Animal Microbiome

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Metabolic pathways associated with *Firmicutes* prevalence in the gut of multiple livestock animals and humans

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Abstract

Dynamic interspecific interactions and environmental factors deeply impact the composition of microbiotic communities in the gut. These factors intertwined with the host's genetic background and social habits cooperate synergistically as a hidden force modulating the host's physiological and health determinants, with certain bacterial species being maintained from generation to generation. *Firmicutes*, one of the dominant bacterial phyla present across vertebrate classes, exhibits a wide range of functional capabilities and colonization strategies. While ecological scenarios involving microbial specialization and metabolic functions have been hypothesized, the specific mechanisms that sustain the persistence of its microbial taxa in a high diversity of hosts remain elusive. This study fills this gap by investigating the *Firmicutes* metabolic mechanisms contributing to their prevalence and heritability in the host gut on metagenomes-assembled bacterial genomes collected from 351 vertebrate samples, covering 18 food-producing animals and humans, specific breeds and closely-related species. We observed that taxa belonging to *Acetivibrionaceae*, *Clostridiaceae*, *Lachnospiraceae*, *Ruminococcaceae*, and the not well understood *CAG-74* family were evolutionarily shared across all hosts. These prevalent taxa exhibit metabolic pathways significantly correlated with extra-host survival mechanisms, cell adhesion, colonization and host transmission, highlighted by sporulation, glycan biosynthesis, bile acid metabolism, and short-chain fatty acid encoded genes. Our findings provide a deeper understanding of the ecological foundations governing distinct transmission modes, effective colonization establishment, and maintenance of *Firmicutes*, offering new perspectives on both well-known and poorly characterized species.

Keywords Bacterial hereditary, Vertebrate gut, *Firmicutes*, Metagenome-assembled genomes, Metabolic pathway inference

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Background

The intricate relationship between vertebrates and their gut microbiota is pivotal for maintaining physiological homeostasis. Serving as a reservoir of diverse microbial life, the gut microbiota is indispensable to the host for food nutrient absorption, modulation and consumption of energy biosynthesis, fortifying the immune system and safeguarding against harmful pathogens [1, 2]. Its efficient functional role depends on the establishment of a resilient and diverse community built through interspecies and species-environment interactions [3]. This complex dynamic is further shaped by several factors, including host's social interactions and environmental exposures, which influence the ever-changing landscape of microbial population, with taxa exhibiting varying degrees of stability and persistence [4, 5].

In the vertebrate gut, microbiota propagation and establishment are driven by multifactorial features such as the host's evolutionary history and morphology, lifestyle (social and environmental exposures), alimentary guild, geographic location and bacterial dispersal mechanisms [6, 7]. The microbial metacommunities present in the host's environment can affect the inherent microbiota acquisition through vertical transmission [8], modulating the shape of the vertebrate gut microbiota [5, 9]. Moreover, horizontal transmission through social interactions has a fundamental role in the dispersal of the intestinal microbiota, important in ecological and evolutionary contexts [4, 5, 8]. Studies dealing with interactions between food-producing animals, for example, reveal that the environment acts continually in the transmission of vertebrate gut microbiota [9–12]. This microbiota shaped under social and environmental influences, intertwined with genetic relationships, acts synergistically as a hidden force in the evolution of health determinants, with some species persisting from one generation to the other [4, 5, 8, 9, 11, 13]. The success of microbial transmission and host colonization depends on the microbe's potential to overcome obstacles such as achieving adequate abundance for shedding and surviving against environmental challenges, endogenous microbiota competition and the host's immune responses [14].

While research on the transmission of parasites and pathogens is extensive, the significance of the transmission of commensal and beneficial microbes has only recently gained recognition [12], and the specific mechanisms facilitating the persistence of microbial taxa remain unclear. Lloyd-Price, Abu-Ali, and Huttenhower (2016) [15] speculate that microbial taxa persistence in the gut ecosystem may be tied to housekeeping functions essential to all microbial life, microbial transmission capabilities, host-specific interactions, and specialized survival pathways crucial for ecosystem stability. The last one includes specific physiological mechanisms implicated for interspecies interactions, functional specialization, and the maintenance of ecosystem stability, such as resistance to bile's bactericidal action, facilitating microbe colonization [16]; host glycans biodegradation, providing access to a more stable nutrient reservoir while promoting microbial adhesion and host interaction [17]; short-chain fatty acids production by complex dietary utilization, acting as chemical signals linked to host-microbe interaction and cross-feeding [18]; specific lipopolysaccharides enrichment; and synthesis of vitamins and essential amino acids, which contribute to microbial interactions and cross-feeding [15]. Interestingly, core phylotypes (i.e., microorganisms grouped by their phenetic relatedness) have also evolved to provide ecological functions that profoundly shape the co-association and outcome of microbial interactions, including butyrate production and protection against pathogens [19–21].

The resilience and persistence of certain microbes within microbial communities are underlined by adaptive traits such as sporulation, allowing them to survive and transmit through spatio-temporal distances, while also allowing recurrent co-association with hosts [2, 5, 7]. In humans, at least 50–60% of the bacterial genera from the intestinal microbiota of a healthy individual produce resilient spores, specialized for host-to-host transmission [22]. *Firmicutes* (also known as *Bacillota*) is a dominant phylum within the intestinal microbiota and their prevalence in humans is an evolutionary trade-off between transmission range and colonization abundance mediated by sporulation [14]. Despite its less extensive interaction with the host when compared to *Bacteroidetes*, another gut dominant phylum, *Firmicutes* exhibit distinct strategies for gut colonization, contributing to the microbial and functional diversity within the intestinal tract [23–25]. There is increasing evidence that some producing-spore *Firmicutes* members can germinate in the gastrointestinal tract and complete their life cycles in both chicken and pigs [26–29], exhibiting their potentially metabolically active forms primarily associated with the breakdown of glycans [25] and the synthesis of butyrate [23], respectively. Dominant *Firmicutes* in cattle are frequently endospore-forming, which enhances their resistance and tolerance to environmental stress and nutrient limitation [30]. This is achieved through their efficient ability to escape low pH and host secretions via spore formation, while in vegetative form can offer vital vitamins and host bile acid metabolism, in addition to their major involvement in carbohydrate breakdown and nutrition absorption [31, 32].

To date, studies that explore vertebrate-related metagenomics primarily aim to clarify microbial diversity and their role in potential disorders and animal health assessment, in improving feed efficiency, or in optimizing livestock growth potential [12, 33–36]. Notably,

metagenome-assembled genomes (MAGs) have aided the taxonomic and functional characterization of bacteria that are difficult to cultivate in vitro due to challenges in mimicking the native gut environment [37–39]. However, there has been very little microbiome research that considers the interplay of transmission, inheritance, and metabolic functions that could support the intestinal stability of uncultured bacteria, primarily associated with *Firmicutes* prevalence in multiple hosts. In this study, we explored the fecal MAGs of humans and livestock animals to investigate the influence of host phylogeny on gut microbial composition, as well as the metabolic mechanisms involved in *Firmicutes* transmission and microbial colonization success among hosts sharing a similar genetic background. Our study aims to contribute to a better understanding of the interaction between vertebrates and common prevalent *Firmicutes* taxa, examining traits that are likely informative for transmission mode and successful colonization establishment.

Results

Diversity and host microbial characterization

The *Firmicutes* transmission and colonization were investigated under metagenomes-assembled genomes from the Brazilian One Health metagenomics study. We recovered 2,915 MAGs, with 1,273 high-quality (≥ 90% completeness and ≤ 5% contamination) and 1,642 medium-quality (≥ 50% completeness and ≤ 10% contamination) MAGs. Considering the additional datasets employed (i.e. conspecific hosts from different countries, different breeds of the farmed hosts and closely-related species) ("Sheet 1" in Additional file 1: Table S1), 1,393 non-redundant MAGs were assembled, being 387 of high-quality and 1,006 of medium-quality. In total, 4,308 MAGs from 18 species were analyzed. The evolutionary relationship among the hosts inferred by phylogenomic inference showed each host clustered in well-defined monophyletic groups, with related-species in an ancestral node, as expected (Fig. 1).

The microbial composition of humans, cattle, swine, and poultry predominantly comprised MAGs from *Firmicutes* (46.7%), *Bacteroidetes* (19.4%), *Proteobacteria* (14.9%), and *Actinobacteria* (7.7%) phyla (Fig. 2 and "Sheets 1–3" in Additional file 2: Table S3). Across these hosts, we identified 612 unique bacterial species, ranging from 6 in swine breeds to 330 in humans ("Sheet 4" in Additional file 2: Table S3). *Firmicutes*, mostly represented by *Ruminiclostridium*, were the most abundant phylum across conspecific, swine breeds and phylogenetically-close species of swine and poultry, while *Bacteroidetes* were notable in cattle, poultry breeds and phylogenetically closest cattle hosts, who exclusively had abundant *Verrucomicrobiota* (Fig. 2). *Firmicutes* and *Bacteroidetes* dominance emphasizes the anciently integrated microbiome members that evolved with vertebrate evolution, leading to conserved gut microbial communities within certain host species [40–42]. Furthermore, the remarkable prevalence of *Verrucomicrobiota* demonstrates their evolutionary adaptation to non-human intestinal environments, which supports emerging evidence that specific microbial pressures have fueled their persistence and adaptability in agricultural animals such as poultry and cattle [40, 43–49].

The gut microbiota richness (Chao estimator), diversity (Shannon index), and evenness (Simpson index) varied significantly among target hosts and breeds, as well as between the targets and their related-species (Fig. 3, Additional file 3: Table S4). Post-hoc Shannon index analyses revealed no significant diversity differences among members belonging to the same group (except for related-swine species that diverged from related-cattle) (Additional file 3: Table S4). Despite the dominance of a

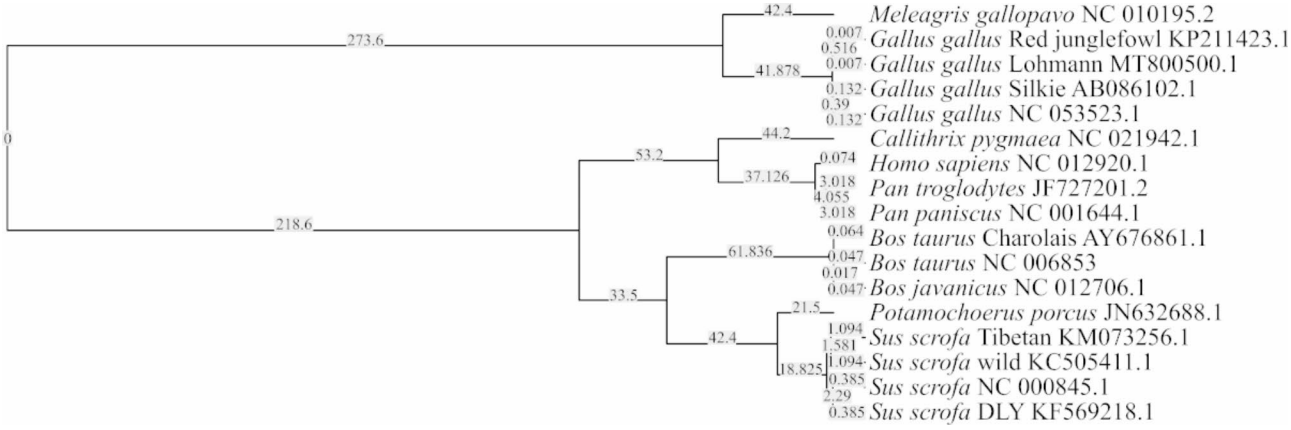

Fig. 1 Time tree of all host species ($n = 17$) based on mitochondrial genomes. The evolutionary history was inferred through maximum likelihood inference considering *Danio rerio* as the outgroup taxon and using GTR + G + I substitution model. Branch lengths are annotated in million years. Mitochondrial DNA from *B. taurus* Luing was unavailable on the NCBI database and thus could not be included in phylogenomic inference

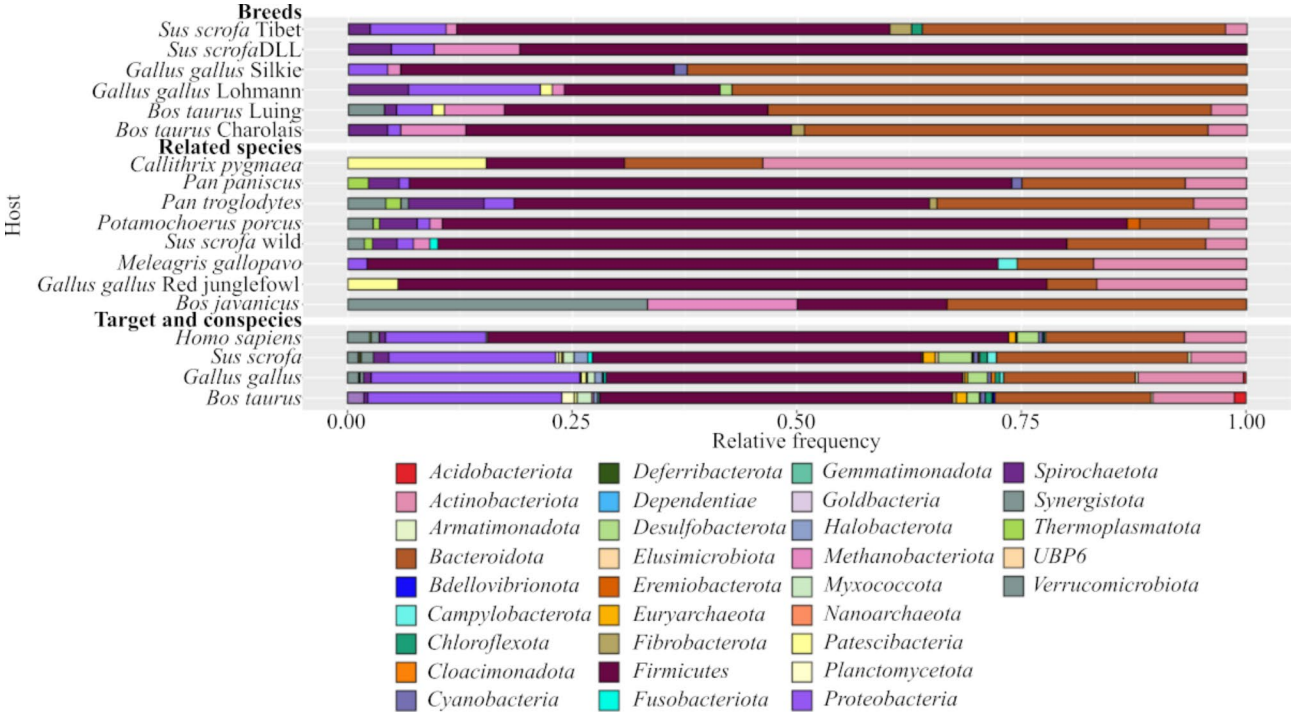

Fig. 2 Relative abundance of bacterial phyla in the microbial compositions of the sampled hosts. The hosts are distributed among conspecifics, breeds, and phylogenetically closest host groups

few bacterial genus, evenness remained consistent across all host groups, with conspecific food-producing animals exhibiting notably similar diversity (Fig. 3b). Overall, conspecific hosts showed more similar diversity than related ones, suggesting that domestication and inbreeding may be important factors modulating the microbial composition of the gut.

The interhost analysis of the microbial diversity by Principal Component Analysis (PCA) demonstrated that members of the target group and their conspecifics had congruent bacterial composition (Fig. 4), except for some human representatives. Furthermore, among non-human groups, pigs and birds exhibited greater beta diversity among themselves than other non-human groups. Host species explained 32.76% of the data variation. Although all host groups clusters overlapped, non-brazilian conspecific hosts showed slightly higher dissimilarities in species composition.

Given the multivariate nature of microbiome data, PERMANOVA analyses were used to investigate the potential effects of ecological (geographic region) and host taxonomy (class, order, and genus) factors on intestinal communities in food-producing animals and humans along with specific breeds and closely-related species. Target and their conspecific species had effect on the bacterial community structure, distinctly of those observed considering all groups (target, conspecifics, breeds and related species) (Additional file 4: Fig. S1). Although conspecific hosts showed a congruent intraspecific microbiota diversity, a consistent variation in bacterial community structure between hosts is predicted only by host phylogeny (R^2 = 0.14960, $p = 0.001$; Betadisper: $F = 1.0721$, $p > 0.05$) (Additional file 5: Table S5). This finding emphasizes that anthropogenic pressures (domestication and inbreeding) may have an impact on interspecific microbiota variance, whereas greater genetic relatedness between hosts can lead to more effective microbial colonization.

Conserved clades of gut *Firmicutes* associated with the vertebrate evolution

Modulation of microbial community structure is not a one-dimensional process under host control, but rather a complex interplay of host and microbial control with microbial interspecies competition. To establish the mechanisms related to bacterial transmission and colonization in their host lineages, we first identified microbial monophyletic clades shared between the target and conspecific vertebrate groups. We obtained 4,237 monophyletic hierarchical clades, some representing bacterial eco-phylogenetic groups conserved throughout host phylogeny ("Sheet 1" in Additional file 8: Table S6). The host groups shared 659 clades, while exclusive clades varied between 85 in swine and 478 in humans (Additional file 6: Fig. S2). Of the shared clades, 533 showed taxa with prevalence of ≥ 50% per host group. Within the prevalent

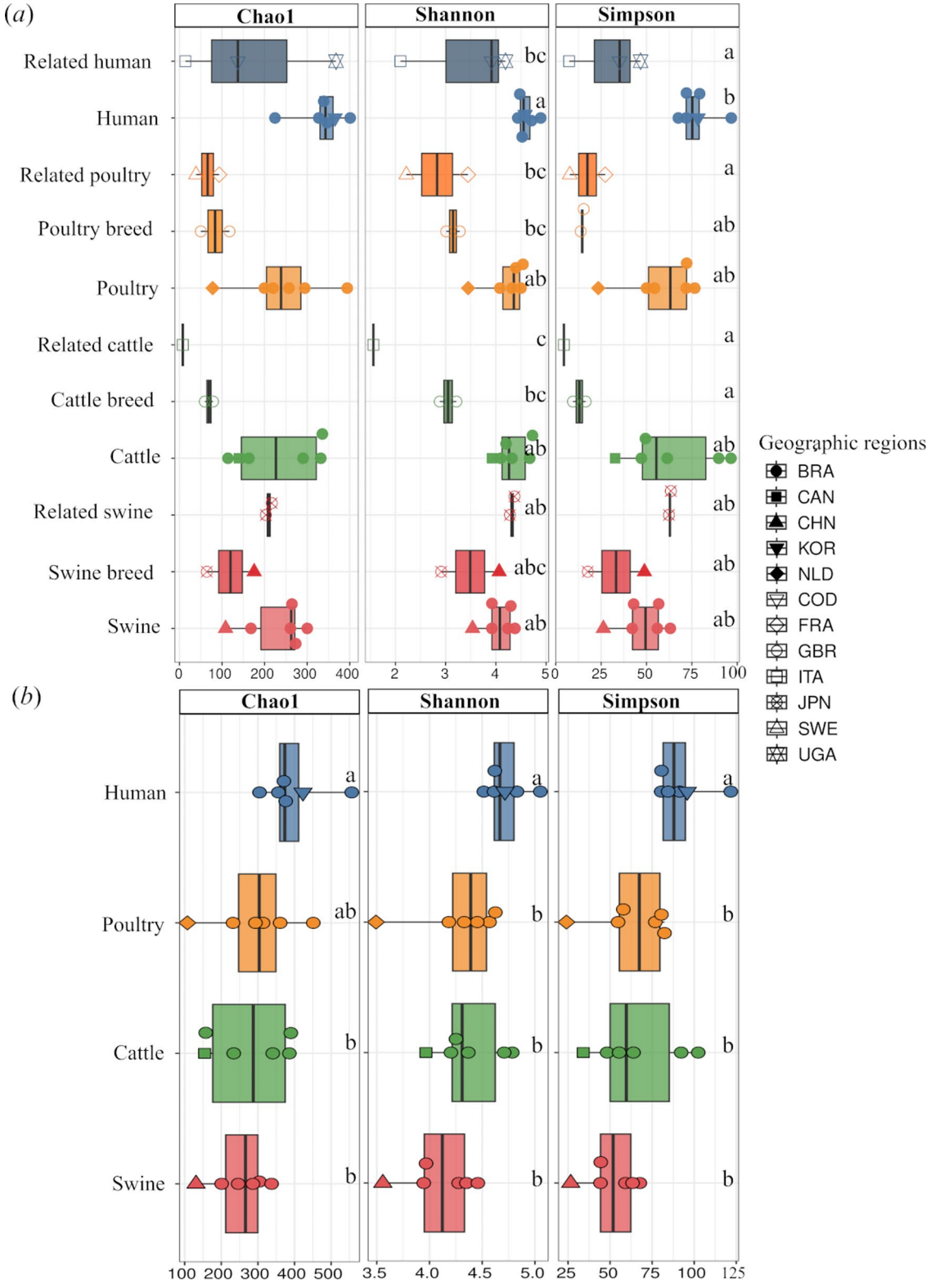

Fig. 3 Alpha-diversity comparison of bacterial genus compositions in poultry, cattle, swine, and humans. **(a)** All host groups from different geographic regions are presented, with conspecies represented by filled points; **(b)** Only conspecies are shown. Brazilian hosts are shown as filled dots. The boxes show the interquartile ranges (IQRs) between the first and third quartiles (25th and 75th percentiles, respectively), while the line within represents the median. Whiskers represent the lowest and greatest values within a 1.5-fold range and the IQRs for the first and third quartiles. Boxes that do not share any letters represent statistically significant comparisons

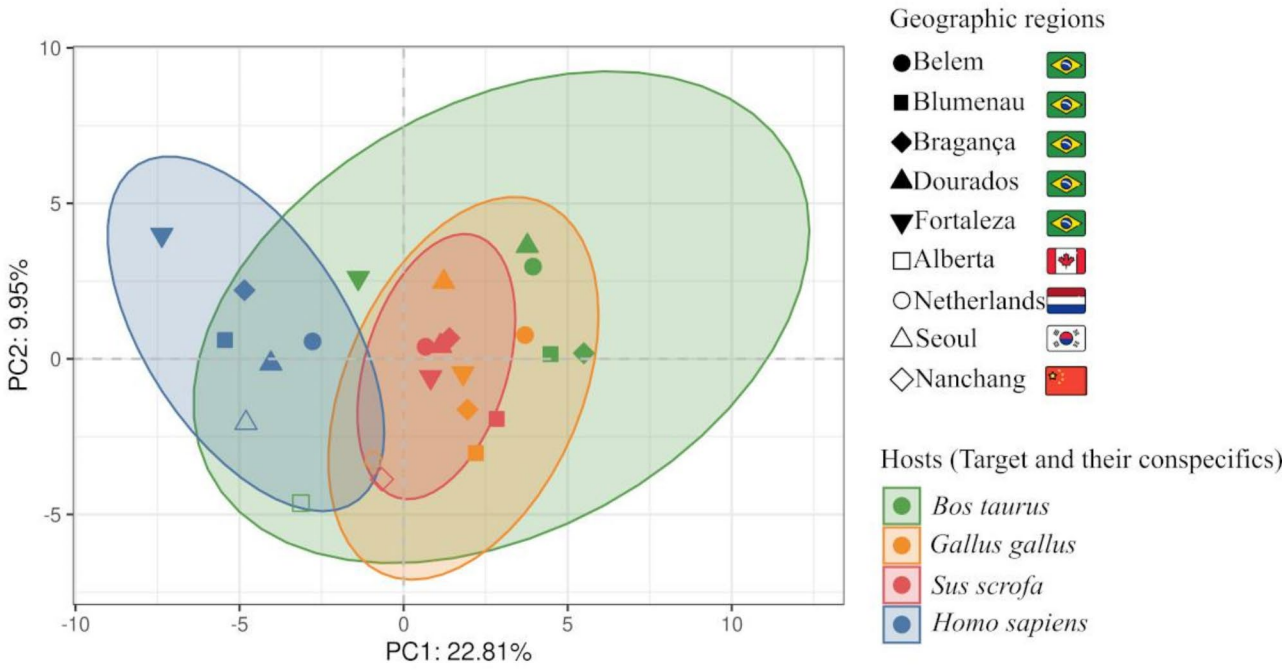

Fig. 4 PCA of Euclidean distances between the gut microbiomes of target hosts and their conspecifics. Each point represents a co-assembled sample based on host species and geographic location, with the shape indicating the geographic region. Euclidean distances were calculated using CLR-transformed abundances of MAGs at the genus level. Principal components one and two explained 22.81% and 9.95% of the variance in gut microbial community structure, respectively

clades, 70 belonged to *Firmicutes* phylum, harboring 1,186 MAGs ("Sheet 2" in Additional file 8: Table S6). Around 8.57% and 7.14% of these belong to the *Clostridia* and *Bacilli* class, distributed in the *Lachnospiraceae* (17.14%), *Acetivibrionaceae* (8.57%), *Clostridiaceae* (10%) and *Ruminococcaceae* families (4.28%) with representatives of *Hungatella* and *Herbinix* genera (2.86%) ("Sheet 4" in Additional file 8: Table S6). From the 70 clades, 16 statistically significant nodes from pigs and humans were composed of 313 MAGs, mainly belonging to *Lachnospiraceae* ("Sheets 3 and 5" in Additional file 8: Table S6). To resolve clades that may be related to critical features underlying their predominance, we sought to identify newly formed clades that are prevalent in all hosts (≥ 50% of individuals per host group) (Fig. 5; Table 1). Although some descendant nodes were variably conserved across host groups, prevalent newly formed clades gave rise to nested clades that were conserved across all investigated host populations (Fig. 5; Table 1). These findings suggest that closely related microorganisms, evolved from a common ancestor, may share critical characteristics that explain their prevalence across hosts.

Table 1. Common nodes discovered at the family, genus, and species levels in all host groups belonging to the *Firmicutes* phylum with a prevalence equal to or more than 50% as detected by ClaaTU.

Mechanisms associated with the transmission of *Firmicutes* in their host lineages

Considering the potential metabolic influence of *Firmicutes* on their host maintenance and evolution, we performed a PCoA analysis of KEGG metabolic profiles for prevalent cladal MAGs. PERMANOVA analysis revealed that host explained approximately 60.5% of the variation in metabolic profiles (R^2 = 0.0435, F = 6.5259, p = 0.001), whereas bacterial family explained approximately 4.3% (R^2 = 0.6051, F = 131.4456, p = 0.001). However, multivariate homogeneity analysis considering family as a predictor indicated that the significant PERMANOVA arises from non-homogeneous intra-group dispersion (F_{HOST} = 1.1662, p = 0.317; F_{FAMILY} = 21.305, p = 0.001). Ellipses in the PCoA are grouped by different monophyletic MAGs from the same family (Fig. 6a) and distinct vertebrates (Fig. 6b) (explaining 74.7% of the variance), reinforcing that MAGs from various monophyletic clades may exhibit functional redundancy regardless of the host.

Since ecologic traits shared by monophyletic clades can drive their apparent ubiquity across hosts, we explored the potential cross-association among prevalent bacterial families and KEGG metabolic pathways that could indicate functional redundancy to multiple species. We observed 211 statistically significant correlations (Fig. 7), consistent with our PCoA analyses. An exception is *Ruminococcaceae*, whose metabolic capabilities were

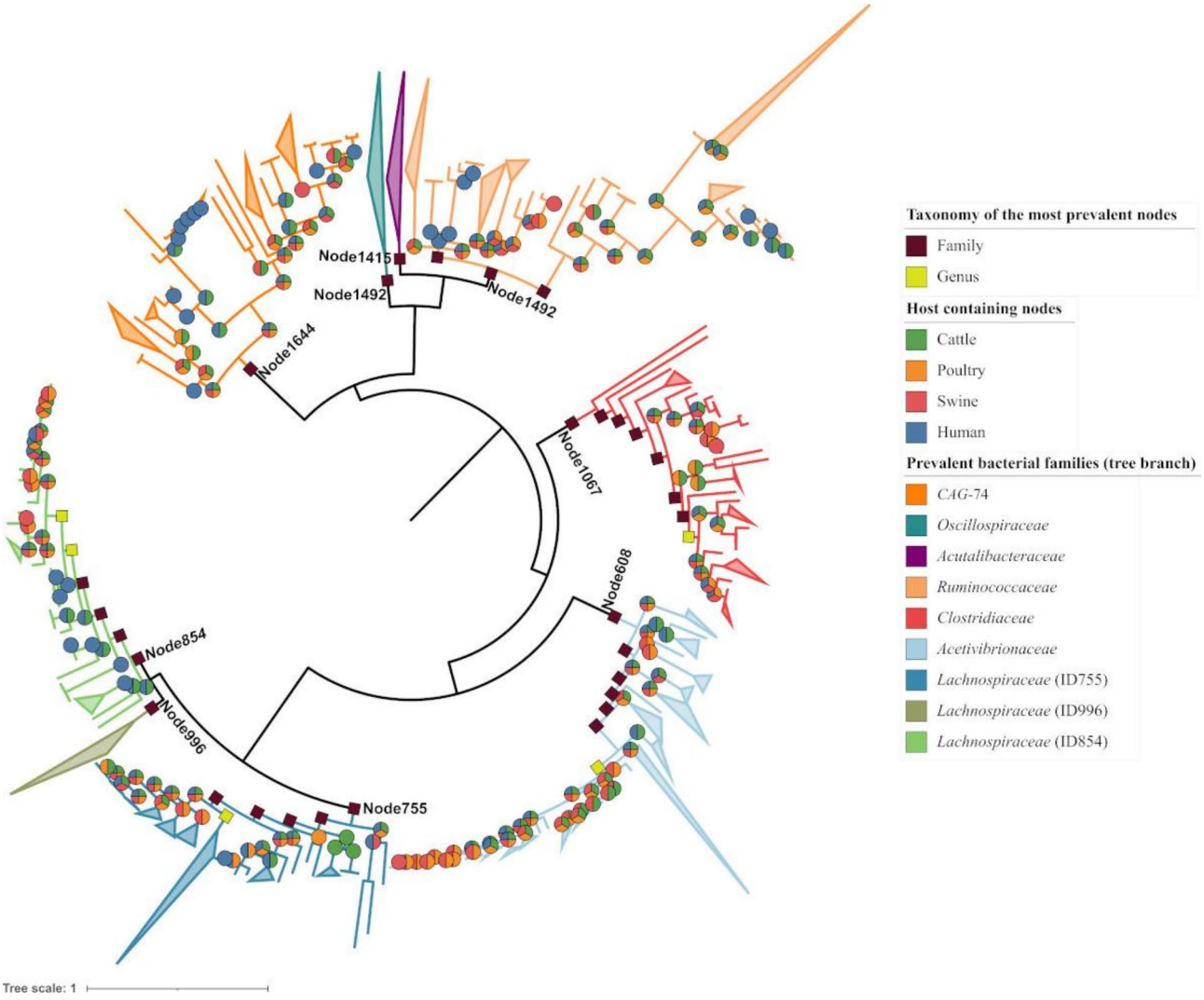

Fig. 5 ClaaTU cladogram showing the common prevalent *Firmicutes* clades among vertebrates. Monophyletic clades at the family level (found in ≥ 50% of individuals per host group) are represented by magenta squares. The taxonomy assignments of these clades, listed in clockwise order in the caption, are associated with branch colors. Lemon squares highlight prevalent nested nodes at the genus level. All prevalent clades shown are conserved across hosts, but their descendants are differentially conserved across host groups, as indicated by pie charts. Collapsed nodes (represented in the triangle aesthetic) correspond to MAGs belonging to the same finer taxonomy level. *Oscillospiraceae*, *Acutalibacteraceae* and *Lachnospiraceae* (ID996) did not comprise vertebrate-shared MAGs with prevalence levels exceeding the predicted threshold (50%)

more heterogeneous. Bacterial families shared among vertebrates, particularly those in non-human hosts, displayed a similar functional profile.

We observed a distinct bacterial taxa cooperation in multiple KEGG pathways within each host (Fig. 7). Briefly, *Acetivibrionaceae* showed two main functional clusters: one containing MAGs commonly found in swine and poultry, associated with host-specific microbiome functions (such as implicated for interaction and nutrient scavenging, for example signaling and cellular processes and membrane transport - see pathways strongly correlated in "Sheet 1" in Additional file 9: Table S7); and another with heterogeneous MAGs dispersed in distinct hosts and exclusive representatives (as *Ruminiclostridium papyrosolvens*, found in food-producing animals) ("Sheet 1" in Additional file 9: Table S7). In this last cluster, the vertebrate-shared *Acetivibrionaceae* had a similar metabolism profile to *Pseudobacteroides* found in cattle, while *Ruminiclostridium* and *UBA*1305 genera showed similar metabolic traits, specially related to cellular communication, metabolism and genetic processes. The *CAG*-74 family also showed two diverse metabolic profiles: one including less-characterized *UMGS*1603 and *UBA*1038, found in cattle and swine, involved in microbial interaction and metabolite biosynthesis; and another containing MAGs exclusive to humans linked to survival, anabolism and catabolism processes (such as cell growth and death and genetic processes, metabolism of glycan, cofactors

Table 1 Common nodes found at the family, genus, and species levels in hosts with ≥ 50% prevalence.[a] node IDs with similar prevalence values are grouped together, and the prevalence and FDR values are described for each one based on the host group where they are found. [b] hosts from target group and their conspecifics are identified by their first initials (C = cattle, P = poultry, S = swine, H = human)

NodeID[a]	Node classification	Node prevalence [a]	FDR [b]
608,615–619	*Acetivibrionaceae*	0.83 (C)*, 0.67 (P)*, 0.83 (S)*, 0.5 (H)*	1 (C), 1 (P), 0.98 (S), 1 (H)
623	*Ruminiclostridium_A*	0.83 (C)*, 0.67 (P)*, 0.83 (S)*, 0.5 (H)*	1 (C), 0.99 (P), 0.98 (S), 1 (H)
755	*Lachnospiraceae*	1 (C)*, 0.83 (P)*, 1 (S)*, 0.83 (H)*	1 (C), 0.99 (P), 0.98 (S), 1 (H)
758,766,768	*Lachnospiraceae*	0.83 (C)*, 0.83 (P)*, 1 (S)*, 0.83 (H)*	1 (C), 0.99 (P), 0.98 (S), 1 (H)
769	*Lachnospiraceae*	0.83 (C)*, 0.83 (P)*, 0.83 (S)*, 0.67 (H)*	1 (C), 0.99 (P), 0.98 (S), 1 (H)
791,799	*Herbinix*	0.83 (C)*, 0.83 (P)*, 0.67 (S)*, 0.5 (H)*	1 (C), 0.99 (P), 0.98 (S), 1 (H)
854	*Lachnospiraceae*	0.83 (C)*, 0.83 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 0.99 (P), 0.98 (S), 0.77 (H)
858	*Lachnospiraceae*	0.83 (C)*, 0.83 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 0.99 (P), 0.98 (S), 0.72 (H)
859	*Lachnospiraceae*	0.83 (C)*, 0.83 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 0.99 (P), 0.98 (S), 0.65 (H)
860	*Lachnospiraceae*	0.67 (C)*, 0.83 (P)*, 0.5 (S)*, 0.83 (H)*	1 (C), 0.98 (P), 0.98 (S), 1 (H)
864	*Hungatella*	0.67 (C)*, 0.83 (P)*, 0.5 (S)*, 0.83 (H)*	1 (C), 0.96 (P), 0.98 (S), 0.99 (H)
865	*Hungatella*	0.67 (C)*, 0.83 (P)*, 0.5 (S)*, 0.5 (H)*	1 (C), 0.96 (P), 0.98 (S), 1 (H)
996	*Lachnospiraceae*	0.5 (C)*, 0.67 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 1 (P), 1 (S), 0.89 (H)
997,998	*Lachnospiraceae*	0.5 (C)*, 0.5 (P)*, 0.5 (S)*, 0.67 (H)*	1 (C), 0.99 (P), 0.98 (S), 1 (H)
1067	*Clostridiaceae*	1 (C)*, 1 (P)*, 0.83 (S)*, 1 (H)*	1 (C), 0.96 (P), 0.98 (S), 0.82 (H)
1068	*Clostridiaceae*	1 (C)*, 0.83 (P)*, 0.83 (S)*, 1 (H)*	1 (C), 0.99 (P), 0.98 (S), 0.81 (H)
1069	*Clostridiaceae*	1 (C)*, 0.83 (P)*, 0.83 (S)*, 1 (H)*	1 (C), 0.99 (P), 0.98 (S), 0.8 (H)
1070	*Clostridiaceae*	1 (C)*, 0.83 (P)*, 0.83 (S)*, 1 (H)*	1 (C), 0.99 (P), 0.98 (S), 0.79 (H)
1071	*Clostridiaceae*	1 (C)*, 0.83 (P)*, 0.83 (S)*, 0.83 (H)*	1 (C), 0.99 (P), 0.98 (S), 1 (H)
1083	*Clostridiaceae*	0.83 (C)*, 0.83 (P)*, 0.67 (S)*, 0.83 (H)*	1 (C), 0.99 (P), 0.98 (S), 1 (H)
1088	*Clostridiaceae*	0.67 (C)*, 0.67 (P)*, 0.67 (S)*, 0.83 (H)*	1 (C), 0.99 (P), 0.98 (S), 0.98 (H)
1089	*Clostridium*	0.67 (C)*, 0.67 (P)*, 0.67 (S)*, 0.83 (H)*	1 (C), 0.99 (P), 0.98 (S), 0.93 (H)
1264	*Ruminococcaceae*	1 (C)*, 0.83 (P)*, 0.67 (S)*, 1 (H)*	1 (C), 0.99 (P), 1 (S), 1 (H)
1265	*Ruminococcaceae*	0.5 (C)*, 0.5 (P)*, 0.67 (S)*, 1 (H)*	1 (C), 1 (P), 0.98 (S), 0.75 (H)
1309	*Ruminococcaceae*	0.83 (C)*, 0.67 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 0.99 (P), 0.98 (S), 0.78 (H)
1415	*Acutalibacteraceae*	0.67 (C)*, 0.67 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 1 (P), 1 (S), 0.89 (H)
1418	*Acutalibacteraceae*	0.67 (C)*, 0.67 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 0.99 (P), 1 (S), 0.89 (H)
1492	*Oscillospiraceae*	0.67 (C)*, 0.83 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 1 (P), 1 (S), 1 (H)
1527	*Oscillospiraceae*	0.5 (C)*, 0.83 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 0.99 (P), 1 (S), 1 (H)
1541	*Oscillospiraceae*	0.5 (C)*, 0.67 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 1 (P), 1 (S), 0.91 (H)
1542	*Oscillospiraceae*	0.5 (C)*, 0.67 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 0.99 (P), 0.99 (S), 0.89 (H)
1543	*Oscillospiraceae*	0.5 (C)*, 0.5 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 1 (P), 0.98 (S), 0.86 (H)
1572	*Oscillospiraceae*	0.5 (C)*, 0.5 (P)*, 0.5 (S)*, 1 (H)*	1 (C), 0.99 (P), 0.98 (S), 0.32 (H)
1644	*CAG-74*	0.83 (C)*, 0.5 (P)*, 0.67 (S)*, 1 (H)*	1 (C), 1 (P), 0.98 (S), 0.89 (H)

and vitamins, nucleotide and xenobiotics compounds) ("Sheet 2" in Additional file 9: Table S7).

Clostridiaceae subgroups also have homogeneous metabolic characteristics. *Clostridium*, present in all hosts, exhibited a metabolic profile comparable to *C. beijerinckii*, found in swine, and *Clostridium* sp000435835, found in humans, swine and poultry. Both taxa are grouped with MAGs characterized by housekeeping functions (such as cell growth and death, amino acid, energy and lipid metabolism and genetic information processing along with signaling and cellular processes also relevant to microbial and host interactions) ("Sheet 3" in Additional file 9: Table S7). Another *Clostridiaceae* major group comprises MAGs exclusive to humans and cattle, linked to microbial interactions functions (such as cellular motility and community).

Lachnospiraceae (ID755) showed three heterogeneous metabolic profile groups: two linked to essential microbial and gut functions (including *Anaerocolumna* members, human MAGs and those found in humans and animals; *Herbinix* and food-producing animals exclusive MAGs) and one comprising MAGs from cattle, associated with motility, microbial signaling and interaction ("Sheet 4" in Additional file 9: Table S7). Microbial signaling and interaction were also highlighted in *Lachnospiraceae* (ID854). This group contains the *Hungatella celerecrescens* found in all vertebrate hosts, clustered with MAGs exclusive to poultry. Additionally, another subgroup in *Lachnospiraceae* (ID854) primarily comprises

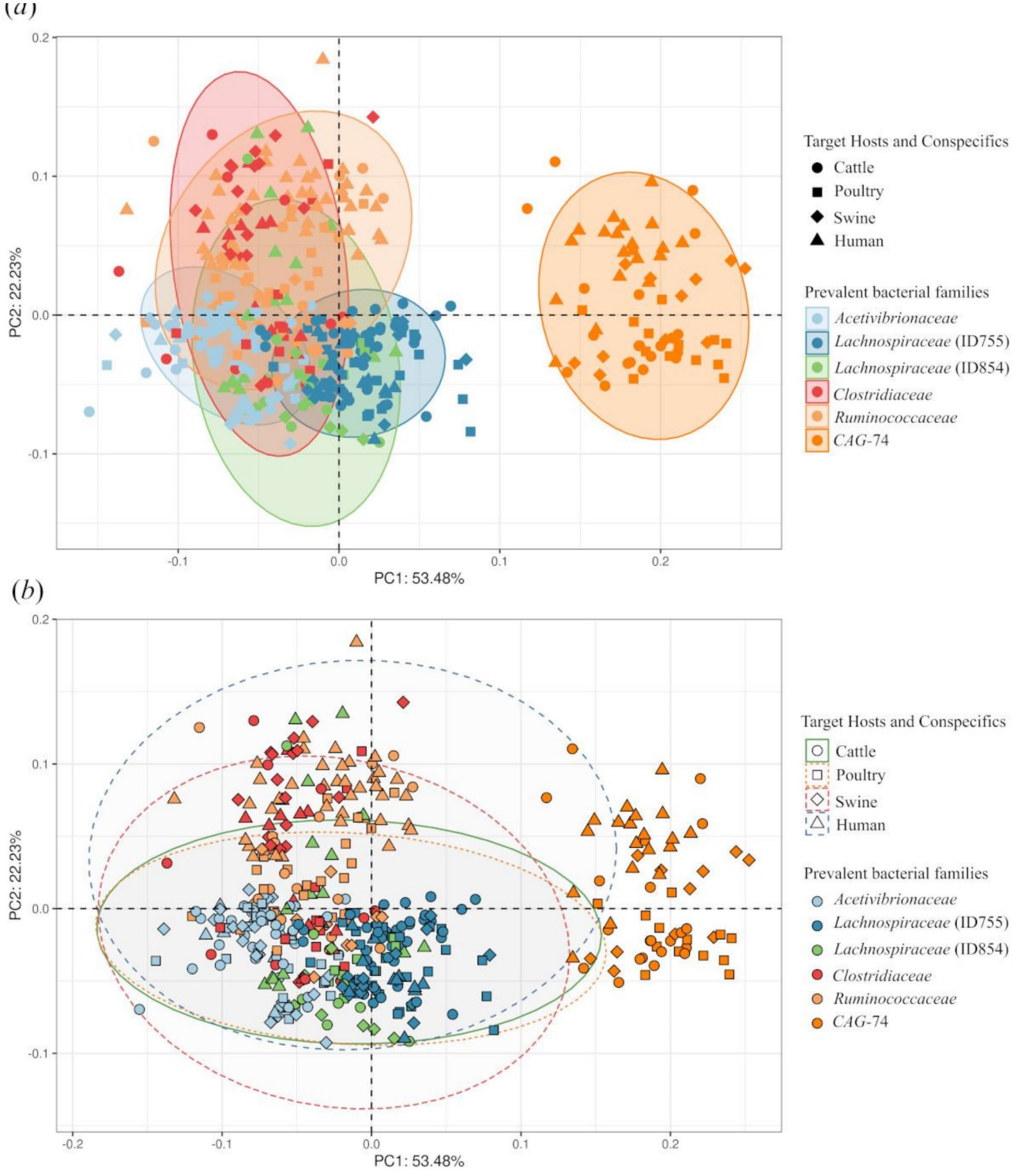

Fig. 6 PCoA of KEGG metabolic profiles from prevalent MAG clades in hosts using Bray-Curtis dissimilarity. Each point represents a metabolic profile from a different MAG, and the shape identifies the host in which it was identified. The impact of **(a)** bacterial family and **(b)** host on the metabolic profile of MAGs from prevalent clades is visually explored by clusters. Principal components one and two accounted for 53.48% and 22.23% of the variation in metabolic profiles among prevalent clades, respectively

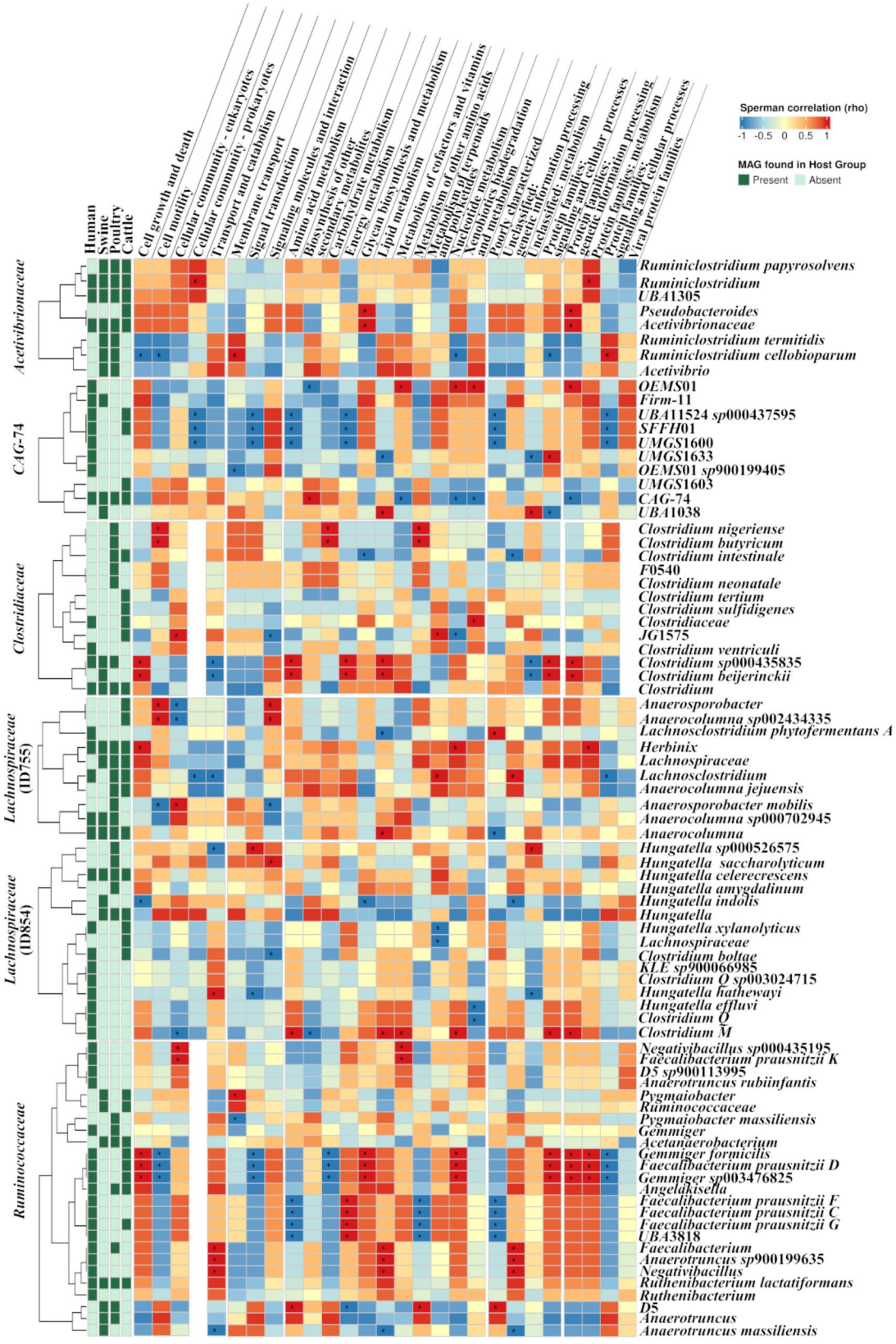

Fig. 7 Correlation between MAGs from prevalent clades and KEGG metabolic pathways (at the hierarchy level 2). Spearman's rank correlations were performed with the MAGs' finer taxonomic levels from each prevalent bacterial family to investigate crucial traits for their transmission and colonization among vertebrate guts. Two monophyletic nodes of *Lachnospiraceae* (ID755 and ID854) are described. The red represents positive correlations; the blue block means negative correlation. "*" indicates a significant association ($|r| > 0.5$, $p < 0.05$)

MAGs associated with humans, focusing on metabolite production and microbial interaction ("Sheet 5" in Additional file 9: Table S7).

Furthermore, within *Ruminococcaceae*, despite two diverse metabolic groups, the shared taxon *Ruthenibacterium lactatiformans* clustered with MAGs exclusively found in humans and correlated to essential microbial and gut-specific functions ("Sheet 6" in Additional file 9: Table S7). Additionally, a group comprising MAGs found in humans displayed functions related to microbial interaction and habitat specificity (as metabolism of cofactors and vitamins, energy metabolism and cellular community, along with strong correlations with xenobiotics biodegradation and metabolism) ("Sheet 6" in Additional file 9: Table S7).

Whitin significant correlations, few taxa show a possible niche-specific specialization consistent with the host associated. An example is the metabolism of cofactors and vitamins exclusively found in humans and associated with MAGs from *CAG*-74 family (*OEMS*01), *Lachnospiraceae* (*Clostridium* M, Node ID854), and *Ruminococcaceae* (*Negativibacillus* sp000435195 and *Faecalibacterium prausnitzii*). Also, carbohydrate metabolism is exclusively positively correlated in poultry and associated with MAGs from the *Clostridiaceae* family (*Clostridium butyricum* and *C. nigeriense*).

The strong and positively correlated metabolic categories with sharing vertebrate taxa (Additional file 7: Fig. S3) were cellular community; glycan biosynthesis and metabolism; cellular growth and death; protein families related to metabolism and genetic information processing; lipid and nucleotide metabolism; and biosynthesis of other secondary metabolites. In addition to the typical functions necessary for microbial survival, these categories encompass processes that influence the outcome of host-microbe interactions, including host-to-host transmission strategies, resistance to acidic environments, adhesion to host cell surfaces, breakdown of complex dietary and structural carbon sources, and production of compounds involved in host-microbe associations. All genes associated with colonization strategies identified in prevalent vertebrate-shared *Firmicutes* species are shown per bacterial family in "Sheets 1–6" in Additional file 10: Table S8. Our results accentuate the complexity and relevance of microbial adaptability in host intestines, and mainly point out the metabolic pathways involvement in the maintaining *Firmicutes* species' function and persistence across multiple vertebrate hosts.

Discussion

Firmicutes is one of the predominant bacterial phyla colonizing the healthy vertebrate gut, with certain species being transmitted across host generations. Accumulating evidence suggests that the intrinsic relationship between vertebrates and *Firmicutes* is orchestrated by dynamic microbial interactions that are intertwined with the host's genetic background, as well as social and environmental factors. However, the specific mechanisms sustaining the persistence of its microbial taxa among multiple vertebrates remain elusive.

In this study, the bacterial microbiota of humans, cattle, swine, and poultry were primarily composed of MAGs from *Firmicutes*, *Bacteroidetes*, *Proteobacteria*, and *Actinobacteria*, consistent with previous meta-analyses [50, 51]. Despite morphological, physiological, and ecological differences, these warm-blooded animals shared a similar gut microbiota composition, with *Firmicutes* as the most prevalent phylum, favored by stable intestinal conditions such as constant temperature, continuous nutrient supply, and anaerobic environments [52]. Interestingly, studies have demonstrated *Firmicutes* to be heritable using SNP-based heritability estimates determined by host genotype [53, 54], with the observed variation possibly related to the host phylogenetic similarity effect [53–58].

The intraspecific microbiota variance in tandem with the reduced bacterial richness observed in breeding animals agrees with findings in purebred cattle [59] and highlights how captive animal inbreeding often leads to genetic homogeneity and reduced microbiome diversity [60]. Furthermore, animals in captivity exhibit heterogeneous alpha diversity when compared to wild vertebrates [5, 60–64]. In our study, captive animals and humans living close to rural properties showed similar alpha diversity. The physical proximity between hosts and also the direct (social) or indirect (abiotic environmental substrates) contact within groups may be contributing to the spread of these microbial members among those vertebrates [5, 61, 64]. Notably, alpha diversity patterns among Brazilian food-producing animals indicate that Brazilian rearing approach supports microbial exchange [5], echoing previous findings of shared bacterial taxa across humans, cattle, and semi-captive chimpanzees in shared environments [65].

We identified that the host phylogeny significantly explained interspecies variation in bacterial community composition, which can be attributed to molecular, anatomical, and physiological changes in captive animals caused by domestication in human-constructed environments such as zoos and farms [59, 66–68], as well as disruptions in microbial colonization preferences influenced by inbreeding mechanisms [69]. Consequently, including these vertebrates in phylogenomic inferences increases microbial community complexity and potentially leads to randomization of compositional changes [7, 70, 71]. Our findings suggest that greater host relatedness may facilitate effective microbial colonization due to a more similar genetic background [5], whereas less closely related hosts may impose physiological filters hindering colonization

efficiency. In this context, convergent physiological adaptations and anatomical specializations shared by phylogenetically related vertebrate hosts can create a gut ecosystem with comparable selection pressures, potentially leading to similar microbial diversity [72, 73].

Furthermore, in this study we found no significant evidence supporting geographical location as a predictor of microbial community variation (Fig. S1). Although Brazilian samples are overrepresented compared to other countries, this finding emphasizes that vertebrates with convergent ecological niches tend to harbor gut microbiota influenced more by shared evolutionary, behavioral, and physiological traits than by geographical factors. While geographical proximity may facilitate microbial dispersal among cohabiting vertebrates, increasing the similarity of gut microbiota composition in different hosts with overlapping habitats [5, 61, 64], region-specific dietary variation, food composition, and availability from livestock management—both within and between countries—shaped by socio-economic and environmental factors such as climate, soil geochemistry, and plant communities, appears to further reinforce the dominant role of host phylogeny [30, 74–77]. As a result, the prominent role of host phylogeny can obscure the influence of geographical locations, consistent with previous research indicating that evolutionary and physiological traits within phylogenetically related host species are important factors shaping microbial communities [75, 78].

Altogether, our findings suggest that rearing practices on food-producing farms may alter gut microbiome communities by increasing microbiota similarity. However, host phylogeny may be the primary factor shaping bacterial microbiome structure across multiple vertebrate clades [6, 70, 72, 79, 80]. Recent research links host-specific patterns to non-mutually exclusive hypotheses: one suggesting host filtering of microbial taxa due to differences in the intestinal environment, and another considering limitations imposed by transmission barriers (i.e., vertical versus horizontal transmission and specific dispersal characteristics) [2, 80–82]. Successful microbial establishment in the gut may also be facilitated by other factors, such as bacteria performing functions critical to host fitness [41]. Moreover, the microbiome-host phylogeny relationship underscores the triangular interaction among host genotype, gut bacteria, and host traits, a connection reinforced by evidence linking host genetics and intestinal physiology to the prevalence of phylogenetically related microbial taxa [53, 56].

Our findings align with these concepts, identifying shared microbial monophyletic clades across target and conspecific vertebrate groups. These phylogenetic patterns suggest that closely related microbial taxa possess inherited traits that facilitate their transmission, colonization, and persistence in specific environments [41, 83, 84]. Such traits may promote a microbial clade conservation through exaptation, environmental filtering, or improved dispersal [41, 83].

The potential pathways for bacterial transmission and establishment in microbial monophyletic clades shared between the target and conspecific vertebrate groups, included descendant clades from ancestral nodes differently conserved within a community, as pointed out by Gaulke and colleagues [41]. Moreover, we observed cladal microorganisms of lower abundance but with functional and ecological importance [85]. Compared to ancient clades (orders and classes), newly formed clades (families) may occur in more hosts than would be expected by chance. They are likely to possess derived traits critical to the microbes' ability to disperse to new hosts and succeed within the gastrointestinal tract [41, 54]. Despite recently formed clades with low abundance sharing *core* genes with abundant clades, promoting functional redundancy, they may also disproportionately contribute to specialized functions that can be triggered under specific environmental conditions, such as pollution degradation and geochemical cycling [86, 87]. Due to their dual roles as a genetic resource reservoir and as a major driver of ecological and functional processes, they are crucial for maintaining host fitness, resilience, and survival [86, 87].

While our findings suggest potential microbial inheritance mediated by host phylogenomics, host social and environmental interactions—particularly livestock animal care practices, stocking density, stress, antibiotics, and nutritional resources [77]—as well as microbial traits such as niche construction, intermicrobial competition, environmental stressor resistance, transmission mechanisms, and influences on host behavior and metabolism, are likely to contribute to microbial distribution [5]. These factors likely work synergistically to establish acquired symbiotic microbes across vertebrates. For example, within the *Firmicutes* phylum, *Clostridia* taxa have been reported as key species in microbial consortia assembly in the chicken caecum [88], human gut [6], swine intestine [6, 89] and bovine rumen [90]. Although these hosts have distinct morphological and physiological gut structures, *Clostridia* commensals possess characteristics that allow interhost or host-environment high migration rates, such as being obligate anaerobic bacteria able to produce resistant spores [91, 92]. These features can contribute to establishing and maintaining prevalence patterns of *Firmicutes*, with biological functions relevant to host fitness (e.g., reproductive years survival, and fertility) underlying these ecological associations [41, 54].

Many spore-forming genera with facilitated interhost propagation and an influential role in the gastrointestinal tract colonization are described for *Firmicutes* [93]. They comprise taxa fundamental to a healthy intestinal

microbiome across vertebrates, including *Oscillospiraceae* representatives (*Clostridium leptum*, *C. scindens*, *C. innocuum*, *Clostridium* XI and XIVa) [22, 94, 95]; members of *Ruminococcaceae* (*Flavonifractor plautii* and *Ruminococcus bromii*) [22, 96]; and *Lachnospiraceae* (*Eubacterium rectale* and *E. elegans*) [22, 97, 98]. The sporulation process creates a source-sink dynamic in gut environments, maintaining ephemeral spore populations replenished through migration between hosts and abiotic substrates [6]. In the gut of birds, pigs and humans, it has been demonstrated that endospore-forming *Firmicutes* are capable of carrying out a complete life cycle in both vegetative cell and spore form [98]. Moreover, a reduced genome and specialized metabolic resources due to the sporulation loss in intestinal *Firmicutes* have favored their successful transmission, with multiple events of colonization and host adaptation, contributing to their evolutionary conservation [14].

Our results demonstrated that host phylogeny explained the KEGG metabolic profile variation in prevalent MAG clades better than the bacterial families. Besides, multivariate homogeneity analysis considering the family as a predictor indicated that the influence over metabolic profile arises from a nonhomogeneous intra-group dispersion. These observations emphasize that bacterial families exploring different host ecosystems possibly have redundancy for some metabolic capacities [99].

Few studies of bacterial dispersal integrate bacterial traits and their transmission mode among hosts [7]. Recent findings show that microbial vertical transmission correlates positively with host specificity: Oxygen-tolerant, spore-forming, and pH-tolerant bacteria tend to be generalists, while those strict anaerobes lacking dispersal traits like spore-forming are more likely to inhabit a single host species [2]. Furthermore, bacterial persistence across hosts is attributable to their ability to resist the host's immune system, evade mechanisms of resident microbiota, and the host's overall ability to establish a commensal relationship [100, 101]. Nevertheless, specific microbial functions that favor high occupancy of persistent taxa in various vertebrates remain unclear [9].

In this study, the MAGs from prevalent bacterial genus and species revealed overlap and differences in metabolism. Indeed, a few host-specific microbial taxa linked with a single or small set of metabolic functions suggest prominent adaptations imposed by the host's intestinal environment [2], whereas cross-associations between prevalent bacterial families and KEGG metabolic pathways point to functional redundancy across certain species, which may contribute to their ubiquity across hosts [41]. Beyond the usual functions required for microbial survival, the metabolic categories most strong and positively correlated with sharing vertebrate taxa contain crucial mechanisms influencing the outcome of host-microbe interactions [15, 102]. These include host-to-host transmission strategies [103], ecosystem-specific capabilities involved in resistance to highly acidic environments [35], adhesion to host cell surfaces [15, 102], breakdown of complex dietary and host structural carbon sources [4, 17, 19], and the production of compounds implicated in host-microbe association [23, 104, 105].

Despite morphological and physiological variations in vertebrate intestines, bacterial communities exhibit generalist characteristics under continuous competition and collaborative efforts [17]. In this complex microbial ecological network, we identify mechanisms of the cellular community, particularly quorum sensing and biofilm formation strategies, that can aid bacterial attachment to the intestinal surface [105, 106]. Sporulation-associated genes, including the main regulator protein for sporulation starting (Spo0A) and signaling protein families, were found across all shared taxa. In addition to facilitating microbial spread from host-to-host, sporulation provides a stress resistance mechanism [16]. The glutamate decarboxylase gene (found in cellular community category), important for bacterial resistance to extremely acidic environments [35], was found exclusively in *Anaerocolumna*, *Herbinix* (both from *Lachnospiraceae*) and *Ruminiclostridium* (*Acetivibrionaceae*). Moreover, we identified fibronectin/fibrinogen-binding proteins (Protein families: genetic information processing category) in all prevalent vertebrate-shared taxa. These proteins facilitate the bacterial aggregation to different gut microbiota members, preferentially those from *Firmicutes*, which may contribute to their successful colonization, predominance and cross-feeding interactions [23].

Enzymes involved in the degradation of host-derived glycans in mucus layers provide a source of nutrients and aiding bacterial cell adhesion and colonization [17]. These glycans, namely glycosaminoglycans (GAGs), are essential components of mammalian extracellular matrix, comprising substances like heparin, chondroitin sulfate, collagen, or hyaluronan [35]. Shared *Firmicutes* here identified had enzymes capable of breaking down GAGs, or at least their disaccharide components. *Herbinix* has the major genes for complete GAGs degradation, except for heparinase, which was only detected in MAGs from the *CAG*-74 family. Unlike prior reports, the majority of MAGs here described have hemagglutinin. The presence of hemagglutinin in symbiotic bacteria highlights their underappreciated role in host cell adherence and colonization, generally linked with cell lysis in pathogenic bacteria [35]. Proteins related to mucin degradation, providing carbon sources and amino acids for bacterial from mucus layer growth [107], are found in all prevalent shared taxa except for *H. celerecrescens* (*Lachnospiraceae*

ID854), *Clostridium* and *Lachnospiraceae* MAGs, where sialidase is likely absent.

Genes in the cellular growth and death category have multiple roles in oxidative stress response and cell regulation, which is critical for linking antioxidant response, redox signaling, and cell cycle based on the environmental context [108]. Lipid metabolism influences microbial physiology, membrane dynamics, and microbe-microbe interactions and inhibits bacterial growth through toxic effects [109, 110]. All vertebrate-shared taxa showed genes associated with resistance to the adverse environment, such as bile acid metabolism assigned to lipid metabolism. Bile acids inhibit microbial colonization by bactericidal action and stimulate germination in spore-forming bacteria [16]. Bacterial capacity of modifying bile acids was reported in *Lachnospiraceae*, *Clostridiaceae* and *Ruminococcaceae* members [16, 111].

Secondary metabolite biosynthesis promotes rapid microbial response in a competitive environment context, leading to collaborative acquisition of metabolic benefits that cannot be acquired individually, promoting the growth and survival of multiple species [104]. This preceding category also includes proteins involved in short-chain fatty acid (SCFA) generation by fermenting dietary and host-derived fibers, supporting the proliferation of fiber-degrading bacteria [112]. Here, the presence of essential enzymes reported for nonstarch polysaccharides digestion [113–117] suggest that *Ruminiclostridium* A, *CAG-74*, *Clostridium*, and *Herbinix celerecrescens* may degrade cellulose and hemicellulose [117]. Together with *Acetivibrionaceae*, *Anaerocolumna* and *Herbinix*, these taxa are potential cooperative pectin degraders [118]. Prevalent taxa also contain members (such as *Ruminiclostridium*, *Acetivibrionaceae*, *Clostridium*, *Anaerecolumna* and *Herbinix*) specialized in the digestion of granules or solubilized starch fragments [113, 115, 119, 120]. Finally, SCFA and other metabolites (e.g., vitamins, lipids, primary bile acid) not only feed other microbial taxa (known as "cross-feeding"), but they also serve as chemical signals to different microbial species and to the host [18].

Altogether, the shared metabolic pathways among prevalent vertebrate-associated *Firmicutes* are crucial for their ability to colonize diverse hosts. These pathways facilitate adaptation to distinct intestinal environments by enabling microbe dispersal between hosts and across gut biogeography via sporulation [16, 121]. They also support the production of key metabolites (e.g., SCFAs and secondary metabolites) that promote both host health and microbial growth, fostering host-microbiome communication [18, 104, 112]. Additionally, mechanisms such as quorum sensing, bile acid metabolism, and GAG degradation enhance resistance to pathogenic invasion [23, 35, 122]. Strategies like fibronectin/fibrinogen-binding, and biofilm formation in combination with quorum sensing and GAG degradation, promote microbial attachment and persistence within the host's intestinal ecosystem [17, 105, 106]. Collectively, these adaptations enable *Firmicutes* to thrive across different vertebrate hosts, ensuring ecological stability and contributing to the functional integrity of the gut microbiome.

On the opposite side of this balanced symbiosis with the host, spore formation in humans, for example, promotes the development of gut-associated lymphoid tissue, which enhances gut immunity by stimulating B cell maturation and IgA secretion, thus improving bacterial tolerance and preventing epithelial leakage [98]. In livestock, spore-forming probiotics have been shown to boost intestinal immunity, inhibit harmful bacteria, and support beneficial microbes, improving growth performance and microbiological status in piglets [123], cattle [124, 125] and chickens [126, 127]. Fibronectin/fibrinogen-binding proteins facilitate bacterial adherence to intestinal niches, optimizing community composition and supporting metabolic interactions, such as butyrate and acetate production in chickens [23, 122].

Additionally, glycosaminoglycan-degrading taxa outcompete pathogens, preventing their colonization in human gut [128] and likely in livestock as well. Genes linked to bile acid metabolism across vertebrate taxa regulate host energy homeostasis, modulate glucose, amino acid and lipid metabolism, and enhance animal carcass quality while reducing susceptibility to infections in both humans and livestock animals [129–132]. Furthermore, taxa capable of degrading cellulose, hemicellulose, and pectin contribute to fiber breakdown, improving feed efficiency and energy harvesting in humans [133], followed by improved growth performance, enhanced health and production in animals [134–136].

In this manner, bacteria in the gastrointestinal tract supply several biological functions that the host lacks. These include increasing nutrient uptake, energy harvest, and carbohydrate metabolism, especially when digesting complex and otherwise inaccessible biological polymers, enhancing digestion and absorption efficiency for the host [137]. They also allow the host to exploit alimentary niches previously intolerable through detoxifying dietary components and preventing oxidative stress [1, 18].

Our study highlighted metabolic mechanisms important to gaining maximal advantage in a competitive environment, along with those essential for *Firmicutes* propagation and survival, as potential key candidates for the maintenance of vertebrate-microbial associations.

Conclusions

Unraveling the potential mechanisms underlying the persistence of specific *Firmicutes* in the vertebrate gut, especially those dominant in a competitive environment,

provides a significant step toward uncovering the mechanisms driving *Firmicutes*-vertebrate and interbacterial associations. Here, we describe bacterial taxa that are evolutionarily shared between food-producing animals and humans. These taxa belong to the bacterial families *Acetivibrionaceae*, *CAG-74*, *Clostridiaceae*, *Lachnospiraceae* and *Ruminococcaceae*. The high prevalence of *Firmicutes* phylum, along with the identified metabolic pathways, supports extrahost survival mechanisms, its transmission to physically or temporally distant hosts, while allowing the recurrent co-association of these taxa and their hosts. Crucial ecosystem functions such as detoxification, resistance to acidic environments, and binding to host cell surfaces are also discussed. Additionally, we analyzed functional categories involved in a network of microbial interactions such as cross-feeding of macro- and micronutrients, production of secondary metabolites and survival to competing microorganisms. Our data contribute to a better understanding of the metabolic mechanisms related to transmission modes, successful colonization, maintenance, and *Firmicutes*-host interactions in known bacterial families and gut microbial members that are poorly characterized.

Methods

Sample collection and animal grouping

This study considered 2,915 metagenome-assembled genomes (MAGs) derived from a Brazilian One-Health-metagenomics study [138], which comprises gut microbiomes samples from 107 healthy individuals, including humans (*Homo sapiens*) ($n = 32$), cattle (*Bos taurus*) ($n = 30$), swines (*Sus scrofa*) ($n = 15$) and poultry (*Gallus gallus*) ($n = 30$). Samples were collected from the five Brazilian geographical regions in triplicates, totaling 321 individual samplings.

The potential effects on the natural intestinal communities caused by domestication and inbreeding processes were investigated using 28 vertebrate gut metagenomic datasets from public databases. This selection aimed to cover a broad spectrum of gut microbiota present in farmed animals and humans, and included: (1) conspecific hosts from different countries (Canada, China, England, Japan, Korea, Netherlands, Scotland and Sweden); (2) different breeds of the farmed hosts; (3) closely-related species [139–145]. The dataset includes 351 samples from 18 species from public studies ("Sheet 1" in Additional file 1: Table S1).

We performed the bioinformatics analyses according to Lemos and colleagues (2022) for the entire dataset to avoid biases in the bioinformatics analysis [138]. We applied a co-assembly strategy according to individual host and geographic location, which included data from public research, using Megahit software with specified parameters [138]. MAGs were reconstructed via Metabat2 with default settings [146]. For subsequent steps, we considered genomes with completeness ≥ 50.0% and contamination ≤ 10.0%, in line with Minimum Information about MAG standards for bacteria and archaea [147] using CheckM software (lineage workflow) [93]. MAGs' taxonomy was assigned using GTDB-Tk v. 1.3.0 (classify_wf workflow) [148]. Downstream analyses were conducted considering four host groups: (i) target (hosts from the Brazilian One Health metagenomics study, such as the farmed animals *B. taurus*, *G. gallu*, *S. scrofa*, and *H. sapiens*) [138], (ii) conspecifics hosts of target group, which are individuals of each target host species from different countries; (iii) breeds specific to each target host and (iv) related species phylogenetically close to each target host, comprising species from the closest phylogenetic vertebrate group with metagenomic studies of its gut microbiota available (detailed below and in "Sheet 1" in Additional file 1: Table S1).

Host phylogenomics

Host evolutionary tree was constructed using complete mitochondrial genome sequences downloaded from the NCBI ("Sheet 2" in Additional file 1: Table S1). mtDNA was chosen due to its little intraspecific variability but sufficient interspecific variation that allows an estimation of degrees of relatedness and divergence times [149]. The Luing breed of *Bos taurus* is not included in this tree due to the absence of its mtDNA in NCBI GenBank.

The mtDNA were aligned with MAFFT v7.123b [150]. A Maximum Likelihood phylogenetic tree was inferred with IQ-TREE v. 2.0.3 [151] using the GTR + G + I nucleotide substitution model with discrete gamma distribution (five categories), selected by the ModelTest algorithm built in IQ-TREE [152]. To root the phylogeny, we used the mtDNA of *Danio rerio* as an outgroup. Branch support was calculated using 1,000 replicate trees generated by ultrafast bootstrap approximation, implemented in IQ-TREE [153]. Divergence time estimates were generated using RelTime in MEGA 11 [154], of which some relative molecular dating among host genus were calibrated as follows: *Sus*/*Potamochoerus*: min 9.7 - max 21.5 MYA; *Sus*/*Bos*: uniform, min 52.0 - max 63.9 MYA; *Sus*/*Homo*: uniform, min 91.5 - max 97.4 MYA; *Homo*/*Pan*: lognormal, mean 1,78, sd 0.085; *Callithrix*/*Homo*: unform, min 40.0 - max 44.2 MYA; *Homo*/*Gallus*: uniform, min 316.0 - max 322.4 MYA; *Meleagris*/*Gallus*: uniform, min 27.9 - max 42.4 MYA. The host phylogenomic tree was visualized with the iTOL web interface [155].

Microbial community analysis

Host gut vertebrate composition was analyzed using taxa with relative abundances > 0.001% to minimize false positives [156]. Unless noted otherwise, the analyses were conducted at the genus bacterial level for its relevance in

conserving microbial traits underscoring growth in the gut environment [157]. The bacterial genus composition diversity within host species was accessed by alpha diversity and richness metrics—Shannon, Chao estimator, and Simpson indices— computed on unfiltered data using the vegan v. 2.6-4 R package [158]. Statistical significance of diversity indices was determined using the Krukal-Wallis test (*kruskal.test* function in R Stats v. 4.3.2 package [159], followed by Dunn's post hoc test (*dunnTest* function in FSA v. 0.9.5 R package [160] or ANOVA ($p < 0.05$; *aov* function in R Stats v. 4.3.2 package [159] with Tukey's post hoc test (*TukeyHSD* function in agricolae R package v. 1.3.0 [161], based on Shapiro-Wilk normality tests (*shapiro.test* function in R Stats v. 4.3.2 package [159]. Stacked barplots of microbial abundance distributions and box plots of alpha diversity metrics were generated using ggplot2 v. 3.5.1 R package [162] with the *ggplot* function.

A centered log-ratio (clr) transformation using *clr_lite* function (with *"unif"* method) in the Microbiome Oriented Compositional Data Toolkit [163] was employed to normalize the microbial abundance data among the hosts [164]. To determine if host taxonomy influences the microbiota beta-diversity, we conducted a multivariate Principal Components Analysis (PCA) using Euclidean distances of CLR-transformed abundances in R Stats v. 4.3.2 [159]. The significance of compositional differences on among-sample Euclidean distances was assessed using permutational multivariate analysis (PERMANOVA) using 999 permutations. The intragroup dispersion homogeneity was checked using *adonis2* and *betadisper* functions from the vegan v. 2.6-4 R package [158, 165]. Factors influencing microbial composition variances may differ across bacterial and host phylogenetic scales [166], so we conducted this analysis with hosts' taxonomy agglomerated into successively higher taxonomic ranks from genus to order and bacterial taxa at the genus and phylum levels. Considering the varied number of samples per host and the asymmetric distribution of microbial species among host groups, we developed an in-house script to perform random subsampling to avoid bias in statistics and correlation values. We also evaluated the robustness of intraspecies variability [6] by generating 100 permutation subsamples, with one randomly selected sample for each host and used a 5% significance level to the hypothesis test.

Ecophylogenetic discovery of prevalent clades

As Linnaean taxonomic classifications may not fully reflect intermediate-level variations in gut microbial communities, bacterial taxa distribution across target and conspecific hosts was analyzed using MAGs abundance and cladal taxonomic units defined by ClaaTU v. 0.1 using default parameters [41, 167]. We used ClaaTU to identify prevalent *Firmicutes* clades among vertebrates, considering a threshold ≥ 50% [85] of individuals per host group. We focused on prevalent known and poorly described bacterial families to discover metabolic traits that support their dominance in vertebrates [41]. To identify significant hereditary clades, we adjusted *p*-values for multiple comparisons using a reasonably permissive false-discovery rate ($q \leq 0.2$) [41, 167] with qvalue v. 2.34.0 R package (using *qvalue* function) [168, 169]. A Venn diagram generated with the ggvenn v. 0.1.9 R program [170] provided an overview of shared and exclusive monophyletic nodes across vertebrates. The ClaaTU microbial dendrogram was visualized and annotated with the iTOL web interface [155].

Relationships between prevalent *Firmicutes* species and metabolic profile

To investigate *Firmicutes*' metabolic influence on their prevalence in hosts, MAGs' open reading frames were predicted using Prodigal v.2.6.3 program (applying the -g 1 -p single options) [171] and ORFs longer than 50 amino acids were functionally annotated using eggNOG-mapper v. 2.0.8 (applying e-value ≤ $1e^{-5}$, identity > 60%, and query/subject coverage > 60%) [172] and the Kyoto Encyclopedia of Genes and Genome Orthology (KEGG) database [173]. The metabolic profiles of prevalent taxa were assessed based on the proportion of genes mapped to KEGG hierarchy level 2, which provides an overview of the MAG role in gut microbiome while remaining functionally specific [174]. The metabolic profile was filtered to functions relevant to the nutritional ecology of mammals and birds [10]. Principal Coordinates Analysis (PCoA) using Bray–Curtis dissimilarity matrices was employed to explore the KEGG metabolic profiles across target and conspecific hosts, using *vegdist* and *cmdscale* functions from the vegan v. 2.6-4 R package [158]. To understand whether host or bacterial taxonomy affects the metabolic profile of prevalent MAGs, we conducted a PERMANOVA analysis on among-sample Bray–Curtis dissimilarity indices using the *adonis2* function in vegan v. 2.6-4 R package [158] with 999 permutations.

To explore the association between prevalent bacterial taxa and their metabolic profiles within target and conspecific hosts, we conducted a Spearman correlation between clr-transformed bacterial abundances and the relative abundances of KEGG metabolism-related genes using the *corr.test* function (with use parameter as "complete" to Spearman method, considering a Benjamini-Hochberg correction with 5% of significance) [168] in psych v. 2.4.3 R program [175]. Spearman's rank correlation coefficients were visualized in a heatmap format using the *pheatmap* function in ComplexHeatmap v. 2.18 R package [176]. Significant correlation coefficients were defined as $|r| > 0.50$ and $p < 0.05$ [177].

KEGG orthology genes were selected to interpret statistically significant correlations by assuming that prevalent monophyletic clades can manifest associations with ecologic traits that drive their apparent ubiquity across hosts. These microbial genes were selected based on their functions associated with different microbiome-host interaction mechanisms [178]. The genes were chosen based on literature evidence that bacteria carrying such genes might interact with the host and influence colonization outcomes of bacterial taxa (detailed gene descriptions in Additional file 11: Table S2).

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42523-025-00379-y.

Supplementary Material 1: Table S1 (xlsx). Detailed information about the data collections. Sheet 1: Number of microbial MAGs (medium and high quality) identified in each host species and grouped according to their respective host phenotype in conspecifics, related and breed hosts. Sheet 2: Hosts mitochondrial genome accession numbers used to construct the estimated phylogenomic tree

Supplementary Material 2: Table S3 (xlsx). Intestinal bacterial community across hosts characterization. Sheet 1: General overview of phyla frequencies (%) across vertebrate hosts. Sheet 2: Frequency (%) of all phyla in vertebrate hosts in each group. Sheet 3: Frequency (%) of phyla in vertebrate hosts from each geographic region. Sheet 4: The exclusively bacterial species found across vertebrate hosts

Supplementary Material 3: Table S4 (xlsx). Pairwise comparisons of alpha-diversity calculated to bacterial communities from host groups (Conspecifics, breed and related-animals), measured by the Chao1, Shannon and Simpson indices

Supplementary Material 4: Fig. S1 (docx). PERMANOVA findings distribution after random subsampling for beta-diversity analysis: (a) microbial community-predictor correlation and (b) adjusted ***p***-value for covariates (host taxonomy and geographic location) explaining variation in bacterial community structure

Supplementary Material 5: Table S5 (xlsx). PERMANOVA analyses for multiple testing factors explaining variation in microbial community structure considering bacterial (a) genus and (b) phylum

Supplementary Material 6: Fig. S2 (docx). Overview of common and exclusive monophyletic nodes among target and conspecific hosts and their conspecifics identified by ClaaTU

Supplementary Material 7: Fig. S3 (docx). Correlation between MAGs from sharing vertebrate clades and KEGG metabolic pathways (at the hierarchy level 2). Spearman's rank correlations were performed with the MAGs' finer taxonomic levels from each prevalent bacterial family to investigate crucial traits for their transmission and colonization among vertebrate guts

Supplementary Material 8: Table S6 (xlsx). Description of monophyletic nodes identified by ClaaTU and their prevalence among hosts. Sheet 1: Node prevalence distribution among host groups established by ClaaTU. Sheet 2: Detailed description of common nodes discovered at the family, genus, and species levels in all host groups belonging to the ***Firmicutes*** phylum with a prevalence equal to or more than 50% as detected by ClaaTU. Sheet 3: MAGs associated to target hosts and their conspecifics considered to ClaaTU analysis. Sheet 4: Detailed quantity of ***Firmicutes*** prevalent nodes found and their taxonomic classification. Sheet 5: MAGs associated to conserved descendant nodes (FDR [***q*** value] < 0.2) belonging to the ***Firmicutes*** phylum with prevalence equal or bigger than 50% identified by ClaaTU

Supplementary Material 9: Table S7 (xlsx). Spearman's rank correlations between prevalent bacterial species and KEGG metabolic pathways. Sheet 1: The Spearman's rank correlations between ***Acetivibrionaceae*** MAGs' finer taxonomic levels and KEGG metabolic pathways (at the hierarchy level 2). Sheet 2: The Spearman's rank correlations between ***CAG***-74 MAGs' finer taxonomic levels and KEGG metabolic pathways (at the hierarchy level 2). Sheet 3: The Spearman's rank correlations between ***Clostridiaceae*** MAGs' finer taxonomic levels and KEGG metabolic pathways (at the hierarchy level 2). Sheet 4: The Spearman's rank correlations between ***Lachnospiraceae*** (ID 755) MAGs' finer taxonomic levels and KEGG metabolic pathways (at the hierarchy level 2). Sheet 5: The Spearman's rank correlations between ***Lachnospiraceae*** (ID 854) MAGs' finer taxonomic levels and KEGG metabolic pathways (at the hierarchy level 2). Sheet 6: The Spearman's rank correlations between ***Ruminococcaceae*** MAGs' finer taxonomic levels and KEGG metabolic pathways (at the hierarchy level 2)

Supplementary Material 10: Table S8 (xlsx). Quantification of KEGG orthology genes involved in host interaction in prevalent shared ***Firmicutes*** taxa. Sheet 1: Total number of KEGG orthology genes related to interaction with the host per bacterial taxa found in at least one ***Acetivibrionaceae*** MAG. Sheet 2: Total number of KEGG orthology genes related to interaction with the host per bacterial taxa found in at least one ***CAG***-74 MAG. Sheet 3: Total number of KEGG orthology genes related to interaction with the host per bacterial taxa found in at least one ***Clostridiaceae*** MAG. Sheet 4: Total number of KEGG orthology genes related to interaction with the host per bacterial taxa found in at least one ***Lachnospiraceae*** (ID 755) MAG. Sheet 5: Total number of KEGG orthology genes related to interaction with the host per bacterial taxa found in at least one ***Lachnospiraceae*** (ID 854) MAG. Sheet 6: Total number of KEGG orthology genes related to interaction with the host per bacterial taxa found in at least one ***Ruminococcaceae*** MAG

Supplementary Material 11: Table S2 (xlsx). List of KO genes associated with different microbiome-host interaction mechanisms that affect bacterial colonization outcome

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Author contributions

B.C.D. formulated the overarching research goals and aims, investigated, analyzed and interpreted the data, and wrote the original manuscript. A.P.L. and V.P.K. contributed to the methodology. D.T.M. contributed to the conceptualization of ideas and the investigation process. Both F.M.C. and A.T.R.V. coordinated and supervised the research activity planning and execution, and helped with data interpretation. A.T.R.V. obtained the financial support for the project leading to this publication. All authors reviewed and edited the manuscript, and approved the final manuscript.

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Data availability
All metagenome-assembled genomes investigated in our study derived from studies publicly available at SRA-NCBI database (http://www.ncbi.nlm.nih.gov/sra). BioProject IDs accessions are presented in "Sheet 1" in Additional file 1: Table S1.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
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Competing interests
The authors declare no competing interests.

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