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Review

Prairie Agroecosystems: Interconnected Microbiomes of Livestock, Soil and Insects

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Abstract: Agroecosystems are comprised of environmental compartments where associated microbial communities interact with one another. These microbial communities, called microbiomes, inhabit livestock, insects, and plants. Microbiomes are also present in the soil and watersheds. Clarifying the nature and extent of microbial interactions between compartments both at intra-farm and global scales can promote sustainable production systems, healthier animals, increased crop yields, and safer meat products. Early research on microbiomes was hindered by a lack of expertise and the high cost of molecular sequencing. However, these limitations have been largely resolved with advances in and reduced costs of sequencing technologies. In this paper, we summarize sequencing and bioinformatics approaches, and review the crucial roles of diverse microbiomes in livestock, plants and soil, as well as pollinators and pest insects. These crucial roles include nutrient cycling, nutrient acquisition, metabolism of toxins and enhanced host immune function. Additionally, we examine potentially undesirable effects of microbiomes associated with climate change and agri-food production such as their role in the release of greenhouse gases from cattle and their impact on meat safety and spoilage. By increasing the awareness of microbiomes and the growing ease with which they can be studied, we hope to foster a greater adoption of microbiome research. Further understanding of the diverse effects and interactions of microbiomes will advance our efforts to increase agricultural production while reducing its negative environmental footprint, thus making the agroecosystems more sustainable.

Keywords: microbiome; agriculture; greenhouse emissions; ecosystem; prairies

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1. Background

A microbiome is the community of microorganisms (bacteria, protozoa, fungi, archaea, and viruses) and their genetic potential within a defined environmental compartment that may include a host such as an animal or plant, or be present in soil and water. The microbiome can mediate multiple metabolic processes that affect plant growth, soil biodiversity, pollinator services, and host health. In many cases, these microbiomes interact across hosts and compartments to affect the production and sustainability of agroecosystems, including agricultural food production on the Canadian Prairies (Prairie Agroecosystem), in unsuspected ways.

Microbiome research focusing on livestock (e.g., cattle, swine) is driven by the desire to optimize animal growth and production, as well as to maintain the safety of animal

products entering the human food chain. A diverse and complex ecosystem of microbes is found on the hide/skin, in the gut, and in manure/feces that interact with microbes in bedding, feed troughs and feed. In addition to food safety, microbial spoilage of meat products is also influenced by the microorganisms associated with food-producing animals. Within the animal, the microbiome is involved in vitamin synthesis, carbohydrate metabolism, digestive health, regulation of the host's immune system, and defense against pathogens. Factors affecting the composition of livestock microbiomes include diet, feed additives, weaning, the environment, and breed/host genetics [1], with diet being the largest determinant of bacterial community structure [2]. For livestock production, and in particular, beef and dairy production, cattle, one important area of concern is the emission of greenhouse gases (GHGs), especially methane, through eructation. Methane is generated largely by the archaea (methanogens) in the rumen through the hydrogenotrophic pathway where hydrogen ions and carbon dioxide produced by fermentative processes are converted to methane. The production of methane reduces environmental accumulation of hydrogen, which can shift the microbial community composition, but also reduces feed efficiency in ruminant production and contributes to GHG emissions. A reduction in methane production could improve the energy capture from feed and thereby increase the efficiency of feed conversion.

Microbiomes associated with livestock, specifically those of the dung, also influence the soil microbiome, which further affects the crop rhizosphere and contributes to enhanced nutrient uptake, drought tolerance, and pathogen or pest resilience [3–5]. Soil is an extraordinarily heterogeneous matrix with a highly variable distribution of nutrients across space and time [6]. As plants take root and grow, they feed soil microbes through root exudation, which can trigger the release of plant-available nutrients and plant-soil feedback. The species or type of crop (e.g., cereal, pulse, oilseed) and associated differences in agronomic practices also drive microbiome assembly [7], which changes predictably with plant phenology [8]. An improved understanding of the processes governing microbiome assembly is emerging as the leading possibility for manipulating plant-soil feedback, inoculation, and shaping desired outcomes such as pest resistance [9].

The microbiomes in dung and, as well as those of plants and their flowers, influence the microbiomes of economically-important pest and beneficial (e.g., pollinators) insects, which are in turn manipulated by crop management practices [10–13]. Insect microbiomes contribute to the nutrient availability of the host, affect sex ratios, or confer protection against parasitoids or pathogens [14]. These microbiomes can be directly or indirectly affected by a complex of factors. These factors include the plant upon which the insect feeds or pollinates [10], the microbiome of the soil in which the plant grows [11,12], agricultural intensification [15,16], and the application of veterinary medicines to livestock [17]. The essence and extent of these interactions are further complicated by climate change [18] and the adoption of new crops and agricultural practices with attendant consequences to the soil microbiome and ecosystem services [18].

Our underlying objectives in this review are three-fold: to (i) increase awareness of the roles that microbiomes play in different hosts and environmental compartments in agroecosystems, (ii) illustrate the interactions of these microbiomes, and (iii) show how these microbiomes and interactions are intimately entwined with agricultural practices. We also wish to increase the familiarity of the reader with research on microbiomes and the growing ease with which their study can be incorporated into research programs. This review addresses our objectives by examining the microbiomes associated with livestock, soil and insects—particularly in the context of prairie agriculture in North America.

In this review, we discuss their environmental effects and future research opportunities and consider how microbiomes are interconnected from an ecological context in our agricultural system.

2. Bioinformatic Methods for Microbiome Analysis

The rapid development of high-throughput sequencing (HTS) and the corresponding tools for bioinformatics analyses in recent years has enabled effective identification of taxa within microbial communities and the genes harboured by individual taxa. Here, we summarize approaches for microbiome sequencing (Section 2.1), bioinformatics methods for analysis (Section 2.2), and relevant terminology and ecological background (Section 2.3) to facilitate reading this review.

2.1. Approaches for Microbiome Sequencing

High-throughput sequencing of microbiomes has enabled data generation on a large scale and increased the affordability of amplicon-based marker gene surveys and shotgun metagenomics. Both amplicon-based marker gene surveys and shotgun metagenomics provide information about the taxonomic composition of a microbial community, but metagenomics sequencing includes all genetic material in a sample, thus providing additional information about gene content and genetic potential of both the microbiome and the host. Generally, a ribosomal RNA (rRNA) gene (16S for prokaryotes, 18S for eukaryotes) is used as the marker gene in amplicon-based studies due to its conserved nature, resulting in a relatively robust representation of taxonomic relationships [19]. Alternative marker genes can be used as well, with a common strategy consisting of targeting metabolic genes to determine the taxonomic composition of microbes with a certain function. One such example is the amplification of the *mcrA* gene (methyl coenzyme M reductase) to uncover the taxonomic affiliations of microbes responsible for methane production in the bovine rumen [20].

The majority of microbiome sequencing studies from the last decade have used second generation sequencing methods, most commonly utilizing the various Illumina platforms. These platforms allow for the high-accuracy, simultaneous sequencing of hundreds of samples and generate short reads ($\leq$300 bp), which require downstream bioinformatic merging or assembly to obtain more useful information. Recently, long-read sequencing platforms, for example, Oxford Nanopore Technologies and Pacific Biosciences, are being used more frequently. These platforms can produce reads longer than 10 kb, and despite a higher error rate, have been used to sequence both amplicon-based marker genes and metagenomes [21–23]. An added feature of Oxford Nanopore Technology is the small size of the MinION instrument, which allows for portability to remote field locations and has the potential to provide real-time sequencing in the field. In situ sequencing could therefore be advantageous for real-time diagnostics of soil and livestock health [24].

2.2. Bioinformatic Methods for Taxonomic Analysis

A multitude of workflows exist for the analysis of amplicon-based marker gene and metagenomic sequences. Amplicon-based marker sequencing pipelines, including Mothur [25], QIIME2 [26], and DADA2 [27], use raw rRNA gene sequences to perform a series of steps leading to data output: quality control, read pair merging, identification of amplicon sequence variants (ASVs) or clustering of similar sequences into operational taxonomic units (OTUs), and lastly, assignment of taxonomy to sequences based on an rRNA-specific taxonomic database; e.g., Silva [28]. The subsequent investigation of diversity and distribution are conducted on the output tables consisting of unique OTUs or ASVs and their relative abundances across the experimental samples. Amplicon sequencing analysis workflows, particularly for the rRNA gene, have become more standardized with increased use. Thus, the main biases in the method are due to the selection of PCR primers, variable copy numbers of the 16S rRNA gene within bacteria, and the low taxonomic resolution (often to genus level) of marker genes [29]. The analysis of shotgun metagenomics sequencing is computationally intensive and can involve different steps depending on the goals of the research. Effectively, two main trajectories for metagenomics analysis exist: gene-centric and genome-centric. Gene-centric metagenomics consists of identifying gene coding regions within reads or within reads assembled into longer continuous sequences

called contigs. The identified genes are then functionally and taxonomically annotated to determine the genetic potential of the microbial community, and possibly which microbes are responsible for this potential. Genome-centric metagenomics involves assembling reads into contigs and then grouping contigs based on characteristics such as frequency of nucleotides and read depth, in a process called binning. These groups are considered representative genomes, or metagenome-assembled-genomes (MAGs), if they are of sufficient quality. MAGs provide information about which microbial species or even strains are present in a sample and also provide higher confidence to taxonomic classification of genetic potential [21].

Metagenomics can provide sequence information from other members of the microbiome including protozoa and viruses, as well as details on the identity and relative abundance of microbial functional genes such as antimicrobial resistance genes [30]. Metagenomics also provides higher taxonomic resolution (species/strain) than marker gene sequencing because more than one gene is sequenced. Two of the present barriers to wider adoption of shotgun metagenomics sequencing in microbiome research are cost and the need for greater computational resources than required for marker-gene surveys. In host-associated samples, the usual practice is to filter out the host genome sequences. However, in some systems such as the honey bee gut microbiome, metagenomics sequencing can provide sufficient information to characterize host-microbiome interactions [31].

2.3. Relevant Terminology and Ecological Background

Microbiome studies use alpha and beta diversity indices to estimate within- and between-sample diversity, respectively. When measuring alpha diversity (i.e., the number of species and their abundance within a sample), indices or metrics used in other sub-fields of ecology can be used, such as the Shannon diversity index, Simpson's diversity index, and the Chao1 index. Beta diversity analyses investigate how similar two samples are in terms of their microbial community composition, and can be used to pinpoint which external factors have the strongest effect on microbial composition. They often require the calculation of distance or dissimilarity metrics, which quantify the difference in microbial composition between samples. There are several user-friendly, open-source software tools available for estimating microbial diversity and determining the factors that affect it, such as the vegan package in R [32], and the rRNA gene workflows Mothur and QIIME2 [26].

3. Livestock and Meat Microbiomes

The gut microbiome is of particular importance in the health of both ruminant and monogastric species. The main role of the commensal population in the gut is the efficient breakdown of feedstuffs and the provision of nutrients for the host, but they also have a key role in the regulation of the host immune system and the competitive exclusion of pathogens. Specifically, bacteria in the gastrointestinal tract (GIT) produce short-chain fatty acids (SCFAs) such as acetate, butyrate, and propionate from otherwise non-digestible polysaccharides [33] and also generate certain vitamins including B_{12} and K [34]. This largely takes place in the lower GIT of monogastric animals and in the rumen (forestomach) of ruminants. There are millions of unique microbial genes within the gut microbiome [35–37] compared to the 20,000 to 25,000 genes found in pig and cattle genomes, thereby greatly expanding the enzymatic repertoire of the host. The microbiome is critical in the early development and maturation of the host immune system [38], and it can provide resistance against colonization by pathogenic microbes through several mechanisms including the production of antimicrobials [39].

The integral role of the gut microbiome in host health and function is made especially evident in the germ-free model. Germ-free animals require dietary supplementation for survival and often need significantly more calories to obtain the same weight as conventionally-raised animals [40]. In conventionally-raised livestock, such as cattle and pigs, succession of the GIT microbiota begins with parturition and exposure to the vagina microbiota of the dam. Further exposure to the environment, and feed (including milk)

continuously introduces new microorganisms to the gut, where the processes of digestion, physiological and immunological development occur [41] and in ruminants specifically, an anaerobic environment develops [42]. Regardless of the animal species, the key influences on the gut microbiome remain the same: diet and nutrient availability, environment, animal genetics and exposure to antibiotics. The combination of these factors impacts the animal variability, GIT ecosystem stability, and the susceptibility to disease.

Because both the physiology and common production practices of monogastric and ruminant livestock are quite different, we discuss some of the aspects unique to cattle and pigs with a focus on the GIT microbiome.

3.1. Ruminant Livestock Microbiome

The gastrointestinal ecosystem of the ruminant is unique in comparison to other livestock based on the highly developed and specialized mode of digestion. Similar to other herbivores, the microbes that inhabit the GIT are the main agents for the digestion of complex carbohydrates. However, in ruminants these carbohydrates are not the primary source of energy for the animal, but instead microbes ferment complex carbohydrates to SCFAs (mostly acetate, butyrate, and propionate) that are used by the host as the primary energy source for metabolism. Their digestive system is characterized by pregastric retention and fermentation with symbiotic microorganisms in three distinct niches: solid-associated bacteria, the free-floating liquid community, and epithelial adherent biofilms. These niches have diverse metabolic functions, but many phenotypes overlap between these communities and those in the hindgut as well. The rumen microbiome consists of a highly diverse and complex ecosystem of protozoa, bacteria, archaea, fungi, and viruses [2]. The most diverse of these groups is the bacteria, which are adapted to function at acidities between pH 5.5 and 7.0, in the absence of oxygen, at a temperature of 39–40 °C, in the presence of moderate concentrations of fermentation products, and at the expense of the ingesta provided by the ruminant. The steady supply of food and the continuous removal of fermentation products and food residues maintain relatively constant conditions in which an extremely dense population can develop.

Rumen bacteria are commonly divided into functional groups including cellulolytic, amylolytic, and proteolytic. The relative proportions of each group vary according to the dietary substrates provided, with the largest diversity found in animals consuming a forage-based diet. Under more energy-dense conditions, the relative proportions of celluloytic bacteria such as *Fibrobacter* and *Ruminococcus* spp. decrease, while the proportions of amylolytic and lactic acid metabolizing bacteria such as *Megasphaera elsdenii* and *Selenomonas ruminantium* increase due to acid sensitivity and lower levels of substrate availability. Despite dietary changes, Henderson et al. [2] were able to show a core set of dominant bacteria in the rumen across a range of ruminant species, diets and geographical locations, including *Prevotella*, *Butyrivibrio*, and *Ruminococcus* spp. The most predominant archaea are members of the *Methanobrevibacter* spp. Similar to the bacteria populations, they are found in all niches of the rumen and increase in relative abundance with the proportion of fibrous feedstuffs consumed by the host. While the protozoal, fungal and more so the viral populations of the rumen remain minimally understood in comparison to the bacterial and archaeal populations, substantial work has shown that their presence in the rumen is a key part of a healthy and functioning digestive system.

A few studies have examined the colonization of the GIT of ruminants and the changes associated with development. Studies that have looked at rumen and fecal communities in ruminants from birth through adult development have noted a succession of specific taxa unique to each animal, with beta-diversity decreasing and alpha-diversity increasing as animals aged, with a transition to an adult-like microbiota between weaning and one year of age. Facultative anaerobes such as *Streptococcus* and *Enterococcus* spp. are known early colonizers [43] that serve to convert the GIT to a fully anaerobic environment. Strictly anaerobic bacteria then establish and dominate the community within the first few days

after birth [44,45]. In contrast, anaerobic fungi and methanogenic archaea do not appear in the rumen until approximately one week after birth [46].

One of the largest areas of inefficiency in the rumen is the process of methanogenesis [47]. The redirecting of energy from methane (CH_4) to fermentation products with a nutritional value would increase energy availability to the host and decrease CH_4 production and reduce environmental impacts of cattle agriculture. Any process to reduce methane production in the rumen must account for how to remove the fermentative hydrogen build-up in the rumen. Martinez-Fernandez et al. [48] showed that supplementation of phloroglucinol together with 3-nitrooxypropanol (3-NOP) promotes the capture of excess hydrogen from methanogenesis, thereby reducing methanogenesis. In recent years there have been considerable efforts to control the formation of CH_4 in the rumen, which represents an energy loss of 2–12% of gross energy intake [49]. Because methane is produced from carbon dioxide and metabolic hydrogen, both the inputs and outputs of this biochemical process are controlled by microbial metabolism, making the most logical targeted solutions to methane reduction microbial-based. Unfortunately, the complex and interconnected web of metabolism and fermentation in the rumen has made targeted solutions difficult and some methods for reducing methane affect the productivity through means unrelated to methanogenesis [47].

Although dietary composition is the most influential factor driving the equilibrium of the population, individual animal variation [50,51] associated with the rumen ecosystem is a critical component to understanding how the rumen microbiome impacts animal performance [52], disease susceptibility [51,53], methane production [54], antimicrobial resistance [55], and pathogen shedding into the environment [56]. A key component to advancing our understanding of these linkages is to elucidate the host-microbial cross-talk within both the rumen and hindgut of the ruminant. Host-microbial interactions are well defined in the GIT of humans, due to their enormous impact on host health. Although metabolic dysfunction and health of the rumen (i.e., subacute acidosis) are also linked to the composition and functions of the rumen microbiome [57], host-microbial interactions in the rumen have mainly been studied to maximize production performance. In that regard, it is well understood that not only does the microbiome drive host development, but also the host drives the microbiome [58]. However, functional redundancy in the rumen and the GIT means that changes in metabolic function and efficiency of the ecosystem are not always reflected in the microbial diversity or relative abundances of specific microbes. This metabolic redundancy combined with the complexity of the ecosystem, the sensitivity to dietary components and the impact of animal variation, means that our understanding of mechanisms of action, cross-talk and targeted intervention strategies for gut health is less than that for other mammalian species.

3.2. Monogastric Livestock Microbiome

As with other mammals, the gut microbiome of pigs is acquired from the sow and the environment. The GIT is initially colonized by bacteria such as *Clostridium*, *Enterococcus*, *Escherichia*, and *Streptococcus* spp. [59,60] and within a few days, anaerobic outnumber aerobic bacteria [61]. The mature pig gut microbiome is typically dominated by members of the *Blautia*, *Lactobacillus*, *Prevotella*, *Ruminococcus*, and *Treponema* genera [62]. In modern swine production, pigs are weaned relatively young, 19 to 22 days old and sometimes younger in North America, and take about five to six months to reach market weight. A number of factors can influence and shape the pig gut microbiome including diet, age, disease state, genetics, gender, and the environment. Of these factors, diet has the strongest effect on the gut microbiome as evidenced by the large alterations that take place pre- and post-weaning when piglets are switched abruptly from a largely milk-based diet to one that is solid and rich in plant polysaccharides [63–65].

The pig gut microbiome reaches a stable state rather quickly, often within a few weeks of weaning [63,64,66]. As with humans, the pig GIT increases in bacterial concentration and diversity from the proximal to the distal end with the highest numbers in the colon

(10^{10} to 10^{12} bacterial cells g^{-1} digesta) [62,67,68]. Pigs receive up to 30% of their energy requirements from SCFAs produced by bacterial fermentation that takes place largely in the colon [69]. Therefore, a number of different studies have attempted to link the composition of the pig gut microbiome to feed efficiency and growth [70–73]. Although bacterial genera such as *Lactobacillus*, *Treponema*, and the archaeal genus *Methanobrevibacter* have consistently been identified as more relatively abundant in feed-efficient pigs, other bacterial genera including *Bacteroides*, *Prevotella*, *Roseburia*, and *Streptococcus* have been reported by different studies to be associated with both feed-efficient and less feed-efficient pigs [74].

Fecal microbiota transplantation (FMT) involves the transfer of a fecal microbial community from a donor to a recipient and has been used to successfully treat refractory *Clostridioides difficile* infections in humans [75]. Recently, FMT has been used in swine with transfer from feed-efficient pigs to gestating sows via gastric intubation. This was shown to improve feed efficiency in their offspring [71] but also negatively affected weight gain in these piglets [76]. However, the preparation for FMT involved the use of antibiotics and purgatives in recipients, which makes it difficult to assign any subsequent observed effect directly to the FMT. Another study orally transferred feces from a breed of minipigs that are more resistant to post-weaning diarrhea into commercial Landrace x Yorkshire piglets prior to weaning. These authors reported a significantly reduced incidence of post-weaning diarrhea comparable to piglets treated with oxytetracycline [77]. Although likely impractical on a large scale, these studies demonstrate the potential of microbiome manipulation in swine.

3.3. Feed Additives

Antimicrobials have long been included in livestock diets in North America to improve growth and feed efficiency in cattle and pigs. Although the exact mechanism behind their growth-promoting effects is largely unknown, it is believed to be due to a direct effect on the gut microbiome [78]. However, concerns regarding the rise of antimicrobial resistance have restricted the use of this feed practice and increased the interest in alternative methods of manipulating livestock microbiomes to enhance weight gain.

One such alternative method is the use of probiotics, which are defined as "live microorganisms that, when administered in adequate amounts, confer a health benefit on the host" [79]. When used in food-producing animals, they are often referred to as direct-fed microbials [80]. The potential mechanisms responsible for beneficial effects on the host include competitive exclusion of pathogens through production of antimicrobial compounds and/or inhibition of colonization, enzyme and SCFA production, and immunomodulatory effects [81]. While other feed additives have been used with varying results in ruminant and monogastric livestock species, the differing microbiomes and associated gastrointestinal physiology and ecology make finding universal products such as antimicrobials incredibly difficult. It is not surprising then that studies using probiotics to improve livestock productivity and health often report results that are inconsistent and highly variable [82,83].

The majority of commercially available probiotics for livestock comprise a relatively small group of microorganisms, namely the lactic acid bacteria, *Bacillus* spp., bifidobacteria, and yeasts [84]. Additionally, the probiotic strain(s) may not have been originally isolated from the species receiving the probiotic. Therefore, increasing the diversity and number of commercially available bacterial species with potential probiotic benefits is desirable. These microbes are sometimes referred to as "next generation probiotics" [85]. Prebiotics, defined as "substrates that are selectively utilized by host microorganisms conferring a health benefit", represent another promising antimicrobial alternative and include fructooligosaccharides, galactooligosaccharides, and mannan oligosaccharides [86]. Some products on the marketplace combine a prebiotic with a probiotic, which is termed a "symbiotic". These additives are typically delivered in feed, and as with probiotics, the effects on animal health and production are highly variable [84]. Microbiome research not only promises to greatly expand the number of microorganisms under study for use as a probiotic, but also the variety of prebiotic substrates that enhance their activity.

3.4. From Livestock to the Meat Microbiomes

The previously sterile meat surface is inevitably contaminated with microorganisms during the dressing process in meat packing plants, e.g., with microorganisms on animal hides and in their GI tracts, and as such, the microbiome on carcasses before chilling largely reflects the microbiome of livestock [87]. Cold temperatures during chilling and fabrication further select for the psychrotolerant members of the carcass microbiome; bacteria on processing equipment surfaces will also contaminate meat during fabrication. Thus, the microbiome of freshly fabricated cuts and trimmings reflects the fraction of the dressed carcass microbiome that survives and grows at cold temperatures and those on equipment surfaces.

Bacteroidetes, Firmicutes and Proteobacteria are the dominant bacterial phyla on both beef [88] and swine [89,90] hot carcasses. The bacterial phyla of the microbiome of hot carcasses correspond with the major phyla of the fecal microbiome of beef cattle [91,92] and domestic pigs [62,93,94], as most bacteria on skinned carcasses would reflect those on the hides of animals. After the meat is further processed, however, the microbiome of finished meat cuts [95] largely differs from that of livestock [96,97], representing only a small fraction of the initial livestock microbiome. However, this small fraction may include significant human pathogens. For instance, Shiga toxin-producing *Escherichia coli* (STEC) has been involved in numerous foodborne outbreaks and product recalls since being implication in a multistate outbreak involving ground beef in the 1990s [98]. Ruminants such as cattle are the primary host of STEC; however, carriage of the microorganism does not cause disease in cattle as they lack the vascular receptor for Shiga toxin(s) [99]. The STEC has been found in all hide samples collected from cattle presented for slaughter in a beef packing plant in the Canadian Prairie region, similar to the prevalence of STEC found on the hides of cattle in a US beef plant [100]. In contrast to the very low incidence of the STEC strain O157:H7 associated with pork worldwide, there has been four major outbreaks associated with pork in Alberta since 2014 and some of these STEC O157:H7 strains carried more potent Shiga toxin subtypes [101]. The evolution of *E. coli* is shaped to a similar extent by their genetic background and their environments [102]. Whether the higher incidence of STEC associated with pork in Alberta is due to the interactions between microbiomes and their habitat, or from contamination during processing, would require further investigation. By the same token, another significant zoonotic pathogen, *Salmonella*, is ubiquitous in cattle and consequently beef in the United States, but is rare in cattle/beef in Alberta [103].

In meat processing facilities, various interventions such as steam and acid washing are applied to reduce pathogens and spoilage microorganisms. Other common interventions include spraying the carcass to reduce bacterial loads using hot water/steam and antimicrobial solutions (low concentrations of lactic/citric/peroxyacetic/acetic acid, chlorine dioxide, or acidified sodium chlorite). Steam vacuuming with or without hot water or lactic acid wash reduces the concentration of mesophilic bacteria including *Enterobacteriaceae* (e.g., *Escherichia coli* and other coliforms) by 2 to 5 log CFU (colony forming units)/cm^2 on beef carcasses [104]. Washing with high pressure water and lactic acid effectively reduces mesophilic bacteria and *Enterobacteriaceae* on hog carcasses [105,106], and organic acids reduce total bacteria on beef carcasses [107]. Despite the diversity of bacterial species found on fresh meat, the meat microbiomes after extended storage at chiller temperatures will be primarily dominated by lactic acid bacteria if stored under vacuum and by pseudomonads if stored in air. However, the exact microbial composition will vary largely with the initial microbiota and treatments or stress that they have encountered during meat processing [108].

4. Soil Microbiome

Soil is a living matrix of microbiomes interacting within physically and chemically heterogeneous environments [109]. Soil is often characterized as teeming with life, yet individual bacteria may actually experience minimal interactions with other individuals [110].

Due to the heterogeneity and complex arrangements of pore space and water films, bacteria and other soil denizens can remain separated from each other, at least in bulk soil.

Soil biological communities form complex interaction networks, and play a vital role in controlling ecological functions. Soil microorganisms are essential in nutrition and carbon cycles, healthy soil formation, and plant disease resistance. Plants are rooted in the soil; therefore, they are influenced by symbiotic and/or pathogenic soil-derived microbes. Recent breakthroughs in technology, especially microbial genomics, have enhanced appreciation of the multiple interactions of soil microorganisms with other environmental compartments. In this section, we attempt to summarize the possible soil microbe-crop interactions along with agronomic practices for improving crop productivity.

4.1. Soil Microbiomes in Agriculture

Well-structured soil is the foundation of successful crop production. Soils differ regionally in physical, chemical, and biological properties that collectively define soil fertility and affect crop productivity. In characterizing soil fertility, chemical and physical properties have received much more attention than biological characteristics, partly because of the complexity of soil. Roots penetrate and explore soils, inject carbon compounds, trigger bacterial proliferation, and feed a complex food web [6]. The communities assembled by these flows and changes are determined by historical biotic and abiotic events. The order of arrival of microbes (priority effects) can determine the outcomes of interactions between populations, and influences the structure of the microbiome [111].

Plants recruit and mediate interactions with microbes in the rhizosphere (the narrow region of soil and associated soil microorganisms) through root exudates [112–115]. Root exudates account for a significant amount of photosynthetically-fixed carbon [116,117] and can be broadly grouped into two categories: low-molecular-weight compounds such as sugars, amino acids and secondary metabolites; and high-molecular-weight molecules such as polysaccharides and proteins [118–122]. The chemical composition of root exudates changes during the course of plant development [115,123] and in response to environmental cues [124,125]. Thus a complex and dynamic interaction between plant genetics, developmental progression and environment shapes the rhizobial microbiome, which in turn has a significant impact on plant and soil health.

The legacy effect of a particular annual crop is enrichment of a unique microbial community, in addition to the incorporation of specific biomass residues with variable composition and effects, which in turn can impact subsequent or co-planted crops. Our fundamental understanding of the microbiome in soils and the impacts of agricultural practices is increasing, leading to the possibilities of manipulating them for the benefit of our agroecosystems.

Rhizosphere microbial community assemblages are species-specific [126,127] and can be affected by plant host genetic differences between cultivars and subspecies [128–131]. Matthews et al. [127] found that different crop species assembled distinct microbial communities and that these communities varied depending on whether they were grown in grassland vs. woodland soils. Howard et al. [132] used soil inoculants from fallow fields of increasing age and found an effect of inoculant age on microbial assemblage and plant growth, though the effects were crop-specific. These results suggest that some plant hosts are more discriminating or better able to manipulate their microbial associations than others.

Microbial community assemblages also change during the course of the growing season in response to plant developmental stages [123,133,134]. This has been shown to be the case in greenhouse studies [123,130,135] and in field grown crops [136–138]. Generally, rhizosphere microbial communities tend to be most diverse at the germination or seedling stages, compared to later vegetative and/or flowering stages [123,138].

4.2. Impact of Environment and Climate

Environment and climate can alter and shift soil microbiomes. Dramatic impacts on organization of populations in soils occur with shifts in pH [139]. Increases in pH, often associated with agriculture practices including nitrate-N-based fertilizer and liming, can dramatically alter carbon use efficiency and reduce the capacity of soils to sequester carbon [140]. Soil microbial communities are also impacted by drought, as lack of water slows diffusion and access to nutrients; with activity peaking in response to a rewetting event [141]. Drought affects the chemical characteristics and amounts of root exudates produced by plants. Because soil microbiomes are fed and manipulated by root exudates, their community structure is inextricably linked to drought conditions [142]. In addition, an increase the frequency of freeze-thaw cycles with climate change may also have an impact, [143], although this has not yet been shown in agricultural systems. Just like other ecological communities, soil microbiomes respond to food quality and quantity, water availability, and temperature.

4.3. Impact of Agricultural Management

Soil and crop management activities in the Prairies alter the soil microbiome through various mechanisms. These activities include tillage, fallowing, crop rotation/intercropping, fertilizer application, organic soil amendments, and pesticide applications.

Tillage: Until recently, soil tillage was the standard seedbed preparation method used to control weeds, manage disease, and promote plant residue decomposition. However, tilling the soil leads to loss of soil organic carbon (C) by erosion of the loosened soil and accelerated decomposition due to breaking up the soil aggregates that protect occluded C from microbial decomposition. Because soil organic C is the main substrate on which most soil microorganisms depend on their metabolism, the soil microbiome and its ecological services are usually disturbed by tillage. A no-till vs. plough-tillage comparison of the soil bacterial community profiles and functions after nearly 50 years of the two systems in Ohio showed that no-till soil had greater bacterial diversity than plough-tillage [144], which is in agreement with most other studies [145]. Quantification of genes involved in nitrogen metabolism suggested that no-till soils had greater microbial capacity to mineralize nitrogen for crop use than tilled soils. With the advent of herbicides and herbicide-tolerant crops, no-till systems, which increase C sequestration and N mineralization rate in the soil, are now common on the Canadian Prairies [144].

Fallowing: Fallow-based cropping, in which one or two years of cropping are followed by a fallow year (without crops), was widely practiced in the past to "recharge" the soil by restoring soil water and fertility [146]. Generally speaking, the absence of crops during fallow periods reduces organic C inputs to the soil, which reduces soil organic C [147,148]. A 10-year fallow vs. continuous winter wheat cropping comparison revealed that continuous wheat had greater relative abundances of the fungal genera *Chaetomium*, *Humicola* and *Cryptococcus* than bare fallow, but the opposite was observed for the bacterial genus *Bacteroides* [149]. In the same study, soil available P was higher in continuous wheat than in bare fallow, but the reverse was true for soil inorganic N.

Crop rotation/intercropping: Crop rotation is successively growing more than one crop on the same piece of land, and intercropping is simultaneously growing more than one crop species on the same piece of land. Both practices increase either temporal or spatial crop diversity, and aboveground diversity usually increases belowground diversity [150]. Often, diversity in the soil microbiome increases functional resilience/stability by increasing the probability that some taxa will exploit differences or changes in resource availability [151]. Yang et al. [152] linked the occurrence of clubroot disease (caused by the protist *Plasmodiophora brassicae*) in oilseed rape to crop rotation-related composition of soil microbial communities. Planting soybean before oilseed rape increased the relative abundances of beneficial soil microbial genera that could reduce the severity of clubroot diseases of *P. brassicae*, including *Sphingomonas*, *Bacillus*, *Streptomyces* and *Trichoderma*. However, continuous cultivation of cruciferous crops accumulated soil-borne plant pathogens includ-

ing *P. brassicae*, *Olpidium* spp. and *Colletotrichum* spp. From a crop nutrition standpoint, legume-based crop rotations are beneficial to subsequent crops because of the N_2 fixed by legumes if residues are incorporated [153]. In a semiarid prairie, legumes in rotation altered soil bacterial community structure, increased bacterial diversity, and increased the N metabolism pathway [154]. However, continuous legumes build up legume-specific fungal disease populations; temporal and spatial crop diversification ensures well-balanced soil microbial communities and their functions in terms of beneficial or detrimental effects on crop growth.

Inorganic fertilizers: Inorganic fertilizers have both positive and negative effects on the soil microbiome, either directly or indirectly. The direct positive effect is provision of nutrients that soil microbes require for their metabolism. Indirect positive fertilizer effects include the increase in plant growth, which boosts the soil microbiome through increased rhizodeposits, and increased soil C and N input from crop residues. One positive example is that after 50 years of nitrogen (N) and phosphorus (P) fertilizer applications to wheat on the Canadian prairies, Li et al. [155] reported that the abundances of bacteria and fungi increased while that of archaea decreased with inorganic fertilizer N. The alpha diversity of the bacteria decreased while fungal and archaeal diversities increased with fertilizer N. Metabolic gene expressions revealed increases in bacterial denitrification, assimilatory nitrate reduction and organic N metabolism, fungal nitrate assimilation, and all archaeal metabolic processes with fertilizer N. In return, the soil microbiome makes otherwise unavailable substrate nutrients available to plants. The contribution of free-living bacteria to mineralization (and competition for) nutrients is one of the most critical aspects of plant-soil interactions [156]. However, the toxicity from inorganic fertilizers can also reduce plant growth, thereby reducing the mass and diversity of the soil microbiome through reduced plant biomass added to the soil. The other indirect negative effect is the soil-acidifying nature of some fertilizers, especially urea and ammonia fertilizers, which produce protons during nitrification [157], because only acid-tolerant soil microbes survive in acid soils.

Organic soil amendments: Amendments, such as animal manures/composts, crop residues, municipal wastes, and biochar, add organic C and nutrients to the soil [158,159]. The chemistry of the organic amendments can influence the composition of the soil microbiome. Bonanomi et al. [160] reported that recalcitrant C amendments were dominated by oligotrophic bacteria like *Acidobacteria*, which are slow growers that live in low-nutrient soils. On the other hand, copiotrophic bacteria including some classes of Proteobacteria and Bacteroidetes, which are fast-growers that flourish in nutrient-rich soils, were dominant where inorganic fertilizer was applied. Similar results were reported by Ding et al. [161] who, after 35 years of manure and inorganic fertilizer applications, also reported that inorganic fertilizers reduced soil bacterial and archaeal alpha diversity but inorganic fertilizers applied relative to the no-fertilizer control together with organic manures increased the diversity. Crop residue removal is an example of a practice that can reduce soil biodiversity. Thus, Kim et al. [162] reported that 10–11 years of residue retention increased the abundance of ammonia-oxidising bacteria, but residue removal increased nitrite reductase *nir*S-denitrifier abundance.

Herbicides: Herbicides are the most widely-used pesticides globally, and glyphosate is at the top of the list [163]. Glyphosate effects on the soil microbiome have been studied extensively. Although the herbicide has been associated with crop mineral imbalances [164] and increased disease incidences [165], presumably resulting from glyphosate effects on the rhizosphere microbiome [166], most studies find that it has no or only transient effects on the soil microbiome when applied at recommended rates [167–169]. However, the long-term effects of repeated applications of herbicides and other agrochemical pesticides are not yet clear and they require long-term trials.

Organic and cover cropping: Principles of organic and cover cropping are based on a system that can involve many management strategies, including optimization of soil biological processes for crop nutrition and protection. Synthetic fertilizers and pesticides are not allowed; plant nutrients are supplied through N_2-fixing legume crops (including

cover crops) and organic soil amendments, and weeds are controlled with tillage and other cropping practices including increased seeding rate, crop rotation, and polyculture. The soil organic amendments usually increase soil biodiversity. A recent meta-analysis showed that, relative to bare fallow, cover crops, which are usually planted in organic cropping, significantly increased soil microbial abundance, activity, and diversity parameters by 27%, 22%, and 2.5%, respectively [170]. These effects were modulated by climate, termination method, and tillage. Tillage in organic cropping reduces some of these benefits by reducing soil organic matter (discussed above). Consequently, some forms of reduced tillage, including non-inversion tillage, are being explored for organic cropping [171].

Despite an explosion in research into soil microbiomes and an increase in understanding of microscale microbial processes, macro-modeling soil microbial responses and feedback loops in agriculture systems requires more relevant experimental data [109]. Large-scale studies are beginning to demonstrate microbiome metabolism patterns [140,172,173], helping clarify underlying mechanisms of how soil microorganisms affect soil health [109]. Agricultural practices, however, can be modified to improve soil health via our current understanding of the soil microbiome. Growing perennial, or deeply-rooted plants, and allowing them to remain in place (no-till) increases rhizosphere inputs. Astute nutrient management, through organic and inorganic nutrient addition, keeps crops vigorous and photosynthesizing thereby generating more carbon for the belowground microbial community [173]. Future work should focus on harnessing the particular soil microbiome through cropping systems or microbial inoculants to achieve desired outcomes, whether they target roots, above-ground diversity, or nutrient management.

5. Insect Microbiomes

Insects and other arthropod species (e.g., isopods, spiders, and mites) occupy many different trophic levels of different ecological niches. Insect herbivores, for example, include pollinators, gall-formers, leaf-miners and detritivores [174]. Many insect species provide valuable ecological services in the form of pollination, seed-dispersal, bioturbation, nutrient cycling, or as food for vertebrate and invertebrate predators. Some species are economic pests that affect humans, livestock and crops. Other species are important natural enemies of these pests and suppress their populations [175].

It is partially because of their associated microorganisms that insects are able to thrive under such diverse and changing circumstances. The general features of insect microbiomes have been reviewed by others [176–180] and are only briefly discussed here. Membership in the microbiome may be either transitory or intimate. Transitory members persist on the external surface or in the gut of the insect. They are acquired by the host from the surrounding environment or from other insects via horizontal transmission. They may not be present in all members of the host population and often include facultative secondary symbionts that are not essential for host survival, but which can influence host biology. Intimate members are normally transmitted vertically from a female to her offspring and persist within their cells or in specialized organs (mycetomes). They are present in all individuals of the population and mostly include obligate (= primary) symbionts that are required for the survival of the host. As a consequence of their close evolutionary relationship with the host, the genomes of obligate symbionts can experience extensive gene loss.

The insect microbiome includes bacteria, archaea, protists, fungi, and viruses [178,179]. Efforts to define a core microbiome common to different insect taxa have focused on gut bacteria [14]. These bacteria are mainly represented by species of Actinobacteria, Bacteroidetes, Firmicutes and Proteobacteria, whose relative abundance is influenced by diet, gut morphology and physicochemical conditions, e.g., gut pH and oxygen levels [178,181,182]. Much less information is available for archaea, which are represented in the insect microbiome by Methanoarchaeota (methanogens), Crenarcheota, Thermoplasmatales and Halobacteriales [178,179,183]. These groups are associated with environments with low

oxygen levels (analogous to the rumen of higher mammals) and have been reported in the hindgut of cockroaches [184], termites [185] and scarab beetle larvae [183].

Most of the research on protist and fungal associates has been limited to single taxa that are either pathogens of, or vectored by, insects of economic or medical importance [178,179]. The best known protist-insect associations are those of termites and wood-feeding cockroaches [178]. These insects harbour unique gut protists from the orders Trichomonadida, Hypermastigida (Phylum Metamonada), and Oxymonada (Phylum Preaxostyla), which are involved in the degradation of lignocellulose [179,186,187]. Research on fungal associates has focused on yeasts and similar taxa [188]. They are most commonly represented in insect microbiomes by *Saccharomyces*, *Pichia*, *Kluyveromyces*, *Candida*, *Hanseniaspora*, *Debaryomyces*, *Metschnikowia*, *Lodderomyces*, and *Cryptococcus* [181,190]. Fungal associates are affected by the feeding habits of the host and the localization of food; within the host, they can influence behavior, fitness, the production of essential nutrients, digestion, and pheromone synthesis [178,179,188].

Studies of the viruses associated with insects identify high levels of abundance and genetic and phylogenetic variability relative to that of vertebrates [189,190]. Some of these viruses may be ingested with food, directly infect the host, or infect micro-organisms within the host [191]. The ancestors of some of these viruses likely infected plants and vertebrates with which the insects interacted and were incorporated into the microbiome over evolutionary time [114,190]. Horizontal gene transfer (HGT) is a non-sexual gene transfer across species that facilitates the acquisition of new functional roles [192]. This process is a source of evolutionary change in microorganisms but there is also evidence of this occurring between microorganisms and insects [192,193]. HGT in bacteria is mediated by mobile genetic elements like transposons, plasmids, and bacteriophages (viruses that infect bacteria; [194]). The high recombination rates of viruses and a vast gene pool facilitate the horizontal transfer of genetic material between bacteria in the microbiome [179,193,194]. HGT in insects is known to happen with bacteria that interact closely with their hosts as in the case of intracellular endosymbionts [193,195]. The type IV secretion system in bacteria is the only confirmed mechanism of HGT between bacteria and eukaryotes, but other systems might involve transposable elements, bacteriophages, giant viruses, and extracellular vesicles [192]. The genome of whiteflies incorporate bacterial genes that allow the host to synthesize the vitamin biotin [196,197]. Bacterial genes in the genomes of lepidopteran species and phytophagous mites allow these arthropods to detoxify cyanide produced by plants as a defense against herbivory [198]. The genome of the pea aphid *Acyrthosiphon pisum* incorporates genes of fungal origin that produce the pigment carotenoid, which alters the aphid's susceptibility to predators and parasitoids [199].

Three areas of research have been the subject of particular focus to clarify how the microbiome affects the survival and reproduction of the insect host, i.e., nutrient acquisition, symbiont mediated defenses, and reproductive parasites. We briefly introduce these topics and discuss some of the potential implications of microbiome-insect interactions in an agricultural and livestock context. We conclude with a section on managed pollinators, which play a unique role in prairie agriculture.

5.1. Effects of the Microbiome on the Insect Host

5.1.1. Nutrient Acquisition

Their microbiomes allow many insect species to survive and thrive on diets that lack essential nutrients, are otherwise toxic, or which are difficult to digest (e.g., sap, seeds, blood, wood, and dung) [178,200–202]. If not present in the diet, and in the absence of their microbiome, insects cannot produce various essential amino acids, generate certain co-factors required for enzyme function, or produce sterols that are used in cell membranes or as precursors for key hormones [203–205]. For example, the pea aphid requires certain amino acids for survival that are absent in the plant phloem upon which it feeds. The aphid obtains these amino acids from its symbiont *Buchnera aphidicola* and, in return, the aphid provides the symbiont with amino acids that are non-essential to the host [206]. As

a second example, the larvae of dung beetles (Scarabaeinae) have a gut microbiome that degrades undigested lignocellulose in herbivore dung [207]. Core members of this gut microbiome are passed from the mother to her offspring through secretions deposited on dung consumed by the larvae shortly after hatching [200,207].

5.1.2. Symbiont-Mediated Defenses

The microbiome may contain defensive symbionts that protect the host from pathogens, parasitoids or predators via one or more of three general types of mechanisms [208–210]. The first mechanism is through resource competition. For example, the fly *Drosophila melanogaster* harbours infections of the symbiont *Spiroplasma poulsonii* and is attacked by parasitoid wasps. The symbiont competes with the immature parasitoid for lipids in the host's hemolymph, which reduces the likelihood of parasitoid survival [211]. The second mechanism is by priming the immune system of the host to enhance its reaction against pathogens and parasites. Caragata et al. [212] review this process as it relates to the microbiome of mosquitoes in mediating infections of arbovirus. The third mechanism is through symbiont-produced chemicals. The symbiont *Hamiltonella defensa* confers protection to its aphid host against parasitism, the mechanism of which appears to be a toxin produced by a phage associated with the symbiont [213].

5.1.3. Reproductive Parasites

Some members of the insect microbiome manipulate the reproduction of their host to enhance their prevalence in the host population [214,215]. These reproductive parasites are typically acquired from the mother via egg cytoplasm. This manipulation results in infected individuals producing more progeny than their uninfected siblings and may take one of four forms: (i) cytoplasmic incompatibility—uninfected females mated with infected males produce sterile eggs, whereas infected females can successfully mate with either infected or uninfected males; (ii) parthenogenesis—unmated females produce female offspring; (iii) male-killing—male offspring die during embryogenesis, and (iv) feminization—genetic males develop into phenotypic females. *Wolbachia* spp. are the best known of these reproductive parasites. They infect an estimated 40% of terrestrial arthropod species [216], including many taxa of agricultural significance [217–219]. Other reproductive parasites include species of *Arsenophonus*, *Cardinium*, *Flavobacterium*, *Rickettsia*, and *Spiroplasma* [220].

5.2. Microbiome-Insect Interactions in an Agricultural and Livestock Context

There is a growing body of literature that documents the ability of microbiomes in herbivorous insects to affect the physiology of the plants upon which they feed, possibly enhancing the status of certain insects as economic pests. The Colorado potato beetle, *Leptinotarsa decemlineata*, is a major pest of potatoes in North America. During feeding, its larvae orally secrete three different species of bacteria. These bacteria activate the plant's chemical defenses against pathogens, reduce the plant's chemical defenses against herbivory, and enhance insect growth and survival [221]. Leaf-mining insects require photosynthetic tissue upon which to feed and can generate local areas of photosynthetic tissue ("green islands") in otherwise senescent leaves. In some species of leaf miners, this green island effect occurs through the action of the insect's microbiome, which causes the plant to increase production of the plant hormone cytokinin [222,223]. The western corn rootworm, *Diabrotica virgifera virgifera* is a major pest of corn. Its microbiome appears to have the ability to down-regulate genes in the plant that confer protection against herbivory [224].

A smaller number of studies document the interconnectedness of agricultural practices and insect microbiomes. By accelerating dung degradation and nutrient cycling, dung beetles provide important ecological services in grassland and pasture systems used for livestock production [225]. Livestock treated with antibiotics can excrete the residues through feces, which can restructure the microbiome of the dung and also the microbiome of dung-feeding beetles in the dung [17]. Livestock treated with parasiticides excrete

residues that can be highly toxic to dung-breeding insects [226,227], but we are unaware of any published studies examining the effect of these residues on insect microbiomes. Certain species of pentatomid bugs acquire bacterial symbionts from the soil. Soils in fields sprayed with fenitrothion can harbour fenitrothion-degrading strains of *Burkholderia* bacteria that, when acquired by these bugs, confer the host with resistance to the insecticide [228]. As a consequence, bugs may acquire resistance to fenitrothion without having been directly exposed to this pesticide.

Given its role in host survival and reproduction, manipulating the microbiome may have application to controlling pest insects or the spread of insect-vectored pathogens in agricultural systems. Madhav et al. [219] reviewed the potential for manipulation of *Wolbachia* spp. in management strategies for arthropod pests of livestock. Types of manipulations include the addition, removal, or genetic modification of taxa that compose the microbiome. The value of the addition strategy is illustrated by the transfer of *Wolbachia* spp. into field populations of mosquitoes, which can reduce the ability of infected individuals to spread arboviruses (e.g., chikungunya, dengue, yellow fever, Zika) that affect hundreds of millions of humans each year [229]. The removal strategy is illustrated with the use of antibiotics to remove infections of *Wolbachia* spp. from their hosts to examine the nature of *Wolbachia*-host interactions [230]. Paratransgenesis refers to the genetic modification of an insect symbiont for the purposes of, for example, producing compounds that adversely affect the animal or plant pathogen being transmitted by the host [231]. We are unaware of any successful application of this approach in agriculture, although it has been studied as a method to control insect-vectored diseases affecting sugarcane [232] and grapes [233]. Elston et al. [234] describe methods for the paratransgenesis of a symbiont of aphids. Mendiola et al. [235] reviewed applications and methods for implementation of paratransgenesis for the control of arthropod-vectored pathogens affecting crops.

5.3. Pollinators—Honey Bees

Knowledge of the microbiome may be equally valuable to promote the health and reproduction of beneficial species such as pollinators. Insects, especially bees (Hymenoptera), are key pollinators in most of the world's agroecosystems. They include both native species, which are present in the environment without human intervention, and managed species, whose numbers are manipulated to increase their pollination services. In Canada, the most common managed pollinator is the European honey bee, *Apis mellifera* [236]. Managed bumble bees (*Bombus* spp.) and leafcutter bees (*Megachile rotundata*) are also significant pollinators in Canadian agriculture. Populations of honey bees and leafcutter bees are established in canola fields each year to pollinate hybrid seed canola plants to enhance oilseed production while bumble bees are released into greenhouses to pollinate different crops, including tomatoes [237,238]. Research on managed honey bees and their associated microbiome is the focus of the next section.

5.3.1. Honey Bees and Their Gut Microbiome

The European honey bee is an indispensable managed pollinator of various crops of economic significance in Canada. Their pollination services are valued at up to $CAD 5.5 billion per year [239]. Major oilseed crops including canola, as well as berries and tree fruit, benefit from honey bee pollination for maximum yield. The health and productivity of honey bee colonies depends on a variety of abiotic and biotic factors that impact their physiology, including the composition of their gut microbiome.

The bacterial composition of the gut microbiome changes throughout the honey bee lifecycle [240]. Larvae and pupae lack gut bacteria; it is only when young honey bees first emerge from brood cells that they have the opportunity to start developing a bacterial population. The majority of the gut microbiome is acquired four days after emergence through trophallaxis (exchange of food or nutritive fluid) and social interaction with nurse bees [241]. In general, the bacterial population in the digestive tract of healthy adult worker bees ranges from 10^8 to 10^9 cells [241,242]. Studies based on 16S rRNA sequence

profiling indicate that up to nine symbiotic bacterial species, or phylotypes, constitute the majority of the honey bee gut population [240,242]. Five of these phylotypes are considered "core" members: *Bifidobacterium asteroides*, *Gilliamella apicola*, *Lactobacillus* Firm-4 and Firm-5, and *Snodgrassella alvi*. Most of the bacteria are found in the hindgut, which is divided into the ileum and rectum [242]. In the ileum, *S. alvi* and *G. apicola* are highly abundant and occupy discrete regions [240]. *S. alvi* lines the gut wall, while *G. apicola* resides in the lumen [240,243]. In the rectum, *B. asteroides* and *Lactobacillus* Firm-4 and Firm-5 are most abundant [244]. Other members found throughout the honey bee gut that occur less frequently include *Bartonella apis*, *Frischella perrara*, and *Lactobacillus kunkeei* [242].

5.3.2. Role of the Honey Bee Gut Microbiome in Nutrition

The characterization of the honey bee gut microbiome has enhanced our understanding of how the resident gut members contribute to honey bee nutrition, health, and immunity [244]. A role for the microbiome in affecting weight gain was identified. Young bees fed a diet containing gut microbes from adult bees had increased body weight compared to bees fed a non-supplemented diet [243]. This is relevant for the digestion of nectar, the main carbohydrate source of honey bees, and pollen—an important food source due to its protein, carbohydrate, and lipid content [245]. Metagenomic sequencing of the *Apis* gut has uncovered specific strains of *Bifidobacterium* and *Gilliamella* that possess polysaccharide catabolism genes involved in the hydrolysis of hemicellulose and pectin, respectively [246]. *G. apicola* strains, for example, can metabolize different sugar substrates including sugars that are toxic to the host, indicating that the bacteria of the honey bee gut microbiome are integral to the bee's nutritional needs [247,248].

5.3.3. Factors Influencing the Honey Bee Gut Microbiome Composition

Honey bees are social insects that perform different tasks inside and outside the hive, and as a consequence, have different gut microbiome compositions. Young nurse bees that remain inside the hive exhibit greater microbial diversity than outside forager bees [249]. Nurse bees harbour more *Bifidobacterium* spp. and *Lactobacillus* Firm-4 compared to foragers [249]. Seasonal variations in the honey bee microbiome composition have also been reported. Winter bees have increased levels of *Bartonella* and *Commensalibacter*, which is likely correlated with their winter diet [250–252].

The interaction of honey bees and their environment exposes them to different stressors; agrochemicals, antibiotics, and pathogens can disrupt the natural balance of the gut microbiome, which is referred to as dysbiosis [253,254]. Exposure to glyphosate, a widely-used herbicide, resulted in a compositional shift for *S. alvi*, compared to unexposed bees [255]. Antibiotic treatment may make honey bees more susceptible to infections with *Nosema ceranae* [256]. Some members of the gut microbiota can become lethal pathogens when the core gut microbiota is disrupted, particularly *Serratia*, which is commonly found at very low frequencies in nurse bee guts (<5%). Honey bees exposed to the insecticide flupyradifurone had an increased level of *Serratia* at day five post-exposure, compared to the non-exposed control [257]. In extreme cases, the core taxa can be displaced by pathogens such as *Melissococcus plutonius*, which is responsible for European foulbrood [258]. Dysbiosis affects honey bee health and the ability of honey bee colonies to effectively pollinate agricultural crops. The sensitivity of the honey bee gut microbiome to various environmental stressors can be used as a promising indicator to monitor bee health, such as through the use of shotgun metagenomic sequencing.

6. Conclusions

Microbiomes play key roles in the productivity of agricultural systems affecting soil, crops, and livestock, as well as beneficial and pest insects. They affect the health and survival of animal hosts, facilitating nutrition acquisition, the metabolism of toxins, and increasing immune defenses. However, they also may have undesired effects on the environment; e.g., the release of methane by archaea inhabiting the rumen of cattle. These

diverse microbiomes are intimately connected, are frequently altered by farm practices, and yet we remain in the early stages of understanding the consequences of these practices. Despite numerous studies characterizing the microbiomes of food-producing animals, there is still uncertainty on what constitutes a "healthy" microbiome. However, there are reports of increased production efficiency when microbial diversity is reduced [259]. One of the challenges in microbiome studies is the inter-individual variation of the gut microbiome and the need to use a large number of subjects (animals, soil, crop or water) to avoid underpowered studies and the lack of inter-study reproducibility. Increased standardization of methods, increased replication, and higher taxonomic resolution will positively impact microbiome research in agriculture.

Animal and plant microbiomes in agriculture are closely connected to the soil microbiome (see graphical abstract). The diversity, structure, and functionality of soil microorganisms are influenced by several factors including soil physical and chemical characteristics, anthropogenic activities (farming practices), and climatic variability. Crops partially rely on soil microbes for nutrient acquisition and protection against biotic and abiotic stress. From the ecosystem perspective, the crop interaction with soil microbes impacts not only net primary production but also an interaction with both pest and beneficial insects. Further, future research on the interconnectedness, such as the interaction between microbiomes of flowers, insects and soil, will allow further understanding of the ecosystem stability, biodiversity and agricultural production [13].

Our increased understanding of the variables affecting agricultural microbiomes and their effects on their hosts and the environment will facilitate the manipulation of microbial communities to increase agricultural productivity and reduce the release of greenhouse gas emissions from livestock production to minimize its contribution to climate change. However, challenges in agricultural microbiome research still exist. Advances in high-throughput sequencing, bioinformatic tools, and machine-learning capacities are helping us to characterize the taxonomic components of microbiomes.

A limitation of our current review is that we have not included methods for studying the functional properties of microbiomes in an ecosystem. However, understanding the functions of these components is difficult, particularly because only a miniscule fraction of microbes has been studied in any detail and many microorganisms are unculturable under typical laboratory conditions, making ex vivo/in vitro studies difficult. Therefore, the current trend in microbiome research focuses on metagenomic assemblies and metatranscriptomics to obtain functional microbiome information. These studies include careful study design and selection of assembly/analysis pipelines most suitable for the research question while considering the available computational resources [260,261]. Another potentially informative approach involves epigenomic studies (analysis of DNA modifications that regulate gene expression) of agricultural metagenomes, or metaepigenomes, by analyzing methyltransferase sequences in the metagenome, for example, with PacBio sequencing and bioinformatics approaches [262]. The integration of host genomics and metagenomics also promises to be a powerful approach. Growing recognition of the association between microbiomes and their host has given rise to the terms "holobiont" (the microbiome plus the host) and "hologenome" (their combined genomes) [263]. Future research will benefit by inclusion of these concepts; for example, the integration of host genomics with metagenomics of bacterial communities, as well as the use of multi-omic technologies. These approaches may capture host-microbe interactions in greater resolution and lead to new insights, especially as we move beyond descriptive studies toward those focusing on the mechanisms responsible for these interactions to understand the complex dynamics at play across the agricultural continuum.

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Abbreviations

GHGs	Greenhouse gases
GIT	Short-chain fatty acids
SCFAs	Gastrointestinal tract
FMT	Fecal microbiota transplantation
HGT	Horizontal gene transfer

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