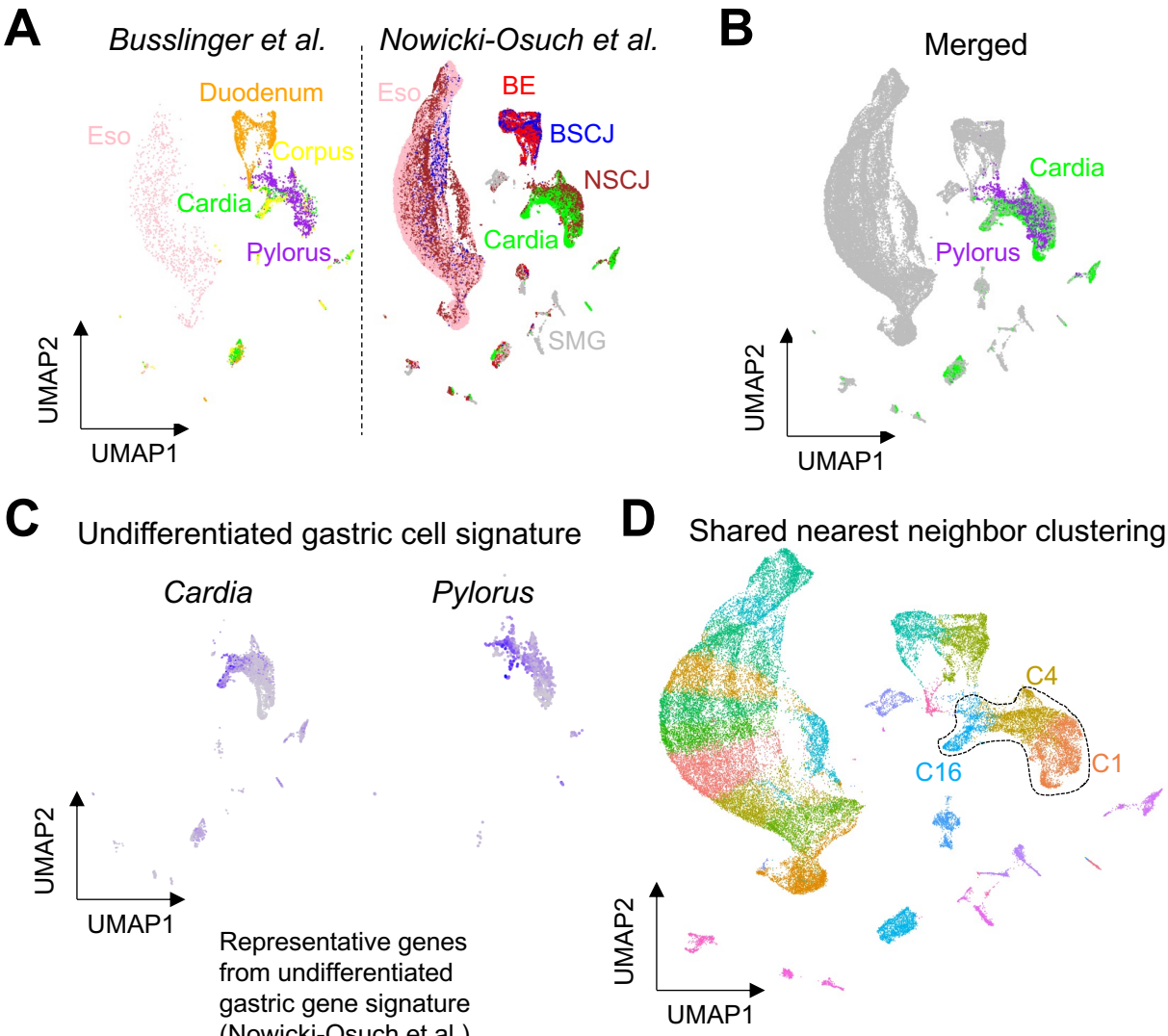


Cluster	Cardia	Corpus	Pylorus
	Number of cells per cluster (% of total cells from that region)		
1 Avg signature score 0.05	1578 (35)	57 (9)	297 (29)
4 Avg signature score 0.10	1109 (24)	62 (10)	452 (44)
16 Avg Signature score 0.25	578 (13)	216 (35)	297 (29)

FIGURE S1. Human stomach cardia and pylorus display similar transcriptional profiles

(A) Single cell RNA-seq data from different regions of the human gastrointestinal tract from two independent studies (Busslinger et al. 2021b; Nowicki-Osuch et al. 2021) were integrated and projected adjacent to each other using uniform manifold approximation (UMAP). Eso: Esophagus, BE: Barrett's esophagus, NSCJ: Normal squamo-columnar junction, BSCJ: Squamo-columnar junction from patients with BE, SMG: Esophageal submucosal glands.

(B) Datasets from above two studies when projected together reveal overlapping transcriptional profiles of the majority of epithelial cells from human stomach cardia and pylorus/antrum.

(C) Undifferentiated gastric cell signature, derived by Nowicki-Osuch et al. and salient genes depicted below, reveals co-aggregation of stem cell like populations in human stomach cardia and pylorus.

(D) Clustering of all cells from the two datasets identifies Clusters 1, 4 and 16 to be enriched for stomach cardia and pylorus cells. Cluster 16 is enriched in cells with an undifferentiated "stem-cell" like phenotype and has contributions from both stomach cardia and pylorus.

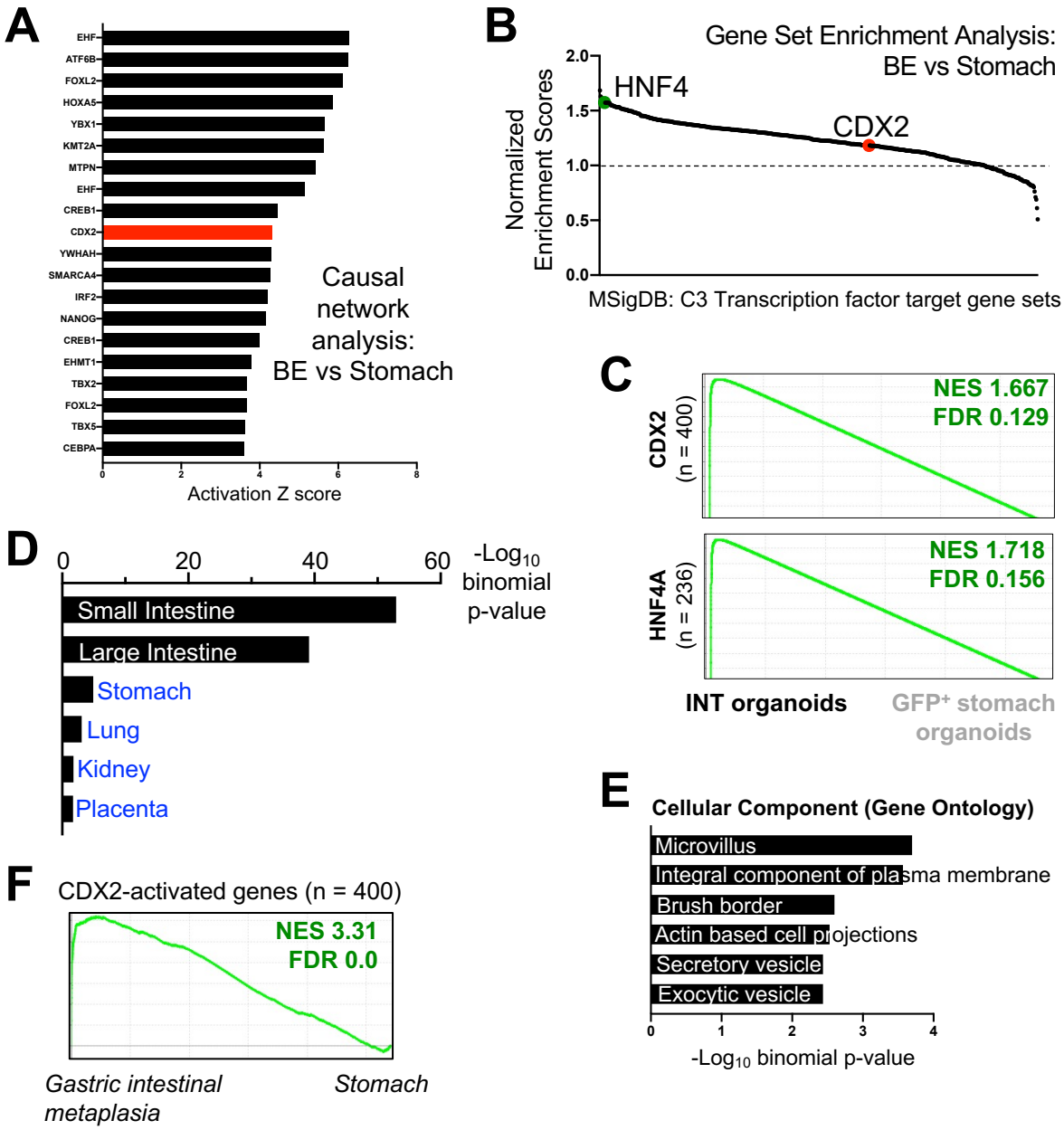

A
EHF
ATF6B
FOXL2
HOXA5
YBX1
KMT2A
MTPN
EHF
CREB1
CDX2
YWHAH
SMARCA4
IRF2
NANOG
CREB1
EHMT1
TBX2
FOXL2
TBX5
CEBPA
0
2
4
6
8
Activation Z score
Causal network analysis: BE vs Stomach
B
Gene Set Enrichment Analysis: BE vs Stomach
Normalized Enrichment Scores
2.0
1.5
1.0
0.5
0.0
HNF4
CDX2
MSigDB: C3 Transcription factor target gene sets
C
CDX2 (n = 400)
NES 1.667
FDR 0.129
HNF4A (n = 236)
NES 1.718
FDR 0.156
INT organoids
GFP+ stomach organoids
D
0
20
40
60
-Log10 binomial p-value
Small Intestine
Large Intestine
Stomach
Lung
Kidney
Placenta
E
Cellular Component (Gene Ontology)
Microvillus
Integral component of plasma membrane
Brush border
Actin based cell projections
Secretory vesicle
Exocytic vesicle
0
1
2
3
4
-Log10 binomial p-value
F
CDX2-activated genes (n = 400)
NES 3.31
FDR 0.0
Gastric intestinal metaplasia
Stomach

FIGURE S2. CDX2 and HNF4A induce intestinal enhancers and genes in mouse stomach organoids.

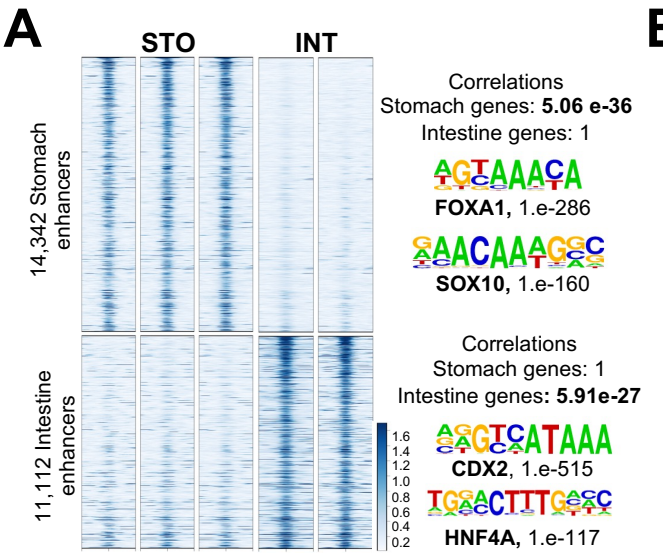
(A) Causal network analysis (Ingenuity pathways) using bulk RNA seq data from BE vs. normal stomach mucosa (Owen et al. 2018) implicates CDX2 in BE pathogenesis.

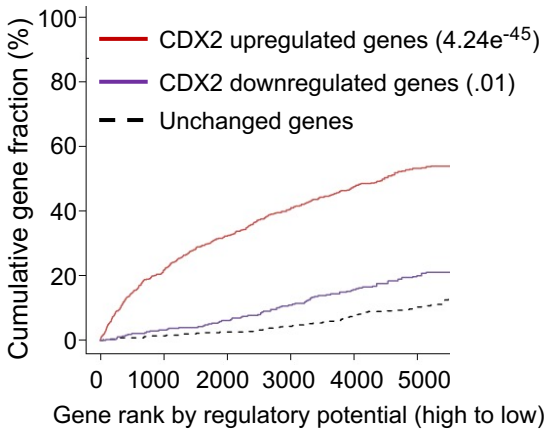
(B) Gene Set Enrichment Analysis (GSEA) of the same bulk RNA seq data (Owen et al. 2018) using curated gene sets (MSigDB C3 Transcription factor targets). HNF4 and CDX2 target genes are upregulated in BE compared to normal stomach mucosa.

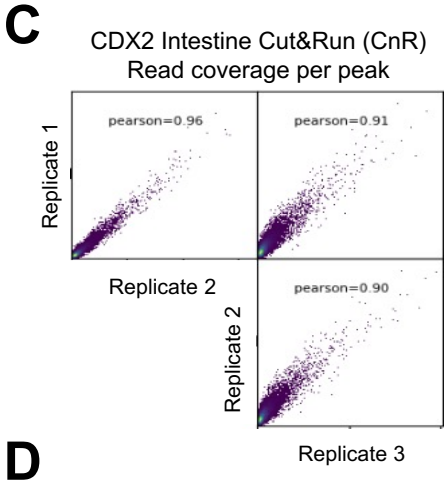
(C) GSEA of genes induced by CDX2 (n = 400) or HNF4A (n = 218) in gastric organoid lines, compared to GFP controls (DESeq2, q <0.05, $\log_2$ fold-increase >1). Both sets are enriched for transcripts expressed in intestinal organoids. NES, normalized enrichment score; FDR, false discovery rate.

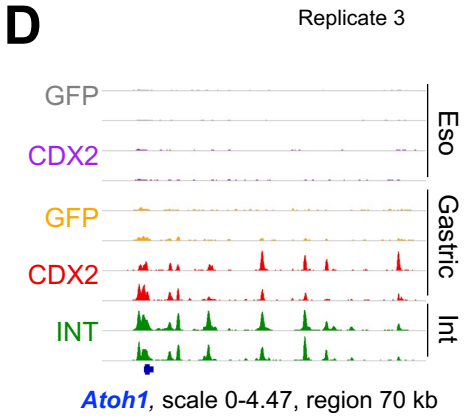
(D-E) Enrichment analysis (enrichR) of CDX2-induced genes reveals a predominant intestinal program (D), and enrichment of CDX2-dependent intestinal features (Gao and Kaestner 2010) such as brush border, microvillus, and actin-based cell projections.

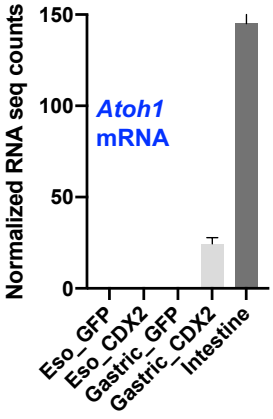
(F) GSEA of 400 genes induced in $CDX2^+$ gastric organoids (DESeq2, $\log_2$ fold-increase >1, q<0.05), showing resemblance to clinical specimens of human GIM (Companioni et al. 2017).











E

Transcription factor	Log fold change
ISX	10.4
TBX3	7.8
CDX1	7.7
CDX2	5.0
ATOH1	4.9
EVX1	3.9
MYB	3.2
MAF	3.1
LEF1	2.8
NR1H4	2.4
HOPX	2.3
AHRR	2.2
NPAS2	2.2
E2F2	1.6
PRDM1	1.4
MLXIPL	1.2
HNF4G	1.1
PAX8	1.1
HNF4A	0.9
ETS1	0.9
PPARG	0.8
MYC	0.7
NR1I2	0.7
ETV4	0.6

FIGURE S3. CDX2 upregulates canonical intestinal transcripts and transcription factors in mouse stomach organoids

(A) Enhancers with differential chromatin accessibility in stomach (left) and intestinal (right) organoids (DESeq2, $\log_2$ fold-difference >1, q <0.05). Tissue-specific enhancers correlate with gene expression profiles (BETA analysis) and are enriched for specific TF-binding motifs.

(B) Genes induced by CDX2 correlate with loci showing significantly higher ATAC-seq signal (<100 kb from TSSs), i.e., genes with high regulatory potential defined by BETA analysis (Wang et al. 2013). In contrast, elevated ATAC signals correlate poorly with reduced expression of nearby genes.

(C) High correlation between signals at called peaks in 3 biological replicates for CDX2 CUT&RUN (CnR) on adult mouse intestinal villus cells.

(D) IGV data tracks of open chromatin at the intestine-restricted *Atoh1* locus in replicate samples. Forced CDX2 expression in stomach but not in esophageal organoids increased accessibility at intestinal enhancers. Altered stomach cell chromatin was accompanied by induced *Atoh1* expression (RNA-seq counts, mean ±SD).

(E) Gene expression changes in $CDX2^+$ gastric organoids reveal upregulation of intestine-restricted TF genes (red) and *Myc* (yellow), which was recently implicated in BE pathogenesis (Nowicki-Osuch et al. 2021).

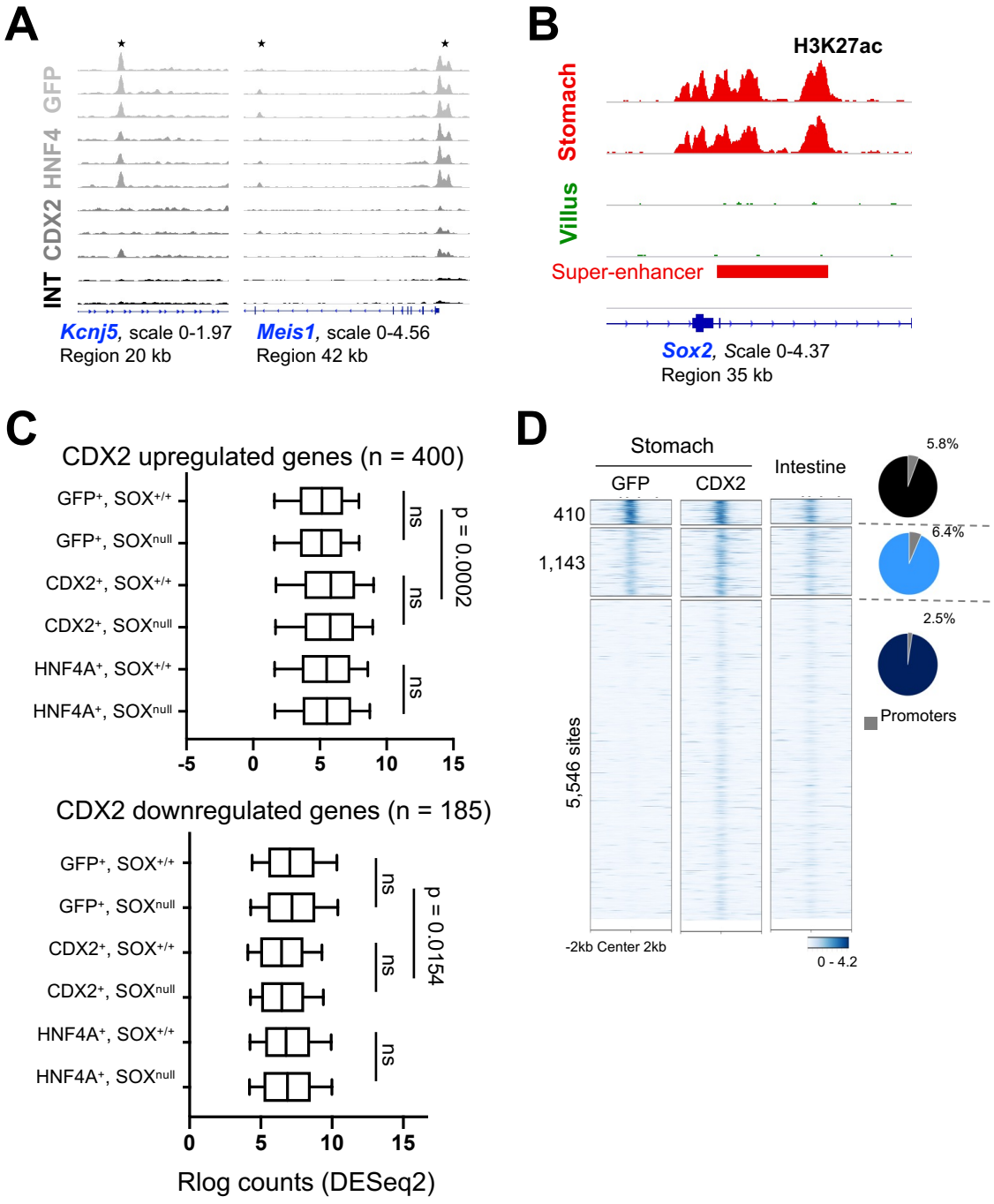

A
GFP
HNF4
CDX2
INT
Kcnj5, scale 0-1.97
Region 20 kb
Meis1, scale 0-4.56
Region 42 kb
B
H3K27ac
Stomach
Villus
Super-enhancer
Sox2, Scale 0-4.37
Region 35 kb
C
CDX2 upregulated genes (n = 400)
GFP+, SOX+/+
GFP+, SOXnull
CDX2+, SOX+/+
CDX2+, SOXnull
HNF4A+, SOX+/+
HNF4A+, SOXnull
ns
p = 0.0002
-5
0
5
10
15
CDX2 downregulated genes (n = 185)
p = 0.0154
Rlog counts (DESeq2)
D
Stomach
Intestine
GFP
CDX2
410
1,143
5,546 sites
-2kb Center 2kb
0 - 4.2
5.8%
6.4%
2.5%
Promoters

FIGURE S4. SOX2 knockout does not impact CDX2 mediated changes in stomach organoids

(A) ATAC-seq data tracks from classic stomach-restricted loci that show decreased chromatin access in $CDX2^+$ organoids. Accessibility was reduced to lesser degrees in $HNF4A^+$ organoids.
(B) H3K27Ac ChIP-seq data from mouse stomach mucosa and intestinal villi, showing a stomach-restricted super-enhancer over the *Sox2* locus.
(C) Left, SOX2 depletion has no statistically significant impact (Kolmogorov-Smirnov test) on expression of HNF4A- or CDX2-responsive genes. Rlog counts of 400 genes upregulated (top) and 185 genes downregulated (bottom) upon CDX2 expression in gastric organoids.
(D) Classes of chromatin access (*k*-means clustering of ATAC-seq data) at 7,099 *cis*-elements unique to gastric organoids (cluster 3 in Fig. 2C). CDX2 binding at 5,546 previously closed sites is associated with small increases in chromatin accessibility, similar to basal levels in intestinal (INT) organoids. To allow cross-comparison, the heatmap scale is identical to Fig. 4B.

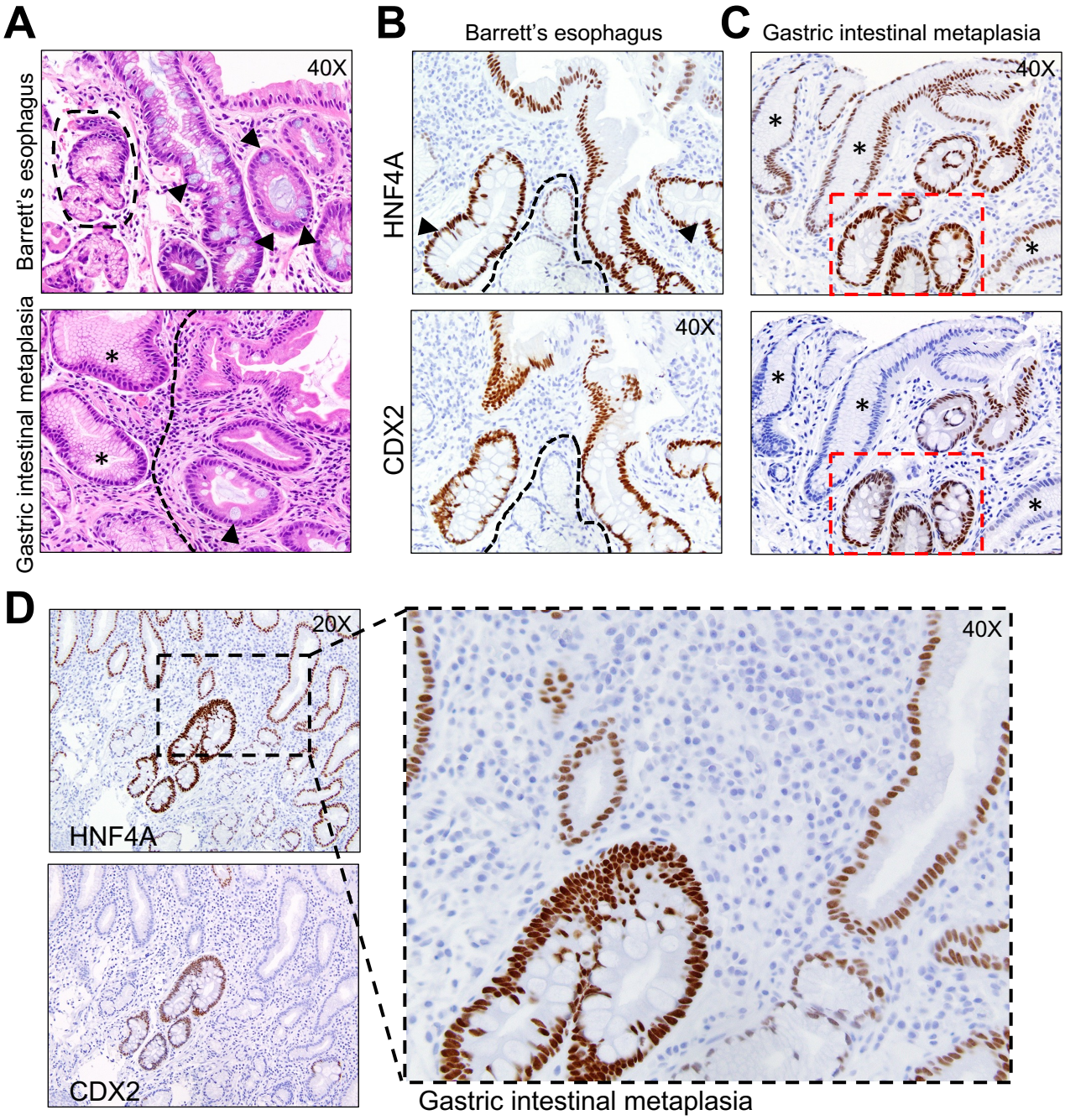

A
Barrett's esophagus
40X
Gastric intestinal metaplasia
B
Barrett's esophagus
HNF4A
CDX2
40X
C
Gastric intestinal metaplasia
40X
D
20X
HNF4A
CDX2
40X
Gastric intestinal metaplasia

FIGURE S5. CDX2 expression in human IM is restricted to HNF4A-overexpressing stomach cells

(A) hematoxylin and eosin (H&E) sections from BE (top) and GIM (bottom) corresponding to serial tissue sections in Fig. 5C-D, showing typical IM morphology. $HNF4A^{low}CDX2^{neg}$ regions seen on IHC correspond to gastric foveolar glands (top, dashed circle; bottom, asterisks) whereas $HNF4A^{high}CDX2^{+}$ glands show intestinal features, including goblet cells (arrowheads). (B-D) Additional examples of BE (B) and GIM (C-D), illustrating low basal HNF4A expression in CDX2-negative areas and the concordance of $HNF4A^{high}$ and $CDX2^{+}$ cells (e.g., red dashed box in C. Original magnifications are indicated and $HNF4A^{low}$ $CDX2^{neg}$ regions are marked with a dashed black perimeter (B) or asterisks (C). Panel D shows a GIM example with a $CDX2^{+}$ $HNF4A^{high}$ gland cluster carrying goblet cells enveloped by normal $HNF4A^{low}$ $CDX2^{neg}$ glands. The dashed box is magnified on the right.

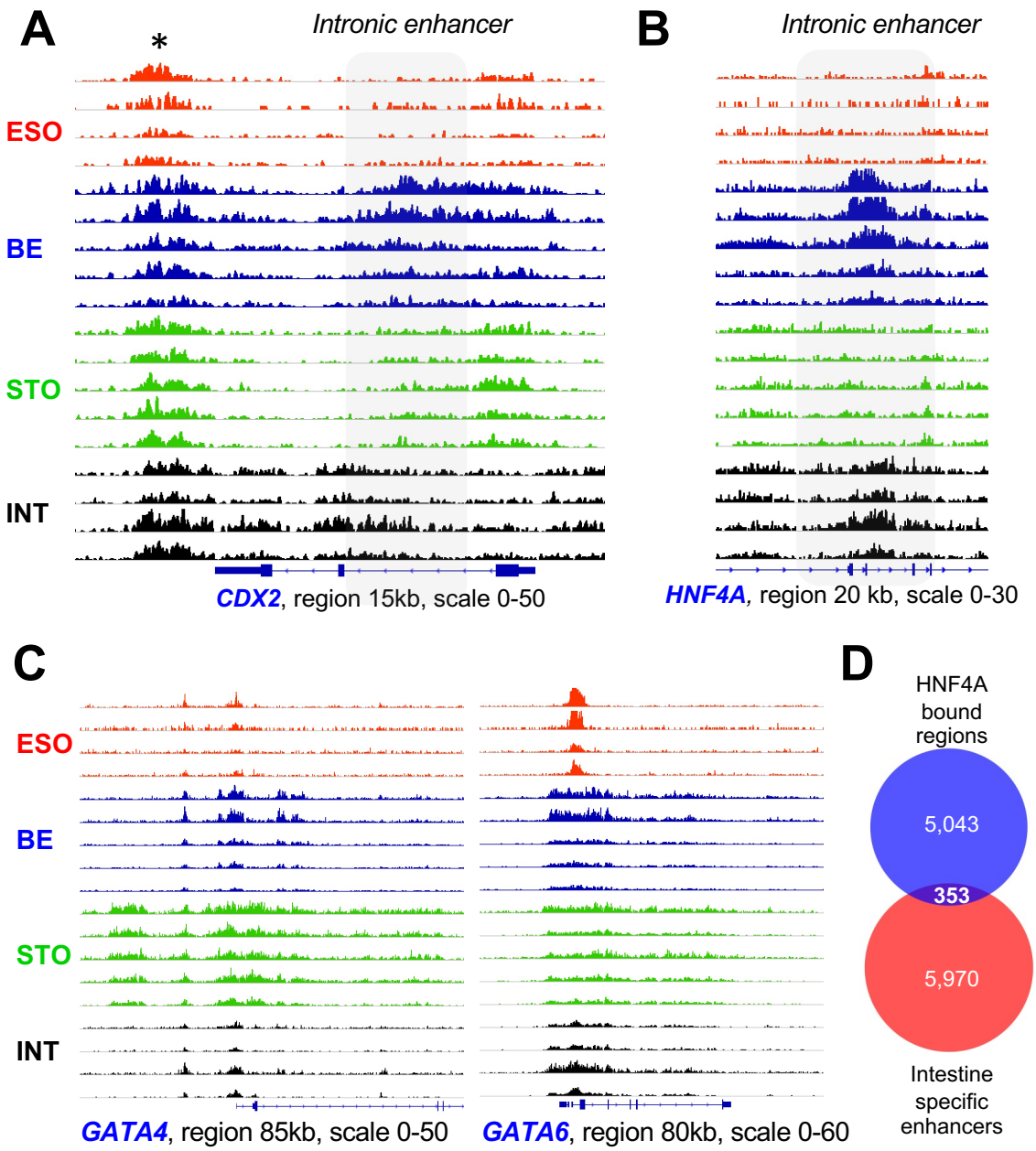
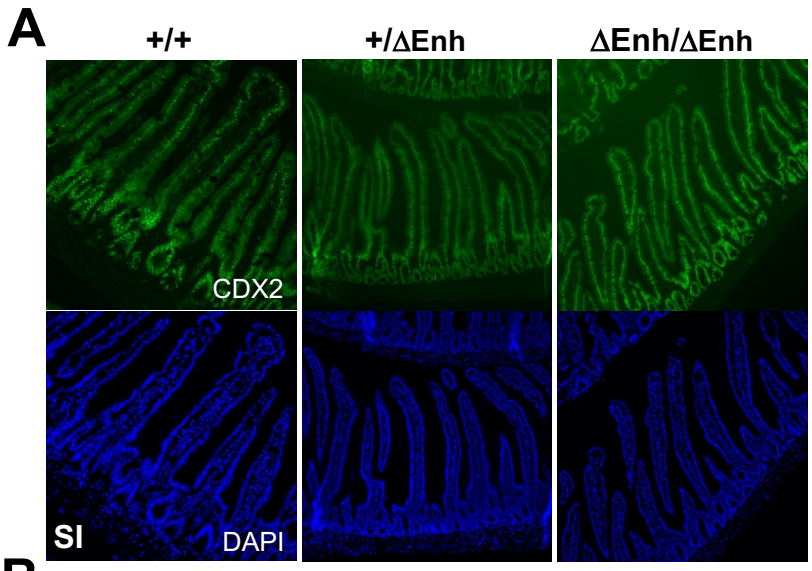

A
Intronic enhancer
*
ESO
BE
STO
INT
CDX2, region 15kb, scale 0-50
B
Intronic enhancer
HNF4A, region 20 kb, scale 0-30
C
ESO
BE
STO
INT
GATA4, region 85kb, scale 0-50
GATA6, region 80kb, scale 0-60
D
HNF4A bound regions
5,043
353
5,970
Intestine specific enhancers

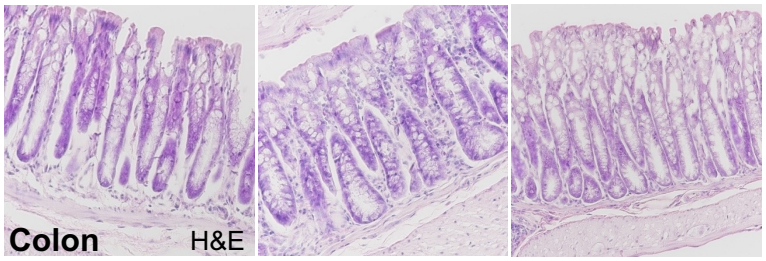
FIGURE S6. Enhancer activity (H3K4me2 FIT-Seq, data from (Singh et al. 2021)) at pertinent TF gene loci in normal and metaplastic human mucosae.

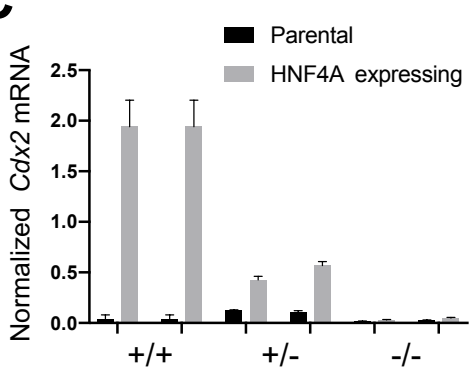
(A-B) IGV tracks from H3K4me2 FIT-Seq at the *CDX2* and *HNF4A* loci, showing increased marking in primary human BE specimens compared to the native stomach (STO) epithelium. ESO, Esophagus; INT, Intestine.

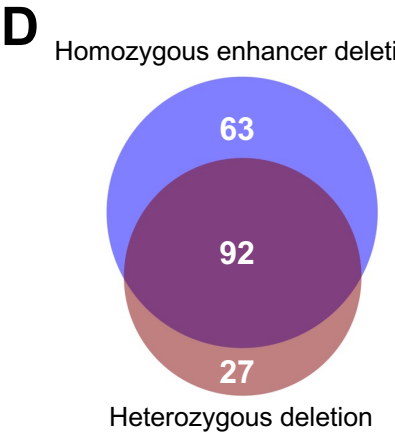
(C) In contrast, other intestinal TF loci, such as *GATA4* and *GATA6* show no clear difference in enhancer profiles in BE compared to normal stomach.

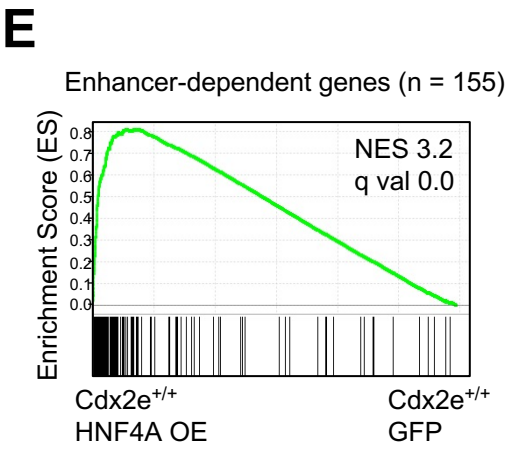
(D) HNF4A-occupied sites in HNF4A^{+} stomach organoids overlap minimally with intestine-specific enhancers.

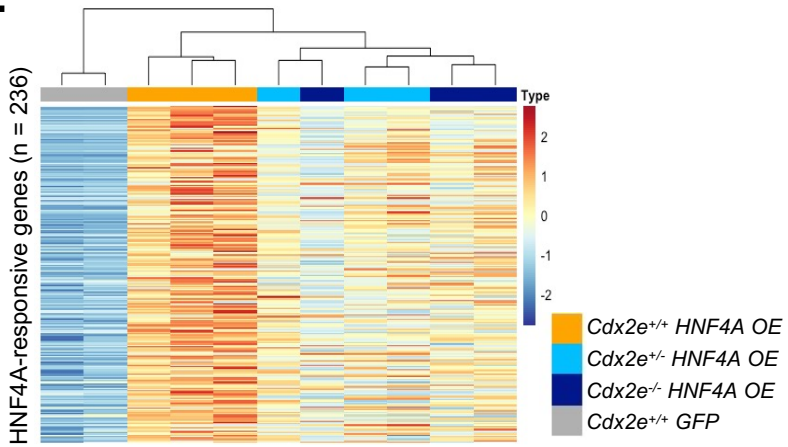












G

Genes	CDX2e$^{+/+}$ GFP		CDX2e$^{+/+}$ HNF4A OE			CDX2e$^{+/-}$ HNF4A OE			CDX2e$^{-/-}$ HNF4A OE		
Cdx2	37	69	541	474	270	171	51	86	2	13	6
Cdx1	0	0	101	22	58	25	17	22	9	5	3
Alpi	0	1	662	1311	85	24	13	12	0	4	7
Akp3	0	0	478	1378	77	15	1	1	0	0	0
Isx*	0	0	102	41	43	35	2	2	5	0	10
Tff3	1	7	234	214	29	16	5	6	0	4	9
Muc13	2	5	736	315	170	50	43	171	31	31	45
Krt20	6	2	277	253	86	20	28	8	18	30	6
B4galt4	17	38	76	77	38	18	11	5	5	4	8
B4galnt2	13	22	757	458	392	60	175	107	16	68	45
Naip1	0	1	201	74	56	35	8	7	7	7	12
Ceacam18	0	0	26	21	12	0	1	2	2	3	0
Ceacam20*	0	2	31	9	23	3	1	10	6	0	1

FIGURE S7. Deletion of a 3' *Cdx2* shadow enhancer attenuates the transcriptional response to HNF4A overexpression in stomach organoids

(A) Duodenal CDX2 is preserved at wild-type levels in heterozygote and homozygote enhancer-deleted (∆enh) mice, shown here by representative immunofluorescence images from groups of 3 independent animals of each genotype.

(B) Colonic architecture is preserved in heterozygote and homozygote enhancer deleted mice, shown here by representative H&E from group of 3 independent animals of each genotype.

(C) qRT-PCR confirmation that HNF4A overexpression in gastric organoids fails to induce *Cdx2* mRNA in homozygous *∆enh* mice. Mono-allelic enhancer loss blunted *Cdx2* induction.

(D) Statistically reduced expression of 155 and 119 genes, respectively, in HNF4A^{+} ∆enh/∆enh and +/∆enh organoids, compared to wild-type HNF4A^{+} organoids. The two groups overlap significantly (92 genes, representative factor 73.2, $p < 5.8e\text{-}171$).

(E) Genes that escape upregulation in enhancer-deleted compared to wild type HNF4A^{+} stomach organoids (DESeq2, Log_2 fold-change >1, $q < 0.05$; n = 155) are enriched in HNF4A^{+} gastric organoids compared to control gastric organoids as shown by GSEA and hence are enhancer responsive genes. This illustrates that this enhancer and in turn endogenous CDX2 activation is important in mediating intestinalization mediated by HNF4A.

(F) Heatmap of 236 genes significantly upregulated by HNF4A overexpression in wild type enhancer organoids (DESeq2, log_2 fold-change >1, $q < 0.05$). Transcriptional response to HNF4A overexpression is broadly attenuated in ∆enh/∆enh and +/∆enh stomach organoids.

(G) Normalized RNA-seq counts for classic intestinal genes in wild type gastric and HNF4A^{+} organoids from wild-type, +/∆enh or ∆enh/∆enh mice. Several genes show near-complete abrogation in enhancer deleted organoids.

SUPPLEMENTAL METHODS

Passaging of Gastric organoids. Gastric organoids grew as spheres requiring passage every 4-6 days, when Matrigel containing mature organoids was dissociated in 0.05% Trypsin at 37°C for 1-3 min with intermittent manual trituration. Dissociation was verified by microscopy and the reaction was quenched with fetal bovine serum (FBS) when small grape-like cell clusters replaced most spheroids. Cells were pelleted and re-plated in Matrigel by 1:3 to 1:5 dilution, depending on starting density and the degree of cell dissociation. *Sox2*$^{fl/fl}$ mice were reported previously (Sarkar et al. 2016) and antral organoids were generated as described above. *Sox2* was excised in vitro using adenoviral CRE delivery at two consecutive passages and confirmed by immunoblotting.

Generation and passaging of esophageal organoids. We incubated fragments of esophageal epithelium in 1 mL 0.25% trypsin-EDTA at 37°C for 10 min, vortexed gently, rinsed the tissue with 8 ml Soybean Trypsin Inhibitor (Sigma Aldrich, T6522), and repeated the digestion and wash cycle once. We filtered the dissociated tissue through a 40 μm strainer and washed the strainer with 9 mL washing medium (100 units/mL penicillin, 0.1 mg/mL streptomycin, 2 mM L-glutamine, and 10% FBS in DMEM/F12 medium (Invitrogen, 11320033) containing HEPES). We centrifuged cells at 200 *g* for 5 min before resuspending the cells in Matrigel (Corning, 356234) and applying organoid medium (advanced DMEM/F12 supplemented with Glutamax, 0.15 mM HEPES, N2 and B27 supplements, 1 mM N-acetylcysteine, 50 ng/ml human EGF, and 3% conditioned medium from L-WRN cells expressing Wnt3a, Noggin, and Rspo1) (Miyoshi and Stappenbeck 2013). For subsequent passages, organoids were dissociated in 0.25% trypsin at 37°C for 10 min and small cell aggregates were embedded in fresh Matrigel.

Isolation of gastric antral and small intestinal Lgr5^{+} *stem cells.* Gastric antral glands were isolated as above from *Lgr5*$^{GFP\text{-}Cre}$ mice (Jackson Labs 008875) and dissociated to single cells in a mixture of 2.5 mL Accumax (Innovative Cell Technologies, AM105), 2.5 mL Dispase (Stem Cell Technologies, 07913), and 0.5 mL 10x TrypLE (ThermoFisher, A1217701) in 4.5 mL phenol red-free Dulbecco's Modified Eagle Medium (DMEM) for 10 min at 37°C. Stem cells from the proximal 1/3 small intestine were isolated as described previously. After gently scraping off villi, the remaining intestine was rinsed, minced into small pieces, and rotated in 5 mM EDTA solution in PBS at 4°C for 45 min. Samples were shaken manually every 10 min and the solution was changed at 30 min. Released crypts were passed through a 70 μm filter and the

eluate was pelleted and digested in 4x TrypLE (ThermoFisher, A1217701) for 30 min at 37°C. Antral or intestinal cells were resuspended in FACS buffer (phenol red-free DMEM, 2% FBS and ROCK inhibitor), labeled with DAPI (BD Biosciences 564907, 1:1000), and sorted by flow cytometry to isolate GFP^+ ($Lgr5^+$) stem cells.

Immunoblotting. Protein was isolated from organoid pellets using RIPA buffer (Sigma, R0278), quantified using the Pierce BCA Protein Assay Kit (Thermo, 23227), and 40 μg was loaded per sample onto SDS-PAGE gels. After electrophoresis, membrane transfer was achieved using the IBlot 2 system (Thermo IB21001). Membranes were blocked with 5% bovine serum albumin (BSA) in Tris-buffered saline (pH 8 + 0.1% Tween-20) for 1 h at room temperature, then stained with primary antibodies (Ab, CDX2 – Cell Signaling Technology, D11D10, 1:1000; HNF4A – Novus Biologicals, NBP1-89679, 1:250; SOX2 – R&D Systems, AF3538, 1:2000) overnight at 4°C. Secondary Ab (horseradish peroxidase (HRP)-conjugated goat anti-rabbit IgG, Invitrogen 656120, 1:2000; or HRP-conjugated mouse anti-goat IgG, Invitrogen 626520, 1:2000) were incubated for 1 h at room temperature and proteins were visualized using ECL Prime reagents (Amersham, RPN2232). For β-Actin we used a HRP-conjugated primary Ab (Abcam, ab49900, 1:25,000) for 1 h. Images were obtained using the GE ImageQuant LAS 4000.

ChIP-seq. CHIP-seq was performed on cross-lined chromatin as described previously (Jadhav et al. 2016; Saxena et al. 2017). Briefly, intact gastric antral glands or duodenal villi were cross-linked at room temperature using 1% formaldehyde for 15 min. Cross-linked tissue was resuspended in cold RIPA lysis buffer, sonicated to obtain DNA fragments between 200 and 800 bp, and incubated overnight with H3K27ac Ab (Active Motif, 39135) at 4°C. The solution was subsequently incubated with Protein A and Protein G beads (ThermoFisher, 10002D and 10004D) at 1:1 ratio for 4h at 4°C and beads were then washed twice in sonication buffer, once in high-salt buffer (20 mM Tris-HCl pH 8, 1 mM EDTA, 0.5 M NaCl, 0.1% SDS, 1% Triton X-100), once in LiCl buffer (10 mM Tris-HCl pH 8, 1 mM EDTA, 250 mM LiCl, 1% NP-40), and once in TE buffer. Formaldehyde cross-links were reversed by heating the eluate overnight at 65°C in the presence of 1% SDS and 0.1 M NaHCO3. Samples were eluted after treatment with proteinase K for 1 h at 55°C using the QIAQuick PCR purification kits. Libraries were prepared using ThruPLEX DNA-seq kits (Rubicon Genomics, R400427) and sequenced on a NextSeq instrument (Illumina).

Computational analyses

ATAC-Seq. Data were analyzed (Tables S2 and S4) according to ENCODE guidelines (https://www.encodeproject.org/pipelines/ENCPL792NWO/). Briefly, DNA sequence tags were aligned to the mouse genome using Bowtie (Langmead et al. 2009) and peaks were called using MACS2 (Zhang et al. 2008) (https://github.com/taoliu/MACS). Bigwig tracks were generated using bamCoverage from DeepTools and quantile normalized using Haystack (Pinello et al. 2018) for individual track visualization, *k*-means clustering, and plotting heatmaps with Deeptools (Ramirez et al. 2014). Bigwig tracks were visualized using integrative genomics viewer (IGV) (Robinson et al. 2011). Raw read counts on merged peaks were obtained using Bamliquidator (https://github.com/BradnerLab/pipeline/wiki/bamliquidator) and used as input for DESeq2 (Love et al. 2014) to identify differential peaks using the Wald test. Motif analysis was performed using HOMER using findMotifsGenome.pl (Heinz et al. 2010). ATAC-seq peaks were associated with mRNA changes using BETA (Wang et al. 2013). Promoters were defined as peaks between 2 kb upstream and 1 kb downstream from a TSS and the remaining peaks were considered enhancers.

To assess motif enrichment at ATAC-seq sites which display corroborative evidence of TF binding such as increased motif footprint depth (FPD) and/or chromatin accessibility flanking motifs (FA), we used Bagfoot (Baek et al. 2017). Briefly, paired-ended ATAC-seq data from $CDX2^{+}$ and control gastric organoids were used as input, adjusted for cut-count bias. Footprint depth (FPD) and flanking accessibility (FA, measured $\pm$200bp from motif centers) were calculated for each motif for the two conditions. The difference between FPD and FA for each motif was calculated between the two conditions and plotted as an XY bag plot, where the “bag” (dark blue) contains ~50% of data points and the surrounding “fence” (light blue) contains 97-100% of data points. Points falling outside the fence represent outliers with significant change between the two conditions.

RNA microarray analysis. Published RNA microarray data from gastric intestinal metaplasia (Companioni et al. 2017) were processed using the Applied Biosystems™ Transcriptome Analysis Console under default settings. The differential table was exported and used in a Pre-ranked Gene Set Enrichment Analysis (GSEA) against various gene sets (Fig. S2F).

RNA-Seq. Data were analyzed using the VIPER pipeline (Cornwell et al. 2018) and differential gene expression was determined by DESeq2 (Love et al. 2014) using the Wald test. Enrichment

for gene sets was performed by GSEA (Subramanian et al. 2005) (http://software.broadinstitute.org/gsea/index.jsp). Mouse genes were compared with human BE (Fig. 1E) on the basis of similar nomenclature. Differential genes identified by a Likelihood Ratio Test (Fig. 3E) were hierarchically clustered using the DEGreport package (http://lpantano.github.io/DEGreport/)(Pantano 2019) and plotted using the pheatmap package (Kolde 2019), both in R. Significant differences between two groups were evaluated using the hypergeometric test at http://nemates.org/MA/progs/overlap_stats.html. Ontologies for genes induced in gastric organoids (Figs. S1B-C) were determined using online tool enrichR (Chen et al. 2013; Kuleshov et al. 2016). Causal pathway analysis (Fig. S2A) was performed using QIAGEN Ingenuity Pathway Analysis (IPA) program under default parameters (Kramer et al. 2014). Differential gene expression between BE and stomach from Owen et al. was calculated using DESeq2 and used as input data for this analysis. Causal pathway analysis results were filtered for transcription factors and the activation z-scores were plotted using GraphPad Prism v9.2.0.

scRNA-seq. Single cell RNA-seq datasets (Busslinger et al. 2021; Nowicki-Osuch et al. 2021) and the respective metadata were downloaded. Normalized count data from Nowicki-Osuch et al. and raw count data from Busslinger et al. were processed into a Seurat format. We restricted further analysis to genes common to both datasets, which were normalized using SCTransform and integrated using Seurat's SCT integration protocol. Cell type assignments from each set's original metadata were retained in the integrated dataset. Cell clustering and UMAP plots were generated for the integrated dataset in Seurat. An undifferentiated gastric cell signature derived by Nowicki-Osuch et al. was determined by the average of the signature gene set counts in a cell (Nowicki-Osuch et al. 2021). Average scores in clusters were obtained by averaging cells within their respective clusters. An inbuilt table function in R was used to find overlapping counts between cell type assignment and cell cluster.

CUT&RUN. Sequence tags were analyzed using CUT&RUNTools (Zhu et al. 2019), a pipeline that includes alignment, trimming, length-based fragment filtering to identify fragments <120 bp, peak calling (MACS2)(Zhang et al. 2008), motif enrichment (Bailey et al. 2009), and DNA footprint analysis (Pique-Regi et al. 2011). A union set of MACS2-called narrow peaks from 3 intestinal villus CDX2 Cut&Run replicates was intersected with a union set of villus ATAC-seq and H3K27ac peaks (Saxena et al. 2017) to delineate the active CDX2-occupied cistrome (promoters and enhancers), which we used as input for the motif and footprint pipelines within

CUT&RUNTools. CDX2 peaks enriched for the motif and footprint were regarded to contact DNA directly, while the remaining regions were considered indirect binding sites.

ChIP-seq. DNA sequence tags were aligned against reference genome Hg19 using Bowtie2 v2.3.4.3(Langmead et al. 2009) and H3K27Ac-marked regions were identified using MACS v2.1.1 (https://github.com/taoliu/MACS) with the default cutoff q <0.01 (Zhang et al. 2008). H3K27Ac-marked regions located >2 kb from TSSs were designated as enhancers and bigwig files were generated by align2rawsignal (https://github.com/akundaje/align2rawsignal). Data were visualized using the Integrative Genomics Viewer(Robinson et al. 2011); heatmaps were prepared using Deeptools (Ramirez et al. 2016) v2.5.0.

Super-enhancers (SEs) were identified using ROSE (Loven et al. 2013; Whyte et al. 2013). Briefly, peaks within 12.5 kb were stitched together and overall signal strength was calculated based on total read counts. Peaks overlapping transcription start sites were excluded using 2.5 kb as the distance threshold. Peak strength and distribution were scaled from 0-1 and peaks with strength above the inflection point (defined as the point on the x-axis where a line with slope=1 was tangential to the curve of signal strength) were identified as SEs.

We used the Coltron algorithm to identify tissue-restricted master TFs (Fig. 4C) (Ott et al. 2018). Briefly, mouse stomach and intestine SEs were identified from H3K27Ac ChIP-seq data and SEs adjacent to or overlapping with TF genes were used to identify tissue master TFs. SE datasets from stomach and intestine were merged and tissue-specific ATAC-seq peaks within SEs were used to identify motif enrichment for master TFs using FIMO (Grant et al. 2011). Total H3K27Ac signal on all promoters was calculated for each tissue and genes with signal higher than the 50^{th} percentile were counted as expressed. If a master TF was not expressed in the stomach or intestine, its motif enrichment was not calculated in that tissue. Inward and outward binding were calculated as motif enrichment of master TFs within their own (inward) or other (outward) SEs. Scores for each master TF between stomach and intestine were subtracted to obtain the difference (Δ) in in/outward binding and hence identify tissue-restricted master TFs.

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Table S1. Genes activated in CDX2+ and HNF4A+ stomach organoids compared to GFP+ controls (Log2 fold-change >1, q <0.05)

CDX2 upregulated

Isx	S100a7a	Maoa	Abcg5	Trim15	Spink4	Aim2	Ahnak
Naip1	H2-Q1	Oxct2b	Ceacam1	Cbr2	Kcnk5	Serpinb9b	Fbp2
Myo7b	Tph1	Car8	Sema3e	Ifi27l2b	Stxbp1	Slc17a3	Prdm1
Gucy2c	Mgat4c	Cdhr2	Nlrp6	Trpv6	Exoc3l4	Pgap1	Steap1
Il5ra	Cldn15	Slc6a7	Dpysl3	Chga	St3gal3	Cdc42ep3	Fabp2
Cdhr5	Tmem236	Abcg8	Tmem200a	Pyy	Arhgap31	Abhd3	Oasl1
Wnt3	Clca4	Anxa13	Ms4a8a	Mall	Naip5	Mapt	Olfm4
Ms4a10	Pcsk5	Guca2a	Anks4b	Rasgrf2	Cd177	Dkk2	Btnl6
Tbx3	Aldob	Cyp2c65	Ctla2a	Myom3	Tmem246	Fads1	Tln2
Prkg2	Cyp2c55	Ddc	Pcsk1	Gp1bb	Il1rn	Epha4	Pde9a
Cdx1	AI747448	Ctss	Dse	Zdhhc14	Ces1g	Cd38	AA467197
Prap1	Rasa4	Pmp22	Nebl	Hpcal4	Reg4	Ehd2	Slc38a1
Muc13	Rhox5	Slc30a10	Ppp1r14d	Disp2	F3	Parp8	Mpp1
Heph	Tm4sf4	Btnl4	Slc17a4	Ly6c1	Aim1l	B4galt4	Slc18a1
Lypd8	Aoc1	Evx1	Bdnf	B3gnt7	Fam13a	Gsta2	Tmc5
Clrn3	Cdx2	Sult1d1	Myb	Nr1h4	Krt20	Ckb	Ggt6
Trim31	Pde4b	Mmd	Ttc7b	Aldh1a3	Ryr3	Plgrkt	Xkr5
B4galnt2	Slco2a1	S100g	Cidec	Cwh43	Cgref1	Gdf15	Tpm2
Gsdmc2	Atoh1	Bmp3	Phgr1	Aqp1	Entpd8	Cdc42ep2	Ank
Cdh17	Nat8l	Dynap	Myl7	Acta1	Akap2	Slc40a1	Sytl5
Gpr128	Clec2h	Ceacam18	Phospho1	Syne1	Gabrp	Rasl11a	Pde5a
Tff3	Cyp2c66	Scg2	Maf	Hopx	Tnfsf13b	Cited2	Cldn3
Tmem181c-ps	Otc	Abi3	Ntrk2	Clec2e	Pdlim1	Tnfrsf14	Pkp1
Serpina1e	Rbm11	Bmp8b	Cd200r2	H2-Q10	Cth	Pycard	Gstm6
Plcl2	Ccl6	Clca6	Dct	Myo1a	Tnfrsf8	Atp10b	Efnb2
Fgf15	Spsb4	Grb10	Slc2a12	Fmo4	Ston1	Pde1b	Mtm1
Gngt2	Abcb1a	Ms4a18	Lgals2	Jag1	Fbp1	Tnfaip2	Ripk3
Tm4sf5	Ugt1a1	Plac8	Cers4	Areg	Fam3c	Tmem158	Slc26a3
Adcyap1	Chst4	Zfp462	Gsta1	Ahrr	Depdc7	Lrp4	Guca2b
Ush1c	Cck	Vipr1	Kcnf1	Calml4	Nlrp9b	Trim36	Neto2
Adh6a	Dhrs9	Syt7	Fsd1l	Hmga2-ps1	Cyyr1	Car12	Gprin1
Gsdmc4	A1cf	Emp1	Rbp2	Wfdc13	Ankrd1	Cytip	Tnik
BC030870	Chgb	Dsg3	Upk3bl	Npas2	Wipf1	Mt3	Slc27a2
Tm4sf20	Ces2a	Mettl7b	Nid1	Chp2	Lgals3	Ky	Pcsk9
Crnn	Fndc1	Mgam	Lef1	Aldh1b1	Pappa2	Hsd17b13	Rph3al
Cyp4f14	H2-Q2	Cav1	Serpinb1a	Alpi	Tubb2b	Ildr1	Mfap3l
Ugt1a7c	Defa17	Btnl5-ps	Sema4g	Ceacam20	Smim24	Fam189a2	Frat2
Greb1	Fcgbp	Slc5a1	Dach1	Il22ra1	Dfna5	Ang4	Lor
Mep1b	Themis3	Ptprb	Rassf2	Mep1a	Rnf157	Lrat	Tmem37
Cyp2d34	Sct	P2rx2	S100a14	Scin	Pipox	Penk	Tm4sf1
Sis	Laptm5	Nt5c1a	Atp2b4	Cds1	E2f2	Rhof	Slc25a43

Scn2b	Hnf4g
Dapk2	Capg
Map6	Ctla2b
Kcnk6	Rab31
Serpina9	Slc39a14
Slc7a11	Grtp1
Lpar1	Krt4
Wbscr25	Utp14b
Cdca7	Syk
Dusp6	Nkain1
Nmnat2	Acot7
B4galt5	Car13
Aprt	Fyn
Pim1	Pax8
Metrnl	Prkca
Cyp2d26	Ces2c
Dock5	Pawr
Stc2	Slc2a9
Edn3	Bdh1
Rhoc	Gulp1
Elovl6	Ifi27
Cd274	Itpk1
Enpp2	Stk32c
Rasa3	Cxcl16
Pip5k1b	Krt8
Mgat5	Vstm5
Mlxipl	Ly6a
Peli1	Epsti1
Cisd3	Pgp
Phf21b	
Slc4a11	
Kalrn	
Gipc2	
Cd55	
St6gal1	
Pvrl3	
Trim40	
Abcg2	
Rnasel	
Fam213a	
Tnfrsf1b	
Atp8a2	
Sytl2	

HNF4A upregulated

Prap1	Agmat	Pla2g12b	Dfna5	Cd38
Cps1	Tfr2	Nid1	Calml4	Fgl2
Myo7b	Cyp2d10	Glod5	Cth	Vipr1
Gucy2c	Cdh17	Cfb	Ush1c	Fabp2
Cdhr5	Btnl4	Myo1a	Nebl	Hnf4a
Apoc2	Mep1a	Cidec	Ifi27l2b	Il22ra1
Aldob	B4galnt2	Abcb1a	Onecut2	Slc39a14
Trim31	Apoa1	Reg3b	Unc5cl	Phospho1
Tm4sf5	Pcsk5	Myb	Exoc3l4	Dak
Clrn3	Plcl2	Ddc	Itga1	Wipf1
A1cf	Hsd17b2	Plac8	Tcea3	Nr1i3
Cyp2d34	Ckb	Wnt3	Hopx	Xylb
Cyp2c66	Rdh7	Ky	Abcg2	Lrp4
Cyp2d26	Tmem82	Lrp2	Igsf23	Reg3g
Cyp3a25	Ppp1r14d	Gsta1	Fcgbp	Oasl1
Isx	Laptm5	Aqp1	Aldh1b1	Disp2
Prkg2	Slco2a1	Smim24	Clca6	Bdh1
Tm4sf20	Btnl5-ps	Nlrp6	Serpinb1a	Trim40
Slc6a7	Aadac	Tmem246	Ggt6	Tpmt
Lyz1	Ugt1a7c	Abcc6	Adtrp	Aqp11
Cyp2c29	Prlr	Cdx2	E2f2	Pcsk9
Naip1	Cdhr2	Slc5a1	Nr1i2	Fbp2
Cyp4f14	Clca4	Mlxipl	Fst	Lef1
Heph	Abcg5	Defa17	Fbln1	Npas2
Cyp2c68	Anks4b	Sema4g	Kcnf1	Kcnk5
Cyp2c55	Gstm3	Lgals2	Fam20a	Ehhadh
Cyp2d9	Ces1g	Pnp2	Zfp462	Angptl4
Adh6a	Fmo4	Alpi	Phgr1	Grtp1
Muc13	H2-Q10	Cgref1	Slc2a9	Tmem54
Cdx1	Acta1	Slc17a4	Tnik	Jag1
Cldn15	Apob	Slc27a2	Cyp3a11	Ston1
Pipox	Cyp2c65	Chgb	Dach1	Gcat
Otc	Sult1d1	Tmc5	H2-Q1	Phf21b
Mep1b	Ttr	Nags	Cyp2d22	Crip1
Lypd8	Ces2a	Dpysl3	Tubb2b	Dse
Aoc1	Tm6sf2	Rasgrf2	Ceacam1	Dnm1
Serpinf2	Sult1b1	H2-Q2	Gprin3	Pde5a
Krt20	Apoa4	Ms4a8a	Pklr	B4galnt3
Mettl7b	Fbp1	Igf2bp3	Eif4e3	Dennd5b
Abcg8	Cyp2b10	Odf3b	Soat2	Cisd3
Tff3	AI507597	Abi3	Cideb	Rnf157
Ms4a10	Ces2e	Akap2	Hmga2-ps1	Ada
Slc7a9	Mgam	Dpyd	Ttc7b	
Hsd17b13	Pnliprp2	Themis3	Naip5	

Table S2. Sequencing and quality parameters for ATAC-seq analysis of organoids

	CDX2+ gastric organoids		
	CDX2_Line1	CDX2_Line2	CDX2_Line3
Total reads	57,389,124	50,559,785	59,056,797
MAPQ score > 30	54,277,560	48,361,195	55,818,503
Fraction of reads in peaks (FRiP) score	0.07	0.06	0.16
Non redundant fraction (NRF)	0.86	0.86	0.85
PCR Bottlenecking coefficient (PBC) 1	0.86	0.86	0.85
PCR Bottlenecking coefficient (PBC) 2	7.35	7.10	6.78

	HNF4A+ gastric organoids		
	HNF4A_Line1	HNF4A_Line2	HNF4A_Line3
Total reads	47,708,767	52,386,610	63,965,066
MAPQ score > 30	45,145,841	49,745,083	61,055,907
Fraction of reads in peaks (FRiP) score	0.08	0.16	0.26
Non redundant fraction (NRF)	0.86	0.85	0.84
PCR Bottlenecking coefficient (PBC) 1	0.86	0.85	0.84
PCR Bottlenecking coefficient (PBC) 2	7.25	6.57	6.41

	GFP+ gastric organoids		
	GFP_Line1	GFP_Line2	GFP_Line3
Total reads	56,588,547	58,990,891	57,596,775
MAPQ score > 30	53,538,131	56,465,451	54,821,685
Fraction of reads in peaks (FRiP) score	0.08	0.18	0.28
Non redundant fraction (NRF)	0.84	0.85	0.84
PCR Bottlenecking coefficient (PBC) 1	0.84	0.85	0.85
PCR Bottlenecking coefficient (PBC) 2	6.34	6.79	6.58

	Intestinal organoids	
	Intorg_Line1	Intorg_Line2
Total reads	67,341,079	51,265,782
MAPQ score > 30	65,140,806	49,121,445
Fraction of reads in peaks (FRiP) score	0.39	0.15
Non redundant fraction (NRF)	0.85	0.86
PCR Bottlenecking coefficient (PBC) 1	0.85	0.86
PCR Bottlenecking coefficient (PBC) 2	6.78	7.35

Suppl. Table S3. HNF4A binding regions identified using CUT&RUN

Binding regions in HNF4A+ gastric organoids			Binding regions in GFP+ (control) gastric organoids		
Chromosome	Coordinates		Chromosome	Cordinates	
chr1	3514903	3515233	chr1	3515024	3515193
chr1	4538499	4538576	chr1	24611652	24612011
chr1	6804604	6804677	chr1	24612106	24612699
chr1	6973725	6974072	chr1	24612864	24613055
chr1	7088772	7088962	chr1	24613216	24615572
chr1	7498656	7498740	chr1	24615664	24616107
chr1	9535826	9535989	chr1	37864965	37865057
chr1	9748426	9748620	chr1	58613905	58614022
chr1	9748730	9748894	chr1	95451936	95452046
chr1	10257307	10257447	chr1	102628211	102628306
chr1	10285560	10285687	chr1	157877278	157877384
chr1	12000529	12000684	chr1	167340306	167340387
chr1	15615741	15615893	chr1	179743686	179743856
chr1	15877207	15877532	chr1	183299149	183299588
chr1	15908675	15908772	chr1	192454038	192454128
chr1	15937671	15937756	chr1	193227811	193227924
chr1	16199476	16199646	chr1	195241698	195241868
chr1	16228292	16228658	chr1	195371720	195371935
chr1	16235033	16235344	chr10	3109929	3110053
chr1	16241015	16241303	chr10	16256467	16256546
chr1	20820341	20820484	chr10	19591789	19591868
chr1	20863905	20864024	chr10	22142299	22142379
chr1	21132468	21132659	chr10	22142493	22143043
chr1	21482870	21483189	chr10	26828817	26828995
chr1	21499900	21500044	chr10	37820461	37820541
chr1	23255987	23256168	chr10	70222386	70222476
chr1	24611581	24612707	chr10	96077627	96077717
chr1	24612797	24613063	chr10	118804654	118804742
chr1	24613180	24616129	chr10	130594790	130594986
chr1	33691579	33691666	chr11	3162631	3162733
chr1	34120702	34120780	chr11	31922693	31922785
chr1	35931097	35931262	chr11	34544920	34544998
chr1	36093918	36094027	chr11	34681855	34682171
chr1	36244280	36244410	chr11	54140080	54140294
chr1	36271726	36271813	chr11	54140523	54140671
chr1	36547241	36547335	chr11	57176103	57176190
chr1	36647709	36647841	chr11	98653099	98653205
chr1	36920181	36920388	chr11	105102990	105103070
chr1	36971358	36971433	chr11	109011650	109012079
chr1	37026038	37026233	chr11	121982367	121982529
chr1	37027039	37027134	chr12	3109871	3110107

chr1	37522233	37522379	chr12	16747816	16747913
chr1	37568459	37568540	chr12	41515115	41515193
chr1	37687765	37687858	chr12	67059372	67059620
chr1	37694780	37694858	chr12	69654102	69654240
chr1	37865103	37865330	chr12	74804398	74804503
chr1	37954712	37955015	chr12	78350921	78351122
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Table S4. Sequencing and quality parameters for ATAC-seq on intestinal and gastric Lgr5+ stem cells and for H3K27ac ChIP-seq on gastric antral epithelium

	Gastric antrum H3K27Ac ChIP-seq	
	Replicate 1	Replicate 2
Total reads	56,073,649	46,095,088
MAPQ score > 30	54,517,407	44,694,576
Fraction of reads in peaks (FRiP) score	0.14	0.17
Non redundant fraction (NRF)	0.90	0.90
PCR Bottlenecking coefficient (PBC) 1	0.90	0.90
PCR Bottlenecking coefficient (PBC) 2	9.49	10.38
	Gastric LGR5+ Stem Cell ATAC-seq	
	Replicate 1	Replicate 2
Total reads	6,557,827	7,437,887
MAPQ score > 30	6,295,518	7,167,308
Fraction of reads in peaks (FRiP) score	0.18	0.17
Non redundant fraction (NRF)	0.69	0.72
PCR Bottlenecking coefficient (PBC) 1	0.68	0.72
PCR Bottlenecking coefficient (PBC) 2	3.14	3.63
	Intestinal LGR5+ stem cell ATAC-seq	
	Replicate 1	Replicate 2
Total reads	24,931,871	33,685,151
MAPQ score > 30	24,540,451	33,268,909
Fraction of reads in peaks (FRiP) score	0.38	0.14
Non redundant fraction (NRF)	0.75	0.83
PCR Bottlenecking coefficient (PBC) 1	0.80	0.85
PCR Bottlenecking coefficient (PBC) 2	5.81	6.84

Suppl. Table S5. Genes downregulated in HNF4A-overexpressing Δenh stomach organoids

Homozygous enhancer deletion vs. wild type enhancer			
Eif2s3y	Lgals2	Mep1b	Aoc1
Ddx3y	Gcnt3	H2-Q2	Gm3336
Uty	Krt79	Trim40	Btc
Akp3	Cdh17	Ms4a10	Col18a1
Kdm5d	LOC102631757	Dmkn	Ripk3
Alpi	Vipr1	S100a14	Jag1
Gkn2	Pcsk5	Ceacam18	Psapl1
Cdx2	Clca4	Gkn1	Myl7
Trim29	Trim31	Clrn3	Sema4b
Ms4a18	Aldob	Bmp8b	Tctex1d4
Uts2	Prl2c2	Tm4sf5	Abhd11os
Tff3	Rptn	Prss22	Mgat5
Mgat4c	Nlrp9b	Abhd3	Spink4
Aldh1a3	Nid1	Hs3st1	Dock8
Ugt1a7c	Mall	Slc17a4	Slc4a11
Dpcr1	Gucy2c	Plac8	Gprc5a
Clca3	Il1rn	Entpd8	Pde5a
Fcgbp	Angptl4	Btnl4	Flnb
Pbp2	Fst	Krt4	Ly6a
Myo7b	Slc6a7	Atp2a3	Cidea
Tff1	Cyp2c65	Sh3kbp1	Cidec
Ereg	F3	Kcnj11	Plau
Heph	Slc2a6	Rhof	Phgr1
B4galnt2	Gsta1	Btnl6	Arhgap40
Lypd8	Abcb1a	Gsta2	Ptgs2
B4galt4	Gml	Sdcbp2	Sema4g
Naip1	Hpcal4	Efnb2	Mapk11
Ivl	Adh6a	Aim1l	Plat
Muc13	Smoc1	Tmem40	Pear1
Ush1c	Cps1	Cyp4f14	Plgrkt
Krt20	Ly6d	Sprr1a	Car12
Tcf23	Oasl1	Hemt1	Sema3e
Prap1	Gm3776	Ildr1	Ceacam1
Areg	Ecm1	Sema7a	Tmem106a
Slc26a3	Fabp2	Epas1	Fhdc1
Abcc8	Cers4	Tspan12	Dhrs11
Cdx1	Dok2	Plk3	Tsku
Slc5a1	S100a7a	Cwh43	Cds1
Cdhr5	Sh2d5	Fam101b	

Heterozygous enhancer deletion vs. wild type enhancer			
Uty	Gcnt3	Sdcbp2	Ubash3b
Eif2s3y	Gm3776	Phgr1	Dll4
Kdm5d	Krt85	Cdhr5	Heph
Ddx3y	Abcb1a	Tm4sf5	Phlda2
Gkn2	Mall	Pax8	Abcc3
Akp3	Nid1	Bmp8b	
Ms4a18	Gsta1	Oasl1	
Dpcr1	Naip1	Hs3st1	
Alpi	B4galt4	H2-Q2	
Ivl	Cdh17	Aim1l	
Uts2	Tnni2	Kcnk5	
Tff3	Fst	Cds1	
Prl2c2	B4galnt2	Entpd8	
Clca3	Slc5a1	Strc	
Tmem236	Ereg	Cdhr2	
Tff1	Btnl6	Stc2	
Fcgbp	Gm3336	Hpcal4	
Krt20	Ecm1	Paqr5	
LOC102631757	Tchh	Gprc5a	
Zg16	Mslnl	Epas1	
Ugt1a7c	F3	Paqr8	
Ceacam18	Slc17a4	Psca	
Krt4	Lgals2	Prkcg	
Trim31	Dmkn	Fam101b	
Gml	Krt79	Tsku	
Lypd8	Cidec	Slc30a10	
Aldh1a3	Cdx2	Plac8	
Prap1	Pcsk5	Hemt1	
Areg	Sprr1a	Trim40	
Pbp2	Ildr1	Kcnj11	
Tcf23	Atp2a3	Cidea	
Slc2a6	Sptssb	Sema4b	
Il1rn	Unc5c	Krt19	
Gkn1	Muc13	Cyp2s1	
Ly6d	Abhd3	Sh2d5	
Il5ra	Rhof	Dhrs11	
Slc26a3	Mep1b	Psapl1	
Cyp2c65	Cyp2d34	S100g	

Suppl. Table S6. Primers and sgRNA sequences to generate and genotype Cdx2 3' enhancer deletion mice

sgRNA target sites	
sgRNA Cdx2_1	ATCTCCCGCAGTCTGAACTT
sgRNA Cdx2_2	GGATGGTTGGGGGTCGCTAA

In vitro transcribed oligonucleotides	
For sgRNA_Cdx2_1	GAAATTAATACGACTCACTATAGGATCTCCCGCAGTCTGAACTTGTTTTAGAGCTAGAAATAGCAAGTTAAAATAAGGCTAGTCCG
For sgRNA_Cdx2_2	GAAATTAATACGACTCACTATAGGGGATGGTTGGGGGTCGCTAAGTTTTAGAGCTAGAAATAGCAAGTTAAAATAAGGCTAGTCCG
DS_IVT_reverse	AAAAAAGCACCGACTCGGTGCCACTTTTTCAAGTTGATAACGGACTAGCCTTATTTTAACTTGC

Genotyping primers	
Cdx2e_F	ACGGTACAAAGGGGCTCTTT
Cdx2e_WT_Reverse	CTGGGAAGAGCTGGGGATTG
Cdx2e_Del_Reverse	TAGACGTGTAGGGGTGGAGG