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Fecal Microbiota and Feeding Habitats of Nomadic Indigenous Animals (Deer, Yak, Sheep and Camel) in Baikal Siberia (Russia)

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Abstract: In the vast expanse of Baikal Siberia, indigenous nomadic animal groups have been conserved, grazing on pastures throughout the year. It is believed that the fecal microbiota of these diverse nomadic animal species is unique to each species and closely tied to their feeding environments. We conducted a pioneering comparative analysis of the taxonomic structure and the diversity of fecal microbiota in indigenous nomadic animals inhabiting Baikal Siberia. Our study encompassed 20 deer, 23 yaks, 24 camels, and 29 sheep, using high-throughput 16S rRNA gene profiling. In the fecal microbiota of these animals, we observed a predominant presence of the phyla *Bacillota*, *Bacteroidota*, and *Verrucomicrobiota*, collectively comprising over 88% of the microbial communities. Moreover, these proportions exhibited variations according to the host species. The unculturable *Bacillota UCG-005* and *UCG-010* are the key groups for all animals. However, at the genus level, distinctive compositions of fecal microbiota were discernible within each animal group. We identified a total of 37 dominant genera across the fecal samples from these four animal species. Principal component analysis (PCA) and cluster analysis demonstrated that the fecal microbiota composition clustered among individuals of the same animal species. Linear discriminant analysis effect size (LEfSe) indicated that camels exhibited higher abundances of the family *Akkermansiaceae* and the uncultured clostridial lineage *UCG-010*, while deer featured *Lachnospiraceae*; sheep had *Ruminococcaceae*; and yaks displayed *Monoglobaceae*, *Bacteroidaceae*, and methanogenic archaea from the family *Methanobacteriaceae* as distinctive marker taxa. Our studies showed that the studied nomadic animals feed mainly on plants belonging to the families *Poaceae*, *Cyperaceae*, *Asteraceae*, and *Rosaceae*. Our research indicated that the identity of the host species and, to a lesser degree, their diets and habitats, significantly shape the composition of fecal microbiota in these studied nomadic ruminant animals.

Keywords: fecal microbiota; high-throughput 16S rRNA gene profiling; feeding habitat; nomadic indigenous animals; deer; yak; sheep; camel; Baikal Siberia

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1. Introduction

The microbial communities of various ruminant species are currently under intense study due to the development of new ideas about the role of the all-microbial population and the composition of individual communities in animal hosts [1–4].

The ruminant gastrointestinal microbiome is a complex and dynamic ecosystem. Previous studies of various ruminants showed that the composition of the ruminal microbiome

can depend on many factors, including animal genotype [1,5], age [6–8], geographic location [9], season of the year [10–12], diet and feeding habitat [1,13–17], health status [18–21], the use of antimicrobial compounds [22], lighting conditions [23], stress [24], and environmental factors [25,26]. Pasture plants included in the diet of nomadic animals can play a key role in the adaptation and formation of resistance of herbivores to a sharply continental climate [27]. Therefore, it is important to assess habitat conditions, diet, and other factors when studying the microbiome of herbivorous animals.

Nomadic species of indigenous animals—*Rangifer tarandus* (Tofalar deer population), *Bos grunniens* (yak of the Okinsky population), *Ovis aries* (coarse-haired Buryat sheep population), and *Camelus bactrianus* (Transbaikal camel population)—are wide-spread in the territory of Baikal Siberia. Deer, yaks, and sheep are true ruminants, while camels are described as pseudoruminants, lacking an omasum and possessing only three stomach chambers [28]. These animals have adapted to year-round grazing. This subsistence model is the result of the long-term selection process of native free-grazing animals [21–23]. These animals are an important part of the nomadic herding economy and the national heritage of the people of Baikal Siberia. According to recent data, the number of Tofalar deer did not exceed 100, while yaks of the Okinsky population numbered 3400, Buryat coarse-wool sheep numbered 4000, and Transbaikal camels numbered 420. According to the Nomadic Herding Revival Program [29,30], these indigenous animals are classified as "Near Threatened".

Differences in digestive systems, extreme environmental conditions, and dietary habits of native animals may result in the formation of a specific gut microbiota [16]. Changes in the fecal microbiota of native animals may be an adaptation to extreme environmental factors such as long, cold winters; short, dry summers' high-altitude hypoxia; and poor pastures.

To date, no studies have been conducted on the gut microbiota of nomadic animals in the territory of Baikal Siberia. The nomadic lifestyle offers certain advantages over the sedentary lifestyle. Firstly, mobile free-grazing animals reduce the load on the forage resources of pastures. Secondly, nomadic animals do not rely on forage reserves in a particular pasture [29]. As a result, nomadic animals are likely to consume a more diverse diet than farmed animals, which means that they likely possess microbes capable of digesting a variety of substrates.

We assumed that the fecal microbiota of different migratory species is species-specific and habitat-dependent. However, limited information exists on the gastrointestinal microbiome of nomadic animals. This study examines the uniqueness and similarity of the fecal microbiota in rare nomadic animals in relation to their feeding habitats by using a uniform analytical protocol, i.e., MiSeq, the sequencing of hypervariable 16S rRNA.

The aim of this study is to determine the composition and diversity of the fecal microbiota of nomadic animals (Tofalar deer, Okinsky yak, Buryat sheep, and Transbaikal camel) and evaluate variations with regard to animal species and their feeding habitats in Baikal Siberia.

2. Materials and Methods

2.1. Study Objects and Area

We determined four species of native nomadic animals inhabiting the territory of Baikal Siberia, most of which overlaps with Buryatia and Zabaikalsky Krai (Figure 1). The region has a strongly continental climate, with an average annual temperature of −1.6 °C and average annual precipitation of 244 mm. Under the influence of the harsh climate of the habitat, nomadic animals graze all year round, and in the process of natural selection, these animals have acquired valuable and economically useful traits such as endurance and dietary adaptability [29].

Figure 1. Information on the sampling site and animal habitats.

1. Deer (*Rangifer tarandus*): As a breed of mountain taiga deer that lives in more northern latitudes, Tofalar deer graze freely in the valleys of high mountain rivers.
2. Yaks (*Bos grunniens*): The Okinsky yak population exhibits a considerable degree of adaptation in order to survive in harsh ecological and geographical conditions, including year-round grazing on high alpine meadows of the Eastern Sayan and Small Khamar-Daban. This adaptation is evident in the yaks' ecology and behavior, marked breeding seasonality, accelerated development of young animals in the warm season, and seasonal rotation of pastures.
3. Sheep (*Ovis aries*): Buryat-native coarse-wool sheep were bred during the era of nomadic pastoralism. This breed shows exceptional adaptability to local conditions and is suited for year-round grazing.
4. Camels (*Camelus bactrianus*): The ransbaikal camel is best adapted to life in a sharply continental climate with pronounced changes in habitat conditions both throughout the year and day. Thanks to their anatomical and physiological features, camels can tolerate unusually long periods without water and are satisfied with the coarsest and most nutritious food sources [29].

The habitat characteristics of each species are shown In Table 1.

Table 1. The habitat characteristics of nomadic animals of Baikal Siberia. The asterisk (*) indicates the number of analyzed fecal samples from individuals.

Animal	Sampling Place	GPS Location N/E	Altitude (m)	Habitat	Monthly Average Temperature, March (°C)	Number of Individuals (N) *	Age (Years)	Diet Preference (Geobotanical Descriptions) [31]
Deer	Russia, Republic of Buryatia, Onot area, deer camp	52.1217 N 101.2553 E	1762	Mountain taiga	−10.2	20	1–9	*Rheum rhubarb*, *Cetraria islandica* (L.) Ach., *Cetraria laevigata* Rassad., *Cladonia amaurocraea* (Florke) Schaer, *Cladonia arbuscula* (Wallr.) Flot., *Carex juncella* (E. Fries) T. Fries, *Agropyron cristatum*, *Eriophorum polystachion* L.

Table 1. *Cont.*

Animal	Sampling Place	GPS Location N/E	Altitude (m)	Habitat	Monthly Average Temperature, March (°C)	Number of Individuals (N) *	Age (Years)	Diet Preference (Geobotanical Descriptions) [31]
Yak	Russia, Republic of Buryatia, Bokson village, livestock camp	52.0939 N 100.9503 E	1360	High mountainous areas and the valleys	−11.4	23	2–7	*Aster alpinus*, *Thermopsis lanceolata*, *Potentilla anserina* L., *Helictotrichon altaicum* Tzvelev, *Allium splendens* Willd. ex Schultes et Schultes fil., *Polygonum viviparum* L., *Potentilla bifurca* L.
Sheep	Russia, Republic of Buryatia, Dabatui area	50.7888 N 107.9373 E	749	Forest-steppe	−7.4	29	2–3	*Aster alpinus* L, *Stipa capillata* L., *Stipa krylovii*, *Dontostemon integrifolius*, *Potentilla bifurca* L., *Carex duriuscula*, *Pulsatilla turczaninovii* Krylov et Serg.
Camel	Russia, Zabaikalsky Krai, Khapshur area	51.4356 N 115.3508 E	687	Steppe	−8.1	24	2–10	*Allium anisopodium*, *Saposhnikovia divaricata*, *Aster alpinus*, *Saussurea salicifolia*. *Stipa krylovii* Roshev, *Carex duriuscula* C.A.Meyer, *Leonurus* L.

2.2. Sample Collection

A total of 96 fresh fecal samples (20 deer, 23 yaks, 29 sheep, and 24 camels) from four different species of native free-grazing animals in the study area were collected during expeditions to hard-to-reach areas in March 2022.

Sample collection followed a standard procedure: fresh animal feces were collected in sterile plastic sealable bags, labeled according to a uniform scheme, metadata were recorded in a field log, samples were transported in dry ice, and DNA isolation was performed within 12 h of sampling.

Using fecal samples allowed us to overcome difficulties in collecting samples from rare native animals and also helped avoid ethical issues associated with obtaining such samples from internal organs. All animals were raised in natural pastures, were in good health, had experienced no human contact, and had not received antibiotics for a minimum of 12 months.

2.3. Ethical Considerations

The animals in this study did not undergo any procedures, so ethical approval was unnecessary.

2.4. DNA Extraction

Total genomic DNA from feces was extracted using a Power Soil DNA isolation kit (MO BIO Laboratories, Inc., Carlsbad, CA, USA) and stored at −20 °C.

2.5. The 16S rRNA Gene Profiling

The PCR amplification of 16S rRNA gene fragments comprising the V3–V4 variable regions was carried out using the universal prokaryotic primers PRK 341F (5′-CCTAYG GGDBGCWSCAG) and PRK 806R (5′-GGA CTA CNVGGG THTCTAAT).

The libraries were indexed using the Nextera XT Index Kit v.2 (Illumina, San Diego, CA, USA) and sequenced on the MiSeq platform in a paired read format (2 × 300 nt). Paired reads were merged using FLASH v.1.2.11 [32]. The 16S rRNA gene sequences were clustered into operational taxonomic units (OTUs) at 97% identity using the USEARCH v. 11 program [33].

Low-quality reads, chimeric sequences, and singletons were removed via the USEARCH algorithm. All sequences were clustered into operational taxonomic units (OTUs) at 97% identity using the USEARCH v. 11 program. The taxonomic assignment of OTUs

was performed by searching against the SILVA v.138 rRNA sequence database using the VSEARCH v. 2.14.1 algorithm [34].

2.6. Data Analysis

The relative abundance of microbial taxa was summarized at the level of phyla, classes, families, and genera, and included only those microbial taxa that represented ≥1% of the total community. The alpha diversity indices at a 97% OTU cut-off level were calculated using the USEARCH v. 11 program. To avoid sequencing depth bias, the number of reads generated for each sample was randomly sub-sampled to the size of the smallest set using the QIIME 2 2022.8 tool [35]. Alpha diversity indices (Chao1, Shannon, Simpson) were plotted using the R software package. Principal component analysis (PCA) and cluster analysis were performed to determine beta diversity using the Sirius program (PRS, Bergen, Norway).

Linear discriminant analysis (LDA) effect size (LEfSe), a method for biomarker discovery, was used to determine the family that best characterizes each animal species [36]. LEfSe scores are a measure of the consistency of relative abundance differences between taxa in analyzed groups, with a higher score indicating greater consistency.

We limited this analysis to prokaryotic families that account for more than 1% of 16S rRNA gene sequences (on average) in at least one animal species, and classified taxa with an LDA score of >2 and a p value of <0.05 as significant [37]. The ordination matrices multidimensional scale (MDS) analysis was built through the ordinate function of the phyloseq package in R. The Jaccard matrix was built using the vegan package in R to measure the differences in the fecal microbiota composition between pairs of animals.

The method of microscopic cuticular coprological and the geobotanical analysis of plants was used to determine the qualitative and quantitative composition of food on the basis of fecal samples. The method is based on the study of the epidermal sculpture of plant cuticles identified in fecal samples and their comparison with basic standards [38].

Pearson's correlation analysis was performed using Statistica 12 software (StatSoft, Tulsa, OK, USA) to evaluate the correlation between the diet and dominant bacterial taxa.

3. Results

A total of 989,305 sequences were obtained from 96 fecal samples based on a 97% sequence identity and clustered into 3537 OTUs with a 97% sequence identity.

In total, the fecal microbial communities of four animal species included two archaeal and 24 bacterial phyla, 35 classes, 76 orders, 122 families, and 252 genera.

The fecal microbiota of the analyzed samples were dominated by the *Bacillota*, *Bacteroidota*, and *Verrucomicrobiota* phyla, which were found in all samples and accounted for more than 88% of microbial communities (Figure 2).

Other prokaryotic sequences (on average ≥ 1% in at least one animal species) were assigned to the phyla *Pseudomonadota*, *Actinomycetota*, *Cyanobacteriota*, *Spirochaetota*, *Thermodesulfobacterota*, *Euryarchaeota*, and *Halobacterota*.

3.1. Fecal Microbiota of Four Animal Species

3.1.1. Fecal Microbiota of Deer

Only four phyla dominated the fecal microbiota of deer (relative abundance ≥ 1% of the total community). *Bacillota* were the most abundant in the microbial communities of the studied animals (on average 67.1%), followed by *Bacteroidota* (24.0%), *Verrucomicrobiota* (3.3%), and *Pseudomonadota* (2.8%). At the genus level, *Prevotella* and uncultivated *UCG-005* dominated the fecal microbiota, accounting on average for 18.6% and 13.6% of the total microbiome, respectively (Figure S1). Other genera (abundance ≥ 2%) were represented by the *[Eubacterium]_coprostanoligenes_group*, *Lachnospiraceae NK4A136*, *Bacteroides*, *Phascolarctobacterium*, *Roseburia*, *Monoglobus*, *Akkermansia*, and the uncultured clostridial lineages *UCG-010*, *UCG-011*, and *UCG-014*.

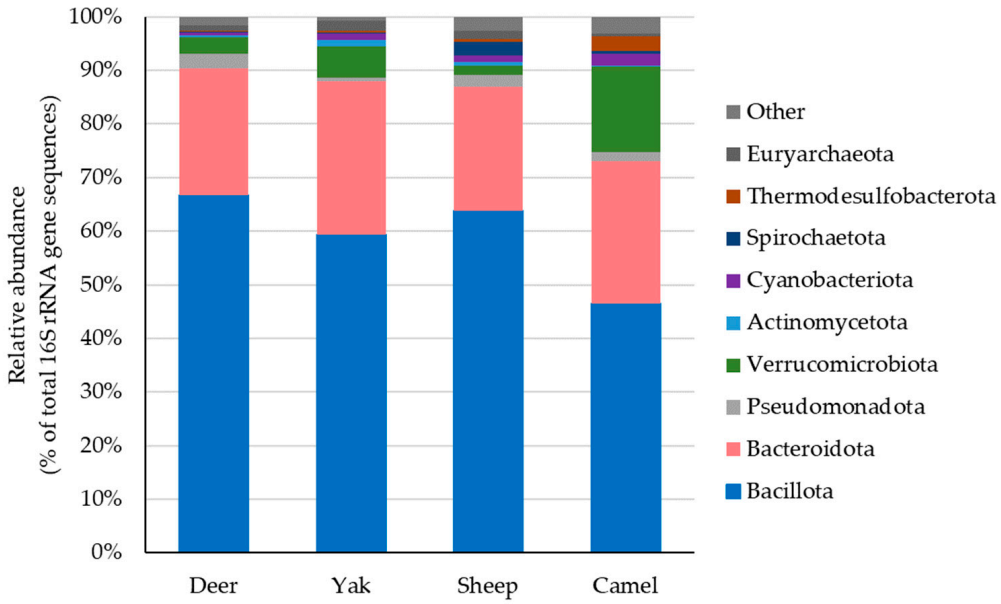

Figure 2. Microbial community composition at the phylum level (revealed by 16S rRNA gene profiling).

3.1.2. Fecal Microbiota of Yaks

The microbiota of yaks were dominated by six main phyla (relative abundance > 1%), namely, *Bacillota* (59.4%), *Bacteroidota* (28.7%), *Verrucomicrobiota* (6.0%), *Euryarchaeota* (1.9%), *Cyanobacteriota* (1.3%), and *Actinomycetota* (1.1%). At the genus level, the yak fecal microbiota were dominated by uncultured lineages *UCG-005* (12.2%) and *Bacteroides* (7.2%), followed by *Monoglobus*, uncultured lineages *UCG-010*, the *[Eubacterium]_coprostanoligenes_group*, *Akkermansia*, and the *Rikenellaceae_RC9_gut_group*, which together accounted for 45.8% microbiota (Figure S2).

3.1.3. Fecal Microbiota of Sheep

Seven main phyla were found in the sheep fecal microbiota, of which *Bacillota* (63.8%) and *Bacteroidota* (23.2%) were the most abundant, accounting for 87% of the total. Other abundant phyla were *Spirochaetota* (2.7%), *Verrucomicrobiota* (1.7%), *Euryarchaeota* (1.5%), *Cyanobacteriota* (1.3%), and *Halobacterota* (1.1%). At the genus level, the fecal microbiota of sheep were dominated by uncultured family-level lineages *UCG-010* (8.9%) and *UCG-005* (9.7%) (Figure S3).

3.1.4. Fecal Microbiota of Camels

The microbiota of camel feces were dominated by *Bacillota* (46.5%), *Bacteroidota* (26.5%), and *Verrucomicrobiota* (16.0%). The codominants were *Thermodesulfobacterota* (2.7%), *Halobacterota* (2.3%), *Cyanobacteriota* (2.3%), and *Pseudomonadota* (1.7%). The most abundant genera were *UCG-010* (12.2%), *Akkermansia* (10.2%), *UCG-005* (6.3%), and *Bacteroides* (5.0%), which together represented 33.4% of the camel fecal microbiota (Figure S4).

3.1.5. LEfSe Analysis

LEfSe was used to identify the prokaryotic lineages that best characterize each animal species. Seven family-level lineages accounting for ≥1% of microbiome in at least one animal species were identified (Figure 3).

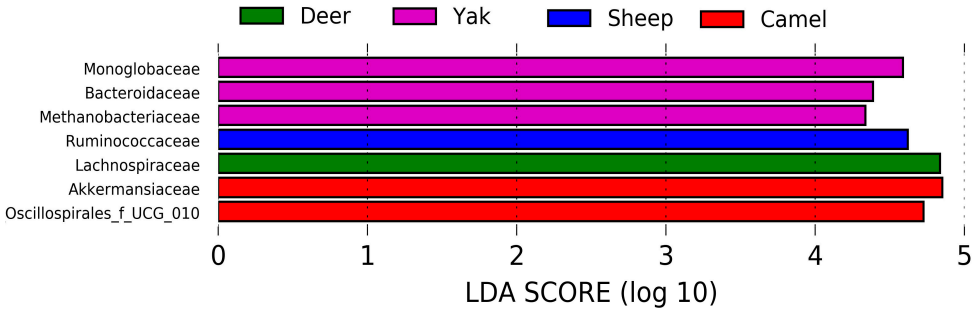

Figure 3. The biomarkers in fecal microbiota were determined by LEfSe among the four groups of free-grazing animals (prokaryotic taxa that best characterize each animal species with LDA scores).

The family *Akkermansiaceae* and the uncultured clostridial lineage *UCG-010* were more abundant for camels, *Lachnospiraceae* for deer, and *Ruminococcaceae* for sheep, while the marker taxa for yaks were *Monoglobaceae*, *Bacteroidaceae*, and methanogenic archaea (family *Methanobacteriaceae*).

Notably, the prevalence of *Akkermansiaceae* was considerably higher in camels (~12%) and yaks (~5%), while this family was much less abundant in most deer individuals and almost nonexistent in sheep. Figure S5 illustrates the relative prevalence of these families in the fecal microbiota of individual animals.

3.2. Diversity Analysis

The α-diversity of fecal microbiota in the four groups of animals is shown in Figure 4. The diversity of the deer fecal microbial community is significantly lower for all defined indices. Minor differences in α-diversity were found in sheep and camels. In general, the highest diversity of fecal microbiota was found in sheep.

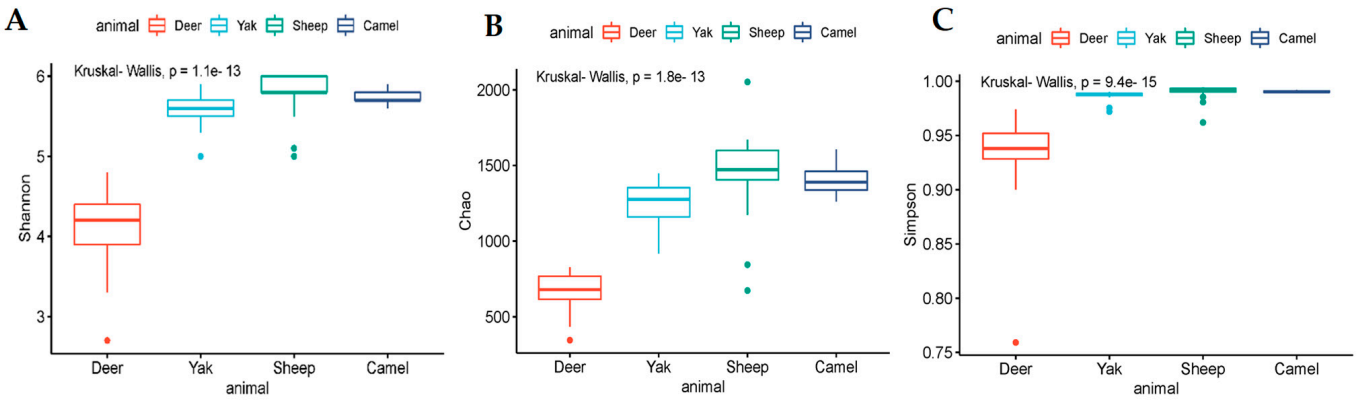

Figure 4. Box-and-whisker plots showing the comparison of the alpha diversity of the fecal microbiota among the animals in each group. The index diversity: Shannon (**A**), Chao1 (**B**), and Simpson (**C**).

The PCA of the fecal microbiota composition in the studied groups of animals was based on the abundance of bacteria with a relative abundance of ≥1% in each group of animals. Scatter plots (Figure 5) were constructed using the values of the first and second principal components.

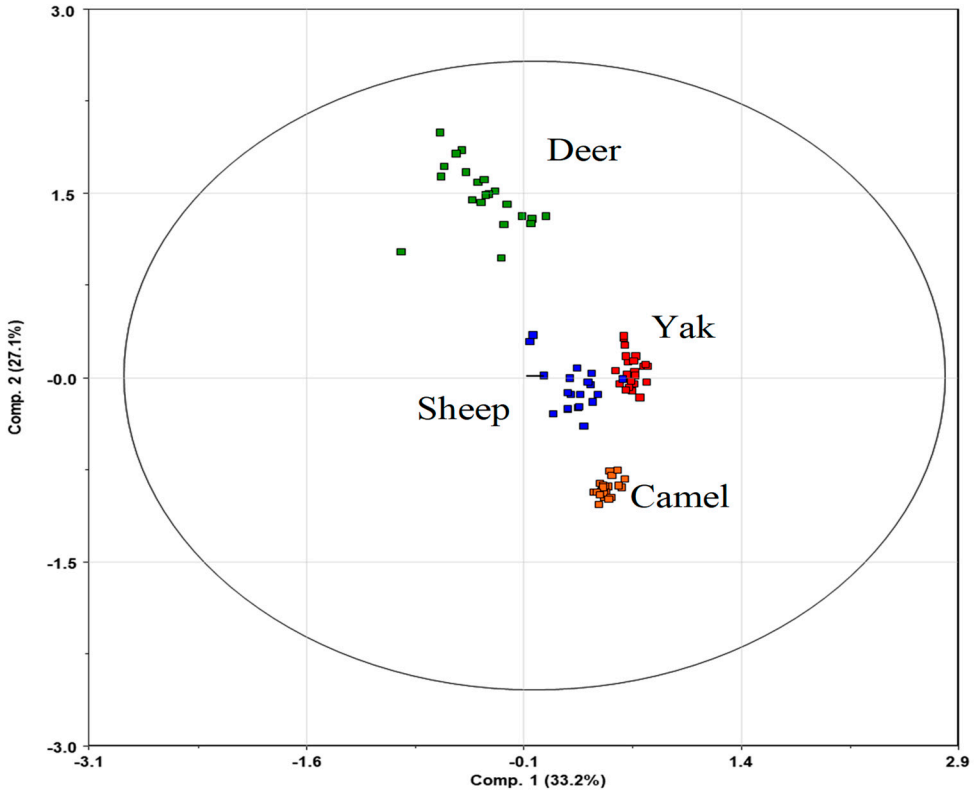

Figure 5. Beta diversity of fecal microbial communities in four groups of animals estimated using PCA at the genus level.

The principal components explain 33.2% (PC1) and 27.1% (PC2) of the variations. The graph clearly shows that the samples of feces were grouped into four groups according to their taxonomic composition, in accordance with the studied animal groups. Deer feces samples are located in the upper part of the biplot, camel feces samples are located in the lower part of the graph. Fecal samples from all yaks and most sheep were located in the center.

We examined the relative abundance (≥1% in each animal group) of prokaryotes in the feces of four animal groups at the genus level (Figure 6). The heatmap analysis showed a division into four clusters of fecal samples from animals according to their species.

3.3. Diet

The diet was studied by comparing the results of cuticular analysis of plant remains in feces with samples of pasture plants from the databases [38].

A total of 1861 plant fragments belonging to 37 species have been detected in deer fecal samples. The dominant species were *Eriophorum polystachion* L. (16.3% of the total), *Rheum rhubarb* (16.2% of the total), *Agropyron cristatum* (L.) Beauv. (15.4%), *Carex juncella* (7%), *Festuca ovina* subsp. sphagnicola (B. Keller) (5.3%), and *Cladonia amaurocraea* (Florke) Schaer (5%). Other species accounted for less than 5% of the total number of plant fragments.

In the yak fecal samples, 2195 fragments of plants belonging to 33 species were found. The dominant species were *Aster alpinus* (12.9% of the total), *Potentilla bifurca* L. (10.8%) *Allium spendens* Willd. ex Schultes et Schultes fil. (9.2%), *Helictotrichon altaicum* Tzvelev (7.4%), and *Thermopsis lanceolata* (6.2%). Other species accounted for less than 5% of the total number of plant fragments.

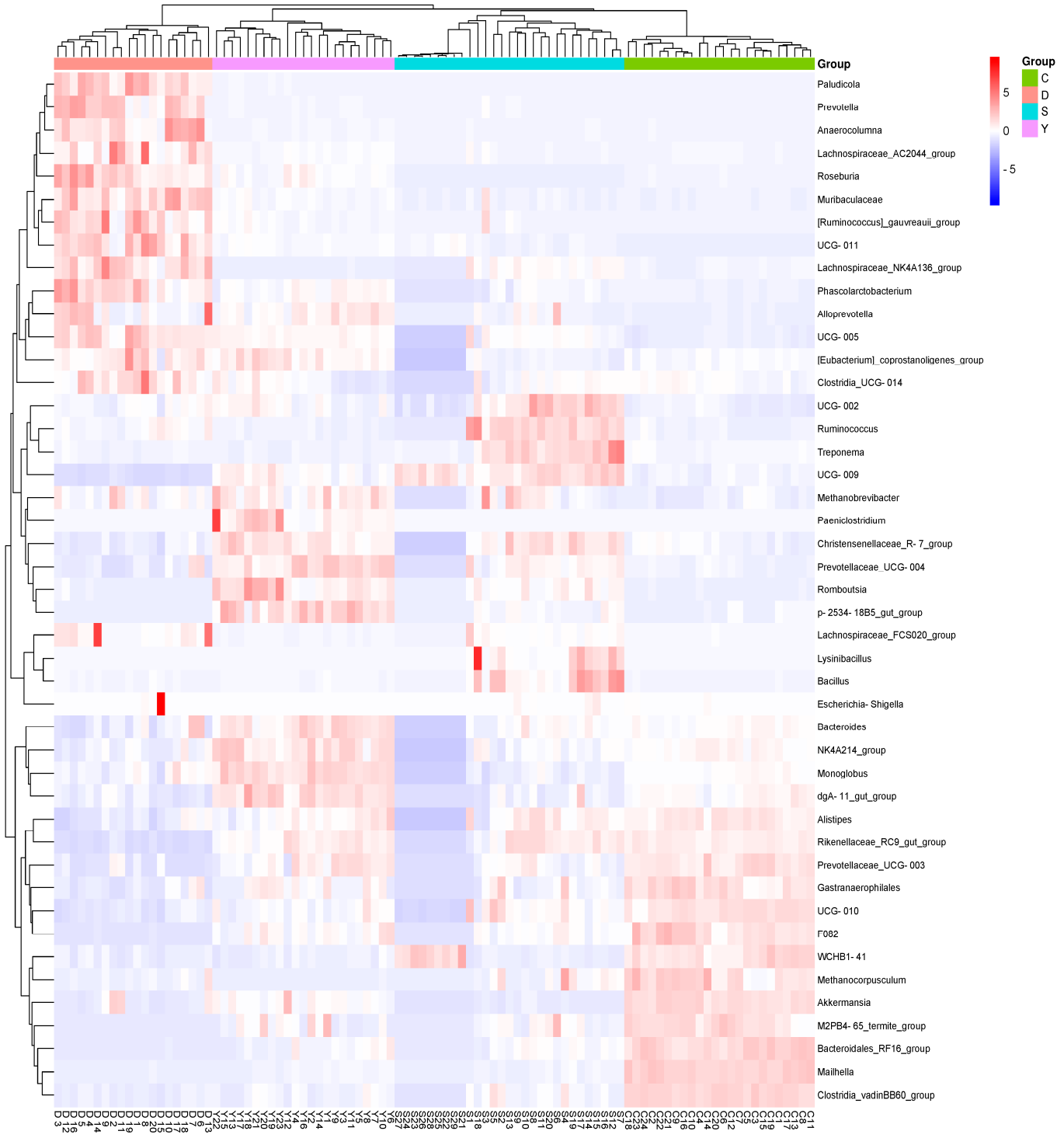

Figure 6. Heatmap showing hierarchical clustering of fecal microbiota composition among the four groups of animals based on 16S rRNA gene profiling. The microbiota shown represents the top 46 bacterial genera across all samples with the greatest mean relative abundance. The color of the heatmap of relative abundance each taxon (blue to red) is based on row-scaled data. The top dendrogram shows the samples with similar microbiomes clustered together, while the side dendrogram shows the bacteria that are commonly found together (D—Deer, Y—Yaks, S—Sheep, and C—Camels).

In the fecal samples of sheep, 2026 fragments of plants belonging to 29 species were identified. The dominant species were *Dontostemon integrifolius* (12.9%), *Aster alpinus* L.

(11.8%), *Stipa capillata* L. (11%), *Potentilla bifurca* L. (11.5%), and *Stipa krylovii* (5.6%). Other species accounted for less than 5% of the total number of plant fragments.

In the fecal samples of camels, 2539 fragments of plants belonging to 20 species were found. The dominant species were *Potentilla longifolia* (28.4%), *Saussurea salicifolia* (15.9%), *Saposhnikovia divaricata* (15.8%), *Aster alpinus* L. (8.3%), and *Leonurus* L. (7.9%). Other species accounted for less than 5% of the total number of plant fragments.

PCA was used to assess differences between fecal samples according to diet (Figure 7). The PCA shows that deer and camel samples are grouped into compact individual loci. Sheep were scattered within their cluster, and yaks were divided into two groups.

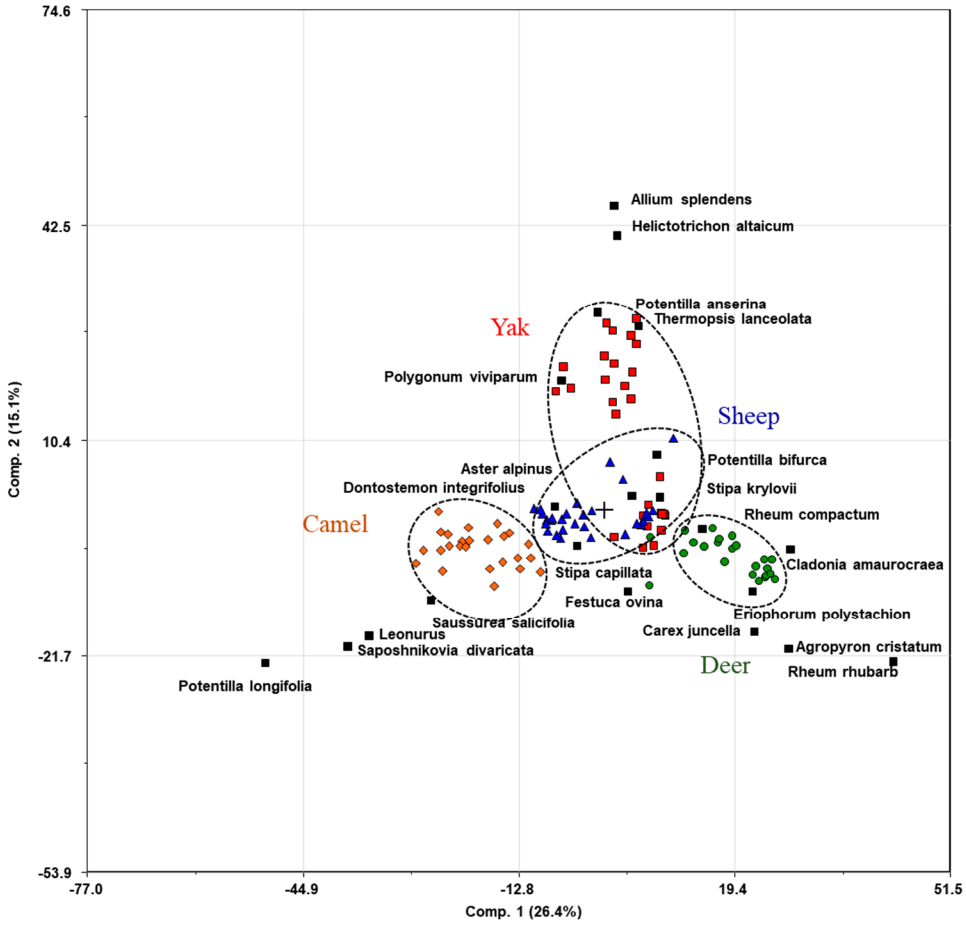

Figure 7. PCA of diet clustering for the four groups of animals.

4. Discussion

Deer, yaks, sheep, and camels are paramount for nomadic pastoralists living in Baikal Siberia as they provide food staples, such as meat and dairy, and wool for the Indigenous Peoples. These native animals are highly adapted to the harsh climatic conditions of the region and require minimal care. Nomadic lifestyles represent a natural subsistence model that has arisen within specific habitat conditions [29].

In this study we attempted to determine how the composition and diversity of fecal microbiota in nomadic animals depends on the animal species and its feeding habitat (for Tofalar deer, Okinsky yak, Buryat sheep, and Transbaikal camel inhabiting the territory of Baikal Siberia).

4.1. The Core Fecal Microbiota of Nomadic Animals (Deer, Yaks, Sheep, and Camels) and Their Species Specificity

This study showed that the fecal microbiota of the four groups of nomadic animals had similarities at the phylum level. The highest relative abundance was observed for the phyla

Bacillota, *Bacteroidota*, and *Verrucomicrobiota* in each group of animals. They can probably be considered the core of the bacterial microbiome in the studied animals. Previously, numerous studies demonstrated that phyla *Bacillota* and *Bacteroidota* are widely distributed in the guts of various mammalian species [17,28,39–42]. This probably indicates their important ecological and functional roles in the gastrointestinal tracts of ruminants [43,44]. Previous studies have shown that *Bacillota* are the major phylum of bacteria that catabolize ingested cellulose to volatile fatty acids in the host [45]. In addition, Li et al. noted that *Bacillota* can also regulate the immune response by suppressing the invasion of opportunistic microorganisms and preventing intestinal inflammation [45]. Representatives of the phylum *Bacteroidota* can utilize starch, xylan, pectin, galactomannan, and arabinogalactan and are among the major degraders of many complex polysaccharides in plant cell walls [46].

It was previously reported that the relative abundance of *Bacillota* was higher than that of *Bacteroidota* in yaks and sheep under grazing conditions, which is consistent with the present study [46]. Shah et al. noted that the dominance of *Bacillota* or *Bacteroidota* may be related to variations in diet, climate, and agricultural practices over a wide geographic area [47]. In addition, the ratio of *Bacillota* to *Bacteroidota* (*Bacillota*/*Bacteroidota*) has been shown to be an important factor in assessing the effect of the gut microbiome on host energy requirements [48,49]. It was found that *Bacillota* participate in the processes of the absorption and circulation of nutrients and are able to participate more efficiently in energy utilization than *Bacteroidota*. Representatives of the latter phylum are responsible for nutrient storage. In our study, the ratio of *Bacillota*/*Bacteroidota* was significantly higher in all studied groups (deer—3.9:1; yaks—2.2:1; sheep—2.8:1; camels—1.85:1). Therefore, it is likely that the microbiomes of these nomadic animals are directed toward energy production. At the end of the cold period, the diets of the ruminants studied were typically low in nutrients, and the elevated *Bacillota*/*Bacteroidota* ratio in the animals we studied suggests that the metabolic efforts of the microbiomes are directed toward nutrient acquisition and absorption rather than storage. This characteristic is consistent with the work of Haworth et al. [50].

Another common phylum among the animal groups we studied was the *Verrucomicrobiota*. Our data are also consistent with the works of Ming et al. and Karnachuk et al. [16,41]. The gut microbiota are known to have anti-inflammatory properties that promote gut health [51]. *Verrucomicrobiota* is closely associated with feed particles and is thought to play an active role in the breakdown of complex polysaccharide [22,52–54].

At the genus level, we identified the most common and widespread groups of bacteria that were identical for all ruminant groups studied. These include the unculturable *Bacillota UCG-005* and *UCG-010*. It can be assumed that these bacteria are the key group for all animals studied. These bacteria are classified as the *Oscillospiraceae* of the phylum *Bacillota* and are obligate anaerobes. *Oscillospiraceae* can efficiently degrade plant material due to genes that allow them to bind to cellulose, hemicellulose, and xylans [55]. Our results are in good agreement with those of Andrade et al., who studied fecal microbial populations of Nelore cattle and found that 16% of the sequences belonged to *UCG-005* and *UCG-010* [56]. These two genera have also been described for the fecal microbiomes of cattle, goats, and musk deer [57–59].

However, as expected, PCA and heatmap analyses revealed a separation into four independent clusters based on fecal microbiota composition [40,60,61]. We assume that this distribution indicates a high degree of species specificity of the samples in terms of microbial content and is probably related to the host species.

At the genus level, dominant/subdominant taxa had their own peculiarities in each group of animals studied. For example, *Prevotella* dominated the fecal microbiota of Tofalar deer (18.6%). *Prevotella* are known to play a key role in the genetic and metabolic diversity of deer rumen microbial communities [42,62,63]. According to Betancur-Murillo et al., this microbe is highly adaptable and can process a wide range of proteins and polysaccharides, including lignocellulose. Furthermore, one of its fermentation products is propionate [64]. Our analysis of fecal microbiota in the Tofalar population of *Rangifer tarandus* showed

the dominant populations of *Ruminococcus* and *Bacteroides* in comparison to the *Rangifer tarandus* population from Spitsbergen [65]. It is likely that differences at the genus level are related to the feeding habitat of these populations. The Spitsbergen population of *Rangifer tarandus* feeds exclusively on natural forage throughout the year but travels insignificant distances to obtain food—less than 0.7 km per day (unlike the Tofalar population of *Rangifer tarandus*). The MDS analysis of fecal microbial communities from these deer populations revealed two distinct clusters, suggesting significant differences. The first cluster comprised fecal samples from the *Rangifer tarandus* of the Spitsbergen population, while the second cluster included fecal samples from the animals we studied (Figure S6 (I)). The microbial community of the Tofalar deer population was more scattered in the plot. Presumably, at the end of winter, when pasture quality is low and snow still covers vegetation, deer are actively foraging. Tofalar deer consume a mixed diet with a high lichen content during this period, relying on the ability of the microbiome to digest poor quality forage with a high lignocellulose content. Yildirim et al. observed that the presence of *Prevotella* species in the rumen improved the adaptation of ruminants to a diet rich in poorly digestible ingredients [66].

In addition to the abovementioned unculturable clostridial lineages, *UCG-005* (12.2%) and *UCG-010* (6.3%), the bacteria of the genera *Bacteroides* (7.2%), *Rikenellaceae_RC9_gut_group* (4.2%), and *Monoglobus* (5.4%) are also dominant groups in the fecal microbiota of yaks. Similar results were obtained when studying fecal samples from yaks in three regions of China [67]. Nie et al. highlighted the significant role of *Bacteroides* in energy metabolism and synthesis of amino acids, which are crucial for the natural growth of yaks in the high-altitude ecological environment of the Qinghai–Tibetan Plateau [68]. The prevalence of the *Bacteroides* and *Rikenellaceae_RC9_gut_group* genera in yaks is supported by Su et al. and Shah et al. [47,69]. The presence of *Monoglobus* bacteria in the gastrointestinal tract of animals is infrequent. Mtshali et al. reported an increase in *Monoglobus* bacteria in cow feces. Nonetheless, the authors underscore the uncertainty surrounding the role of *Monoglobus* in the gastrointestinal tract [70]. In this study, representatives of the *p-2534-18B5_gut_group* were only detected in yak feces. As per Wu et al., the abundance of the *p-2534-18B5_gut_group* in the intestine of yaks decreased markedly with the effect of diarrhea [71]. It could be proposed that the abundance of the uncultured *p-2534-18B5_gut_group* of the phylum *Bacteroidota* is an indirect indicator of the absence of dysbacteriosis manifestations in the studied yaks. The MDS analysis of fecal microbial communities from the two yak (*Bos grunniens*) populations (Okinsky and the Qinghai-Tibetan Plateau) showed a separation into two distinct clusters with significant differences [67]. One cluster contained fecal samples of yak from the Qinghai–Tibetan Plateau population, and the other cluster contained fecal samples from the yak population we studied (Figure S6 (II)). Meanwhile, fecal samples of yaks belonging to the Qinghai–Tibetan Plateau population but inhabiting different areas were also separated from each other on the plot. Overall, despite sharing common dominant taxa, yaks from different study areas had their own distinct gut microbiota. It is likely that harsh environmental conditions (low oxygen, high altitude, temperature) limit food quality and availability.

Similar to our findings in other ruminant groups studied, the fecal samples from sheep exhibited a dominance of unculturable clostridial lines *UCG-005* (9.4%) and *UCG-010* (7.06%). Additionally, the fecal microbiota of sheep exhibited enriched anaerobic *Ruminococcus* bacteria (5%). These bacteria, belonging to the *Oscillospiraceae* family, play a role in the degradation of cellulose, a major component of the typical ruminant plant diet. Shah et al. observed that the availability of high-quality forage and sufficient nutrients in pastures contributed to the relative abundance of fiber-digesting bacteria such as *Oscillospiraceae* and *Rikenellaceae* [47]. It has been noted that *Oscillospiraceae* are considered potentially useful bacteria because they are involved in the positive regulation of the intestinal environment and are associated with immunomodulation and healthy homeostasis [20,72]. Interestingly, our study found bacteria representatives from the genera *Treponema*, *Bacillus*, and *Lysinibacillus* exclusively in the fecal microbiota of sheep. Previous research by Tanca et al. and Chang

et al. demonstrated that a substantial number of functionally active spirochetes in the sheep fecal microbiota belonged to the genus *Treponema*, which were previously described as large pectinolytic spirochetes that reside in the rumen [73,74]. Previously, this phylum was found to be the fourth most abundant in the ruminant gastrointestinal microbiota [75]. *Bacillus* is the major genus of cellulose-degrading bacteria in the gut of animals [75]. The dominant cellulose degrading bacteria were found to differ among animals [76]. Recently, Shabana et al. identified the genus *Lysinibacillus* as a core bacterial genus in sheep [77]. The genus *Lysinibacillus* was also found in the intestine of various breeds of sheep [74]. MDS analysis was performed to compare the fecal microbiota of the studied sheep with sheep from Hebei Province, China [78]. As shown in Figure S6 (III), there was a distinct clustering of fecal microbial community samples from sheep of the Buryat population and sheep from Hebei Province, China.

Akkermansia (10.2%) is one of the dominant genera in the fecal microbiota of Transbaikal camels, along with the uncultivated family lineages *Bacillota UCG-005* (6.5%) and *UCG-010* (12.2%). *Akkermansia* has been found to play an important role in the biology of the Bactrian camels [19]. It has been suggested that bacteria belonging to the genus *Akkermansia* contribute to lower blood glucose levels and provide the ability to tolerate high dietary salt intake [19]. This genus is thought to be a potential biomarker of gut health [21]. It is a highly specialized bacterium capable of utilizing mucins as its sole source of carbon and nitrogen. As a result of mucin degradation, *Akkermansia* releases acetate and propionate, which are readily available to the host [79,80]. A representative of the phylum *Thermodesulfobacteriota*, genus *Mailhella*, was found only in the fecal microbiota of camels. Previously, Karnachuk et al. showed that a significant proportion of *Desulfovibrionaceae* from Altai camel feces was related to '*Mailhella*' sp. [41]. MDS analysis showed that the structure of bacterial communities also differed among various populations of *Camelus bactrianus*. Each group had its own microbial community profile, so samples from each population were grouped separately: the Transbaikal population and the Altai population (Russia) (Figure S6 (IV)) [41]. It is likely that the different gut microbial communities are related to host diet and/or environment.

Archaea in the studied animal groups were mainly represented by methanogenic archaea from the phyla *Euryarchaeota* and *Halobacterota*. The archaeal domain in feces consists mainly of methanogenic archaea from the phylum *Euryarchaeota*. *Methanobrevibacter* is the predominant genus of the *Euryarchaeota* community and the highest abundance in this study was found in deer (2.03%). The high abundance of halophilic archaea in animals living in high salinity habitats suggests that habitat also plays an important role [81]. In our study, *Halobacterota* are found only in representatives of steppe pastures—sheep (up to 1%) and camels (up to 2.4%). Henderson et al. noted that the dominant archaeal groups in ruminants are similar in all regions of the world [2].

4.2. Diet Preferences Is an Important Factor That Affects Fecal Microbiota

Diet is considered one of the most important environmental factors influencing the composition of the gut microbiota [82,83]. Despite a common core of bacteria and archaea in the rumen of animals, differences in microbial community composition have been mainly attributed to diet [2]. To date, studies have been conducted on the relationship between animal nutrition and their microbiota (usually using artificial diets, supplementation of different components, and variations thereof) [84,85].

However, there are few studies on the effect of nutrition on the composition of animal microbiota in natural conditions [86–89]. It should be emphasized that little is known about the relationship between diet and fecal microbiota diversity in nomadic animals. Our studies showed that the studied nomadic animals feed mainly on plants belonging to the families *Poaceae*, *Cyperaceae*, and *Asteraceae* (such as *Stipa krylovii*, *Agropyron cristatum*, *Eriophorum polystachion*, *Artemisia dracunculus*, and *Aster alpinus*). Among the dominant plant species available to the animals, we also found representatives of the *Rosaceae* family.

The diet of deer was based on sedges (*Eriophorum polystachion* L.), grasses (*Rheum rhubarb*), cereals (*Agropyron cristatum* (L.) Beauv.), and lichens (*Cladonia amaurocraea* (Florke) Schaer). The diet of yaks consisted mainly of grasses *Potentilla bifurca* L., *Aster alpinus*, *Allium spendens* Willd. ex Schultes et Schultes fil., legumes *Thermopsis lanceolata*, and cereals *Helictotrichon altaicum* Tzvelev. Sheep preferred grasses of *Dontostemon integrifolius*, *Aster alpinus* L., *Potentilla longifolia*, *P. bifurca* L., and cereals *Stipa capillata* L. In camel feces, *Potentilla longifolia*, *Saussurea salicifolia*, and *Saposhnikovia divaricata* prevailed.

All detected dominant plant species are widely spread in the pastures, which indicates the reliability of our results. Our data are also consistent with results on the diet of free-ranging and semi-free-ranging animals. The identified dominant plant species are prevalent in the pastures, confirming the reliability of our findings. Furthermore, our data are consistent with previous studies on the diet of free-ranging and semi-free-ranging animals [87–90].

We used Pearson's correlation analysis to assess the relationship between diet and dominant microbial taxa. By including fragments of all plant species and dominant microbial taxa in the analysis, we found generally significant positive correlations ($p < 0.05$) between microbiota and plant species found in feces (Figure S7). *Paludicola*, *Prevotella*, *Lachnospiraceae_AC2044_group*, *Muribaculaceae [Ruminococcus]_gauvreauii_group*, and *UCG-011* dominating the fecal microbiota of deer showed significant positive correlations (r = 0.7 and r = 0.8) with plants of *Rheum rhubarb*, *Cladonia amaurocraea* (Florke) Schaer, *Eriophorum polystachion*, *Agropyron cristatum*, *Carex juncella*, and *Artemisia dracunculus*. *Mailhella* was found to be most closely related to *Potentilla longifolia* (r = 0.9) in the fecal microbiota of camels. It should also be noted that almost all bacteria commonly found in camels were positively correlated with *Potentilla longifolia* ($r \geq 0.7$). The microbiota of yaks and sheep showed less pronounced relationships ($r \leq 0.6$) with the analyzed plant spectrum.

PCA analysis based on plant community composition confirmed interspecific differences in the diet of the four animal groups. Indeed, the diet of deer and camels differs significantly, forming compact, distinct clusters. The deer cluster was associated with *Eriophorum polystachion* L., *Rheum rhubarb*, *Agropyron cristatum* (L.) Beauv., *Cladonia amaurocraea* (Florke) Schaer, and *Carex juncella*. For camels, the main contributors to clustering were *Potentilla longifolia*, *Saussurea salicifolia*, *Saposhnikovia divaricate*, and *Leonurus* L. However, overlapping clusters were observed for yaks and sheep. Some of the yaks merged with a widely dispersed group of sheep. This is probably due to the ecological plasticity of yaks, which are able to move from mountainous areas to flat areas of mesoxerophytic steppes in search of food in early spring [29]. These two groups of animals consume common plants found in the steppe regions of Baikal Siberia, including *Potentilla bifurca* L., *Aster alpinus*, and *Stipa krylovii*. These plants are able to maintain their nutritional value in pastures even under a layer of snow [90].

In our study, we identified associations between the fragments of plants and specific bacterial taxa. We observed significant correlations between some plants and the relative abundance of certain bacterial taxa (r = 0.8 and r = 0.9). A close relationship was found between bacteria of the genus *Prevotella* and *Agropyron cristatum*. Previous studies by Wei et al. showed *Prevotella* dominance in the distal microbiota of ruminants, with *Agropyron cristatum* predominating in forage grasses [91]. In addition, some lower abundance taxa including *Muribaculaceae*, *Mailhella*, *Bacteroidales_RF16*, and *Clostridia_vadinBB60* were strongly positively correlated with *Eriophorum polystachion* and *Potentilla longifolia*. Probably, certain nutrient components in the diet contribute to the proliferation of these bacteria.

Thus, in this study, we accumulated knowledge about the similarity and uniqueness of the fecal microbiota in rare nomadic animals of Baikal Siberia in relation to the feeding habitat. This study showed that the fecal microbiota of the studied groups of nomadic animals had similarities at higher taxonomic levels. In general, the studied animal groups were very similar in microbial composition at the phylum level. *Oscillospiraceae*, *Lachnospiraceae*, and *Rikenellaceae* dominated as major bacterial families, and the uncultivated *Bacillota* lineages *UCG-005* and *UCG-010* dominated at the genus level. A characteristic

feature of all animal groups studied was the dominance of bacteria capable of efficient cellulose degradation. However, intergroup species-specific differences in the structure and diversity of major bacterial genera were found among the studied animal groups. These studies have revealed that the co-dominant bacteria differed among animal groups. The results have shown the characteristics of the taxonomic composition of the fecal microbial community of the studied groups of nomadic animals. These findings suggest that various factors such as animal species and feeding habitat may influence the composition of fecal microbiota. Principal component and diversity analyses have confirmed the substantial impact of the host on the fecal microbiota. PCA analysis based on plant community composition confirmed interspecific differences in the diet of the four animal groups. Pearson's correlation analysis revealed a relationship between diet and fecal microbiota of the studied nomadic animals, with each group of animals showing a strong correlation with their diet. These animals show high resistance to nutrient-poor diets due to their microbial communities. A large number of unculturable bacteria (up to 40%) were found in the fecal microbial community, demonstrating the unique potential of the microbiota contained in these indigenous nomadic animals living in Baikal Siberia.

5. Conclusions

High-throughput 16S rRNA gene profiling was used for the first time to analyze the fecal microbiota of indigenous nomadic animals inhabiting in Baikal Siberia. This study provides the first insight into the composition and structure of the fecal microbiota of native nomadic animals living in Baikal Siberia and contributes to our understanding of the interplay between microbiota and feeding habitats specific to each animal group. This pilot study showed that host species as well as diet and habitat determine the taxonomic structure and diversity of the fecal microbiota of the studied nomadic animals. Nomadic animal husbandry typically uses livestock of rare and even endangered species. For this reason, more research and effective management are needed to conserve these rare native animals.

In future research, implementing the whole metagenome sequencing could enhance the comprehension of microbiota of nomadic animals living in Baikal Siberia. The taxonomic composition of the microbial community of the studied species of native rare livestock can be considered a model community of the fecal microbiota of nomadic animals that are pasture-fed in natural habitats year-round. These studies can serve as a guide for further applications in animal husbandry under harsh climatic conditions for the conservation of rare indigenous animals.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16010052/s1. Figure S1: Relative abundance of fecal microbiota of Deer; Figure S2: Relative abundance of fecal microbiota of Yaks; Figure S3: Relative abundance of fecal microbiota of Sheep; Figure S4: Relative abundance of fecal microbiota of Camels; Figure S5: Linear discriminant analysis (LDA) effect size (LEfSe) of fecal microbiomes of nomadic animals; Figure S6: Multidimensional scaling (MDS) plots of the fecal microbiota in different animals; Figure S7: Pearson's correlation of diet and fecal microbial taxa; Table S1: The raw data generated from 16S rRNA gene sequencing have been deposited in the NCBI Sequence Read Archive (SRA).

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