# Avi I. Flamholz Ph.D.

#### ASSISTANT PROFESSOR & HEAD OF LAB · THE ROCKEFELLER UNIVERSITY

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## Summary \_\_\_\_

I am excited when physical and mathematical principles help explain the behavior and evolution of cells, organisms and ecosystems. When possible, I strive to connect theory and laboratory experiments to real-world environments. I am focused on Earth's carbon cycle and working towards quantitative understanding of the metabolic rates of spatially-structured microbial communities in 3D environments like soils. Beyond understanding, we must also build technologies that erase our impacts on the Earth. I apply synthetic biology towards developing an engineered microbial agriculture with radically reduced land, water and emissions.

#### Education

#### **University of California, Berkeley**

Berkeley, CA

PHD, MOLECULAR AND CELL BIOLOGY

2013 - 2019

• Dissertation: "Analysis and Reconstitution of a Bacterial CO<sub>2</sub>-Concentrating Mechanism"; Advisor: Prof. David Savage

**Princeton University**Princeton, NJ

B.S.E., COMPUTER SCIENCE

2003 - 2007

• Graduated magna cum laude, certificate in Applied & Computational Mathematics; Thesis advisor: Prof. Kai Li

# Professional Experience \_\_\_\_\_

2025-	Asst. Prof. & Head of The Laboratory of Environmental Microbiology, The Rockefeller University
2020-2024	Postdoctoral Scholar in Biology & Bioengineering, Dianne Newman & Rob Phillips Groups, Caltech
2013-2019	Graduate Student Researcher, David Savage Group, UC Berkeley
2012-2013	Founding Technical Lead, Via Transportation, New York City
2010-2012	Pre-doctoral Researcher, Ron Milo Group, Weizmann Institute, Israel
2007-2010	Software Engineer II, Google, New York City

### Awards & Honors \_\_\_\_\_

2025-2029	Irma T. Hirschl Trust, Career Scientist Award
2024-2029	Burroughs Wellcome Fund, Careers at the Scientific Interface Transitional Award
2023	Caltech Center for Environmental Microbial Interactions, CEMI Travel Award
2022	Western Photosynthesis Annual Meeting, Best Talk Award
2021-2024	Jane Coffin Childs Memorial Foundation, Postdoctoral Fellowship
2020	Caltech Center for Environmental Microbial Interactions, CEMI Pilot Award
2015	UC Berkeley MCB Department, Travel Award
2019	American Chemical Society, Editor's Choice Award (Flamholz et al. Biochem.)
2014-2019	National Science Foundation, Graduate Research Fellowship
2007	Princeton University Department of Computer Science, Department Service Award
2007	Elected to Sigma Xi. Research Honors Society

#### Publications .

equal contribution, †mentored undergraduate, ^mentored graduate student

#### IN PREPARATION

Chure G, Razo-Mejia M, Goyal A, **Flamholz AI**. Feast-famine cycles select for fast growth even when time-averaged growth rates are slow.

Richter P, Goldford J, Flamholz AI. Selenoprotein annotation in microbial genomes using protein language models.

**Flamholz AI**, Goyal A. A theory of microbial carbon use efficiency.

Bar-On YM, Flamholz AI, Frankenberg C, Fischer WW. Accurate parameter-sparse models of soil carbon degradation.

Flamholz AI, Blikstad C, Dugan EJ, Fischer WW, Savage DF. CO<sub>2</sub> fertilization of heterotrophic growth.

#### In Submission

Eshel G, Flamholz AI, Shepon A, Milo R. Carbon budget and grassland needs of grassfed beef. In revision at PNAS.

#### ACCEPTED FOR PUBLICATION

Lovat S, Ben-Nissan R, Milshtein E, Leger D, **Flamholz AI**, Tzachor A, Noor E, Milo R. *Microbial production back-of-the-envelope techno-economic analysis exploring feasibility of global environmental benefits*. Accepted at Nature Biotechnology.

#### **PUBLISHED**

- Prywes N, Phillips NR, Oltrogge LM, Lindner S, Tsai YCC, de Pins B, Cowan AE, Taylor-Kearney LJ, Chang HA, Hall LN, Bellieny-Rabelo D, HM Nisonoff, Weissman RF, **Flamholz AI**, Ding D, Bhat AY, Shih PM, Mueller-Cajar O, Milo R, Savage DF. *A map of the rubisco biochemical landscape*. Nature. 2025; 1-6. doi:10.1038/s41586-024-08455-0
- **Flamholz AI**, Goyal A, Fischer WW, Newman DK, Phillips R. *The proteome is a terminal electron acceptor*. PNAS. 2025; 122 (1): e2404048121. doi:/10.1073/pnas.2404048121.
- **Flamholz AI**, Goldford J, Richter PA, Larsson EM, Jinich A, Fischer WW, Newman DK. *Annotation-free prediction of microbial oxygen utilization*. mSystems. 2024; e0076324. doi:10.1128/msystems.00763-24.
- Goyal A, **Flamholz AI**, Petroff A, Murugan A. *Closed ecosystems extract energy through self-organized nutrient cycles*. PNAS. 2024; 120: e2309387120. doi:10.1073/pnas.2309387120
- Wang RZ $^{\circ}$ , Nichols RJ, Liu AK, **Flamholz AI**, Artier J, Banda DM, Savage DF, Eiler JM, Shih PM, Fischer WW. Carbon isotope fractionation by an ancestral rubisco suggests biological proxies for  $CO_2$  through geologic time should be re-evaluated. PNAS. 2023; 120: e2300466120. doi:10.1073/pnas.2300466120 **Commentary by Sven Kranz in PNAS.**
- **Flamholz AI**, Goyal A. *Spotlight: Matching metabolic supply to demand optimizes microbial growth*. Trends Microbiol. 2023; 31, 769–771. doi:10.1016/j.tim.2023.06.003
- Lammers NC, **Flamholz AI**, Garcia HG. *Competing constraints shape the nonequilibrium limits of cellular decision-making*. PNAS. 2023;120: e2211203120 doi:10.1073/pnas.2211203120
- **Flamholz AI**\*, Dugan E\*+, Panich J, Desmarais JJ, Oltrogge LM, Fischer WW, Singer SW, Savage DF. *Trajectories for the evolution of bacterial CO*<sub>2</sub>-concentrating mechanisms. PNAS. 2022;119: e2210539119. doi:10.1073/pnas.2210539119 **Highlighted by Phys.org, Caltech News, & Innovative Genomics.org.**
- **Flamholz AI**, Saccomano S, Cash K, Newman DK. Optical  $O_2$  Sensors Also Respond to Redox Active Molecules Commonly Secreted by Bacteria. MBio. 2022; e0207622. doi:10.1128/mbio.02076-22
- Chure G<sup>\*</sup>, Banks RA<sup>\*</sup>, **Flamholz AI**, Sarai NS, Kamb M, Lopez-Gomez I, Bar-On Y, Milo R, Phillips R. Anthroponumbers.org: A quantitative database of human impacts on Planet Earth. Patterns. 2022;3: 100552. doi:10.1016/j.patter.2022.100552 *Highlighted in Wired, Phys.org, & ScienceDaily.*
- Noor E\*, **Flamholz AI**\*, Jayaraman V\*, Ross BL\*, Cohen Y, Patrick WM, Gruic-Sovulj I, Tawfik DS. *Uniform binding and negative catalysis at the origin of enzymes*. Protein Science. 2022;31: e4381. doi:10.1002/pro.4381 **Special issue posthumously honoring Dan Salah Tawfik**.
- Goldford JE, George AB, **Flamholz AI**, Segrè D. *Protein cost minimization promotes the emergence of coenzyme redundancy*. PNAS. 2022;119: e2110787119. doi:10.1073/pnas.2110787119

- **Flamholz AI**, Newman DK. *Microbial communities: The metabolic rate is the trait*. Current Biology. 2022;32: R215–R218. doi:10.1016/j.cub.2022.02.002
- Beber ME, Gollub MG, Mozaffari D, Shebek KM, **Flamholz AI**, Milo R, Noor E. *eQuilibrator 3.0: a database solution for thermo-dynamic constant estimation*. Nucleic Acids Research. 2021;50: D603–D609. doi:10.1093/nar/gkab1106
- Greenwald HD, Kennedy LC, Hinkle A, Whitney ON, Fan VB, Crits-Christoph A, Harris-Lovett S, **Flamholz AI**, Al-Shayeb B, Liao LD, Beyers M, Brown D, Chakrabarti AR, Dow J, Frost D, Koekemoer M, Lynch C, Sarkar P, White E, Kantor R, Nelson KL. *Tools for interpretation of wastewater SARS-CoV-2 temporal and spatial trends demonstrated with data collected in the San Francisco Bay Area*. Water Research X. 2021;12: 100111. doi:10.1016/j.wroa.2021.100111
- Sender R, Bar-On YM, Gleizer S, Bernshtein B, **Flamholz AI**, Phillips R, Milo R. *The total number and mass of SARS-CoV-2 virions*. PNAS. 2021;118: e2024815118. doi:10.1073/pnas.2024815118
- Crits-Christoph A, Kantor RS, Olm MR, Whitney ON, Al-Shayeb B, Lou YC, **Flamholz AI**, Kennedy LC, Greenwald H, Hinkle A, Hetzel J, Spitzer S, Koble J, Tan A, Hyde F, Schroth G, Kuersten S, Banfield JF, Nelson KL. *Genome sequencing of sewage detects regionally prevalent SARS-CoV-2 variants*. MBio. 2021;12: e02703–20. doi:10.1128/mBio.02703-20
- Claassens NJ, Scarinci G, Fischer A, **Flamholz AI**, Newell W, Frielingsdorf S, Lenz O, Bar-Even A. *Phosphoglycolate salvage in a chemolithoautotroph using the Calvin cycle*. PNAS. 2020;117: 22452–22461. doi:10.1073/pnas.2012288117
- **Flamholz AI**, Dugan E<sup>+</sup>, Blikstad C, Gleizer S, Ben-Nissan R, Amram S, Antonovsky N, Ravishankar S, Noor E, Bar-Even A, Milo R, Savage DF. *Functional reconstitution of a bacterial CO*<sub>2</sub> *concentrating mechanism in Escherichia coli*. Elife. 2020;9: e59882.
  - Commentary by Franklin & Jonikas in ELife, highlighted in Nature, Faculty Opinions.
- Davidi D, Shamshoum M, Guo Z, Bar-On YM, Prywes N, Oz A, Jablonska J, **Flamholz AI**, Wernick DG, Antonovsky N, De Pins B, Shachar L, Hochhauser D, Peleg Y, Albeck S, Sharon I, Mueller-Cajar O, Milo R. *Highly active rubiscos discovered by systematic interrogation of natural sequence diversity*. EMBO Journal. 2020;39: e104081. doi:10.15252/embj.2019104081
- **Flamholz AI**, Shih PM. *Cell biology of photosynthesis over geologic time*. Current Biology. 2020;30: R490–R494. doi:10.1016/j.cub.2020.01.076
- Bar-On YM, **Flamholz AI**, Phillips R, Milo R. *Science Forum: SARS-CoV-2 (COVID-19) by the numbers*. Elife. 2020;9: e57309. **Highlighted in Small Things Considered.**
- Desmarais JJ<sup>^</sup>, **Flamholz AI**, Blikstad C, Dugan EJ<sup>+</sup>, Laughlin TG, Oltrogge LM, Chen AW<sup>+</sup>, Wetmore K, Diamond S, Wang JY, Savage DF. *DABs are inorganic carbon pumps found throughout prokaryotic phyla. Nature Microbiology.* 2019;4: 2204–2215. doi:10.1038/s41564-019-0520-8
  - Commentary by Price, Long & Forster in Nature Microbiology
- **Flamholz AI**, Prywes N, Moran U, Davidi D, Bar-On YM, Oltrogge LM, Alves R, Savage DF, Milo R. *Revisiting trade-offs between Rubisco kinetic parameters*. Biochemistry. 2019;58: 3365–3376. doi:10.1021/acs.biochem.9b00237 *Editor's Choice Award*
- Blikstad C, **Flamholz AI**, Oltrogge LM, Savage DF. *Learning to Build a*  $\beta$ -*Carboxysome*. Biochemistry. 2019. pp. 2091–2092.
- Jinich A, **Flamholz AI**, Ren H, Kim S-J, Sanchez-Lengeling B, Cotton CAR, Noor E, Aspuru-Guzik A, Bar-Even A. *Quantum chemistry reveals thermodynamic principles of redox biochemistry*. PLoS Comput Biology. 2018;14: e1006471. doi:10.1371/journal.pcbi.1006471
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- Davidi D, Noor E, Liebermeister W, Bar-Even A, **Flamholz AI**, Tummler K, Barenholz U, Goldenfeld M, Shlomi T, Milo R. *Global characterization of in vivo enzyme catalytic rates and their correspondence to in vitro*  $k_{cat}$  *measurements*. PNAS. 2016;113: 3401–3406.

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- Noor E, **Flamholz AI**, Liebermeister W, Bar-Even A, Milo R. *A note on the kinetics of enzyme action: a decomposition that highlights thermodynamic effects.* FEBS Letters. 2013;587: 2772–2777. doi:10.1016/j.febslet.2013.07.028
- **Flamholz AI**\*, Noor E\*, Bar-Even A, Liebermeister W, Milo R. *Glycolytic strategy as a tradeoff between energy yield and protein cost.* PNAS. 2013;110: 10039–10044. doi:10.1073/pnas.1215283110 **Commentary by Stettner & Segre in PNAS**
- Zelcbuch L, Antonovsky N, Bar-Even A, Levin-Karp A, Barenholz U, Dayagi M, Liebermeister W, **Flamholz AI**, Noor E, Amram S, Brandis A, Bareia T, Yofe I, Jubran H, Milo R. *Spanning high-dimensional expression space using ribosome-binding site combinatorics*. Nucleic Acids Research. 2013;41: e98–e98. doi:10.1093/nar/gkt151
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- Huttenhower C, **Flamholz AI**, Landis JN, Sahi S, Myers CL, Olszewski KL, Hibbs MA, Siemers NO, Troyanskaya OG, Coller HA. *Nearest Neighbor Networks: clustering expression data based on gene neighborhoods*. BMC Bioinformatics. 2007;8: 1–13. doi:10.1186/1471-2105-8-250

# Funded Research Proposals

- January 2025. *Understanding and engineering microbial contributions to the global carbon cycle*. **Irma T. Hirschl Trust** Careers Scientist Award.
- June 2023.  $Predicting\ microbial\ CO_2\ production\ in\ global\ soils$ . Burroughs Wellcome Fund Careers at the Scientific Interface Transitional Fellowship.
- February 2023. Predicting the Fate of Carbon in Soils using Language Models on Sequence Data from Microbial Communities. **Schmidt Academy for Software Engineering.** With W. Fischer; supporting Philippa Richter for 2 years.
- July 2021. Developing bacterial biofilms as a model for predicting tissue metabolism. Jane Coffin Childs Memorial Foundation Postdoctoral Fellowship.
- September 2020. Experimental and theoretical approaches to studying the physiology of single cells in structured environments. Caltech Center for Emerging Microbial Interactions Pilot Grant.
- May 2020. Early detection of COVID-19 reemergence via wastewater surveillance of SARS-CoV-2 written with Profs. Kara Nelson & Jill Banfield's groups. Innovative Genomics Institute at UC Berkeley Rapid Response COVID-19 Research Grant.
- September 2018. Mapping sequence-function landscapes to isolate improved Rubiscos with Prof. David Savage. **National Science Foundation** award #1818377

September 2013. Interrogating Overflow Metabolism with Laboratory Evolution National Science Foundation Graduate Research Fellowship

#### Presentations\_

#### SEMINARS AND CONFERENCE TALKS

November 2024. Using engineered bacteria to study the history of Earth's atmosphere. Salk Institute (Invited)

November 2024. The proteome is a terminal electron acceptor. USC Systems Biology Guest Lecture (Invited)

November 2024. *Using engineered bacteria to study the history of Earth's atmosphere.* USC Department of Marine and Environmental Sciences (Invited)

Oct 2024. The proteome is a terminal electron acceptor. Joint BioEnergy Institute (Invited)

May 2024. The evolution of bacterial CO<sub>2</sub>-concentrating mechanisms. Caltech Center for Evolutionary Science

April 2024. The proteome is a terminal electron acceptor. Southern CA Geobiology meeting

April 2024. Studying microbial physiology to predict the fate of soil carbon.

MIT Department of Earth and Planetary Sciences (Invited)

March 2024. The function and evolution of bacterial CO<sub>2</sub> concentrating mechanisms. Rockefeller University (Invited)

March 2024. The proteome is a terminal electron acceptor. American Physical Society annual meeting (Invited)

February 2024. *Understanding and engineering the carbon cycle with synthetic biology.*Stanford University Department of Bioengineering (Invited)

February 2024. *Understanding and engineering the carbon cycle with synthetic biology.*Harvard Medical School Department of Systems Biology (Invited)

February 2024. Studying microbial physiology to predict the fate of soil carbon. Rockefeller University (Invited)

December 2023. Studying microbial physiology to predict the fate of soil carbon Caltech Division of Geology and Planetary Sciences (Invited)

March 2023. Engineering microbes to learn about the Earth: lessons for the global carbon cycle MIT Department of Earth and Planetary Sciences (Invited)

March 2023. The proteome is a terminal electron acceptor. American Physical Society annual meeting

July 2022. *Using engineered bacteria to study the history of Earth's atmosphere*. CCM10 Conference, Princeton University (Invited)

May 2022. *Trajectories for the evolution of bacterial* CO<sub>2</sub>-concentrating mechanisms. Caltech Center for Emerging Microbial Interactions monthly seminar

March 2022. Building a bacterial CO<sub>2</sub> concentrating mechanism.
Western Photosynthesis Virtual Conference. "Best Talk" award.

July 2021. *Microbial energy conservation when*  $O_2$  *is scarce*. Jointly delivered with Prof. Dianne Newman. Microbial Ecology and Evolution summer course, Kavli Institute for Theoretical Physics at UC Santa Barbara (Invited).

August 2020. Building a bacterial CO<sub>2</sub> concentrating mechanism. Online seminar.

Department of Plant Biology at Australian National University, Canberra, Australia (Invited)

July 2020. Building a bacterial CO<sub>2</sub> concentrating mechanism. Online seminar. Department of Plant Biology at York University, York, United Kingdom (Invited).

December 2019. An engineered E. coli fixes CO<sub>2</sub> from ambient air. West Coast Bacterial Physiology Meeting, Asilomar, CA.

July 2018. Rubisco: Why are you not better? International Geobiology Course, Catalina Island, CA (Invited).

May 2017. The cost of protein production. Amyris Inc, Emeryville, CA (Invited).

January 2017. Carboxysomes: What are they good for?

UC Berkeley MCB Department, Biochemistry, Biophysics & Structural Biology (BBS) Divisional Retreat

November 2013. Thermodynamic Tradeoffs in Glycolysis UC San Francisco Theory Lunch (Invited).

# Teaching Experience \_\_\_\_\_

Fall 2024	The history and future of atmospheric dioxygen, Co-teaching with Woody Fischer	Caltech
Sum. 2019	The Microverse, Introduction to microscopy & programming, Clubes de Ciencia	Monterrey, MX
Spring 2016	Biochemistry: Pathways, Mechanisms, and Regulation, Graduate Student Instructor	UC Berkeley
Sum. 2015	QB3 Python Programming Bootcamp, Teaching Assistant	UC Berkeley
Fall 2015	General Microbiology, Graduate Student Instructor	UC Berkeley
Fall 2011	English as a Second Language, Mesila program for refugees	Tel Aviv, Israel
Fall 2009	Introduction to Programming, 5th-8th Grades, Citizen Schools Volunteer	Brooklyn, NY
2005-2007	Head laboratory teaching assistant for intro courses, Dept. of Computer Science	Princeton

# Formal Mentorship \_\_\_\_\_

2025-	James Wang, Graduate Student	Rockefeller
2022-	Philippa Richter, Schmidt Scholar in Software Engineering in the Fischer Lab	Caltech
2022	Gia Han Vuong, Caltech CEMI-WAVE Summer Research Fellow in the Newman Lab	Caltech
2021	Elin Larsson, Rotation student in the Newman Lab - joined for PhD	Caltech
2019	Alejandra Zapata, UCB Transfers to Excellence Summer Research Fellow in the Savage Lab	UC Berkeley
2017	Edward Koleski, Rotation student in the Savage Lab	UC Berkeley
2017	Julia Borden, Rotation student in the Savage Lab - joined for PhD	UC Berkeley
2017-2020	Eli Dugan, Savage Lab technician - now a PhD student at UCSF Tetrad Program	UC Berkeley
2015-2017	Eli Dugan, Savage Lab Undergraduate Researcher	UC Berkeley
2016-2018	Allen Chen, Savage Lab Undergraduate Researcher - now a PhD student at Caltech	UC Berkeley
2015-2016	Sumedha Ravishankar, Savage Lab Undergrad Researcher - now a PhD student at UCSD	UC Berkeley
2015	Dylan McLung, Rotation student in the Savage Lab	UC Berkeley

### Service and Outreach \_

- 2011-Present. Maintain and develop eQuilibrator the biochemical thermodynamics calculator. With Elad Noor; 500-1000 students and researchers use eQuilibrator each month. equilibrator.weizmann.ac.il
- Summer 2022. Caltech PCC CEMI-WAVE summer research mentor. Volunteer mentor for a summer program bringing Pasadena Community College students to Caltech for paid summer research.
- Summer 2019. Clubes de Ciencias, Monterrey, Mexico. Volunteer teacher. Designed and co-taught "The Microverse" a one-week course on microscopy and introductory programming for 20 students. With Alejandro Balderas of Tecnológico de Monterrey.
- Summer 2019. *UC Berkeley Transfers to Excellence*. Volunteer mentor for a summer program bringing prospective transfer students to UC Berkeley for paid research internships.
- 2018. Student representative to Graduate Admissions Committee. UC Berkeley Department of Molecular and Cell Biology.
- 2017. Student representative to "host-microbe interactions" Faculty Search Committee. UC Berkeley Department of Molecular and Cell Biology.
- 2017-2019. Primary organizer of annual 100-person campus-wide symposium "Photosynthesis, Carbon-Fixation and the Environment." UC Berkeley.
- 2017. Student organizer of Biophysics, Biochemistry and Structural Biology divisional retreat. UC Berkeley Department of Molecular and Cell Biology.
- 2013-2017. Primary organizer of UC Berkeley Systems Biology Reading Group.

#### PEER REVIEW

I have refereed papers for ACS Synthetic Biology, Biophysical Journal, BioEssays, Cell, Current Opinion in Chemical Biology, ELife, Free Radical Biology and Medicine, mSystems, Nature, PLoS One, PNAS and Science.

Advisors		

B.S.E Junior Research Paper Prof. Hilary Coller, Princeton University, Department of Molecular Biology (now UCLA)

B.S.E. Senior Thesis Prof. Kai Li, Princeton University, Department of Computer Science

Pre-doctoral Research Mentor **Prof. Ron Milo**, Weizmann Institute for Science, Department of Plant and Environmental Sciences

PhD Mentor Prof. David Savage, University of California, Berkeley, Department of Molecular and Cell Biology

Postdoc Co-mentors at Caltech

**Prof. Dianne Newman** Divisions of Biology & Biological Engineering, Geological and Planetary Science **Prof. Rob Phillips** Department of Physics, Division of Biology and Biological Engineering

### Additional References\_\_\_

**Woodward Fischer**, Professor of Geobiology, California Institute of Technology **Hernan Garcia**, Associate Professor of Physics, Genetics and Development, University of California, Berkeley **Niall Mangan**, Assistant Professor of Engineering Sciences and Applied Mathematics, Northwestern University **Arvind Murugan**, Assistant Professor of Physics, University of Chicago