Systematic evaluation of the gut microbiome of swamp eel (*Monopterus albus*) by 16S rRNA gene sequencing

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Abstract

The contribution of gut microbiome in fish growth and health is being increasingly recognized. However, little was known about the microbial community in the intestine of swamp eel (*Monopterus albus*). Here, we analyzed microbial communities of five distinct gut compartments (foregut content and mucosa, hindgut content and mucosa, and stools) of swamp eel based on high-throughput 16S rRNA gene sequencing. The results showed that the number of observed OTUs decreased from proximal to distal of intestine and samples from different gut compartments showed significant separations. Nevertheless, there were 54 core OTUs shared by all gut compartments and 36 out of 54 core OTUs significantly varied in the abundances in different gut compartments. Furthermore, we discovered 66 compartment-specific enriched KEGG pathways. These compartment-specific enriched microbial taxa (e.g., *Bacillus*, *Lactobacillus*) and potential function capacities (e.g., amino acid metabolism, carbohydrate metabolism) might play vital roles in nutrients metabolism, immune modulation, and host-microbe interactions of swamp eel. This study should provide basic insights into the gut microbiome of swamp eel.

Key words: *Monopterus albus*; 16S rRNA sequencing; microbial taxa; function capacities

Introduction

Swamp eel (*Monopterus albus*) taxonomically belongs to Order Synbranchiformes, Family Synbranchidae, and is an economically important fish species (Li et al., 2017). Due to its great growth performance and rich nutrient content, swamp eel has become a commercially important farmed species in China, and in 2016 the production of swamp eel reached 367,547 tons. Diseases and low feed efficiency are two major factors restricting the development of swamp eel aquaculture (Chen et al., 2015; Xu et al., 2016). Previous studies revealed that the administration of probiotics could reduce disease susceptibility and improve feed efficiency (Hai, 2015; Newaj-Fyzul, Austin, 2015). Probiotics are live microbial feed supplements which can regulate balance of intestinal bacterial community. It suggested that the dysbiosis and homeostasis of gut microbiota might be associated with swamp eel's diseases pathogenesis and food digestion.

Earlier researches on gut microbiota of freshwater and marine fishes had demonstrated that gut

59 microbiota played a crucial role in host nutrients metabolism, growth and health. Wu *et al.*
60 reported that many cellulose-decomposing bacteria, such as *Anoxybacillus*, *Actinomyces*, and
61 *Citrobacter*, harbored in the intestine of grass carp (*Ctenopharyngodon idellus*) (Wu et al., 2012).
62 Pompano (*Trachinotus blochii*) showed high abundance of *Clostridia* which was associated with
63 polysaccharides degradation, when fed with commercial pellet (Rasheeda et al., 2017). Yan *et al.*
64 observed the alpha diversity and the dominant bacterial taxa significantly changed with the
65 development of *Siniperca chuatsi (Yan et al., 2016)*. Small *et.al* revealed that interactions
66 between threespine stickleback (*Gasterosteus aculeatus*) and gut microbiota play a key role in the
67 development of gut innate immunity (Small et al., 2017). What's more, gut microbial
68 communities in the different gut compartments exhibited distinct differences in diversity and
69 richness. Ye observed significantly higher alpha-diversity indices in the foregut than the hindgut
70 in both Asian silver carp and gizzard shad(Ye et al., 2014). In salmon, microbial richness was
71 greater in the digesta than in the mucosa, however, in the rabbitfish (*Siganus fuscescens*), the
72 microbial richness significantly increased from content compartment to mucosal compartment
73 (Gajardo et al., 2016; Nielsen et al., 2017). Since gut microbiome are complex and dynamic
74 communities which have profound influences on fishes, it is important to systematically
75 characterize the bacterial communities in different gut compartments. However, to the best of our
76 knowledge, there is few study about the gut microbiome of swamp eel.
77 The main objective of this study was to investigate gut microbial structures, compositions, and
78 function capacities of different gut compartments of swamp eel using 16S rRNA gene
79 sequencing. We wondered whether the different structural and functional characteristics of gut
80 microbial community in different compartments were correlated with swamp eel's nutrients
81 metabolism, immune modulation, and host-microbe interactions. This study would provide the
82 first glimpse of gut microbiome of swamp eel.
83

84 **Methods**

85 **Sample collection**

86 Swamp eel individuals were sampled from different net cages of a commercial swamp eel farm,
87 and then acclimated in dechlorinated tap water and fed the same surimi diet in the same 10 L

aquarium tanks for 8 weeks until dissection. Fecal samples were collected immediately and separately before euthanasia. Four individuals were anesthetized with tricaine methanesulfonate and the whole intestine were aseptically removed from the abdominal cavity. The intestine was further dissected using sterile instruments to separate the foregut (immediately after the stomach) and the hindgut (immediately before the anus) sections. The contents in each gut section were squeezed out and collected separately. The proximal and distal sections of the intestine were then washed with sterile PBS three times to remove remnants of the gut content. All procedures for handling and euthanasia of swamp eel were approved by Animal Care and Use Committee of Jangxi Agricultural University.

DNA extraction and 16S rRNA gene sequencing

Total DNA was extracted from gut content and gut mucosa using the PowerSoil® DNA Isolation Kit (Mo Bio, San Diego, CA, USA) according to the manufacturer's instruction. Fecal DNA extraction was performed using the QIAamp Stool Mini Kit (QIAGEN, Germany). The barcoded fusion forward primer 338F (5'-ACTCCTACGGGAGGCAGCA-3') and the reverse primer 806R (5'-GGACTACHVGGGTWTCTAAT-3') were used to amplify the V3-V4 hyper variable region of the 16S rRNA gene. The Barcoded V3-V4 amplicons were sequenced using the paired-end method on Illumina MiSeq platform (Illumina, USA) following the standard protocols.

16S rRNA gene sequencing data analysis

The raw sequencing data were removed the barcodes and low quality sequences to obtain the clean data using FASTX-Toolkit. FLASH software was used to merge high-quality paired-end reads into tags (Magoc, Salzberg, 2011). Operational Taxonomic Unit (OTU) picking was performed using the USEARCH pipeline with a 97% sequence identity (Edgar, 2010). We performed taxonomic assignments for the aligned sequences using the Ribosomal Database Project (RDP) classifier program with 80% confidence threshold (Wang et al., 2007). Microbial taxa abundance and diversity indices were generated using Quantitative Insights Into Microbial Ecology (QIIME) (Caporaso et al., 2010). Phylogenetic investigation of communities by reconstruction of unobserved states (PICRUSt) was used to predict the functional profile of the microbial community (Yang et al., 2017). We extracted the closed reference OTU table from quality control reads in QIIME against the Greengenes database. OTU normalization, gene

family abundances prediction, and function categorization based on KEGG (Kyoto Encyclopedia of Genes and Genomes) pathway was performed by PICRUSt according to the default settings.

Statistical analysis

Microbial species richness was analyzed using the observed number of OTUs. Principal Coordinate Analysis (PCoA) of the beta diversity was performed based on the unweighted distance matrix (Donaldson et al., 2016). Permutation multivariate analysis of variance (PERMANOVA) was performed to identify compartment specific enriched microbial taxa and functional capacities (Nielsen, Wilkes Walburn, Verges, Thomas, Egan, 2017). The output results were visualized using ggplot2 and gplots in R package except the Venn diagrams which were drawn using the online tool (bioinformatics.psb.ugent.be/webtools/Venn/).

Results

Both data sets are accessible through NCBI's SRA, under study accession number SRP [145040].

Microbial diversities and compositions in different gut compartments

At first, 405, 642, 227, 372 and 171 OTUs were found presented in the foregut content, foregut mucosa, hindgut content, hindgut mucosa, and stools, respectively (Figure 1). Then, we identified specific and common OTUs in different compartments via a Venn diagram. 63 common OTUs were detected among foregut content, hindgut content, and stools. 315 OTUs were shared by both the foregut mucosa and hindgut mucosa. Importantly, we found 54 common OTUs as a core microbiota presented in all intestinal compartments, while 53, 254, 5, 16 and 37 specific OTUs were also detected for foregut content, foregut mucosa, hindgut content, hindgut mucosa, and stools, respectively. What's more, PCoA analysis also revealed significant separations among samples from different gut compartments (Figure 2).

To further uncover characteristics of microbial compositions in different gut compartments, relative abundances of OTUs assigned for the phylum level and the genus level were analyzed (Figure 3). At phylum level, *Firmicutes*, *Fusobacteria*, *Proteobacteria*, *Bacteroidetes*, and *Actinobacteria* were the five most dominant phyla. At genus level, *Cetobacterium*, *Ralstonia*, and *Rhodococcus* were the most predominant genera. Interestingly, the abundances of these microbial taxa changed significantly among different gut compartments. For instances, *Firmicutes* occupied

a large proportion of the gut microbiota in both foregut and hindgut regardless of the locations sample obtained, but it only occupied a small proportion of the gut microbiota in stools samples. *Fusobacteria* accounted for a higher proportion of gut microbiota in the content compartment than in the mucosal compartment. *Cetobacterium* was predominant in all samples, but a lower abundance in the foregut was observed when compared to the hindgut and stools. In contrast, the abundance of *Rhodococcus* in foregut was higher than that in hindgut and stools.

Core microbial taxa enriched in different gut compartments

To identify the differential enrichment of the core microbial taxa in specific gut compartment, we analyzed the abundance of the 54 core OTUs across all compartments. As shown in Figure 4, total 36 compartment-specific enriched OTUs were observed. In the foregut content, seven enriched OTUs were annotated to *Enhydrobacter*, *Comamonadaceae*, *Caulobacteraceae*, *Microbacteriaceae*, *Peptostreptococcaceae*, *Bradyrhizobium*, and *Deinococcus*, respectively. Meanwhile, OTUs annotated to each of *Roseburia*, *S24-7*, *Bacillus*, *Acidobacteria*, *Paracoccus*, *Lactococcus*, and *Oxalobacteraceae* were enriched in the foregut mucosa. On the other hand, OTUs enriched in the hindgut content were annotated to *Cetobacterium somerae*, *Arthrobacter*, *Coprococcus*, *Bacteroidaceae*, *Ruminococcaceae*, *Epulopiscium*, and *Citrobacter*. OTUs annotated to *Clostridium*, *Pseudomonas*, *Rhodococcus*, *Ralstonia*, *Achromobacter*, *Streptococcus*, and *Lactobacillus* showed great abundance in the hindgut mucosa. Besides, 8 OTUs derived from *Chryseobacterium*, *Comamonas*, *Serratia*, *Acinetobacter johnsonii*, *Pedobacter*, *Plesiomonas shigelloides*, *Pseudoxanthomonas Mexicana*, and *Aeromonadaceae* increased in abundance in the stools samples.

Comparison of microbial potential capacities in different gut compartments

To compare the potential functional capacity of microbial community in different gut compartments, the relative abundances of KEGG pathways were predicted by PICRUSt. The results showed that 66 KEGG pathways exhibited significant differences in abundances across different gut compartments (Figure 5). Among these, 26 pathways from the foregut samples, 28 pathways from the hindgut samples, and 12 pathways from stools samples. Notably, we found some characteristics of the distribution of differential pathways in specific gut compartment. For example, amino acid metabolism pathways such as lysine degradation, arginine and proline

metabolism, and valine, leucine and isoleucine degradation were predominant in the foregut content. Cofactor and vitamins metabolism and signal transduction related pathways were overrepresented in the foregut mucosa. In the hindgut, carbohydrate and lipid metabolism pathways were prominent in the content, while bacterial replication, transcription, and translation related pathways were outstanding in the mucosa. What's more, we observed that microbial community was more capable of metabolizing secondary metabolites and xenobiotics in the stools.

Discussion

In this study, 16S rRNA sequencing analysis revealed the diversity, composition, and potential functional capacity of microbial community across different gut compartments in swamp eel. To our best knowledge, this is the first study systematically evaluating the gut microbiome of swamp eel (*Monopterus albus*).

It was found that the number of observed OTUs decreased from the proximal section to the distal section of intestine in swamp eel. This result was different from many vertebrate microbiome studies which revealed that the distal section of intestine had higher richness and diversity than the proximal section. This difference might be associated with the specific physiological structure of the intestine in swamp eel. Swamp eel's intestine is short and straight, however, many other freshwater-cultured fishes and mammals have long and coiled intestines (He et al., 2017; Steinert et al., 2013; Tan et al., 2018; Tok et al., 2011). Due to this special physiological structure, nutrients metabolism in swamp eel's intestine is faster than other freshwater-cultured fishes (Zhou, Qin, 2007). Considering the crucial role of gut microbiota in host nutrients metabolism, we speculated that much more microbes inhabitation in the proximal section of swamp eel's intestine should benefit to host fast digestion and absorption of nutrients. Furthermore, much more OTUs presented in the mucosal compartment than the content compartment regardless of the locations that samples obtained. This result was consistent with gut microbiome studies in rabbitfish (*Siganus fuscescens*) and loach (Nielsen et al., 2017; Yanget al., 2017) and reinforced the previous findings that the intestinal mucosa might serve as a reservoir of diverse bacterial species (Lu et al., 2014). OTUs assigned for the phylum level and

genus level further revealed some specific features of microbial compositions of swamp eel. Previous study demonstrated that the high abundance of *Firmicutes* was observed in the gut microbiome of omnivorous fishes and *Fusobacteria* was the predominant phylum in the gut microbiome of carnivorous fishes (Liu et al., 2016). Here, the microbial communities of swamp eel were dominated by *Firmicutes*, *Fusobacteria*, *Proteobacteria*, *Bacteroidetes*, and *Actinobacteria*. It implied that gut microbial composition of swamp eel may be associated with its varied feeding habits. What's more, we found that *Firmicutes* was more predominant in the foregut and hindgut than the stools, while the abundance of *Fusobacteria* was higher in the content compartment than the mucosal compartment. The most dominant genus *Cetobacterium* and *Rhodococcus* also varied in the abundances across different gut compartments. These results suggested that using samples from single gut compartment to represent an overview of gut microbiota would likely fail to detect community variation responding to physiological variations of the gut (Durban et al., 2011).

Although the gut microbiota showed distinct spatial heterogeneity, we still identified a core microbiota consisting of 54 common OTUs in all gut compartment. It was in line with previous fishes gut microbiome studies indicating that specific microbial taxa could form a stable core microbota in the intestine (Baldo et al., 2015; Rudi et al., 2018). Furthermore, we found that the enrichments of these microbial taxa were associated with nutrients metabolism, immune modulation, and habitat adaptions. In the content compartment, most of the enriched microbial taxa were associated with nutrients metabolism. For example, dietary fiber degradation associated bacteria *Enhydrobacter* and *Comamonadaceae* and amino acid metabolism associated bacteria *Comamonadaceae* and *Microbacteriaceae* were enriched in the foregut content (Premalatha et al., 2015; Sakurai et al., 2017; Yin et al., 2017). Gut microbial taxa equipped with multiple carbohydrate active enzymes such as *Bacteroidaceae*, *Ruminococcaceae*, *Coprococcus*, and *Citrobacter* which involved in non-digestible dietary carbohydrates metabolism showed great abundance in the hindgut content (Luo et al., 2017; Tap et al., 2015; Wu et al., 2012). Notably, *Cetobacterium somerae* as a vitamin B-12 and antimicrobial metabolites producing species had a higher abundance in the hindgut content. It was in agreement with the results from many fishes gut microbiota studies (Bledsoe et al., 2016; Larsen et al., 2014). Interestingly, stools samples as

an end product of nutrients metabolism in the content compartment, several potential aquatic pathogenic bacteria were enriched including *Serratia*, *Acinetobacter johnsonii*, *Plesiomonas shigelloides*, and *Aeromonadaceae (Gonzalez et al., 2000; Martins et al., 2013; Nadirah et al., 2012; Sheikhlar et al., 2017)*. However, they did not cause any infections or diseases in our feeding swamp eels. It indicated that they were native inhabitants of swamp eel's stools. Meanwhile, many immune modulation associated bacteria were found inhabiting in the mucosal compartment. For instance, *S24-7* modulated mucosal immune homeostasis, *Roseburia* regulated innate immunity, and potential probiotics including *Bacillus*, *Acidobacteria*, and *Lactococcus* were predominant in the foregut mucosa (Bernardeau et al., 2017; Liu et al., 2017; Lv et al., 2016; Patterson et al., 2017; Wu et al., 2018). *Clostridium* and *Lactobacillus* involved in immune response, *Pseudomonas* and *Achromobacter* had strong antimicrobial activities, and *Rhodococcus* showed properties of probiotic were overrepresented in the hindgut mucosa (Nayak, 2010; Sharifuzzaman et al., 2017; Zothanpuia et al., 2016). Besides, it was noteworthy that the distributions of compartment-specific enriched microbial taxa also reflected their adaptions to habitat, particularly to the oxygen concentration. Aerobic bacteria *Bradyrhizobium*, *Deinococcus*, *Arthrobacter*, and *Comamonas* preferred to thrive in the content compartment. Anaerobes and obligate anaerobes such as *Paracoccus*, *Ralstonia* and *Streptococcus* were more prevalent in the mucosal compartment.

The potential functional capacities of microbial communities were distinctly different across different gut compartments and these differential microbial functional capacities should be related to host physiological functions and host-microbes interactions. Amino acid metabolism pathways were more abundant in the foregut content. It was correlated with foregut as a major segment for amino acid metabolism and suggested that gut microbiota in the foregut content might help swamp eel to digest dietary amino acids (Oliva-Teles, 2012). Cofactors and vitamins metabolism and cellular signals processing pathways were enriched in the foregut mucosa. Since fishes lack the biosynthetic capacity for most vitamins, vitamins produced by gut microbiota will play a key role in host growth, intestinal mucosal immune and signaling molecules expression (Feng et al., 2016; Li et al., 2015). In the hindgut content, a high level of carbohydrate and lipid metabolism was identified. It was in line with previous studies that gut microbiome of fish

hindgut fermented dietary non-digestible polysaccharides to short-chain fatty acids (SCFAs) (Geraylou et al., 2013; Mountfort et al., 2002). In the hindgut mucosa, microbial replications, transcriptions and translations related pathways were concentrated and this was in consistent with that hindgut mucosa was an essential gut region where interactions between gut microbiota and host cells happened (Morgan et al., 2015; Sellers, Morton, 2014). Intriguingly, we observed that microbial xenobiotics and secondary metabolites metabolism pathways were more predominant in the stools samples. This result and the enriched microbial taxa in stools above indicated that stools may service as a "wastes dump" of swamp eel and microbial community.

Conclusions

In the present study, we comprehensively characterized the microbial communities in different gut compartments of swamp eel. Our results showed that the microbial diversity, composition, and function capacity were varied substantially in longitudinal and radial parts of the intestine. The microbial diversity and composition across different gut compartments could reflect the characteristics of swamp eel's intestine structures and feeding habit. The gut compartment-specific enriched core microbial taxa and function capacities may exert an important role in swamp eel's nutrients metabolism, immune modulation, and host-microbe interactions. Taken together, these results should provide a basis for further research on gut microbiome of swamp eel.

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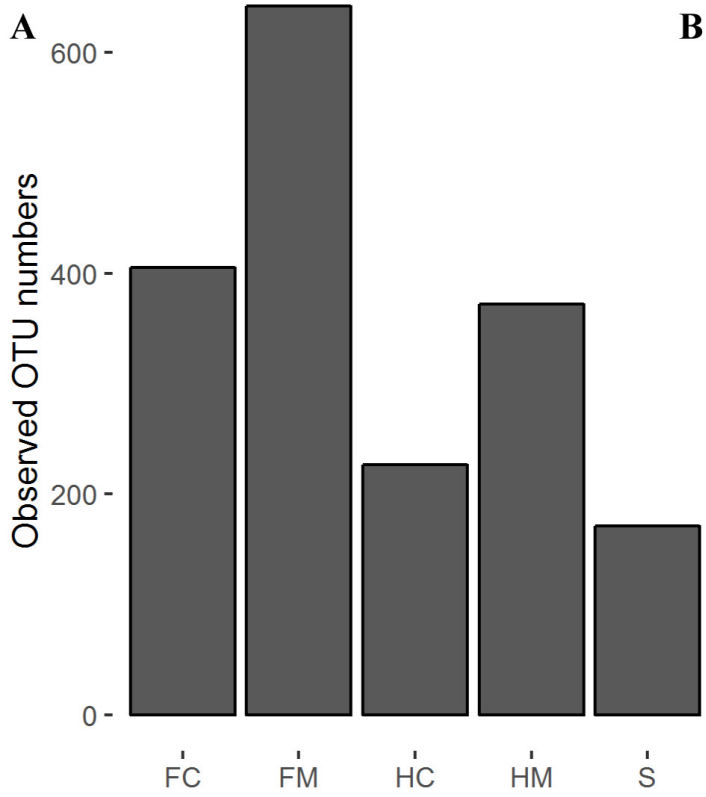
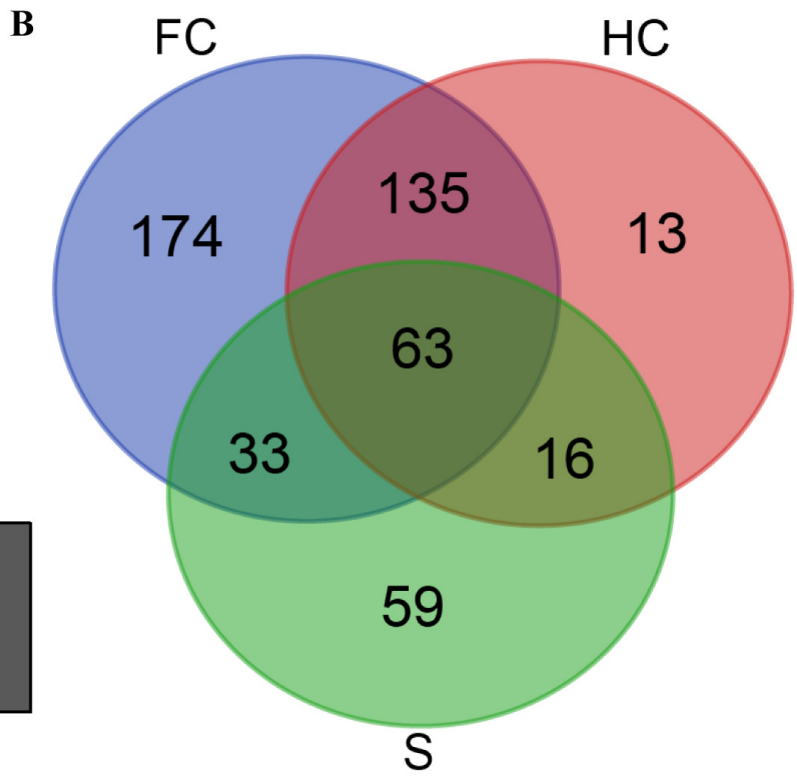
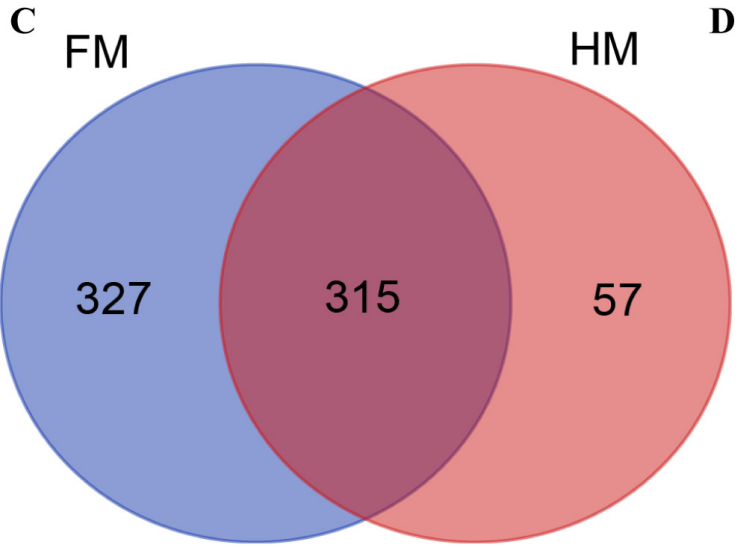
Figure 1(on next page)

The observed OTU numbers, unique and shared OTUs in different gut compartments.

(A) Bar plot shows the observed OTU numbers in foregut content (FC), foregut mucosa (FM), hindgut content (HC), hindgut mucosa (HM), and stools (S). (B) Venn diagram displays the number of shared and unique OTUs among foregut content (FC), hindgut content (HC), and stools (S). (C) Venn diagram displays the number of shared and unique OTUs between foregut mucosa (FM) and hindgut mucosa (HM). (D) Venn diagram displays the number of core OTUs shared by all gut compartments.


A
600
400
200
0
Observed OTU numbers
FC
FM
HC
HM
S


B
FC
HC
174
135
13
63
33
16
59
S


C
FM
HM
327
315
57

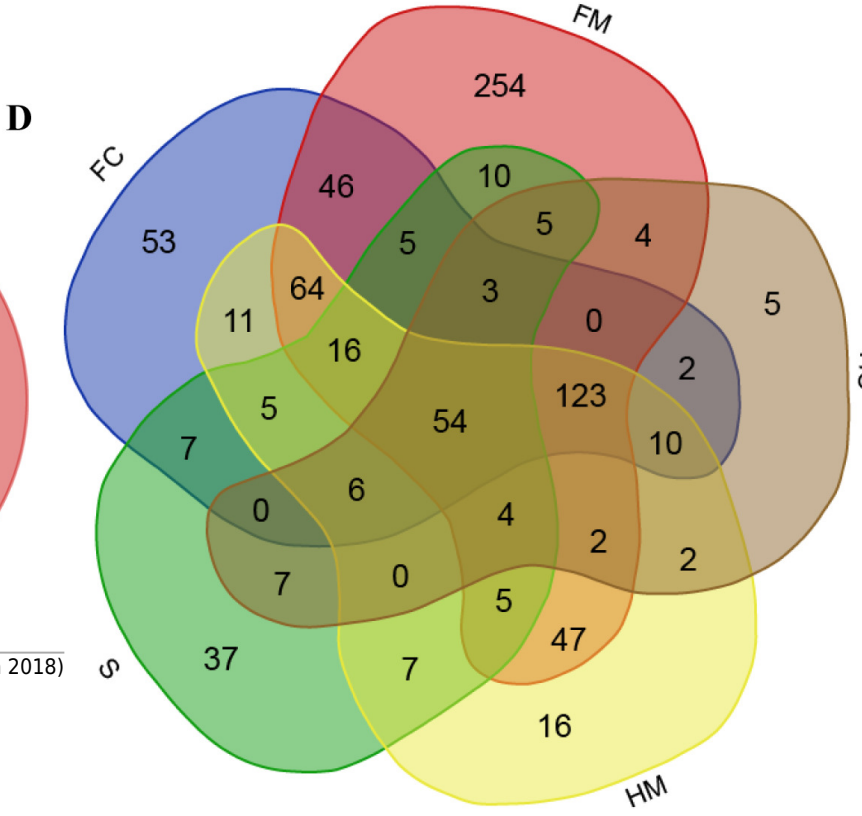

D
FM
254
FC
53
46
10
5
4
64
3
5
11
0
16
2
HC
5
123
54
10
7
6
0
4
2
2
7
0
5
47
37
7
16
S
HM

Figure 2(on next page)

Principal Coordinate Analysis (PCoA) of microbial community in different gut compartments based on the Unweighted UniFrac distance matrix.

The individual samples are color- and shape-coordinated according to the gut compartment. FC : foregut content, FM: foregut compartment, HC: hindgut content , HM: hindgut mucosa, S: stools.

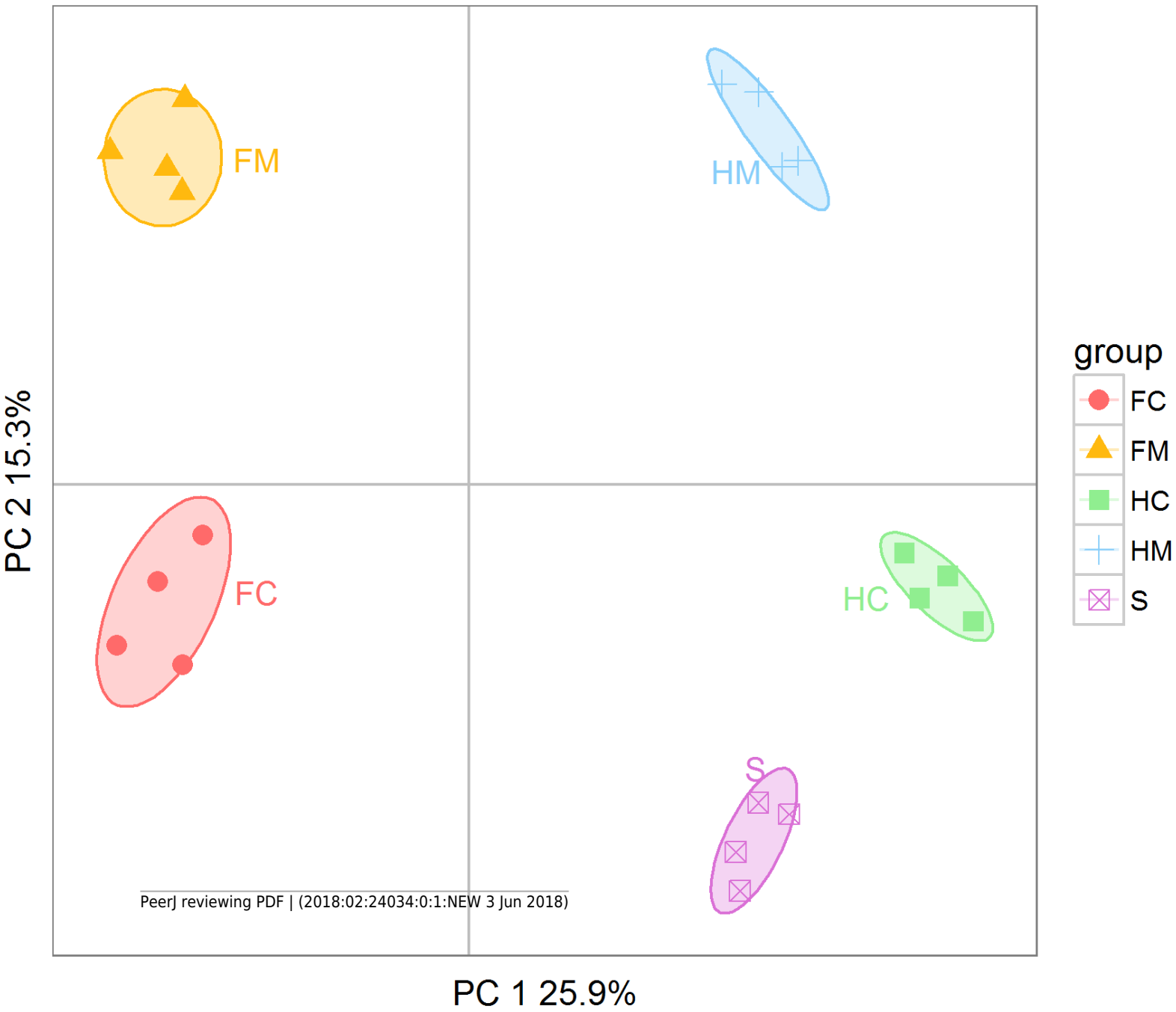

FM
HM
FC
HC
S
group
FC
FM
HC
HM
S
PC 2 15.3%
PC 1 25.9%

Figure 3(on next page)

Gut microbial compositions at the phylum level and genus level.

(A) Each bar represents average relative abundance of each phylum of gut microbiota in foregut content (FC), foregut mucosa (FM), hindgut content (HC), hindgut mucosa (HM), and stools (S). (B) Each bar represents average relative abundance of each genra of gut microbiota in foregut content (FC), foregut mucosa (FM), hindgut content (HC), hindgut mucosa (HM), and stools (S). t

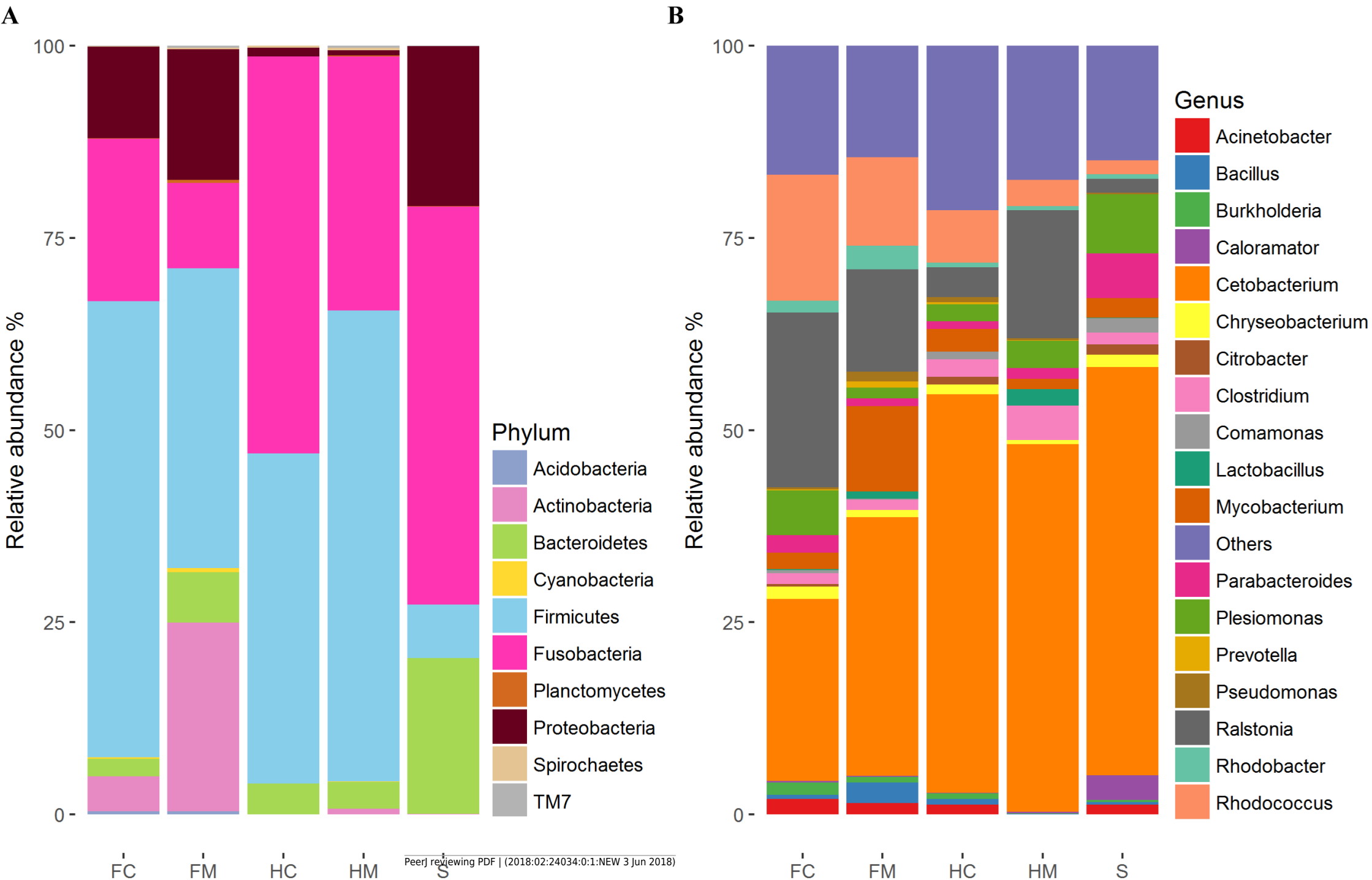

A
B
100
75
50
25
0
Relative abundance %
FC
FM
HC
HM
S
Phylum
Acidobacteria
Actinobacteria
Bacteroidetes
Cyanobacteria
Firmicutes
Fusobacteria
Planctomycetes
Proteobacteria
Spirochaetes
TM7
Genus
Acinetobacter
Bacillus
Burkholderia
Caloramator
Cetobacterium
Chryseobacterium
Citrobacter
Clostridium
Comamonas
Lactobacillus
Mycobacterium
Others
Parabacteroides
Plesiomonas
Prevotella
Pseudomonas
Ralstonia
Rhodobacter
Rhodococcus

Figure 4(on next page)

Gut compartment-specific enriched core OTUs.

Heat map shows core OTUs significantly varied in abundances in different gut compartments (cell note on the heat map represents differentially abundant OTUs annotated to microbial taxa).

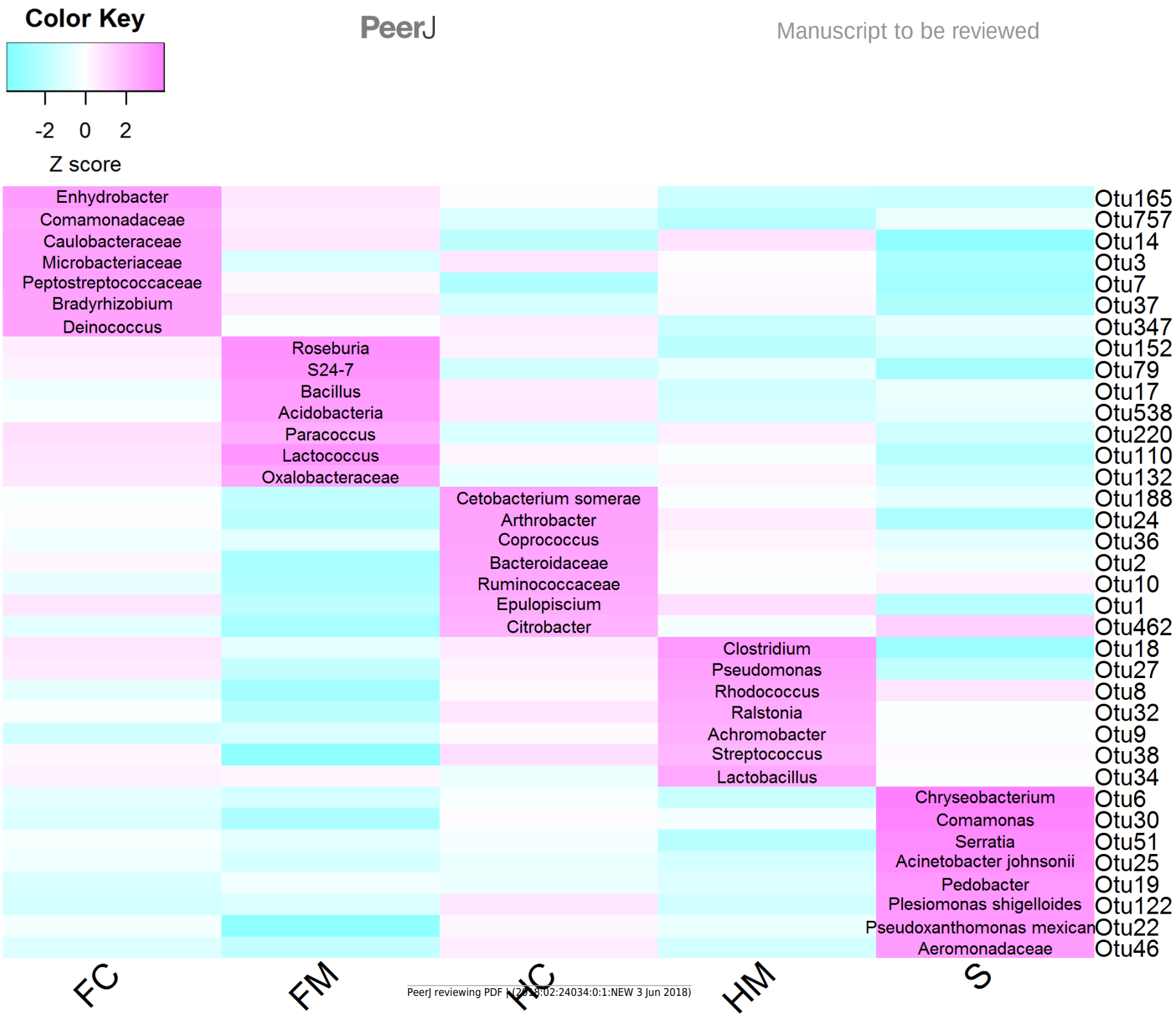
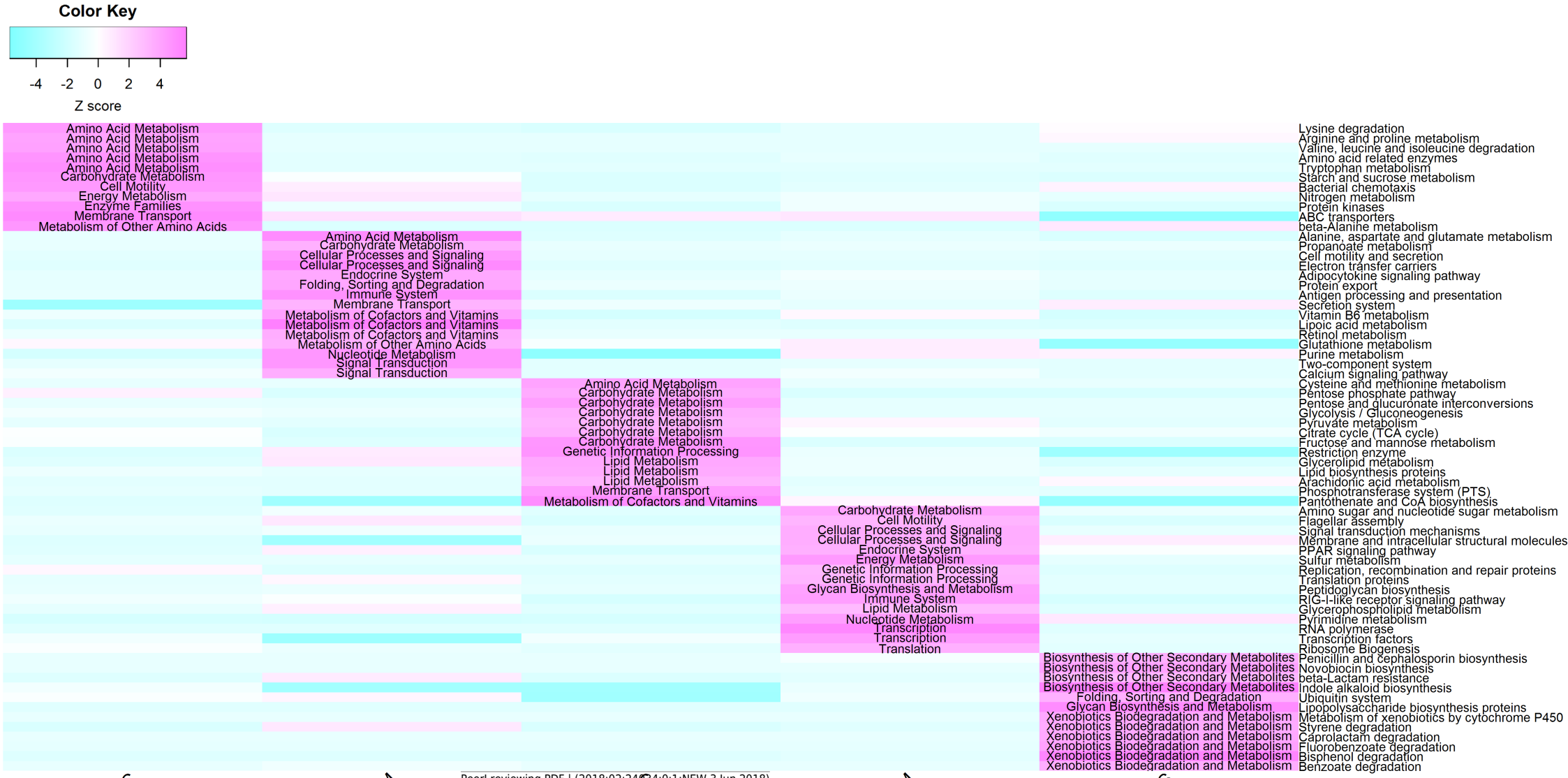

Color Key
-2
0
2
Z score
Enhydrobacter
Comamonadaceae
Caulobacteraceae
Microbacteriaceae
Peptostreptococcaceae
Bradyrhizobium
Deinococcus
Roseburia
S24-7
Bacillus
Acidobacteria
Paracoccus
Lactococcus
Oxalobacteraceae
Cetobacterium somerae
Arthrobacter
Coprococcus
Bacteroidaceae
Ruminococcaceae
Epulopiscium
Citrobacter
Clostridium
Pseudomonas
Rhodococcus
Ralstonia
Achromobacter
Streptococcus
Lactobacillus
Chryseobacterium
Comamonas
Serratia
Acinetobacter johnsonii
Pedobacter
Plesiomonas shigelloides
Pseudoxanthomonas mexican
Aeromonadaceae
Otu165
Otu757
Otu14
Otu3
Otu7
Otu37
Otu347
Otu152
Otu79
Otu17
Otu538
Otu220
Otu110
Otu132
Otu188
Otu24
Otu36
Otu2
Otu10
Otu1
Otu462
Otu18
Otu27
Otu8
Otu32
Otu9
Otu38
Otu34
Otu6
Otu30
Otu51
Otu25
Otu19
Otu122
Otu22
Otu46
FC
FM
HC
HM
S

Figure 5(on next page)

Comparison in the abundance of gut microbial potential function capacities in different gut compartments.

Heat map shows the abundances of gut microbial KEGG pathways (level 3) significantly changed in different gut compartments (cell note on the heat map represents differentially abundant KEGG pathways at level 2).


Color Key
-4
-2
0
2
4
Z score
Amino Acid Metabolism
Amino Acid Metabolism
Amino Acid Metabolism
Amino Acid Metabolism
Amino Acid Metabolism
Carbohydrate Metabolism
Cell Motility
Energy Metabolism
Enzyme Families
Membrane Transport
Metabolism of Other Amino Acids
Amino Acid Metabolism
Carbohydrate Metabolism
Cellular Processes and Signaling
Cellular Processes and Signaling
Endocrine System
Folding, Sorting and Degradation
Immune System
Membrane Transport
Metabolism of Cofactors and Vitamins
Metabolism of Cofactors and Vitamins
Metabolism of Cofactors and Vitamins
Metabolism of Other Amino Acids
Nucleotide Metabolism
Signal Transduction
Signal Transduction
Amino Acid Metabolism
Carbohydrate Metabolism
Carbohydrate Metabolism
Carbohydrate Metabolism
Carbohydrate Metabolism
Carbohydrate Metabolism
Carbohydrate Metabolism
Genetic Information Processing
Lipid Metabolism
Lipid Metabolism
Lipid Metabolism
Membrane Transport
Metabolism of Cofactors and Vitamins
Carbohydrate Metabolism
Cell Motility
Cellular Processes and Signaling
Cellular Processes and Signaling
Endocrine System
Energy Metabolism
Genetic Information Processing
Genetic Information Processing
Glycan Biosynthesis and Metabolism
Immune System
Lipid Metabolism
Nucleotide Metabolism
Transcription
Transcription
Translation
Biosynthesis of Other Secondary Metabolites
Biosynthesis of Other Secondary Metabolites
Biosynthesis of Other Secondary Metabolites
Biosynthesis of Other Secondary Metabolites
Folding, Sorting and Degradation
Glycan Biosynthesis and Metabolism
Xenobiotics Biodegradation and Metabolism
Xenobiotics Biodegradation and Metabolism
Xenobiotics Biodegradation and Metabolism
Xenobiotics Biodegradation and Metabolism
Xenobiotics Biodegradation and Metabolism
Xenobiotics Biodegradation and Metabolism
Lysine degradation
Arginine and proline metabolism
Valine, leucine and isoleucine degradation
Amino acid related enzymes
Tryptophan metabolism
Starch and sucrose metabolism
Bacterial chemotaxis
Nitrogen metabolism
Protein kinases
ABC transporters
beta-Alanine metabolism
Alanine, aspartate and glutamate metabolism
Propanoate metabolism
Cell motility and secretion
Electron transfer carriers
Adipocytokine signaling pathway
Protein export
Antigen processing and presentation
Secretion system
Vitamin B6 metabolism
Lipoic acid metabolism
Retinol metabolism
Glutathione metabolism
Purine metabolism
Two-component system
Calcium signaling pathway
Cysteine and methionine metabolism
Pentose phosphate pathway
Pentose and glucuronate interconversions
Glycolysis / Gluconeogenesis
Pyruvate metabolism
Citrate cycle (TCA cycle)
Fructose and mannose metabolism
Restriction enzyme
Glycerolipid metabolism
Lipid biosynthesis proteins
Arachidonic acid metabolism
Phosphotransferase system (PTS)
Pantothenate and CoA biosynthesis
Amino sugar and nucleotide sugar metabolism
Flagellar assembly
Signal transduction mechanisms
Membrane and intracellular structural molecules
PPAR signaling pathway
Sulfur metabolism
Replication, recombination and repair proteins
Translation proteins
Peptidoglycan biosynthesis
RIG-I-like receptor signaling pathway
Glycerophospholipid metabolism
Pyrimidine metabolism
RNA polymerase
Transcription factors
Ribosome Biogenesis
Penicillin and cephalosporin biosynthesis
Novobiocin biosynthesis
beta-Lactam resistance
Indole alkaloid biosynthesis
Ubiquitin system
Lipopolysaccharide biosynthesis proteins
Metabolism of xenobiotics by cytochrome P450
Styrene degradation
Caprolactam degradation
Fluorobenzoate degradation
Bisphenol degradation
Benzoate degradation
FC
FM
HC
HM
S