The identification of DNA binding regions of the σ54 factor using artificial neural network

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Abstract

Transcription of many bacterial genes is regulated by alternative RNA polymerase sigma factors as the sigma 54 (σ54). A single essential σ promotes transcription of thousands of genes and many alternative σ factors promote transcription of multiple specialized genes required for coping with stress or development. Bacterial genomes have two families of sigma factors, sigma 70 (σ70) and sigma 54 (σ54). σ54 uses a more complex mechanism with specialized enhancers-binding proteins and DNA melting and is well known for its role in regulation of nitrogen metabolism in proteobacteria. The identification of these regulatory elements is the main step to understand the metabolic networks. In this study, we propose a supervised pattern recognition model with neural network to identify Transcription Factor Binding Sites (TFBSs) for σ54. This approach is capable of detecting σ54 TFBSs with sensitivity higher than 98% in recent published data. False positives are reduced with the addition of ANN and feature extraction, which increase the specificity of the program. We also propose a free, fast and friendly tool for σ54 recognition and a σ54 related genes database, available for consult. S54Finder can analyze from short DNA sequences to complete genomes and is available online. The software was used to determine σ54 TFBSs on the complete bacterial genomes database from NCBI and the result is available for comparison. S54Finder does the identification of σ54 regulated genes for a large set of genomes allowing evolutionary and conservation studies of the regulation system between the organisms.

Keywords: Artificial intelligence, pattern recognition, feature extraction.

1. Background

Prokaryotic transcription process starts from the recognition of binding site on DNA sequence by RNA polymerase. The DNA dependent RNA Polymerase (RNAP) is the main enzyme in the transcription and gene expression [1]. It is composed of two subunits, the core enzyme α2ββ with the catalytic site of polymerization and the sigma factors, responsible for promoter recognition [1]. When the enzyme is linked with the sigma factor protein, the complex is called of RNAP holoenzyme (α2ββ'σ) and is ready for transcription [2].

Bacterial genomes have two families of sigma factors, sigma 70 (σ70) and sigma 54 (σ54). σ70 is the best studied and is responsible for transcription of the most bacterial genes in the exponential growth [3]. σ54 uses a more complex mechanism with specialized enhancers-binding proteins and DNA melting and is well known for its role in regulation of nitrogen metabolism in proteobacteria [4].

Each sigma factor recognizes different binding sites in the DNA sequence and is responsible for changing the transcription pattern mediated thorough redirection of transcription initiation [5]. The identification of these regulatory elements is the main step to understand the metabolic networks [6].

A single essential σ promotes transcription of thousands of genes and many alternative σ factors promote transcription of multiple specialized genes required for coping with stress or development [7].

The number of sigma factors varies from one in *Mycoplasma genitalia* [8], seven in *Escherichia coli* [9] to more than 60 in *Streptomyces coelicolor* [10].

It was already shown that σ70 recognize a consensus sequence of hexamers placed between -10/-35 nucleotides upstream the start site and σ54 recognize high GC sequences located -24/-12 nucleotides upstream from the start site [11].

The σ54 factor has an important role in agriculture, due to the control of gene transcription, regulating the nitrogen fixation process that provides ammonia for the plant. This process dispenses chemical soil fertilization, reduces costs and protects the environment [12].

The classical approach for promoter prediction involves the development of algorithms that uses position weight matrices (PWMs) [13-17]. More recently, several methods propose the automatic identification of Transcription Factor Binding Sites (TFBSs) like Gibbs sampling algorithm [18, 19], genetic algorithms [20], and statistical over-representation [21, 22]. These methods works with single and double motifs identification but with a high false positive rate [23], and don't allow complete genome sequences.

In this study, we propose the use of a supervised pattern recognition model with neural network to identify TFBSs for σ54 for whole genome sequence. The advantages of using neural network in pattern recognition include its generalization ability considering both the nonlinear and the diffuse nature of the datasets [24] and also can achieve high performance when processing extended genome sequences [25].

We also propose a free, fast and friendly tool for σ54 recognition and a σ54 database available for consult.

2. Methods

2.1. Candidates sequences for σ54 TFBS and features extraction

The set of intergenic regions to search for σ54 TFBSs candidates was defined as a range of 200 bases from the transcriptional start site of each coding sequence. Candidate sequences were set on 16 bases. The selection was done considering the presence of conserved bases (GG and GC) located in -14/-15 and -2/-3 positions [11]. 18 features were extracted from the candidate sequences. The first sixteen were the nucleotides encoded to numbers (A: 0.0; C: 1.0; G: 2.0; T: 3.0); the 17th feature was the result of the alignment of the candidate sequence with the consensus sequence, extracted from experimentally confirmed sequences available in literature [11, 26, 27]; and the 18th feature was the result of the alignment of the sequence candidate with a consensus of the less frequent bases (present in the true sequences- called as anti-consensus).

2.2. Training data set

Networks were trained using groups of positive sequences collected in the literature and sequences artificially generated, considered as negatives. Those sequences were generated using the MatLab algorithm of string generation. The artificially generated strings were divided into two groups, the first group have only nucleotide base pairs and the same string length of positive sequences. In other side the second group uses also the same length, but it also includes the conserved base pairs shown in the positive sequences.
Positive patterns were defined by sequences experimentally retrieved [26, 27] and a database with 5662 sequences from more than 60 genomes, available in www.sigma54.ca web site [28]. The artificial dataset comprised two groups of random sequences. The groups had the same number of bases observed in the positive pattern and differ by the presence and absence of the highly conserved bases (GG and GC).

2.3. ANN test

Tests with MLP (*Multilayer perceptron*), FAN (*Free Associative Neurons*), RBF (*Radial Basis Function*) and SVM (*Support Vector Machine*) neural networks were performed. RBF and SVM did not show better results than MLP and FAN neural networks. The best architecture used to classify the sequences using MLP neural network had 7 neurons in the first hidden layer and three neurons in the second one. For FAN neural network we used the default setting with fuzzy set support of 100, diffuse neighboring of 6, shuffling the training set every time. The accuracy for each neural network tested on the same database was 95.19% for MLP and 97.95% for the chosen one, the FAN network (**Table 1**).

Table 1. Performance comparison for neural networks.

	MLP	FAN
True positives, %	92.15	**95.51**
False positives, %	3.29	2.09
True negatives, %	96.71	97.91
False negatives, %	7.85	4.49
Accuracy, %	95.19	**97.95**

The ANN test was performed using 3 datasets from published studies comprising 281 proposed σ54 TFBS sequences that were not used for training (**Table 2**). For more recent data, the sensitivity test showed more than 98% of right predictions for σ54 binding sites sequences. The decrease of sensitivity observed on Barrios database was due to the presence of candidate sequences in the σ54 TFBS database.

Table 2. ANN sensitivity in comparison with published data.

Dataset	ANN Positive	Total	Sensitivity (%)
Studholme, 2000 [29]	34	34	100
Leang, 2009 [30]	90	91	98.9
Barrios, 1999 [11]	127	156	81.4

The sequences that did not had the conserved bases GG and GC and without known amino acids, were excluded from the test.

2.4. S54Finder tool

S54Finder is a fast tool developed to work with complete genome sequences. It works with annotated sequences stored in a gbk file format parsing the information to perform the analysis. If the query is a flat fasta file the software uses an in-house ORFinder to identify and annotate the coding regions and extract the intergenic sequences. The output of the S54Finder is 2 files, a new gbk file with the predicted σ54 sequences marked and a text file with the predicted sequences and related ORFs positions to download.

3. Results and discussion

There is no TFBSs consensus for σ54, with only few sequences confirmed in laboratory. Several studies present candidate sequences as consensus but the size usually is not the same, since it differs between species. What is observed is that among the vast majority of the sequences there are at least 4 (GG and GC) conserved bases. This scenario turns difficult the pattern recognition since it increases the false positive rate. To overcome this problem we added the anti-consensus feature, which allow us to decrease candidate number usually observed in other tools. To test S54Finder false positive rate we used 20^{12} sequences generated by combination of bases preserving the high conserved ones (GG and GC). The results showed that S54Finder identified, from the total of possibilities, 1.89% of σ54 candidate sequences. This result confirms a high specificity of the S54Finder software.

We tried to compare S54Finder with other available tools such as GenomeMatScan, but the test was not possible since GenomeMatScan does not perform whole genome predictions. The main features between the two software applications are contrasted in **Table 3**.

Table 3. Comparison between S54Finder and GenomeMatScan software.

	S54Finder	GenomeMatScan
Web version	Yes	Yes
Local processing	Yes	No
Method	FAN	HMM
Data entry	Genbank file (.gbk)	Input data copy-pasted into the browser
Results	Output in Genbank formats (.gbk), MatLab (.mat) and text	Shown in browser
Processing large regions of DNA	Yes (complete genomes)	No

HMM: Hidden Markov Models.

The distinguish feature of S54Finder is the ability to perform fast whole genome predictions. This allowed us to search for TFBSs in complete bacterial genomes across the entire NCBI database. From the complete genomes, s54finder obtained 79626 CDS sequences which could be ranked by the level of TFBSs occurrence next to homologous genes of different species.

An in house tool was employed to cluster the CDS. A set of 9417 homologous CDS groups, within 2 or more homologous occurrences were determined. The minimal relative score considered to group a pair of genes was 0.5. To determine the annotation to be considered for each gene cluster we implemented a kmeans to support the choice in the set of original annotations.   The generated data – TFBSs, CDSs, annotation, Homologous clusters – were gathered to perform a FASTA/BLAST formatted data base available and a web site (http://200.236.3.16/s54.php), that is available to validate the S54Finder predictions. **Table 4** presents a list with the 29 groups that occurred 100 or more times. The glutamine synthetase protein and the nitrogen regulatory protein P II appears in the top of the list with 379 and 329 occurrences, respectively. Due to the importance of these proteins in the biologic nitrogen fixation their presence in the top predicted list was expected. We proposed a score to determine the correlation of a word present in an NCBI annotation found by s54finde with conserved clusters of genes related to TFBS. A binary matrix where columns represent the occurrence of each word and the lines the homologous groups, was joined to a column containing the number of occurrences of the respective homologous group, T. The ws54score of a word is then the Pearson correlation between the column that represent the word and homologous amount column, T. Our purpose was to identify possibly related words to σ54 regulated genes. Highest ws54scores were associated to gene names like glnL (0.3711), glnB (0.2959), glnE (0.2959) and PII (0.2959), whose association with the σ54 promoter is well known. However, words like MtrA and Thi1, also appeared in the top 10 list though not common in the literature; unknown conserved domains also appeared - DUF2233 (4) and DUF2971 (11) - in the top 15 list and we suppose they are likely related to the σ54. The list with annotation words and s54scores is in the **Additional File**.

4. Conclusion

The S54Finder presents good results regarding research in bacterial genomes. The main advantage is the fact that it is faster than other available tools. The pre-selection of candidates without the use of neural networks has shown that the pattern of conservation, based on published sequences and biologically confirmed, is capable of locating binding sites in bacterial genomes, but generates many false positives.

False positives are reduced with the addition of ANN and feature extraction, which increase the specificity of the program. S54Finder allows the user the identification of σ54-regulated genes for a large set of genomes allowing evolutionary and conservation studies of the regulation system between the organisms. The tool and the σ54 database are freely available in web.

5. Authors' contributions

Following are the contributions of the authors to the work described in this paper. LMF: acquisition of data; analysis and interpretation of data; RTR: made substantial contributions to conception and design of the study; analysis and interpretation of data; JNM: have been involved in drafting the manuscript or revising it critically for important intellectual content; have given final approval of the version to be published; VAW: have been involved in drafting the manuscript or revising it critically for important intellectual content; have given final approval of the version to be published; ICRSW:

have been involved in drafting the manuscript or revising it critically for important intellectual content; have given final approval of the version to be published; PAB: analysis and interpretation of data; RV: participated in the website development and revising the manuscript; LUR: made substantial contributions to conception and design of the study. All authors read and approved the final manuscript.

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Order Word                              Score

    1  glnL                             0.3711
    2  MtrA                             0.3398
    3  ThiI                             0.3398
    4  DUF2233                          0.3398
    5  decaheme                         0.3398
    6  GlnB4                            0.29591
    7  GlnE                             0.29591
    8  MEMO                             0.29591
    9  urydylation                      0.29591
   10  ATase                            0.29591
   11  DUF2971                          0.29591
   12  P2                               0.29591
   13  putative                         0.28231
   14  fused                            0.27864
   15  GlnA                             0.27173
   16  of                               0.26583
   17  subunit                          0.26494
   18  GlnG                             0.25621
   19  system                           0.25578
   20  BipA                             0.2491
   21  GlnK                             0.24069
   22  ISBma2                           0.24005
   23  HscA                             0.23875
   24  for                              0.23822
   25  Pentoside                        0.23811
   26  regulator                        0.23229
   27  QueC                             0.23164
   28  membrane                         0.22939
   29  component                        0.22563
   30  specific                         0.22547
   31  AmtB                             0.22453
   32  transcriptional                  0.21938
   33  muropeptide                      0.21612
   34  transporter                      0.21596
   35  binding                          0.2138
   36  DNA                              0.21159
   37  ammonia                          0.21119
   38  by                               0.21095
   39  periplasmic                      0.20893
   40  YjeF                             0.20772
   41  interface                        0.20637
   42  phosphate                        0.2039
   43  family                           0.19994
   44  protein                          0.19695
   45  permease                         0.19668
   46  NtrC                             0.19423
   47  RarD                             0.19317
   48  in                               0.19213
   49  Flags                            0.18908
   50  ClpX                             0.18842
   51  queuosine                        0.18842
   52  glutamate                        0.18803
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53	unknown	0.18234
54	type	0.18205
55	dependent	0.182
56	function	0.18026
57	SufB	0.17839
58	xanthine	0.17827
59	diffusion	0.17625
60	murein	0.17586
61	Empty	0.17556
62	dehydrogenase	0.17545
63	galaxtoside	0.17522
64	connecting	0.17522
65	HBP	0.17522
66	PdxB	0.17522
67	locus	0.17241
68	ABC	0.17221
69	biosynthesis	0.17205
70	pectin	0.17205
71	polar	0.17027
72	inner	0.17015
73	like	0.17004
74	GlnB	0.16994
75	kinase	0.1689
76	PAP2	0.16888
77	acid	0.16851
78	Hexuronide	0.1685
79	tricarboxylate	0.1683
80	PTS	0.16826
81	PadR	0.16758
82	RecG	0.16667
83	sensing	0.16576
84	III	0.16425
85	YVTN	0.16424
86	ExaC	0.16424
87	achromobactin	0.16424
88	XkdN	0.16424
89	TctA	0.16424
90	synthetase	0.16413
91	formation	0.16385
92	sigma	0.16298
93	and	0.16239
94	20S	0.16059
95	nitrogen	0.1603
96	GTP	0.15945
97	Predicted	0.15833
98	portion	0.15793
99	glucitol	0.15752
100	II	0.15708
101	NR	0.15673
102	reductase	0.15659
103	arsenate	0.1557
104	acetylmuramoyl	0.15565
105	FhlA	0.1541
106	TypA	0.15374

107	assimilatory	0.15368
108	hydrolase	0.15311
109	Tyr	0.15262
110	chain	0.15088
111	guanosine	0.15075
112	RNA	0.15043
113	CsiR	0.14888
114	superfamily	0.14845
115	LivK	0.14829
116	NS2	0.14758
117	factor	0.14732
118	beta	0.14723
119	diaminohydroxyphosphoribosylaminopyrimidine	0.14694
120	FeS	0.14671
121	gamma	0.14658
122	protoporphyrin	0.14647
123	camphor	0.14609
124	nucleotide	0.14574
125	ATP	0.14555
126	modulated	0.14538
127	ISSfl2	0.145
128	into	0.145
129	coproporphyrinogen	0.14478
130	AsmA	0.14478
131	IIBC	0.14426
132	ribosomal	0.14386
133	StyLTI	0.14321
134	PrpR	0.14321
135	PrpB	0.14321
136	repressor	0.14184
137	CrcB	0.141
138	efflux	0.14097
139	RetS	0.14047
140	IS1665	0.14047
141	UrtC	0.14047
142	UrtE	0.14047
143	uera	0.14047
144	AmiC	0.14047
145	TTT	0.14047
146	invasin	0.13984
147	La	0.1396
148	signal	0.13906
149	Precursor	0.13905
150	activase	0.13903
151	carboxypeptidase	0.138
152	TC	0.13733
153	multidrug	0.13704
154	IS902	0.13694
155	IS116	0.13694
156	54	0.13639
157	operon	0.13596
158	interaction	0.13523
159	bound	0.13383
160	lyase	0.13326

161	synthase	0.13302
162	EIIB	0.13298
163	transaldolase	0.13284
164	Lysine	0.13231
165	chb	0.13224
166	chitobiose	0.13224
167	YeaH	0.13224
168	AstC	0.13224
169	ArgM	0.13224
170	pentulose	0.13224
171	tyrosyl	0.1317
172	Two	0.1316
173	Ntr	0.13142
174	alpha	0.13059
175	Ile	0.13039
176	chelatase	0.12978
177	Fis	0.12977
178	sigma54	0.1296
179	accessory	0.12953
180	resistance	0.12938
181	thioesterase	0.12915
182	ArgT	0.12883
183	HU	0.12872
184	containing	0.12778
185	val	0.12735
186	leu	0.12735
187	arginine	0.12685
188	succunate	0.12675
189	CoxI	0.12675
190	PhoQ	0.12675
191	nifK	0.12675
192	NifH2	0.12675
193	nifD	0.12675
194	DedA	0.12648
195	with	0.12616
196	racemase	0.12577
197	lytic	0.12495
198	acetaldehyde	0.12453
199	oligosaccharide	0.12401
200	salt	0.12401
201	CelA	0.12401
202	YeaG	0.12401
203	autokinase	0.12401
204	LicB	0.12401
205	TrmB	0.12401
206	sulfur	0.12294
207	transmembrane	0.12257
208	IIA	0.1224
209	oxidoreductase	0.12235
210	the	0.12145
211	amide	0.12137
212	residue	0.12107
213	expression	0.12063
214	IS110	0.12063

215	glucan	0.12051
216	Mg	0.12051
217	HypA	0.1203
218	IIC	0.11999
219	CheR	0.11989
220	enzyme	0.11979
221	isoenzymes	0.11913
222	NtrB	0.11898
223	domain	0.11895
224	outer	0.11894
225	protease	0.11873
226	RbsR	0.11852
227	inversion	0.11852
228	HBsu	0.11852
229	HupB	0.11852
230	DUF1481	0.11852
231	aminotransferase	0.11816
232	ZraS	0.11784
233	ZraR	0.11784
234	alternative	0.11767
235	nitrite	0.11767
236	histidine	0.11719
237	Methyltransferase	0.11677
238	ligase	0.11673
239	Peptidase	0.11637
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265	FlRd	0.11212
266	AexT	0.11212
267	TTSS	0.11212
268	proW	0.11212

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271	mandelate	0.11179
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273	small	0.11101
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276	phenylalanyl	0.10953
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278	translocation	0.10883
279	tripartite	0.10869
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285	manno	0.10813
286	transglycosylase	0.10813
287	Response	0.108
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289	cysQ	0.10755
290	DUF1107	0.10755
291	PapS	0.10755
292	amidophosphoribosyltransferase	0.10744
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321	HycA	0.1022
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911	Low	0.046244
912	antibiotic	0.046214
913	CRP	0.045921
914	suppresses	0.04592
915	HflX	0.045866
916	2S	0.04578

917	2Fe	0.04578
918	23S	0.045744
919	ACP	0.045735
920	yddR	0.045422
921	deacetylase	0.045419
922	SugE	0.045338
923	quaternary	0.045338
924	AtoS	0.045338
925	homocysteine	0.045316
926	Exonuclease	0.045111
927	Luciferase	0.045085
928	converting	0.04507
929	FtsE	0.04504
930	entericidin	0.045038
931	deoxyheptonate	0.04495
932	UPF0319	0.04481
933	deoxyguanosinetriphosphate	0.044627
934	U8	0.044461
935	ACN	0.044461
936	siderophore	0.044365
937	MS	0.044222
938	butyrate	0.044124
939	60	0.044124
940	sodium	0.044078
941	aminopeptidase	0.043999
942	Mal	0.043965
943	dipeptidyl	0.043921
944	biotin	0.043693
945	trancsriptional	0.043667
946	rubrerythrin	0.043657
947	box	0.043624
948	Glutaredoxin	0.043465
949	VII	0.043341
950	HflC	0.043226
951	Insulin	0.043226
952	EF	0.04301
953	delta	0.042956
954	SoxR	0.042698
955	subIIB	0.042632
956	manL	0.042632
957	hydratase	0.042452
958	FlhF	0.042295
959	aminohexanoate	0.042098
960	release	0.042058
961	pyrimidine	0.041727
962	sulfatase	0.041721
963	zeaxanthin	0.041717
964	Aba2	0.041717
965	thiol	0.041712
966	undecaprenyl	0.041646
967	mutH	0.041543
968	Icc	0.041543
969	M28	0.041543
970	Trk	0.04138

971	bicarbonate	0.041196
972	aromatic	0.041196
973	compound	0.041149
974	M50	0.041114
975	IV	0.041091
976	aldo	0.041036
977	hypoxanthine	0.04095
978	AtoC	0.040896
979	universal	0.040859
980	xylulokinase	0.040802
981	diphosphate	0.040773
982	Cas1	0.040586
983	porter	0.040586
984	acetoacetyl	0.040511
985	DctM	0.040466
986	CspD	0.040249
987	6x	0.040249
988	FxsA	0.040249
989	gene	0.040231
990	FliR	0.04023
991	selenium	0.04023
992	including	0.040099
993	FtsW	0.040058
994	PEP	0.04001
995	SohA	0.039889
996	YhaV	0.039889
997	TupA	0.039889
998	MFS	0.039854
999	Electron	0.039808
1000	inhibitor	0.039804
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1002	RecB	0.039603
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1015	alkaline	0.038637
1016	channel	0.038455
1017	recognition	0.038425
1018	FlaA	0.03831
1019	IS2	0.03831
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1021	RecBCD	0.03831
1022	CheW	0.038232
1023	hydrocarbon	0.03818
1024	prophage	0.038167

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1028   mgtE                               0.03806
1029   LemA                              0.037946
1030   sequence                          0.037888
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1032   cobalamin                         0.037672
1033   vanX                              0.037663
1034   M15D                              0.037663
1035   YaeQ                              0.037663
1036   proton                             0.03756
1037   oxo                               0.037464
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1039   GroEL                             0.037418
1040   RocR                              0.037418
1041   control                           0.037394
1042   import                            0.037388
1043   exchanger                         0.037369
1044   CheA                              0.037265
1045   sulfoxide                         0.037201
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1050   DdpX                              0.037146
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1062   lipoyl                            0.036427
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1064   Sel1                               0.03637
1065   EIIAB                             0.036362
1066   receptor                          0.036324
1067   oxalurate                         0.036231
1068   Ggt                               0.036231
1069   ywrD                              0.036231
1070   Heat                              0.036043
1071   Hfq                               0.036042
1072   L7                                0.035893
1073   L12                               0.035893
1074   adenine                            0.03587
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1076   core                              0.035864
1077   genetic                           0.035835
1078   tetrahydropyridine                0.035775
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1099	redoxin	0.035044
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1107	Internalin	0.034443
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1114	CoxL	0.034251
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1131	Cystathionine	0.032764
1132	rotamase	0.032667

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1139  host                         0.03251
1140  Man                          0.03249
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1143  rhs                         0.032235
1144  L33                         0.032235
1145  S2                          0.032205
1146  IS5                         0.032139
1147  E1                          0.031954
1148  light                       0.031952
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1154  replication                 0.031692
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1159  ptxB                        0.031659
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1166  sporulation                 0.031558
1167  antigen                     0.031464
1168  thiosulfate                 0.031367
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1172  chloramphenicol             0.031197
1173  bisphosphatase              0.031113
1174  diacylglyceryl              0.030991
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1176  Hemolysin                   0.030881
1177  thermostable                0.030863
1178  lauroyl                     0.030863
1179  glutathione                 0.030838
1180  guanylate                     0.0308
1181  Chitooligosaccharide        0.030745
1182  uricase                     0.030745
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1184  Yen8                        0.030745
1185  avirulence                  0.030745
1186  DsdX                        0.030745
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1198   region                                  0.030479
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1200   plastoquinone                           0.030406
1201   filamentation                           0.030397
1202   preprotein                              0.030183
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1204   MoFe                                    0.029904
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1206   GabT                                    0.029831
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1227   desuccinylase                           0.029029
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1262   colicin                                           0.027044
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1264   PE                                                0.026789
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1522	part	0.018574
1523	SecD	0.018455
1524	depolymerase	0.018455
1525	fhuC	0.018265
1526	RecX	0.018265
1527	inactive	0.018265
1528	FliF	0.018104
1529	Hpt	0.01806
1530	HydA	0.01806
1531	Chorismate	0.018006
1532	cyanophycin	0.017944
1533	fusaric	0.017944
1534	UgpC	0.017944
1535	dnaC	0.017944
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1537	OruR	0.017944
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1539	NorA	0.017944
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2126	Idh	0.0069713
2127	DSG	0.0069713
2128	GlyA	0.0069713
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2130	CPA2	0.0069713
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2136	MdtF	0.0069713
2137	SirA	0.0067962
2138	monophosphatase	0.0067319
2139	homocitrate	0.0066286
2140	lysophospholipase	0.0066286
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2149	LON	0.0066264
2150	HPA2	0.0066264
2151	ribotide	0.0066264
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2154	LD	0.0066264
2155	s4	0.0066256
2156	RuvB	0.0065934
2157	XerD	0.0065934
2158	CsbD	0.0065934

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2173   MiaB                          0.0061844
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2226   DsbC                             0.0057402
2227   duplication                      0.0057141
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2231   desaturase                       0.0055662
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2233   twitching                        0.0053663
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2235   iditol                           0.0053332
2236   IS407A                           0.0053332
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2238   RluD                             0.0053332
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3829	exo	-0.0030868
3830	some	-0.0030868
3831	M17	-0.0030868
3832	proper	-0.0030868

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3833  C40                    -0.0030868
3834  rusticyanin            -0.0030868
3835  holin                  -0.0030868
3836  PilP                   -0.0030868
3837  RegB                   -0.0030868
3838  BNR                    -0.0030868
3839  m75                    -0.0030868
3840  imelysin               -0.0030868
3841  PrrB                   -0.0030868
3842  MobC                   -0.0030868
3843  COQ5                   -0.0030868
3844  Dam                    -0.0030868
3845  DrsE                   -0.0030868
3846  cobalbumin             -0.0030868
3847  flanked                -0.0030868
3848  yfgL                   -0.0030868
3849  YqgF                   -0.0030868
3850  trafficking            -0.0030868
3851  psi                    -0.0030868
3852  SleB                   -0.0030868
3853  PhhR                   -0.0030868
3854  transription           -0.0030868
3855  s51                    -0.0030868
3856  strictosidine          -0.0030868
3857  LamG                   -0.0030868
3858  HisD                   -0.0030868
3859  dienelactone           -0.0030868
3860  Gin                    -0.0030868
3861  MauE                   -0.0030868
3862  pore                   -0.0030868
3863  Appr                   -0.0030868
3864  DapA                   -0.0030868
3865  550                    -0.0030868
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3867  L10Ae                  -0.0030868
3868  polyferredoxin         -0.0030868
3869  YbiR                   -0.0030868
3870  Pyl                    -0.0030868
3871  RseB                   -0.0030868
3872  MucB                   -0.0030868
3873  VanZ                   -0.0030868
3874  potF                   -0.0030868
3875  OprG                   -0.0030868
3876  YbbN                   -0.0030868
3877  HrpQ                   -0.0030868
3878  GalcD                  -0.0030868
3879  NADB                   -0.0030868
3880  NnrS                   -0.0030868
3881  XylG                   -0.0030868
3882  DnrD                   -0.0030868
3883  FruR                   -0.0030868
3884  L44e                   -0.0030868
3885  broad                  -0.0030868
3886  561                    -0.0030868
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3887   AGT                          -0.0030868
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3892   Ibp                          -0.0030868
3893   HutI                         -0.0030868
3894   CcpA                         -0.0030868
3895   Vat                          -0.0030868
3896   DUF1217                      -0.0030868
3897   S58                          -0.0030868
3898   DmpA                         -0.0030868
3899   LPXTG                        -0.0030868
3900   CaCA                         -0.0030868
3901   Ca                           -0.0030868
3902   FUN14                        -0.0030868
3903   DUF1599                      -0.0030868
3904   S54                          -0.0030868
3905   Rrx2                         -0.0030868
3906   HpaG2                        -0.0030868
3907   Vsr                          -0.0030868
3908   27A                          -0.0030868
3909   YNFM                         -0.0030868
3910   ImpI                         -0.0030868
3911   TagF                         -0.0030868
3912   DUF2874                      -0.0030868
3913   former                       -0.0030868
3914   fasciclin                    -0.0030868
3915   YajL                         -0.0030868
3916   Hsp31                        -0.0030868
3917   h3                           -0.0030868
3918   HemP                         -0.0030868
3919   parkinsonism                 -0.0030868
3920   cone                         -0.0030868
3921   UreJ                         -0.0030868
3922   HupE                         -0.0030868
3923   fimb                         -0.0030868
3924   N2N2                         -0.0030868
3925   vinyl                        -0.0030868
3926   4VR                          -0.0030868
3927   S26B                         -0.0030868
3928   S26A                         -0.0030868
3929   S24                          -0.0030868
3930   organocation                 -0.0030868
3931   Virb6                        -0.0030868
3932   PucR                         -0.0030868
3933   VirB2                        -0.0030868
3934   SusD                         -0.0030868
3935   IB                           -0.0030868
3936   DUF1713                      -0.0030868
3937   SPOA                         -0.0030868
3938   ACR3                         -0.0030868
3939   TrmA                         -0.0030868
3940   oxopent                      -0.0030868
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3943   yccT                            -0.0030868
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3945   ade1                            -0.0030868
3946   pur7                            -0.0030868
3947   fucosidase                      -0.0030868
3948   S16P                            -0.0030868
3949   Caffeoyl                        -0.0030868
3950   IS1354                          -0.0030868
3951   amd                             -0.0030868
3952   MdtJ                            -0.0030868
3953   band                            -0.0030868
3954   MotA3                           -0.0030868
3955   CdaR                            -0.0030868
3956   CUT1                            -0.0030868
3957   iso                             -0.0030868
3958   within                          -0.0030868
3959   BAIF                            -0.0030868
3960   GspD                            -0.0030868
3961   YhnG                            -0.0030868
3962   AglR                            -0.0030868
3963   Fha1                            -0.0030868
3964   ssDNA                           -0.0030868
3965   comigratory                     -0.0030868
3966   DgcB                            -0.0030868
3967   RecJ                            -0.0030868
3968   glxK                            -0.0030868
3969   citA                            -0.0030868
3970   MntR                            -0.0030868
3971   MttB2                           -0.0030868
3972   MttB1                           -0.0030868
3973   DtxR                            -0.0030868
3974   FpvR                            -0.0030868
3975   scafolding                      -0.0030868
3976   SoxY                            -0.0030868
3977   HpnH                            -0.0030868
3978   TraG                            -0.0030868
3979   TraD                            -0.0030868
3980   curing                          -0.0030868
3981   MazE                            -0.0030868
3982   Fae                             -0.0030868
3983   glycanase                       -0.0030868
3984   gp229                           -0.0030868
3985   intrrupted                      -0.0030868
3986   PhsA                            -0.0030868
3987   Taq                             -0.0030868
3988   GlcC                            -0.0030868
3989   Usg                             -0.0030868
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3991   IroE                            -0.0030868
3992   A24                             -0.0030868
3993   AbgT                            -0.0030868
3994   BioD                            -0.0030868
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3997   MurJ                                           -0.0030868
3998   YghU                                           -0.0030868
3999   Mlr3171                                        -0.0030868
4000   angiotensin                                    -0.0030868
4001   XylA                                           -0.0030868
4002   ISSod13                                        -0.0030868
4003   ISBmu27                                        -0.0030868
4004   ISPg1                                          -0.0030868
4005   partial                                        -0.0030868
4006   YapH                                           -0.0030868
4007   FlhD                                           -0.0030868
4008   GtrA                                           -0.0030868
4009   dATP                                           -0.0030868
4010   UbiD                                           -0.0030868
4011   tim44                                          -0.0030868
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4013   WhiB7                                          -0.0030868
4014   pra                                            -0.0030868
4015   NrdI                                           -0.0030868
4016   HyuE                                           -0.0030868
4017   FadD32                                         -0.0030868
4018   FadD                                           -0.0030868
4019   LprB                                           -0.0030868
4020   ComEA                                          -0.0030868
4021   CelD                                           -0.0030868
4022   hairpin                                        -0.0030868
4023   PedF                                           -0.0030868
4024   arylsulfatase                                  -0.0030868
4025   PBS                                            -0.0030868
4026   SnoaL                                          -0.0030868
4027   NapC                                           -0.0030868
4028   CM55                                           -0.0030868
4029   antitrypsin                                    -0.0030868
4030   uup                                            -0.0030868
4031   unique                                         -0.0030868
4032   CyaY                                           -0.0030868
4033   donor                                          -0.0030868
4034   SBP56                                          -0.0030868
4035   56kDa                                          -0.0030868
4036   67                                             -0.0030868
4037   hemimethylated                                 -0.0030868
4038   DHA1                                           -0.0030868
4039   NifD5                                          -0.0030868
4040   GumN                                           -0.0030868
4041   caspase                                        -0.0030868
4042   ethylaminohydrolase                            -0.0030868
4043   MecA                                           -0.0030868
4044   sulfotransferase                               -0.0030868
4045   WGR                                            -0.0030868
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4047   QseB                                           -0.0030868
4048   CadC                                           -0.0030868
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4049   endoprotease              -0.0030868
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4053   CoxF                      -0.0030868
4054   mutarotase                -0.0030868
4055   GP55                      -0.0030868
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4057   GPD                       -0.0030868
4058   HhH                       -0.0030868
4059   DUF2933                   -0.0030868
4060   MucD                      -0.0030868
4061   ISRSO5                    -0.0030868
4062   SciS                      -0.0030868
4063   DivIVA                    -0.0030868
4064   sun                       -0.0030868
4065   npd                       -0.0030868
4066   tola                      -0.0030868
4067   PbpG                      -0.0030868
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4069   pgap1                     -0.0030868
4070   L14                       -0.0030868
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4073   proenzyme                 -0.0030868
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4095   PrpF                      -0.0030868
4096   AlgA                      -0.0030868
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4098   enolpyruvyl               -0.0030868
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4102   P0                        -0.0030868
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4108   IniC                          -0.0030868
4109   inductible                    -0.0030868
4110   vanw                          -0.0030868
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4115   pgaC                          -0.0030868
4116   argninine                     -0.0030868
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4118   DmsD                          -0.0030868
4119   SycD                          -0.0030868
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4121   PhnG                          -0.0030868
4122   TomA0                         -0.0030868
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4124   sulphonates                   -0.0030868
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4127   COQ7                          -0.0030868
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4130   WPhi                          -0.0030868
4131   maintenance                   -0.0030868
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4134   GcrA                          -0.0030868
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4136   Fpg                           -0.0030868
4137   UptF                          -0.0030868
4138   ErpA                          -0.0030868
4139   GlpE                          -0.0030868
4140   raxR                          -0.0030868
4141   AvrXa21                       -0.0030868
4142   batB                          -0.0030868
4143   sigW                          -0.0030868
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4145   SCP                           -0.0030868
4146   SbcCD                         -0.0030868
4147   coadecarboxylase              -0.0030868
4148   XadA                          -0.0030868
4149   conditioned                   -0.0030868
4150   density                       -0.0030868
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4152   sigma28                       -0.0030868
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4155   CipB                          -0.0030868
4156   inclusion                     -0.0030868
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4162  TM2                                          -0.0030868
4163  domin                                        -0.0030868
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4165  TraX                                         -0.0030868
4166  OprM                                         -0.0030868
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4169  IS1548                                       -0.0030868
4170  NirV                                         -0.0030868
4171  haloperoxidase                               -0.0030868
4172  ToxS                                         -0.0030868
4173  ToxR                                         -0.0030868
4174  CitG                                         -0.0030868
4175  LuxS                                         -0.0030868
4176  ScpA                                         -0.0030868
4177  BtpA                                         -0.0030868
4178  PcxA                                         -0.0030868
4179  enol                                         -0.0030868
4180  arcA                                         -0.0030868
4181  autoagglutination                            -0.0030868
4182  cbiO                                         -0.0030868
4183  CbiQ                                         -0.0030868
4184  YloV                                         -0.0030868
4185  Octanoyltransferase                          -0.0030868
4186  OprD                                         -0.0030868
4187  Aha1                                         -0.0030868
4188  HyaE2                                        -0.0030868
4189  SotB                                         -0.0030868
4190  blue                                         -0.0030868
4191  AroB                                         -0.0030868
4192  LlpA1                                        -0.0030868
4193  PcaK                                         -0.0030868
4194  Rex                                          -0.0030868
4195  YbhD                                         -0.0030868
4196  PaaI                                         -0.0030868
4197  oxydoreductase                               -0.0030868
4198  ExoA                                         -0.0030868
4199  HisZ                                         -0.0030868
4200  frataxin                                     -0.0030868
4201  HmcD                                         -0.0030868
4202  COP                                          -0.0030868
4203  FtrA                                         -0.0030868
4204  Legionaminic                                 -0.0030868
4205  exposed                                      -0.0030868
4206  BCCP                                         -0.0030868
4207  GSPF                                         -0.0030868
4208  ISRSO10                                      -0.0030868
4209  C14                                          -0.0030868
4210  yir2                                         -0.0030868
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4216   TssM                                -0.0030868
4217   syringe                             -0.0030868
4218   needle                              -0.0030868
4219   TssI                                -0.0030868
4220   PA2                                 -0.0030868
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4223   44H                                 -0.0030868
4224   bidirectional                       -0.0030868
4225   diaphorase                          -0.0030868
4226   Cbc6                                -0.0030868
4227   SPOR                                -0.0030868
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4229   TssG                                -0.0030868
4230   TssH                                -0.0030868
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4232   articulin                           -0.0030868
4233   FrpC                                -0.0030868
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4236   MraW                                -0.0030868
4237   LPPG                                -0.0030868
4238   rbsC                                -0.0030868
4239   AcrR                                -0.0032228
4240   killer                              -0.0032353
4241   ectoine                             -0.0032353
4242   aminocyclopropane                   -0.0032353
4243   CarD                                -0.0032353
4244   prevent                             -0.0032353
4245   chlorite                            -0.0032364
4246   formamidase                         -0.0034018
4247   stationary                          -0.0034311
4248   phase                               -0.0034311
4249   CTERM                               -0.0034311
4250   Fic                                 -0.0034311
4251   SLT                                 -0.0034311
4252   FliJ                                -0.0034311
4253   reverse                             -0.0034311
4254   transhydrogenase                    -0.0036754
4255   partitioning                        -0.0036754
4256   Cobyrinic                           -0.0036911
4257   acylaminoacyl                       -0.0037191
4258   cyp141                              -0.0037191
4259   141                                 -0.0037191
4260   Hsp33                               -0.0037191
4261   subtype                             -0.0037191
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4263   different                           -0.0037191
4264   HIT                                 -0.0037191
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4270  plasma                           -0.0037191
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4272  CflA                             -0.0037191
4273  RsbU                             -0.0037191
4274  ketosteroid                      -0.0037191
4275  YbjL                             -0.0037191
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4277  arylformamidase                  -0.0037191
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4289  ech                              -0.0037191
4290  3S                               -0.0037191
4291  HisF                             -0.0037191
4292  GFA                              -0.0037191
4293  1C                               -0.0037191
4294  DprA                             -0.0037191
4295  pyranopterin                     -0.0037191
4296  TctC                             -0.0037191
4297  helper                           -0.0037191
4298  DUF1555                          -0.0037191
4299  main                             -0.0037191
4300  Mg2                              -0.0037632
4301  MOSC                             -0.0037632
4302  PqqB                             -0.0037632
4303  LamB                             -0.0037632
4304  ricin                            -0.0037632
4305  lectin                           -0.0037632
4306  minor                            -0.0037632
4307  AbrB                             -0.0037632
4308  ester                            -0.0037632
4309  mota                             -0.0038832
4310  exbb                             -0.0038832
4311  tolq                             -0.0038832
4312  autotransporter                  -0.0038832
4313  water                            -0.0038884
4314  PcrA                             -0.0038884
4315  Alginate                         -0.0038884
4316  bond                             -0.0038884
4317  phenol                           -0.0040211
4318  WecB                             -0.0040408
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4320   CpsF                         -0.0042027
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4322   carnitine                    -0.0042294
4323   s11                          -0.0042912
4324   VacJ                         -0.0042912
4325   MucR                         -0.0042912
4326   IM30                         -0.0042912
4327   DL                           -0.0042912
4328   ribokinase                   -0.0042912
4329   Folate                       -0.0042912
4330   YgfZ                         -0.0042912
4331   Met                          -0.0043456
4332   death                        -0.0043456
4333   extradiol                    -0.0043456
4334   outermembrane                -0.0043456
4335   SpeA                         -0.0043657
4336   Pcs                          -0.0043657
4337   NreB                         -0.0043657
4338   DD                           -0.0043657
4339   steroid                      -0.0043657
4340   RibF                         -0.0043657
4341   IS256                        -0.0043657
4342   prime                        -0.0043657
4343   dbpA                         -0.0043657
4344   WhiE                         -0.0043657
4345   F390                         -0.0043657
4346   enoate                       -0.0043657
4347   mycelium                     -0.0043657
4348   aerial                       -0.0043657
4349   sialoglycoprotein            -0.0043657
4350   monomethyl                   -0.0043657
4351   Carotenoid                   -0.0043657
4352   L5                           -0.0043657
4353   RuvA                         -0.0043657
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4355   choloyL                      -0.0043657
4356   SET                          -0.0043657
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4358   abortive                     -0.0043657
4359   d1                           -0.0043657
4360   RecN                         -0.0043657
4361   ISXoo2                       -0.0043657
4362   layer                        -0.0043657
4363   ISPsy6                       -0.0043657
4364   molydopterin                 -0.0043657
4365   WD40                         -0.0043657
4366   ispsy11                      -0.0043657
4367   sheath                       -0.0043657
4368   AhpD                         -0.0043657
4369   CAIB                         -0.0043657
4370   RecF                         -0.0043657
4371   MraZ                         -0.0043657
4372   DRTGG                        -0.0043657
```

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4373   BvgS                         -0.0043657
4374   HTR                          -0.0043657
4375   DEXX                         -0.0043657
4376   MarC                         -0.0043657
4377   12                           -0.0044498
4378   PA                           -0.0045761
4379   PilZ                         -0.0045761
4380   diamide                      -0.0046907
4381   indolepyruvate               -0.0048029
4382   cyclo                        -0.0048192
4383   triad                        -0.0048192
4384   ResB                         -0.0048192
4385   CcmA                         -0.0048192
4386   MCPs                         -0.0048192
4387   IS1328                       -0.0048192
4388   IS1533                       -0.0048192
4389   IS111A                       -0.0048192
4390   cutinase                     -0.0048192
4391   CHASE                        -0.0048192
4392   IS630                        -0.0048192
4393   ComEC                        -0.0048192
4394   Rec2                         -0.0048192
4395   WhiB                         -0.0048192
4396   b561                         -0.0048192
4397   teichoic                     -0.0048192
4398   CobB                         -0.0048192
4399   reacting                     -0.0048588
4400   DMT                          -0.0052602
4401   trypsin                      -0.0052602
4402   CobQ                         -0.0052602
4403   coat                         -0.0052678
4404   sites                        -0.0053471
4405   G2445                        -0.0053471
4406   SpoIIIE                      -0.0053471
4407   recr                         -0.0053471
4408   mitochondrial                -0.0053471
4409   Gingipain                    -0.0053471
4410   crossover                    -0.0053471
4411   endodeoxyribonuclease        -0.0053471
4412   amylase                      -0.0054172
4413   Fur                          -0.0055002
4414   thiouridylate                -0.0056768
4415   P60                          -0.0056963
4416   typically                    -0.0057174
4417   TagA                         -0.0057174
4418   LysM                         -0.0057174
4419   subtilisin                   -0.0057497
4420   MutS                         -0.0061747
4421   RuvC                         -0.0061747
4422   RecQ                         -0.0061747
4423   autolysis                    -0.0061747
4424   globin                       -0.0064411
4425   mutator                      -0.0064411
4426   MinD                          -0.006443
```

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4427   formaldehyde                          -0.0066574
4428   auxin                                 -0.0067938
4429   MotB                                  -0.0068666
4430   OmpA                                  -0.0072839
4431   GDP                                   -0.0074782
4432   motif                                 -0.0077608
4433   nitroreductase                        -0.0080366
```