



Cross-tissue multi-omics analyses reveal the gut microbiota's absence impacts organ morphology, immune homeostasis, bile acid and lipid metabolism.

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Introduction

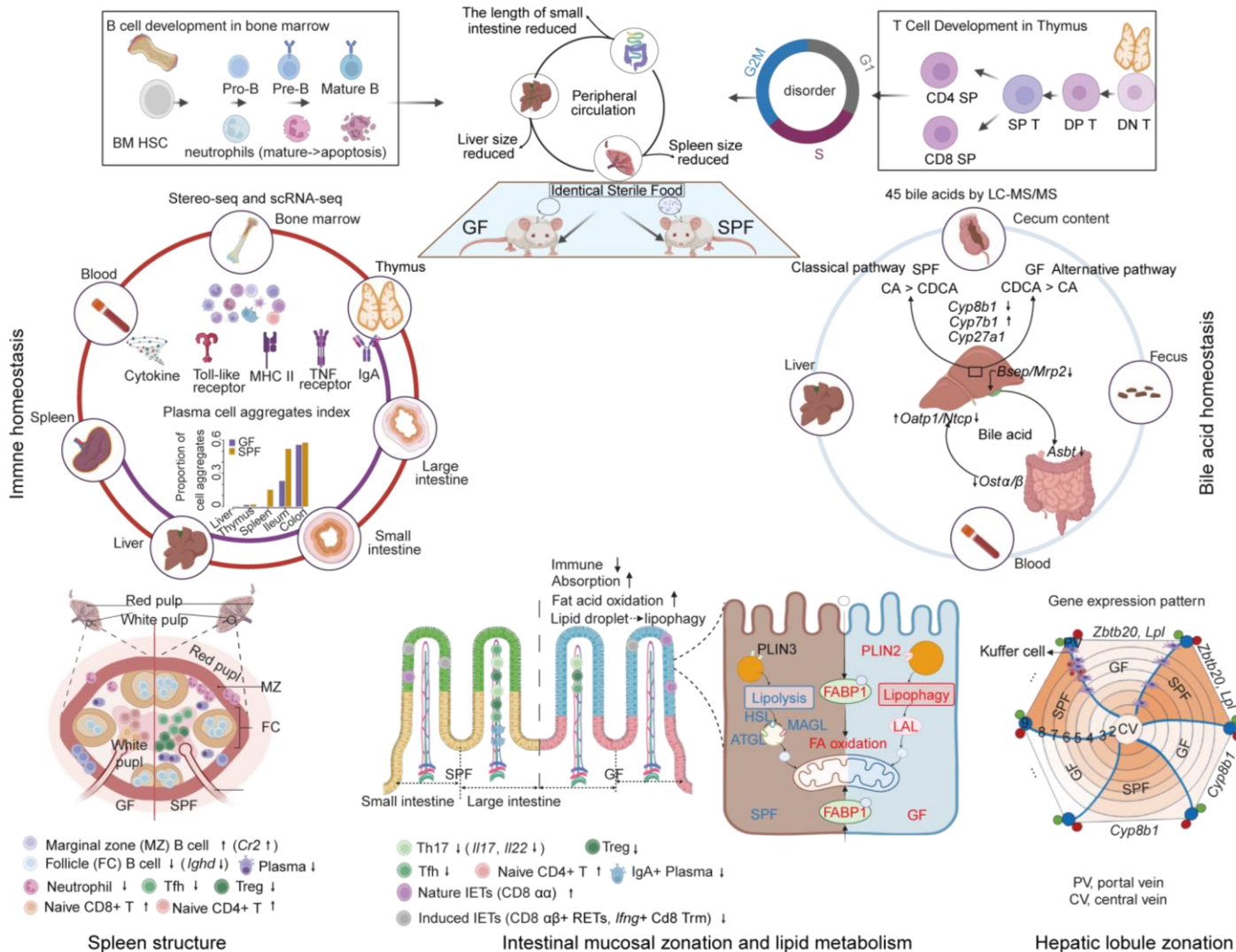
| Test item | Physiological-Biochemical index | Abbreviation | GF | | | SPF | | | p |
|---|----------------------------------|---------------------|-------------------|-------------------------|----------------------------|-------------------------|-------------------------|----------------------------|--------------------------|
| | | | n | Mean ± SD | Median (Min, Max) | n | Mean ± SD | Median (Min, Max) | |
| Hepatic function test | Alanine aminotransferase | ALT (U/L) | 11 | 28.80 ± 10.10 | 28.80 (12.00, 50.40) | 10 | 28.11 ± 18.89 | 17.50 (12.10, 61.50) | 0.917 |
| | Aspartate aminotransferase | AST (U/L) | 11 | 129.55 ± 27.05 | 136.80 (90.90, 163.60) | 10 | 140.36 ± 78.09 | 106.80 (66.60, 279.30) | 0.686 |
| | Alkaline phosphatase | ALP (U/L) | 11 | 109.02 ± 21.07 | 111.90 (63.68, 134.70) | 10 | 101.99 ± 19.54 | 97.05 (76.50, 137.66) | 0.439 |
| | γ-glutamyl transpeptidase | GGT (U/L) | 11 | 2.23 ± 1.52 | 2.00 (0.30, 4.50) | 10 | 5.90 ± 3.26 | 4.90 (1.60, 12.80) | 0.007 |
| | Total protein | TP (g/L) | 11 | 58.45 ± 5.47 | 57.60 (48.90, 66.90) | 10 | 54.94 ± 13.81 | 55.60 (28.60, 74.40) | 0.468 |
| | Albumin | ALB (g/L) | 11 | 24.90 ± 2.09 | 25.20 (21.60, 27.60) | 10 | 23.40 ± 3.46 | 23.20 (17.60, 28.20) | 0.239 |
| | Total bilirubin | TBIL (umol/L) | 11 | 2.10 ± 0.48 | 2.10 (1.50, 2.93) | 10 | 2.38 ± 0.70 | 2.40 (1.50, 3.40) | 0.286 |
| | Direct bilirubin | DBIL (umol/L) | 11 | 1.74 ± 0.64 | 1.50 (0.80, 3.00) | 10 | 1.39 ± 0.94 | 1.15 (0.30, 3.00) | 0.331 |
| | Indirect bilirubin | IBIL (umol/L) | 11 | 0.56 ± 0.63 | 0.60 (0, 2.10) | 10 | 1.03 ± 0.43 | 1.15 (0.33, 1.60) | 0.068 |
| | Renal function test | Blood urea nitrogen | UREA/BUN (umol/L) | 11 | 8.96 ± 1.26 | 9.12 (6.68, 10.62) | 10 | 8.00 ± 1.09 | 8.13 (6.16, 10.15) |
| Uric acid | | UA (umol/L) | 11 | 38.93 ± 27.56 | 32.40 (8.80, 90.90) | 10 | 71.89 ± 72.43 | 52.10 (0, 224.40) | 0.202 |
| Creatinine | | CRE (umol/L) | 9 | 3.72 ± 1.54 | 3.60 (1.80, 6.75) | 8 | 4.42 ± 4.01 | 4.35 (0.40, 12.00) | 0.65 |
| Cystatin C | | CYSC (umol/L) | 10 | 0.53 ± 0.03 | 0.54 (0.46, 0.59) | 6 | 0.53 ± 0.04 | 0.53 (0.47, 0.59) | 0.754 |
| Cardiac function test | | Creatine kinase | CK (U/L) | 11 | 471.26 ± 174.86 | 520.20 (154.80, 724.80) | 10 | 472.12 ± 343.95 | 413.50 (142.80, 1072.20) |
| | Creatine kinase-MB | CKMB (U/L) | 11 | 240.88 ± 70.11 | 256.50 (102.00, 377.70) | 10 | 261.80 ± 96.97 | 259.25 (145.20, 438.51) | 0.575 |
| | Lactate dehydrogenase | LDH (U/L) | 11 | 1594.68 ± 273.66 | 1539.60 (1205.40, 2197.58) | 10 | 1620.87 ± 431.38 | 1469.80 (1185.00, 2409.30) | 0.868 |
| | α-hydroxybutyric dehydrogenase | alpha_HBDH (U/L) | 8 | 461.25 ± 125.31 | 460.50 (273.00, 681.00) | 6 | 561.00 ± 189.27 | 602.50 (330.00, 804.00) | 0.257 |
| | Blood and biochemical indexes | Triglycerides | TG (mmol/L) | 11 | 1.18 ± 0.62 | 1.29 (0.45, 2.59) | 9 | 1.55 ± 0.73 | 1.54 (0.63, 2.93) |
| Cholesterol | | TC (mmol/L) | 11 | 3.25 ± 0.65 | 3.00 (2.10, 4.50) | 9 | 3.76 ± 0.86 | 3.60 (2.40, 5.00) | 0.154 |
| High-Density Lipoprotein Cholesterol | | HDL (mmol/L) | 11 | 1.99 ± 0.28 | 2.04 (1.46, 2.54) | 7 | 2.50 ± 0.44 | 2.34 (1.88, 3.12) | 0.009 |
| Low-Density Lipoprotein Cholesterol | | LDL (mmol/L) | 11 | 0.40 ± 0.18 | 0.36 (0.08, 0.69) | 7 | 0.26 ± 0.06 | 0.27 (0.18, 0.36) | 0.04 |
| C-reactive protein | | CRP (mg/L) | 8 | 0.74 ± 0.07 | 0.77 (0.63, 0.81) | 4 | 0.74 ± 0.09 | 0.78 (0.62, 0.81) | 0.969 |
| Cholinesterase | | CHE (U/L) | 5 | 549.60 ± 134.86 | 519.00 (378.00, 714.00) | 4 | 816.75 ± 72.34 | 822.00 (726.00, 897.00) | 0.009 |
| Acetylcholine | | Ach (ug/ml) | 10 | 776.28 ± 58.71 | 764.10 (698.50, 865.00) | 6 | 405.96 ± 56.48 | 395.20 (325.19, 492.89) | <0.01 |
| White blood cell count | | WBC | 11 | 1.76 ± 0.98 | 1.31 (0.90, 3.61) | 10 | 3.40 ± 1.98 | 3.08 (0.60, 6.42) | 0.034 |
| Lymphocyte count | | LYM | 11 | 1.39 ± 0.84 | 1.04 (0.58, 2.94) | 10 | 2.45 ± 1.56 | 2.27 (0.34, 4.90) | 0.063 |
| Monocyte count | | MON | 11 | 0.06 ± 0.03 | 0.05 (0.01, 0.11) | 10 | 0.15 ± 0.07 | 0.15 (0.06, 0.30) | 0.002 |
| Neutrophil count | | NEU | 11 | 0.29 ± 0.10 | 0.28 (0.14, 0.49) | 10 | 0.78 ± 0.48 | 0.64 (0.20, 1.62) | 0.011 |
| Lymphocyte ratio | | LYM% | 11 | 77.77 ± 6.57 | 75.90 (64.80, 87.80) | 10 | 69.66 ± 12.05 | 73.75 (46.40, 84.60) | 0.067 |
| Monocyte ratio | | MON% | 11 | 3.39 ± 2.05 | 3.40 (0.50, 7.55) | 10 | 5.72 ± 2.57 | 5.95 (1.40, 9.80) | 0.032 |
| Neutrophil percentage | | NEU% | 11 | 18.81 ± 6.46 | 19.00 (9.20, 31.10) | 10 | 24.62 ± 10.61 | 21.75 (11.70, 47.50) | 0.142 |
| Red blood cell | | RBC | 11 | 11.01 ± 0.78 | 11.15 (9.51, 12.05) | 10 | 10.74 ± 0.91 | 10.84 (8.78, 11.75) | 0.469 |
| Hemoglobin | | HGB | 11 | 14.44 ± 1.31 | 14.50 (12.10, 16.30) | 10 | 13.76 ± 1.69 | 14.35 (10.70, 15.80) | 0.317 |
| Hematocrit | | HCT | 11 | 51.62 ± 6.29 | 50.88 (41.96, 63.00) | 10 | 50.62 ± 5.70 | 50.24 (40.20, 59.53) | 0.706 |
| Mean corpuscular volume | | MCV | 11 | 46.05 ± 1.55 | 46.00 (44.00, 48.75) | 10 | 47.50 ± 2.80 | 47.00 (43.00, 52.00) | 0.152 |
| Mean corpuscular hemoglobin | | MCH | 11 | 13.15 ± 0.34 | 13.10 (12.70, 13.70) | 10 | 12.94 ± 0.71 | 13.10 (11.46, 13.90) | 0.391 |
| Mean corpuscular hemoglobin concentration | | MCHC | 11 | 28.47 ± 0.84 | 28.60 (27.10, 29.90) | 10 | 27.40 ± 1.53 | 27.35 (24.41, 29.60) | 0.058 |
| Red blood cell volume distribution width | RDWB | 11 | 20.12 ± 0.97 | 20.20 (18.60, 21.80) | 10 | 19.43 ± 0.93 | 19.65 (18.00, 20.60) | 0.115 | |
| Red blood cell distribution width | RDW | 11 | 34.77 ± 2.21 | 34.40 (32.00, 38.48) | 10 | 34.53 ± 1.68 | 34.80 (32.00, 36.70) | 0.786 | |
| Platelet count | PLT | 11 | 464.55 ± 144.97 | 485.00 (245.00, 674.00) | 10 | 540.00 ± 135.75 | 534.50 (362.00, 755.00) | 0.235 | |
| Mean platelet volume | MPV | 11 | 6.78 ± 0.28 | 6.80 (6.30, 7.20) | 10 | 7.75 ± 1.09 | 7.45 (6.70, 10.03) | 0.021 | |
| Plateletocrit | PCT | 11 | 0.32 ± 0.10 | 0.35 (0.17, 0.44) | 10 | 0.41 ± 0.12 | 0.42 (0.24, 0.60) | 0.067 | |
| Platelet volume distribution width | PDWc | 11 | 31.89 ± 2.48 | 31.40 (27.90, 35.80) | 10 | 35.03 ± 3.30 | 34.50 (31.40, 41.00) | 0.023 | |
| Platelet distribution width | PDWs | 11 | 10.47 ± 1.98 | 9.90 (7.70, 13.80) | 10 | 13.66 ± 3.80 | 13.15 (9.90, 21.50) | 0.024 | |

| Organ coefficient | Organ | n | Mean ± SD | Median (Min, Max) | p |
|-------------------------------|-------|--------------|-----------|-------------------|-----------------|
| | | | | | |
| Weight (g) | 10 | 41.65 ± 1.39 | 10 | 41.81 ± 1.76 | 0.827 |
| Small intestine_L (mm) | 5 | 61.14 ± 3.49 | 5 | 52.92 ± 3.38 | 0.005 |
| Large intestine_L (mm) | 5 | 10.08 ± 0.68 | 5 | 9.86 ± 1.20 | 0.73 |
| Liver (g) | 7 | 1.32 ± 0.15 | 7 | 1.73 ± 0.14 | <0.01 |
| Thymus (g) | 7 | 0.06 ± 0.01 | 7 | 0.06 ± 0.01 | 0.76 |
| Pancreas (g) | 8 | 0.18 ± 0.02 | 8 | 0.20 ± 0.04 | 0.318 |
| Spleen (g) | 8 | 0.08 ± 0.01 | 8 | 0.11 ± 0.02 | 0.007 |
| L_Gast (g) | 5 | 0.21 ± 0.02 | 5 | 0.18 ± 0.01 | 0.048 |
| R_Gast (g) | 5 | 0.20 ± 0.03 | 5 | 0.22 ± 0.02 | 0.347 |
| L_Tibialis Anterior (g) | 5 | 0.07 ± 0.01 | 5 | 0.08 ± 0.01 | 0.439 |
| R_Tibialis Anterior (g) | 5 | 0.07 ± 0.00 | 5 | 0.07 ± 0.01 | 0.479 |
| L_Quad (g) | 5 | 0.23 ± 0.02 | 5 | 0.26 ± 0.04 | 0.175 |
| R_Quad (g) | 5 | 0.26 ± 0.03 | 5 | 0.28 ± 0.04 | 0.333 |
| Caecum_WWWR | 10 | 9.12 ± 2.37 | 10 | 0.84 ± 0.17 | <0.01 |
| Liver_WWWR | 7 | 3.21 ± 0.31 | 7 | 4.12 ± 0.37 | <0.01 |
| Thymus_WWWR | 7 | 0.13 ± 0.03 | 7 | 0.14 ± 0.03 | 0.885 |
| Pancreas_WWWR | 8 | 0.43 ± 0.05 | 8 | 0.47 ± 0.09 | 0.378 |
| Spleen_WWWR | 8 | 0.19 ± 0.02 | 8 | 0.25 ± 0.05 | 0.012 |

Germ-free (GF) mice exhibit a range of anatomical and physiological characteristics, such as reduced liver weight, splenic atrophy, enlarged caecum, increased small intestine length, dyslipidemia, and aberrant immune cell function. These phenotypes highlight the critical role of the microbiota in host development and physiological homeostasis. We chose to conduct spatial and single-cell studies on GF mice to comprehensively dissect the impact of microbiota deficiency on the physiological, immune, and metabolic systems, thereby elucidating the broad spectrum and heterogeneity of microbiota-host interactions.



Highlights



◆ Single-cell, spatial transcriptomics, and bile acidomics atlases in germ-free mice.

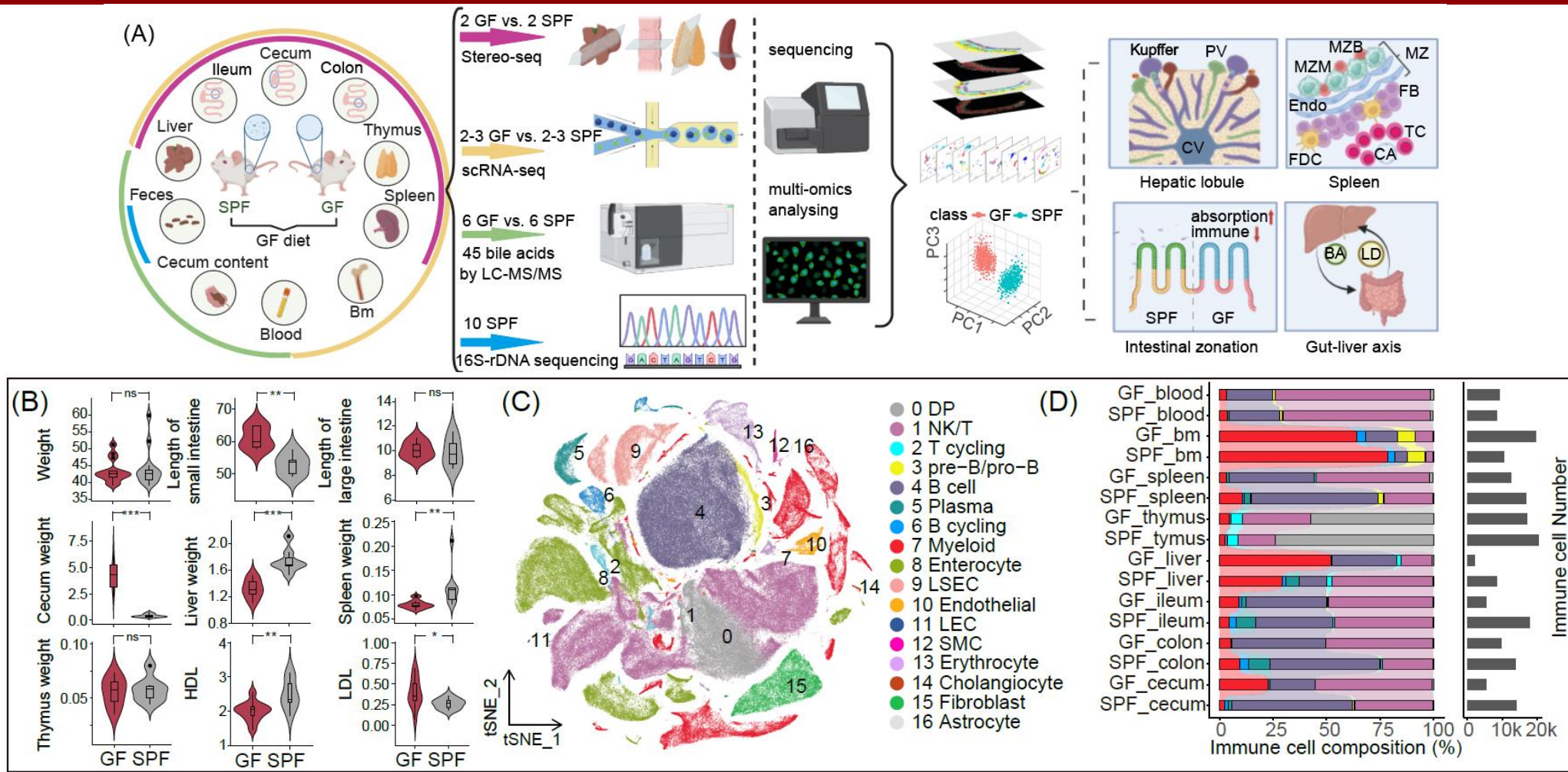
◆ Marked aberration and tissue heterogeneity in B, myeloid, and T/NK cells in germ-free mice.

◆ Microbiota shapes mucosal zonation, modulates lipid dynamics of small intestine.

◆ Germ-free mice show liver bile acid synthesis and ileal reabsorption anomalies.



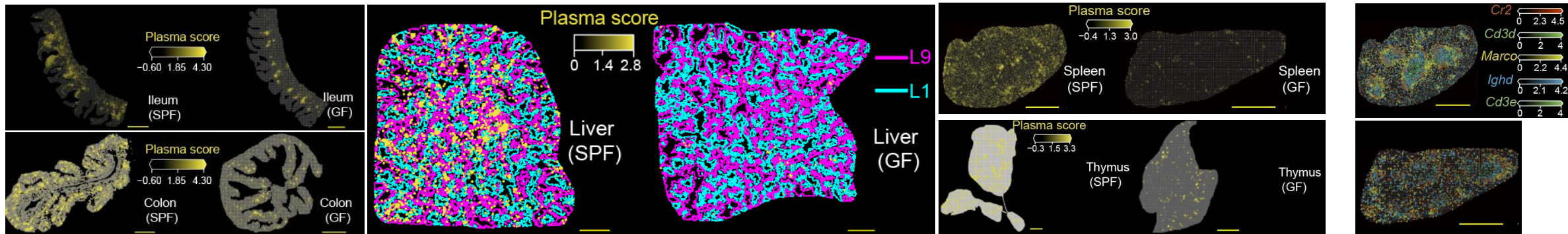
Integrated cross-organ multi-omics maps of tissues in SPF and GF mice



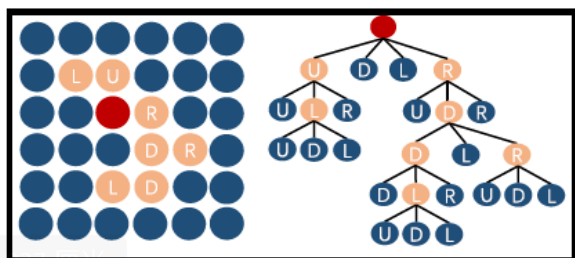
◆ Eight tissues including primary (bone marrow and thymus) and secondary (spleen) lymphoid organs, mucosal tissues (gut), as well as blood and liver were used for scRNA-seq. After filtering, a total of 269,105 cells were retained for unsupervised clustering and we identified 17 major cell populations with 85.2% immune cells and epithelial cells (22.89% B cells, 33.83% NKT cells, 12.32% myeloid cells, and 16.37% epithelial cells).



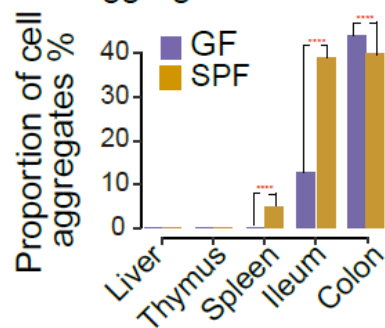
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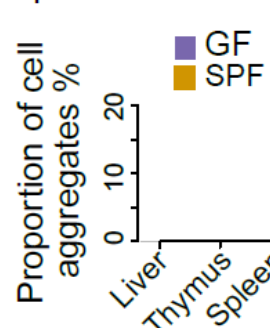
(F) Cell aggregation index



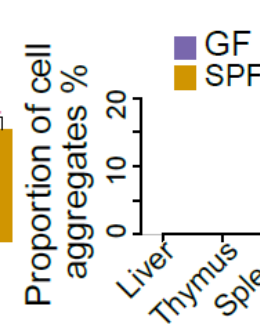
(G) Plasma cell Aggregates index ≥ 30 spots



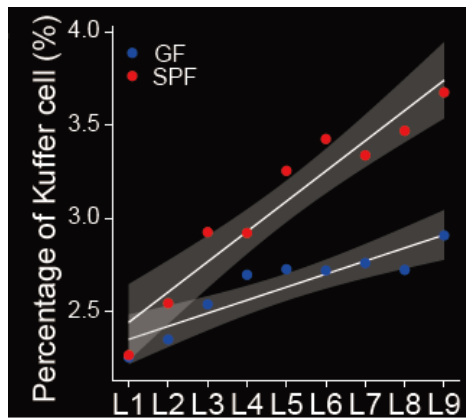
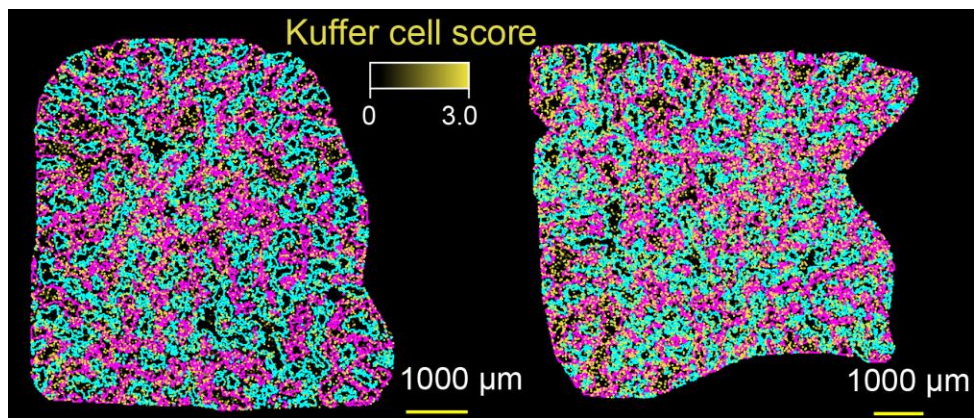
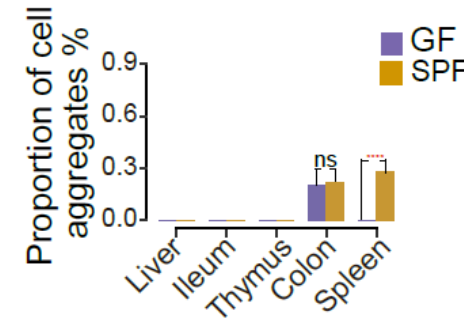
Plasma cell ≥ 500 spots



Plasma cell ≥ 1000 spots

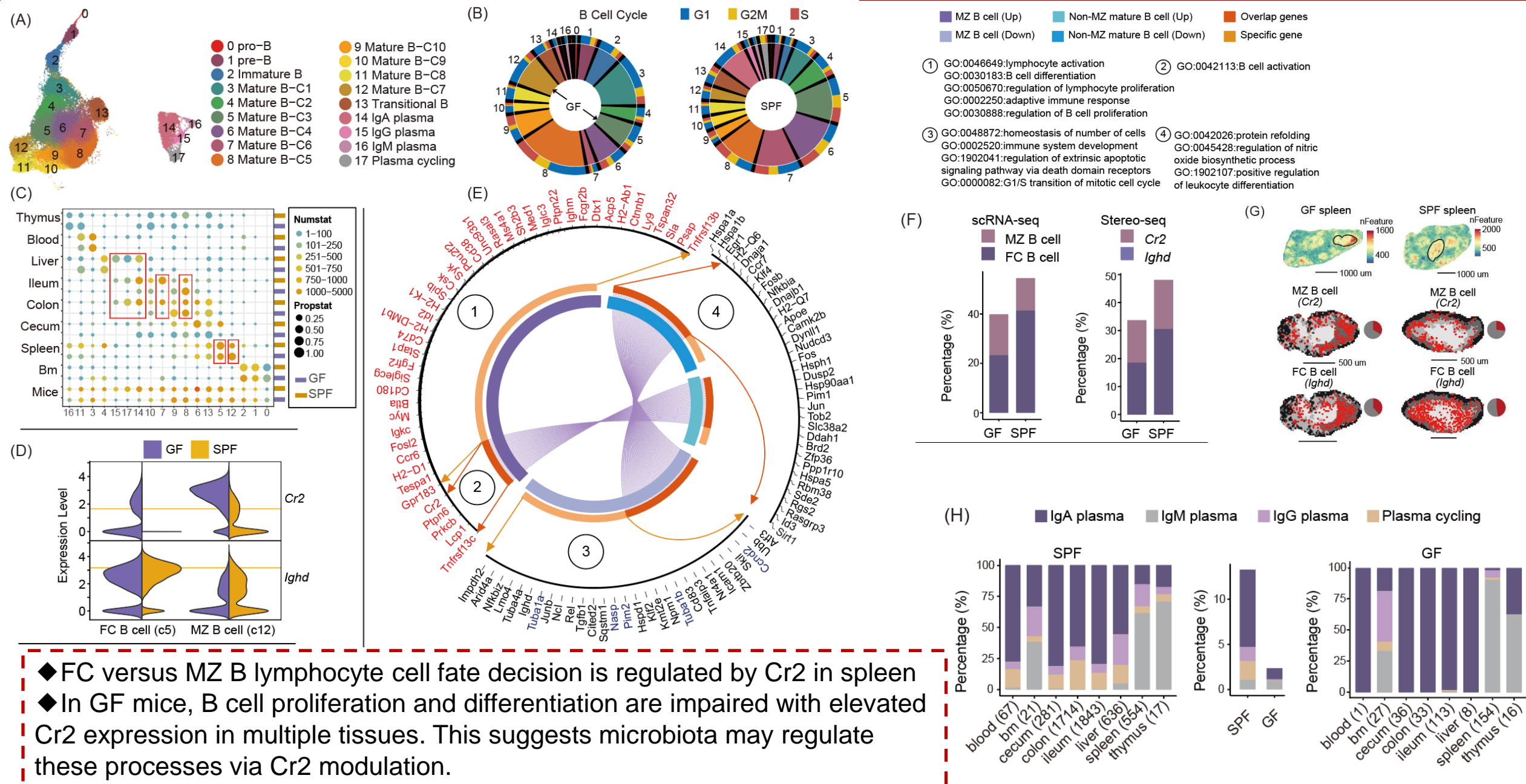


Macrophage ≥ 30 spots

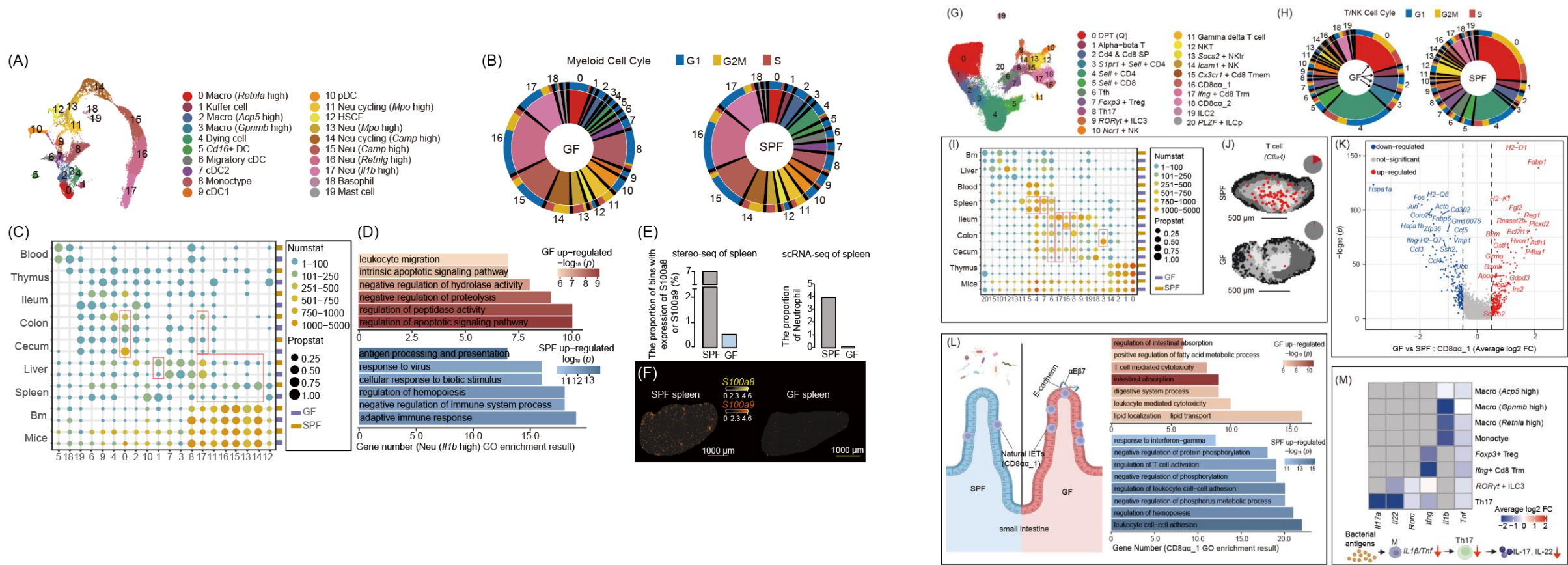


◆ The spatial aggregation index highlights tissue-specific differences in plasma cell clustering, with microbial stimulation having a stronger impact than food-derived antigens. In GF mice, splenic macrophage aggregation is diminished, indicating immature or disordered marginal zone development (marked by Marco). The liver shows microbiota-driven Kupffer cell enrichment around the portal vein, which becomes more random in the absence of microbiota.

The microbiota exhibits organ-specific heterogeneity in the regulation of B cell development and plasma cells composition



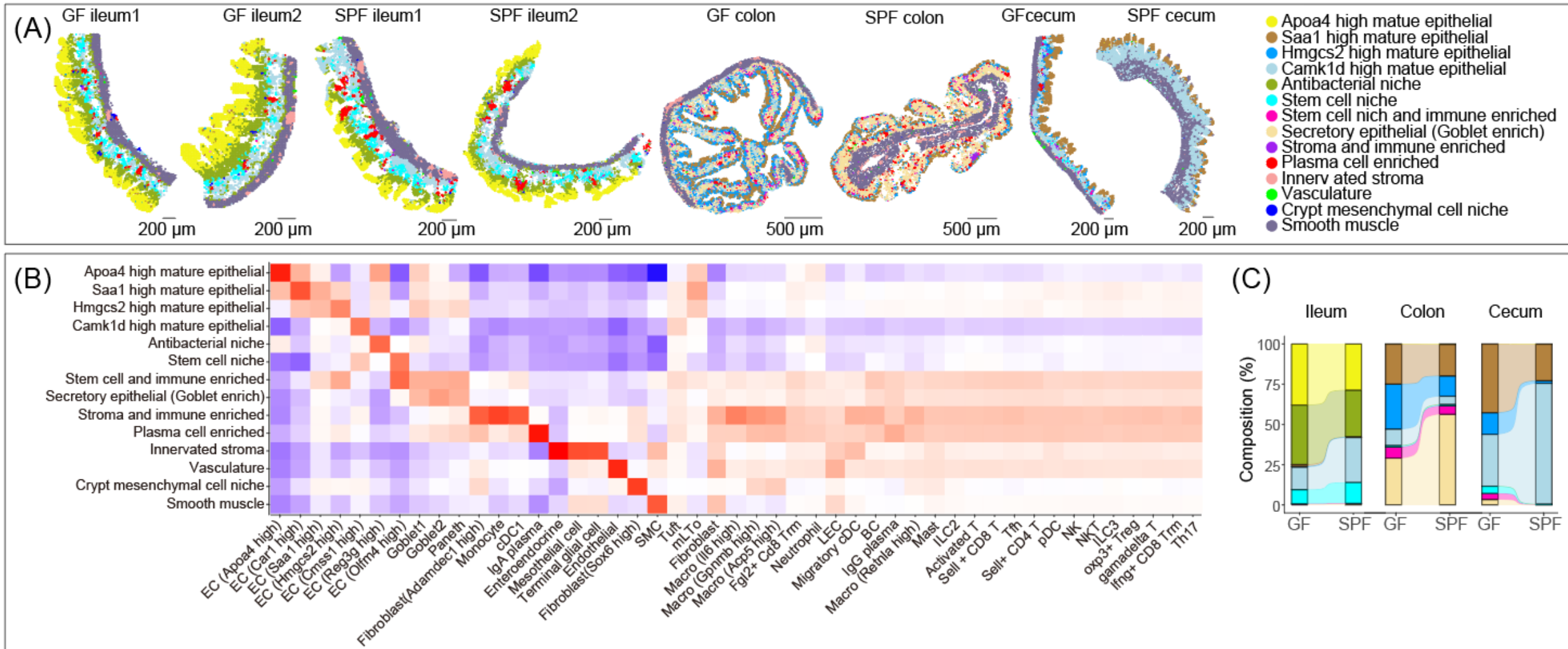
The microbiota exhibits organ-specific heterogeneity in the regulation of myeloid cell function



- ◆ Microbes do not influence the number of neutrophils in the bone marrow but regulate neutrophil development and survival, resulting in a significant reduction of neutrophils in peripheral organs
- ◆ Microbiota deficiency disrupts the cell cycle of thymic T progenitor cells, leading to an accumulation of naïve T cells in peripheral organs, particularly the spleen and gut, and aberrant T cell activation
- ◆ By examining the homing of T cells from the gut, we reveal the heterogeneity differences of T cells and intraepithelial lymphocytes between small and large intestinal



The microbiota regulates zonation, function, and nutrient absorption of intestinal mucosa

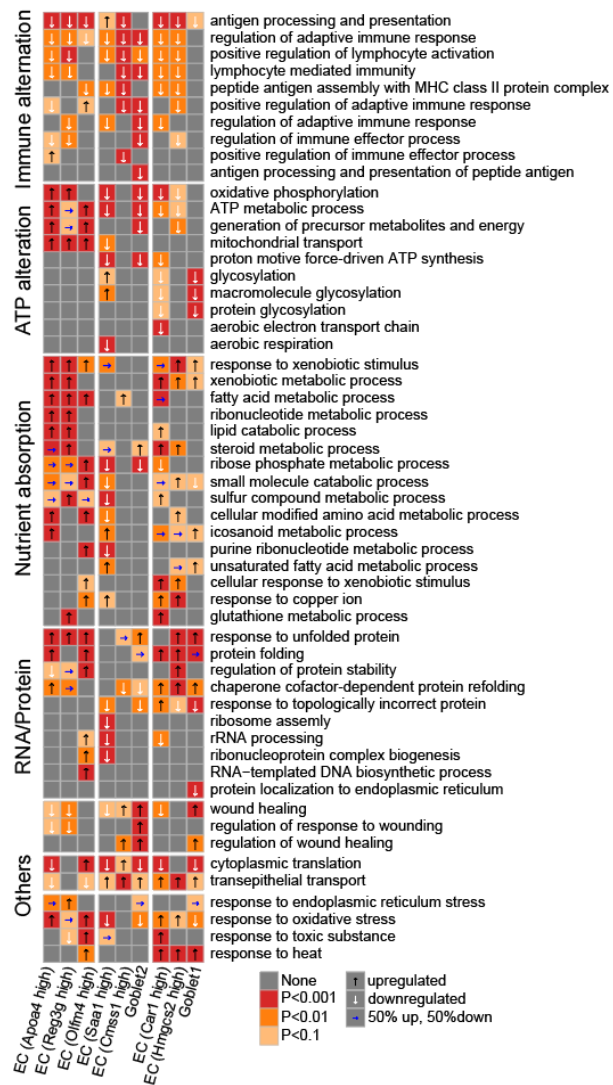


◆ Both scRNA-seq and Stereo-seq data analysis showed significant changes in epithelial zonation in GF mice compared to SPF mice, including thicker apical absorption zone in the ileum (*Apoa4* high mature epithelium), colon (*Saa1* high and *Hmgcs2* high mature epithelium), and cecum (*Saa1* high and *Hmgcs2* high mature epithelium), but thinner secretory zone (Goblet cell enriched) in the colon of GF mice

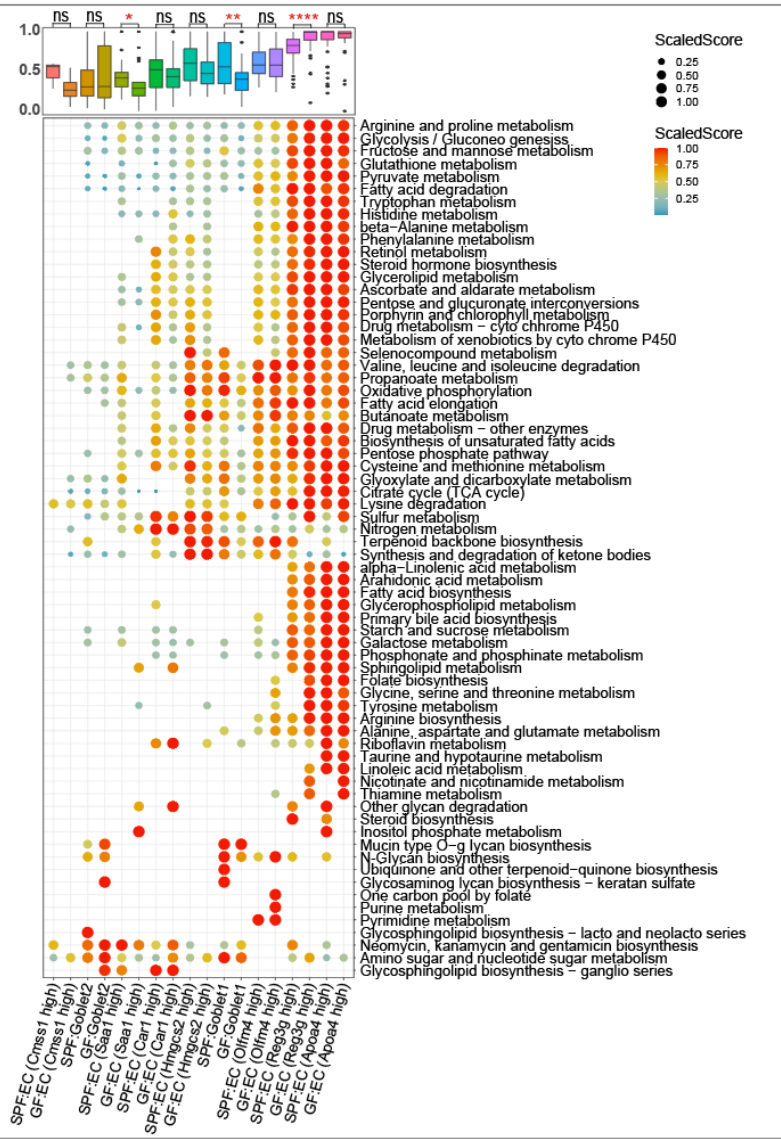


The microbiota regulates zonation, function, and nutrient absorption of intestinal mucosa

(D)



(E)



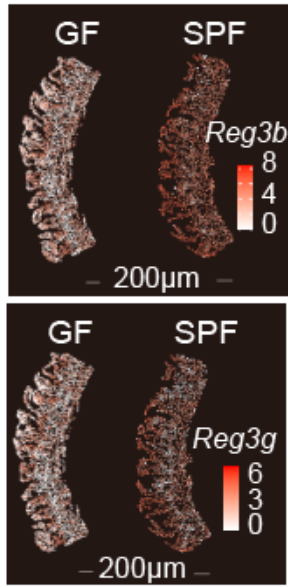
Microbes regulate epithelial function as follows:

- ◆ The overall immune function of intestinal epithelial cells is reduced in GF mice.
- ◆ The nutrient absorption capacity of the ileum is significantly enhanced in GF mice.
- ◆ The energy metabolism function of the large intestine is downregulated in GF mice.
- ◆ The metabolic function of the epithelial subtype (Reg3g high) enterocytes is enhanced in GF mice.

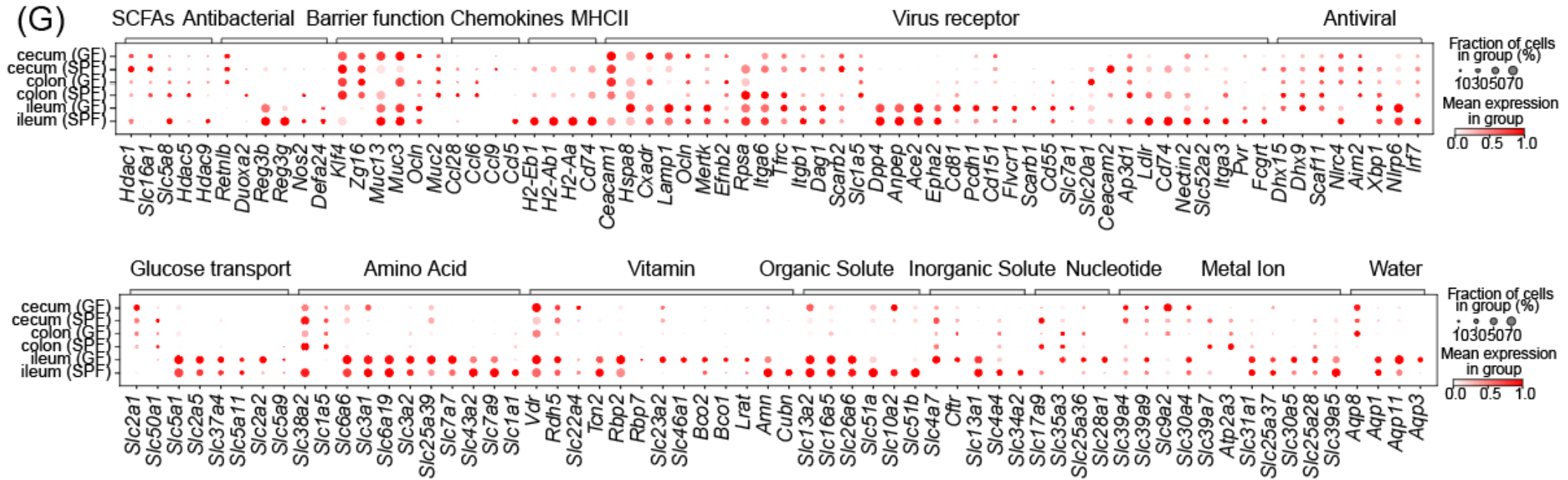


The microbiota regulates zonation, function, and nutrient absorption of intestinal mucosa

(F)

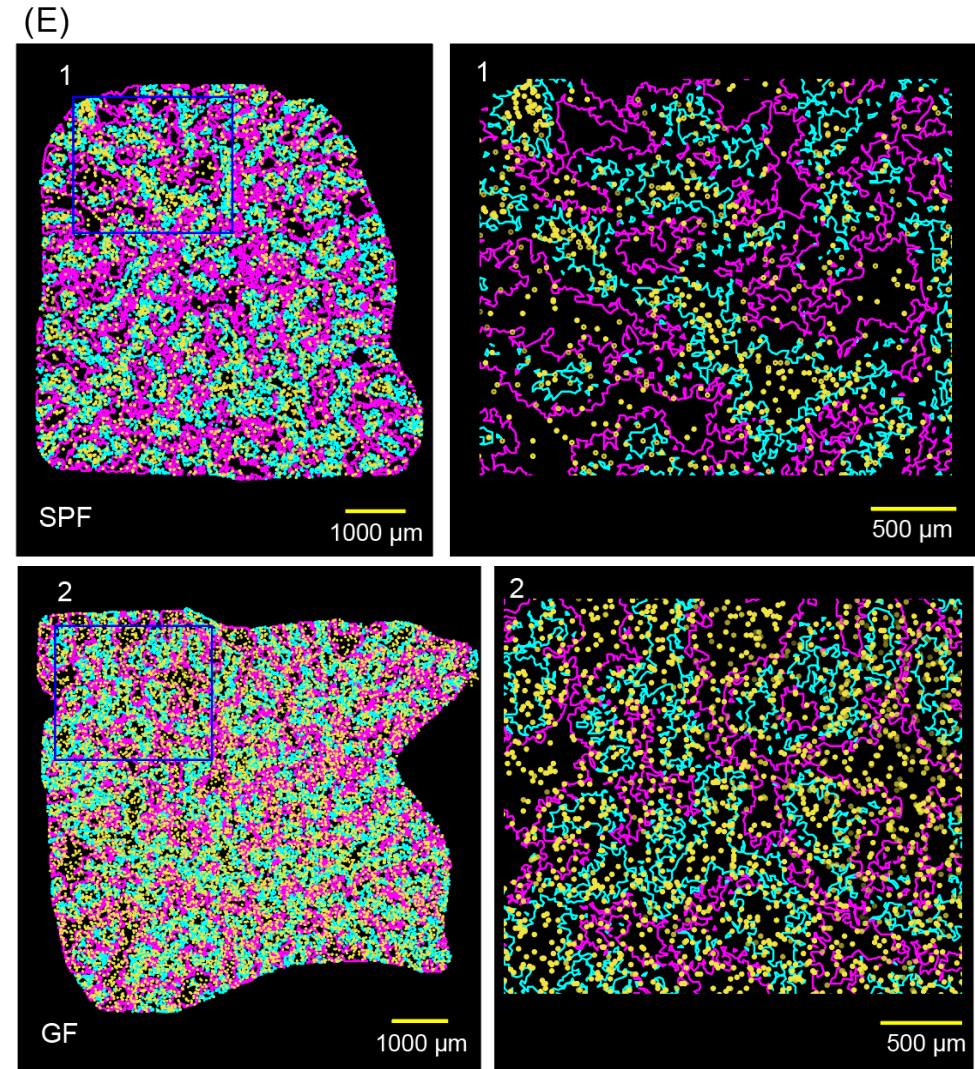
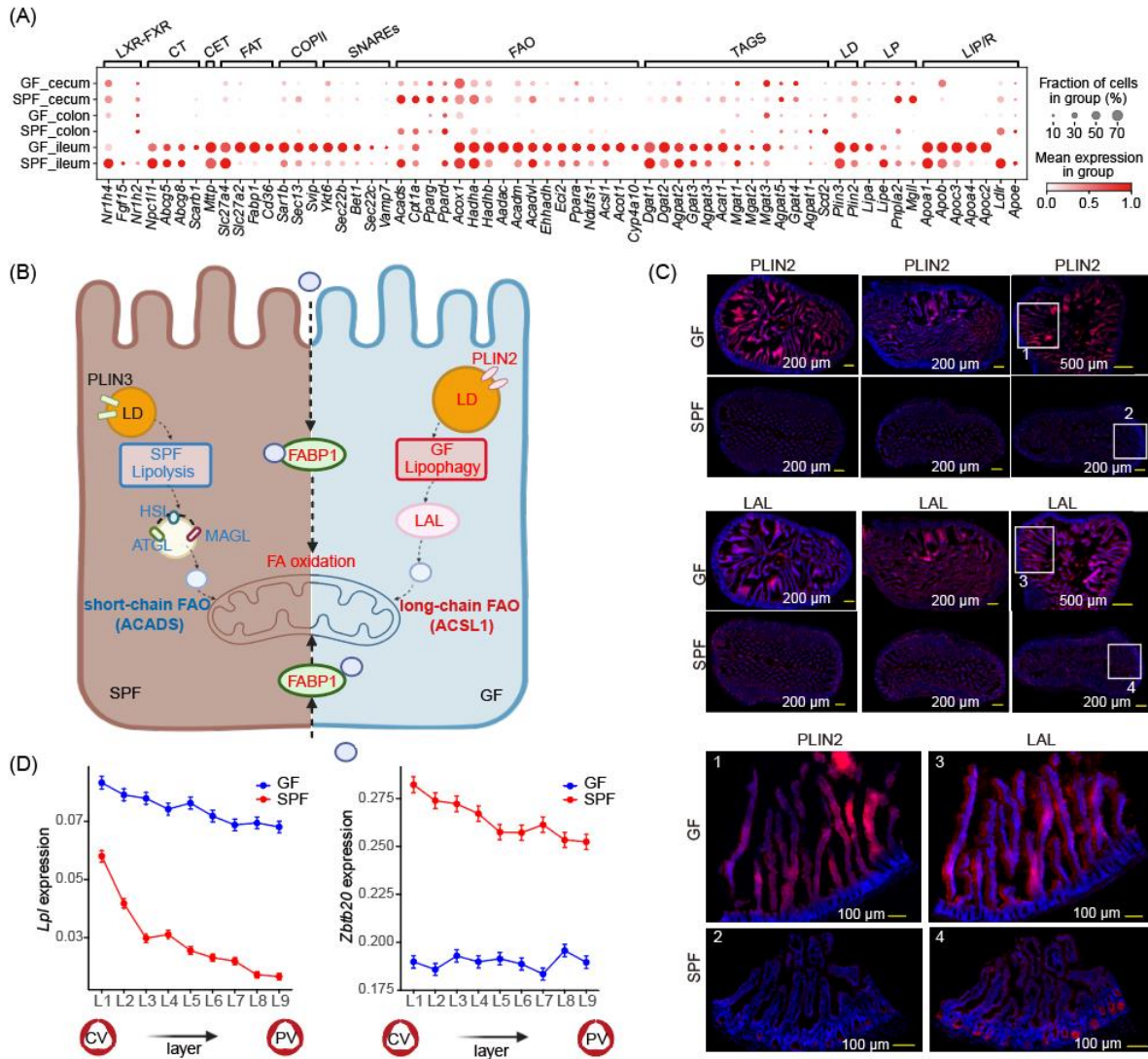


(G)



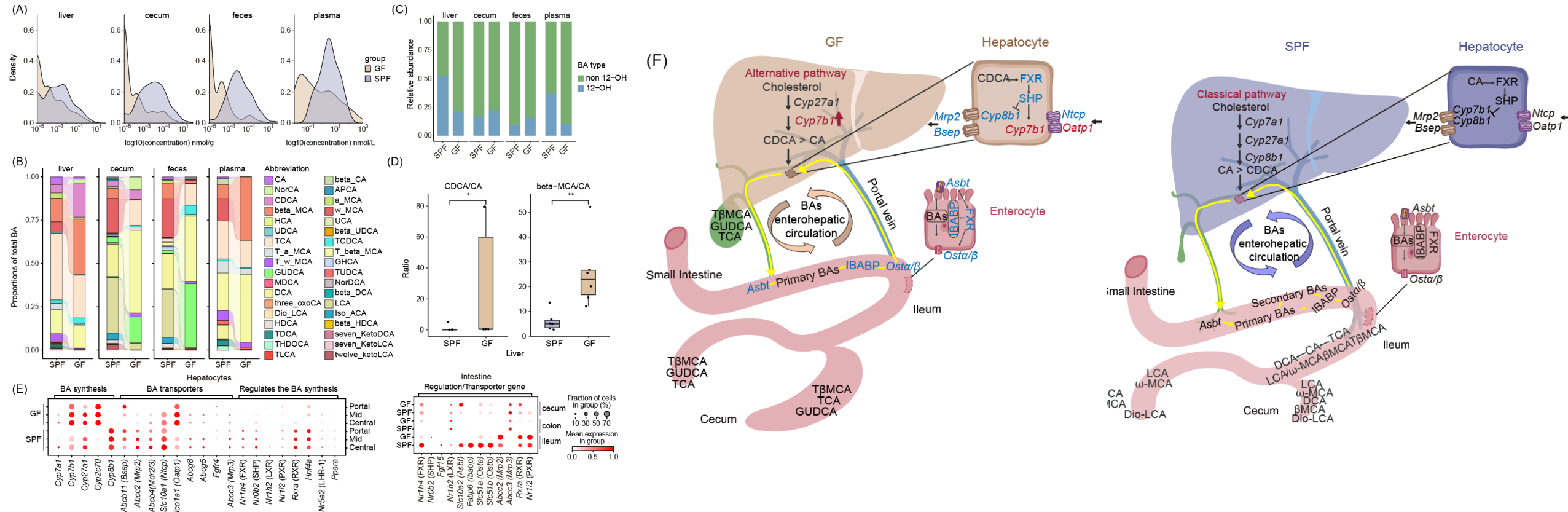
◆ As far as intestinal epithelial immunity is concerned, it appeared that GF mice have adaptive immune deficiencies associated with antigen processing and presentation, while innate immune activation associated with antiviral activity was maintained in GF mice.

The microbiota regulates dietary lipid processing by intestinal enterocytes and regulates blood lipid levels by ZBTB20- LPL axis in the liver



◆ Our study reveals unique lipid droplet characteristics and autophagy features in GF mice.
 ◆ We demonstrate for the first time that the microbiota regulates the expression of Lpl-Zbtb20 and its zonation within liver lobules, contributing to lipid metabolism regulation in GF mice

Integrative analysis reveals that depletion of microbiota alters the synthesis pathway and reabsorption capacity of bile acids



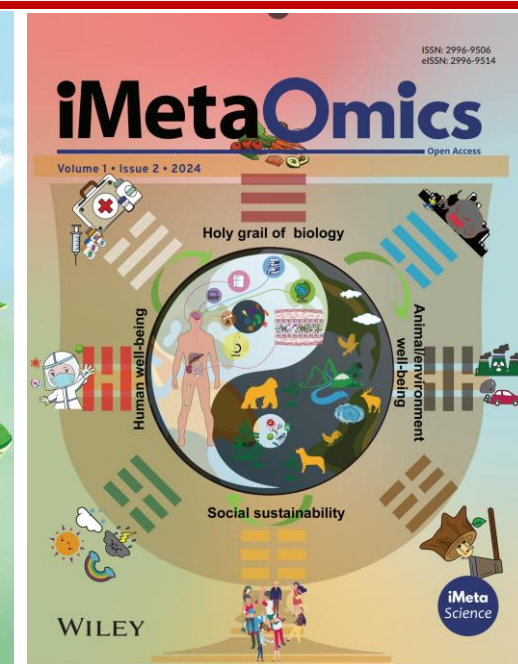
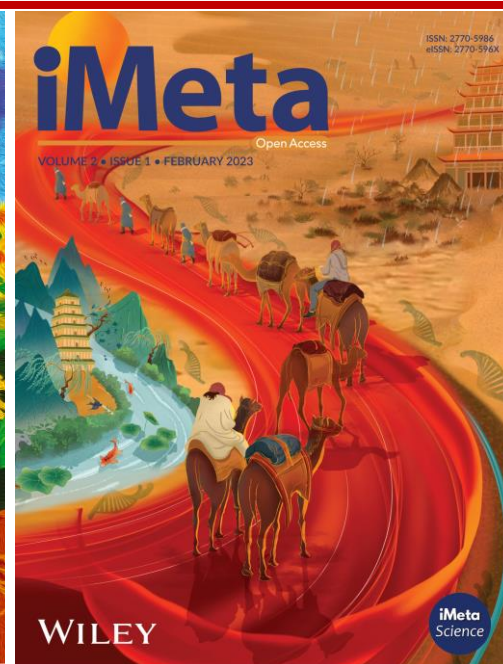
- ◆ GF mice exhibit reduced bile acid concentrations in multiple tissues and significant changes in hepatic bile acid composition, suggesting a shift in bile acid synthesis pathways from the classical to the alternative route.
- ◆ Key genes involved in bile acid synthesis and enterohepatic circulation reabsorption are also significantly altered in GF mice.



Conclusions


- ◆ Our study present a multi-organ single-cell, spatial transcriptomics, and bile acid omics atlas of SPF and GF mice.
- ◆ Plasma cell aggregation displays significant tissue heterogeneity depending on the gut microbiota.
- ◆ GF mice exhibit impaired follicular and marginal zone B cell maturation, linked to microbiota-mediated modulation of *Cr2* gene expression.
- ◆ The microbiota regulates the development and survival of neutrophils in the bone marrow, influences the development and differentiation of T cells in the thymus, and modulates intraepithelial $\gamma\delta$ T cell composition and lipid absorption in the small intestine.
- ◆ Notably, spatial transcriptomics of gut have, for the first time, revealed significant changes in the functional zonation of the intestinal mucosa in GF mice, with an enlargement of lipid droplets in absorptive enterocytes of the small intestine, transitioning towards lipophagy and enhanced fatty acid oxidation, underscoring a key pathway in GF mice' resistance to obesity.
- ◆ Concurrently, spatial transcriptomics of liver have also, for the first time, revealed that the zinc finger and BTB domain containing protein (ZBTB20)- Lipoprotein lipase (LPL) (ZBTB20-LPL) axis, which regulates blood lipids, exhibits a gradient expression pattern in the liver that is modulated by microbes.

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