human health (Clay et al., 2020; Van Vliet et al., 2020). Moreover, food policy now questions whether red meat should even be consumed as part of environmentally friendly and healthy diets by future generations (Lucas and Horton, 2019; Willett et al., 2019; WBCSD, 2020), despite having nourished *Homo Sapiens* and its ancestors for the last 1.5 to 3 million years (Gupta, 2016; Andrews and Johnson, 2020).

CONCLUSION

Plant diversity—and associated phytochemical richness—links animal, human, and environmental health (Provenza et al., 2019). In addition to reducing per capita consumption of meat in industrialized countries (Godfray et al., 2018), human and environmental health can be enhanced through livestock management practices that promote good land stewardship, limit environmental impacts (Wepking et al., 2019; Andrews and Johnson, 2020; Richter et al., 2020; Rosenzweig et al., 2020), and enhance the healthfulness of meat and dairy products (Provenza et al., 2019). While public health recommendations are for reducing red meat consumption to reduce risk of metabolic disease, no consideration is given to animal production practices in these dietary recommendations. That is likely because the literature on animal production systems and human health is limited.

Forage selection by livestock impacts the phytochemical richness of meat and dairy products, with greater botanical diversity resulting in both a wider variety and higher concentrations of health-promoting phytonutrients in meat and milk (**Figure 1**). Conversely, these phytonutrients are typically undetectable or present in lower concentrations in meat and milk from animals fed grain-based concentrates in confinement. The presence of phytonutrients in animal foods currently remains underappreciated, and is virtually unheard-of in discussions of nutritional differences between pasture-raised (grass-fed) and feedlot-finished (grain-fed) meat and milk, which have focused myopically on omega-3 fatty acids and CLA (Provenza et al., 2019). For this reason, is it often stated that little to no differences exist between grass-fed or grain-fed meat and milk; however, the reductionist focus on fatty acids vastly underestimates the complexity of natural food matrices. It is in the expanded pool of phytonutrients (e.g., terpenoids, phenolics, carotenoids, and tocopherols) where substantial differences between grass-fed and grain-fed meat and milk are observed.

The expanded pool of phytonutrients must be considered in attempts to understand the effects of meat and dairy consumption on human health, such as the dampening of inflammation and oxidative stress linked with cancer, heart disease, and metabolic syndrome—diseases that have been associated with red meat and dairy consumption (Ganmaa et al., 2002; Micha et al., 2012; Zheng et al., 2019; Fraser et al., 2020; Zhong et al., 2020). Though research is sparse, several studies show a potential for anti-inflammatory effects and improved lipoprotein profiles when people consume pasture-raised meat and dairy. How increasing the phytonutrient density of animal foods will modify potential relationships between consumption and metabolic health of consumers needs to be further addressed in clinical studies.

Future research should systematically assess the linkages between phytochemical richness of herbivore diets, the nutrient density of animal products, and their subsequent effects on human metabolic health. This is important as a rich body of agricultural literature exists on the presence of health-promoting phytonutrients—terpenoids, phenols, carotenoids, and tocopherols—in grass-fed meat and milk that have rarely been evaluated in clinical trials for their potential to modulate human health responses to meat and milk consumption. Given the concerns about red meat consumption on human health and the growing interest among producers and consumers in grass-fed meat and dairy products, clinical nutrition studies evaluating cardiometabolic risk biomarkers in response to phytochemically-rich meat and dairy represents a logical next step in the field. Finally, future studies should elucidate critical—and as yet unstudied—linkages between soil health, plant diversity, and the health of livestock and humans. Addressing this research gap will require greater collaborative efforts from the fields of agriculture and medicine.

AUTHOR CONTRIBUTIONS

SV wrote the first draft of the manuscript. FP and SK provided many suggestions to improve the manuscript. All authors approved the final version of the manuscript.

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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.