iJO1366 *Escherichia coli* Model
“iJO1366 E.coli Model” Learning Objectives

Each student should be able to:

• Describe the major differences between the iAF1260 and iJO1366 E.coli models.
• Describe the properties of the gaps and orphans found in the iJO1366 model
• Outline the subsystems included in the iJO1366 model
• Describe the supplementary material available for the iJO1366 model
“iJO1366 E.coli Model” Lesson Outline

• Overview
• iAF1260 vs iJO1366 Comparison
• iJO1366 Gaps and Orphans
• iJO1366 Subsystems
• Supplementary Material

The initial genome-scale reconstruction of the metabolic network of Escherichia coli K-12 MG1655 was assembled in 2000. It has been updated and periodically released since then based on new and curated genomic and biochemical knowledge.

An update has now been built, named iJO1366, which accounts for 1366 genes, 2251 metabolic reactions, and 1136 unique metabolites. iJO1366 was

(1) updated in part using a new experimental screen of 1075 gene knockout strains, illuminating cases where alternative pathways and isozymes are yet to be discovered,
(2) compared with its predecessor and to experimental data sets to confirm that it continues to make accurate phenotypic predictions of growth on different substrates and for gene knockout strains, and
(3) mapped to the genomes of all available sequenced E. coli strains, including pathogens, leading to the identification of hundreds of unannotated genes in these organisms.

Like its predecessors, the iJO1366 reconstruction is expected to be widely deployed for studying the systems biology of E. coli and for metabolic engineering applications.

History of Constraint-based *E. coli* Models

- The first genome-scale reconstruction of *E. coli* was *iJE660* (Edwards and Palsson, 2000). This network was constructed through extensive searches of literature and databases to ensure correct stoichiometry and cofactor usage, and was the most extensive metabolic network reconstruction in existence at that time.

- An updated version of this reconstruction, *iJR904* (Reed et al, 2003), had an expanded scope, including pathways for the consumption of alternate carbon sources and more specific quinone usage in the electron transport system. Hundreds of new genes and reactions were added, gene-protein-reaction associations (GPRs) were included for the first time to connect reactions with genes, and all reactions were elementally and charged balanced through the inclusion of protons.

- In the next update, *iAF1260* (Feist et al, 2007), the scope of the network was expanded again, now including many reactions for the synthesis of cell wall components, and all metabolites were assigned to the cytoplasm, periplasm, or extracellular space. The thermodynamic properties of each reaction were calculated, and this was used to set lower bounds on predicted irreversible reactions. *iAF1260* contained 2077 reactions, 1039 metabolites, and 1260 genes.

- The *iJO1366* model includes many newly characterized genes and reactions. Since the *iAF1260* model was a very complete representation of the known metabolism of *E. coli*, only minor expansions in the scope of the network were made. Still, new discoveries since 2007 have made this model update necessary. Several genes were added based on the results of an experimental screen of *E. coli* knockout strains in four different media conditions. The gaps in the *iAF1260* network were identified and characterized, and new reactions and genes were added to reduce the total number of gaps.

- The *iJO1366* reconstruction can serve as a basis for metabolic network reconstructions of other *E. coli* strains and closely related organisms.

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• iAF1260 vs iJO1366 Comparison

• iJO1366 Gaps and Orphans

• iJO1366 Subsystems

• Supplementary Material

### Properties of iJO1366 and iAF1260

<table>
<thead>
<tr>
<th></th>
<th>iJO1366 (this study)</th>
<th>iAF1260 (Feist et al., 2007)</th>
</tr>
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<tbody>
<tr>
<td><strong>Included genes</strong></td>
<td>1366 (32%)</td>
<td>1260 (29%)</td>
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<tr>
<td>Experimentally based</td>
<td>1328 (97%)</td>
<td>1227 (97%)</td>
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<td>function</td>
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<td>Computationally</td>
<td>38 (3%)</td>
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<td><strong>Unique functional</strong></td>
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<td>extracellular</td>
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**Gene–protein–reaction associations**

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<td>transport)</td>
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<td>Spontaneous/diffusion reactions</td>
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<td>Total (gene associated and</td>
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**Exchange reactions**

- 330

**Metabolites**

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Properties of iJO1366

(A) The number of reactions in each of 11 functional categories. Non-gene-associated (orphan) reactions are indicated by the lighter portion at the far right of each bar.

(B) The number of genes with associated reactions in each category. The number of genes unique to each category (i.e. associated only with reactions in one category) is given as a percentage.

(C) The number of unique metabolites that participate in at least one reaction in each category, with the number of metabolites unique to each category indicated.

Properties of iJO1366(II)

(D) Histogram of the years in which the function of each of the 107 new genes was first unambiguously identified.

(E) Classification of each of the 107 new genes in iJO1366. 'New content added' includes genes associated with new (non-gap-filling) pathways and systems in the model. 'Orphan fill' includes genes associated with orphan reactions from iAF1260. 'New gene with existing reaction' includes new isozymes for existing gene-associated reactions in iAF1260. 'Gap fill' includes genes associated with new gap-filling reactions. 'Others' includes genes that are associated both with new, non-gap-filling reactions, and with a previous orphan reaction or as a new isozyme.

A total of 180 of the 285 possible carbon sources were found to be growth supporting. There are several reasons why a carbon containing metabolite cannot serve as a carbon source.

First, not all extracellular compounds have transport reactions that allow them to enter the cell. Some may only have efflux reactions that allow them to be excreted.

Second, some compounds are not connected to the central reactions of metabolism from which all essential biomass components are constructed. For example, cob(II)alamin can be converted only to vitamin B12, but not to any other biomass components.

Third, carbon sources must also generally serve as energy sources for E. coli, so a highly oxidized compound such as CO2 cannot be growth supporting.

Not all compounds can serve as nitrogen, phosphorus, and sulfur sources for similar reasons. Some compounds may serve as a source of more than one essential element, such as L-alanine, which can provide both carbon and nitrogen simultaneously.

The potential growth supporting carbon, nitrogen, phosphorus, and sulfur sources were also predicted using the iAF1260 E. coli model. iJO1366 contains the same number of growth supporting phosphorus and sulfur sources, but has new sources for carbon and nitrogen. Thus, the scope of the environmental conditions that can be analyzed through modeling has now been increased.

Gene Essentiality Predictions

The GPR associations of every reaction in iJO1366 allow this model to predict the effects of gene knockouts. FBA was used to predict the optimal growth rate of *E. coli* growing on both glucose and glycerol with all 1366 genes knocked out one at a time. These computational knockout screens were then compared to experimental screens of the entire Keio. The final iJO1366 model was used to make these predictions.

There are four possible outcomes, TP, TN, FP, and FN, when one compares computationally predicted to experimental gene essentiality data.

FP predictions can be made when a model contains some unrealistic capabilities, such as pathways that are normally not expressed during the particular growth conditions. Because iJO1366 is a metabolic network model that does not contain regulatory systems, FP predictions are possible.

FN cases, on the other hand, indicate that some realistic content such as an essential transport or enzymatic reaction may be missing from the model.

When compared to the experimental gene essentiality data, most of the predictions made by iJO1366 are correct, confirming its overall accuracy (91%). Still, there are 80 FPs and 39 FNs among the 1366 predictions for growth on glucose minimal media. Predictions of growth on glycerol minimal media achieved similar accuracy.

“iJO1366 *E. coli* Model” Lesson Outline

- Overview
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Properties of the Gaps and Orphan Reactions in iJO1366

(A) Numbers of root no-production, root no-consumption, no-production downstream, and no-consumption upstream gaps in the network.

(B) Histogram of the number of downstream or upstream blocked metabolites for each root gap. Most root gaps only result in one downstream gap.

Properties of the Gaps and Orphan Reactions in iJO1366 (II)

(C) The 85 knowledge gaps (no scope gaps) in iJO1366 by type of gap. “Others” includes special cases such as metabolites that are both root and downstream gaps.

(D) The 85 knowledge gaps by the primary metabolic functional category (see Figure 1) of the reactions in which the blocked metabolites participate.

(E) The 127 orphan reactions (excluding the artificial reaction ATPM) by functional category.

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iJO1366 Subsystems

1. Alanine and Aspartate Metabolism
2. Alternate Carbon Metabolism
3. Anaplerotic Reactions
4. Arginine and Proline Metabolism
5. Biomass and maintenance functions
6. Cell Envelope Biosynthesis
7. Citric Acid Cycle
8. Cofactor and Prosthetic Group Biosynthesis
9. Cysteine Metabolism
10. Extracellular exchange
11. Folate Metabolism
12. Glutamate Metabolism
13. Glycerophospholipid Metabolism
14. Glycine and Serine Metabolism
15. Glycolysis/Gluconeogenesis
16. Glyoxylate Metabolism
17. Histidine Metabolism
18. Inorganic Ion Transport and Metabolism
19. Intracellular demand
20. Lipopolysaccharide Biosynthesis / Recycling

21. Membrane Lipid Metabolism
22. Methionine Metabolism
23. Methylglyoxal Metabolism
24. Murein Biosynthesis
25. Murein Recycling
26. Nitrogen Metabolism
27. Nucleotide Salvage Pathway
28. Oxidative Phosphorylation
29. Pentose Phosphate Pathway
30. Purine and Pyrimidine Biosynthesis
31. Pyruvate Metabolism
32. Threonine and Lysine Metabolism
33. Transport, Inner Membrane
34. Transport, Outer Membrane
35. Transport, Outer Membrane Porin
36. Tyrosine, Tryptophan, and Phenylalanine Metabolism
37. Unassigned
38. Valine, Leucine, and Isoleucine Metabolism
39. trRNA Charging
“Alanine and Aspartate” Subsystem
(Includes Asparagine)
“Alternate Carbon Metabolism” Subsystem

Alternate Carbon Metabolism Subsystem.json
“Anaplerotic Reactions” Subsystem

Anaplerotic Reaction Subsystem.json
“Arginine and Proline Metabolism” Subsystem

Arginine and Proline Metabolism Subsystem.json
“Biomass and Maintenance Functions” Subsystem

Biomass and Maintenance Functions Subsystem.json
“Cell Envelope Biosynthesis” Subsystem

• The Cell Envelope Biosynthesis Subsystem contains the following pathways.
  ✓ The synthesis of saturated fatty acids attached to an acyl carrier protein (ACP)
  ✓ The synthesis of unsaturated fatty acids attached to an acyl carrier protein (ACP)
  ✓ The synthesis of Murein (peptidoglycan) precursors
  ✓ The synthesis of Antigen precursors

Cell Envelope Biosynthesis Subsystem.json
"Citric Acid Cycle" Subsystem
“Cofactor and Prosthetic Group Biosynthesis” Subsystem
"Cysteine Metabolism" Subsystem
“Folate Metabolism” Subsystem

Folate Metabolism Subsystem.json
"Glutamate Metabolism Subsystem" (including Glutamine)

The ability to synthesize both L-Glutamate and L-Glutamine within *E.coli* has importance since it is the only route to incorporate inorganic nitrogen into the cell structure. In *E.coli* all inorganic nitrogen must be first converted into ammonium ('nh4_c'), which is then incorporated as an amino group of L-Glutamate and L-Glutamine. The amino group from these amino acids is then transferred to other nitrogen containing compounds within the cell.
“Glycerophospholipids Metabolism” Subsystem

- The Glycerophospholipids Metabolism Subsystem contains the saturated and unsaturated lipids that can be produced by *E. coli*, they include:
  - Phosphatidylethanolamine
  - Phosphatidylglycerol
  - Cardiolipin

- The length of the lipids spans from 12 to 18 carbons.

- The lipids actively included in simulations are determined by the biomass function.
"Glycine and Serine Metabolism" Subsystem

Glycine_Serine_Subsystem.json
“Glycolysis/Gluconeogenesis” Subsystem

Glycolysis/Gluconeogenesis Subsystem.json
“Glyoxylate Metabolism” Subsystem

Glyoxylate Metabolism Subsystem.json
"Histidine Metabolism" Subsystem

Precursor
Alpha-D-Ribose 5-phosphate

Histidine Metabolism Subsystem.json
"Inorganic Ion Transport and Metabolism" Subsystem

- The Inorganic Ion Transport and Metabolism contains the transport and secretion reactions for the following metabolites.
  - Iron derivatives, including ferric 2,3-dihydroxybenzoylserine, fe(III)dicitrate, enterochelin, fe(III)hydroxamate, ferrichrome, ferroxamine, coprogen, and aerobactin.
  - Ammonia, calcium, cadmium, chloride, cobalt, copper, sulfur dioxide, sulfate, sulfite, thiosulfate, tungstate, zinc, silver, mercury, potassium, magnesium, manganese, molybdate, nickel, nitric oxide, nitrous oxide, nitrite, nitrate, oxygen, phosphate, selenite, selenite, and sodium.
"Intracellular Demand" Subsystem

5'-deoxyribose

Aminoacetaldehyde

S-Adenosyl-4-methylthio-2-oxobutanoate

P-Cresol

Oxamate

(2R,4S)-2-methyl-2,3,3,4-tetrahydroxytetrahydrofuran

Intracellular demand Subsystem.json
“Lipopolysaccharide Biosynthesis/Recycling” Subsystem

- The Lipopolysaccharide (LPS) Biosynthesis - Recycling Subsystem contains the following pathways.
  - The synthesis of Lipid A
  - The synthesis of KDO and the LPS core
  - The synthesis of antigens including the enterobacterial common antigen, the O16 antigen, the lipid A diphosphate antigen, and the Ara4N antigen
  - The biomass function is used to determine the antigen included in the model simulations.
“Membrane Lipid Metabolism” Subsystem

- The Membrane Lipid Metabolism Subsystem contains the pathway for fatty acid catabolism.
- This subsystem is not used in the synthesis of the cell envelope.
- When fatty acids are not used as a carbon source this pathway needs to be disabled of the optimization software will select it over the natural pathway included in the Cell Envelope Biosynthesis Subsystem.

Membrane Lipid Metabolism Subsystem.json
"L-Methionine Metabolism" Subsystem
"Methylglyoxal Metabolism" Subsystem

Methylglyoxal Metabolism Subsystem.json
“Murein Biosynthesis” Subsystem

• This subsystem models the production of the murein repeating units used to create the murein sacculus.

• The murein sacculus is modeled through the biomass function that determines the assumed murein molecules required for cell growth.

✓ The Core biomass function ("BF_Core") only assumes one murein peptide.

✓ The Wild Type biomass function ("BF_WT") assumes five different murein peptides,
**“Murein Recycling” Subsystem**

- *E. coli* contains up to 20 murein hydrolases.
- Murein hydrolases are enzymes that digest murein or murein fragments into small, soluble fragments.
- These hydrolases include autolysins and lytic transglycosylases.
- About 40-50% of the murein in the murein sacculus recycled per generation.
- About 90% of the recycled murein is reinserted back into the murein sacculus.
“Nitrogen Metabolism” Subsystem

Nitrogen Metabolism Subsystem.json
"Nucleotide Salvage Pathway" Subsystem
“Oxidative Phosphorylation” Subsystem

Oxidative Phosphorylation Subsystem.json
"Pentose Phosphate Pathway" Subsystem

Pentose Phosphate Pathway Subsystem.json
“Purine and Pyrimidine Biosynthesis” Subsystem

Purine and Pyrimidine Biosynthesis Subsystem.json
"Pyruvate Metabolism" Subsystem
"Threonine and Lysine" Metabolism Subsystem

Threonine_Lysine_Subsystem.json
**“Transport, Inner Membrane” Subsystem**

- The Transport, Inner Membrane Subsystem contains the following:
  - 332 Reactions
  - Passive bidirectional and unidirectional diffusion
  - Facilitated irreversible diffusion
  - Active unidirectional transport using the ABC system
  - Active unidirectional transport using the PTS system
  - Active symporters and antiporters
  - Reductases
  - Permeases
“Transport, Outer Membrane” Subsystem

- The Transport, Outer Membrane Subsystem contains the following:
  - 46 reactions
  - Passive bidirectional diffusion of 10 metabolites,
  - Passive unidirectional diffusion of 9 metabolites using an undefined system,
  - Facilitated irreversible diffusion of 7 metabolites,
  - Active TonB system unidirectional transport of 11 metabolites,
  - Active proton antiport transport of 1 metabolites,
  - Active TolC system unidirectional secretion of 7 metabolites,
  - Active unidirectional secretion of 1 metabolites using an undefined system.
“Transport, Outer Membrane Porin” Subsystem

The Transport, Outer Membrane Porin Subsystem includes the passive bidirectional diffusion of 270 metabolites.

- Diffusion of metabolites from the extracellular space to the periplasm.
- Uses the “tex” suffix for each reaction name.

Diagram: Passive Diffusion

- H$_2$O$_{tex}$
- O$_2$_tex
- CO$_2$_tex
- H$_2$O$_p$
- O$_2_p$
- CO$_2_p$

Diagram: Diffusion through Outer Membrane Porin

- H$_2$O, O$_2$, CO$_2$
"Tyrosine, Tryptophan, and Phenylalanine Metabolism" Subsystem

Tyrosine\_Tryptophan\_Phenylalanine\_Subsystem.json
"Valine, Leucine, and Isoleucine Metabolism" Subsystem

Valine_Leucine_Isoleucine_Metabolism_Subsystem.json
"tRNA Charging" Subsystem

tRNA Charging Subsystem.json
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iJO1366 Supplementary Tables (Excel File)

- Supplementary Table 1 - Results of the experimental growth phenotype screen
- Supplementary Table 2 - All reactions in iJO1366
- Supplementary Table 3 - All metabolites in iJO1366
- Supplementary Table 4 - All references used in constructing iJO1366
- Supplementary Table 5 - New genes, reactions, and metabolites in iJO1366
- Supplementary Table 6 - The iJO1366 wild-type and core biomass reactions
- Supplementary Table 7 - Number of abstracts for each E. coli gene in Medline
- Supplementary Table 8 - Comparison of genes in iJO1366 and Seed83333.1 V20.21
- Supplementary Table 9 - Comparison of genes in iJO166 and the EchoLocation database
- Supplementary Table 10 - All gaps and orphan reactions in iAF1260 and iJO1366
- Supplementary Table 11 - Predictions of orphan-filling genes from iJR904
- Supplementary Table 12 - All growth supporting carbon, nitrogen, phosphorus, and sulfur sources in iJO1366
- Supplementary Table 13 - Essential and non-essential genes in iJO1366
- Supplementary Table 14 - Mapping iJO1366 to 38 E. coli and Shigella strains

# Supplementary PDF Document


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- Comparison of iJO1366 to the EchoLocation database: Pg. 6
- Gaps and orphan reactions in the iJO1366 reconstruction: Pg. 6
- Prediction of all growth supporting carbon, nitrogen, phosphorus, and sulfur sources: Pg. 9
- Prediction of gene essentiality: Pg. 9
- Mapping iJO1366 to closely related strains: Pg. 10

Lesson/Course Website Supplementary Material

https://systemsbiology.usu.edu/E_coli_iJO1366.php

- Additional Presentations
  - iJO1366 Amino Acid Overview (PDF)
  - iJO1366 Cell Envelope Operation (PDF)

- Matlab Live Scripts (ZIP)
  - iJO1366 Amino Acid Overview (PDF, MLX [zipped])
  - iJO1366 Cell Membrane (PDF, MLX [zipped])
  - iJO1366 Energy Management (PDF, MLX [zipped])
  - iJO1366 Subsystems (Matlab Overview: PDF, MLX [zipped])

- iJO1366 Escher Maps
  - iJO1366 Escher Maps (Zipped)
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Extra Material
Mapping *E. coli* and *Shigella* Strains

- (A) The number of strain models capable of producing all components of the iJO1366 core biomass reaction at different PID cutoffs.

- The PID of 40% used in parts (B, C) of this figure is indicated with a yellow square. At a PID of 40%, only four strains are incapable of complete biomass synthesis.

- (B) Biomass components that cannot be produced in one or more models with a PID of 40%. The strains are indicated by their KEGG organism code.

- (C) The fraction of iJO1366 genes present in all 38 strains at a PID of 40%. Strains are listed by their KEGG organism code. Laboratory strains are colored blue, commensal and environmental strains are in green, and pathogens are in red. A dashed line indicates the average fraction of genes present (97%).

## Strains Used in iJO1366 Mapping

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<th>Strain Name</th>
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