

# Benjamin H Good, PhD

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(last updated: April 26, 2025)

## Education

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| <b>Harvard University</b> , Cambridge, MA<br>Ph.D. (2016) in Physics<br>Thesis: Molecular evolution in rapidly evolving populations<br>Advisor: Michael M. Desai | 2010-2016 |
| <b>Swarthmore College</b> , Swarthmore, PA<br>B.A. (2010) in Physics and Mathematics with Highest Honors   | 2006-2010 |

## Employment and Research Experience

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| <b>Stanford University</b> , Stanford, CA<br><i>Alden H. and Winifred Hubbard Brown Faculty Fellow</i>   | 2024-present |
| <b>Stanford University</b> , Stanford, CA<br><i>Assistant Professor of Applied Physics and, by courtesy, of Biology</i>  | 2019-present |
| <b>University of California at Berkeley</b> , Berkeley, CA<br><i>Miller Research Fellow, Departments of Physics and Bioengineering</i><br>Advisor: Oskar Hallatschek | 2016-2019    |
| <b>Harvard University</b> , Cambridge, MA<br><i>Postdoctoral Fellow, Department of Organismic and Evolutionary Biology</i><br>Advisor: Michael M. Desai              | 2016         |
| <b>Harvard University</b> , Cambridge, MA<br><i>Graduate student, Department of Physics and FAS Center for Systems Biology</i><br>Advisor: Michael M. Desai          | 2010-2016    |
| <b>Santa Fe Institute</b> , Santa Fe, NM<br><i>Undergraduate researcher</i><br>Advisor: Aaron Clauset  | 2008-2010    |
| <b>Gettysburg College</b> , Gettysburg, PA<br><i>Research Assistant, Department of Computer Science</i><br>Advisor: Rodney S. Tosten                                 | 2004-2005    |

## Fellowships and Awards

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






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| Philippe Meyer Prize in Theoretical Physics, <i>Ecole Normale Supérieure</i> .....                  | 2024      |
| Alden H. and Winifred Hubbard Brown Faculty Fellow, <i>Stanford University</i> .....                | 2024-2025 |
| Dean's Award for Distinguished Teaching (First Years in Teaching), <i>Stanford University</i> ..... | 2023      |
| Chan Zuckerberg Biohub Investigator Award, <i>Chan Zuckerberg Biohub</i> .....                      | 2022-2027 |
| Alfred P. Sloan Research Fellowship, <i>Alfred P. Sloan Foundation</i> .....                        | 2021-2023 |
| Bio-X Undergraduate Star Mentor Award, <i>Stanford University</i> .....                             | 2021      |
| Terman Fellowship, <i>Stanford University</i> .....   | 2019-2022 |
| Miller Postdoctoral Fellowship, <i>Miller Institute for Basic Research in Science</i> .....         | 2016-2019 |
| Walter M. Fitch Award Finalist, <i>Society for Molecular Biology and Evolution</i> .....            | 2015      |
| Certificate of Distinction in Teaching, <i>Harvard University</i> .....                             | 2015      |
| Doctoral Dissertation Improvement Grant, <i>National Science Foundation</i> .....                   | 2015      |
| Graduate Research Fellowship, <i>National Science Foundation</i> .....                              | 2011-2014 |
| Leroy Apker Award Finalist, <i>American Physical Society</i> .....                                  | 2010      |
| Lang Award, <i>Swarthmore College</i> .....   | 2010      |
| William C. Elmore Prize in Physics, <i>Swarthmore College</i> .....                                 | 2010      |
| Phi Beta Kappa.....   | 2010      |
| Goldwater Scholar .....   | 2009-2010 |
| National Merit Scholar .....  | 2006      |

## Publications

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(in anti-chronological order, \*=co-first authors, †=corresponding authors, ②=undergraduate author)

1. Good, B.H.†, A.S. Bhatt, and M.J. McDonald†. Unraveling the tempo and mode of horizontal gene transfer in bacteria. *Trends in Microbiology* (in press, 2025).
2. Ghosh, O.M., G. Kinsler, B.H. Good, and D.A. Petrov. Low-dimensional genotype-fitness mapping across divergent environments suggests a limiting functions model of fitness. *bioRxiv* doi:10.1101/2025.04.05.647371 (2025).
3. Lopez, J.A., S. McKeithen-Mead, H. Shi, T. Nguyen, K.C. Huang†, and B.H. Good†. Abundance measurements reveal the balance between lysis and lysogeny in the human gut microbiome. *Current Biology* (in press, 2025).

4. Husain, K.\* , V. Sachdeva\*, R. Ravasio, M. Peruzzo, Wangqiang Liu, B. H. Good, and Arvind Murugan. Direct and indirect selection in a proofreading polymerase. *bioRxiv* doi:10.1101/2024.10.14.618309 (2024).
5. Shiver, A.L., J. Sun, R. Culver, A. Violette, C. Wynter, M. Nieckarz, S.P. Mattiello, P.K. Sekhon, F. Bottacini, L. Friess, H.K. Carlson, D.P.G.H. Wong, S. Higginbottom, M. Weglarz, W. Wang, B.D. Knapp, E. Guiberson, J. Sanchez, P. Huang, P.A. Garcia, C.R. Buie, B.H. Good, B. DeFelice, F. Cava, J. Scaria, J.L. Sonnenburg, D. Van Sinderen, A.M. Deutschbauer, and K.C. Huang. Genome-scale resources in the infant gut symbiont *Bifidobacterium breve* reveal genetic determinants of colonization and host-microbe interactions. *Cell* 188(7):2003-2021 (2025).
6. Lyulina A.\*, Z. Liu\*, and B.H. Good. Linkage equilibrium between rare mutations. *Genetics* 15(3): iyae145 (2024).
7. Vasquez, K.S.\* , D.P.G.H. Wong\*, M.F. Pedro, F.B. Yu, S. Jain, X. Meng, S.K. Higginbottom, B.C. DeFelice, N. Neff, A.S. Bhatt, C. Tropini, K.B. Xavier, J.L. Sonnenburg†, B.H. Good†, and K.C. Huang†. Within-host evolution and strain transmission of a human gut symbiont across ecological scales. *bioRxiv* doi:10.1101/2024.02.17.580834 (2024).
8. Goldman, D.A.\*, Goldman, K.S. Xue\*†, A.B. Parrott, R.R. Jeeda, L.R. Franzese, J.G. Lopez, J.C.C. Vila, D.A. Petrov, B.H. Good, D.A. Relman, K.C. Huang†. Competition for shared resources increases dependence on initial population size during coalescence of gut microbial communities. *PNAS* 122(11): e2322440122 (2025).
9. Xue, K.S.†, S.J. Walton, D.A. Goldman, M.L. Morrison, A.J. Verster, A.B. Parrott, F.B. Yu, N. Neff, N.A. Rosenberg, B.D. Ross, D.A. Petrov, K.C. Huang, B.H. Good†, and D. Relman†. Prolonged delays in human microbiota transmission after a controlled antibiotic perturbation. *bioRxiv* doi: 10.1101/2023.09.26.559480 (2023).
10. McEnany, J.D. and B.H. Good. Predicting the first steps of evolution in randomly assembled communities. *Nature Communications* 15: 8495 (2024).
11. Ferrare, J.T. and B.H. Good. Evolution of evolvability in rapidly evolving populations. *Nature Ecology & Evolution* 8: 2085–2096 (2024).
12. Good, B.H.. Limited codiversification of the gut microbiota with humans. *bioRxiv*, doi:10.1101/2022.10.27.514143 (2022).
13. Wong, D.P.G.H. and B.H. Good. Quantifying the adaptive landscape of commensal gut bacteria using high-resolution lineage tracking. *Nature Communications* 15: 1605 (2024).
14. Liu, Z. and B.H. Good. Dynamics of bacterial recombination in the human gut microbiome. Dynamics of bacterial recombination in the human gut microbiome. *PLoS Biology* 22(2): e3002472 (2024).
15. Good, B.H.†, L.B. Rosenfeld, Eco-evolutionary feedbacks in the human gut microbiome. *Nature Communications* 74: 7146 (2023).
16. Ascensao, J.A., K.M. Wetmore, B.H. Good, A.P. Arkin, and O. Hallatschek. Quantifying the local adaptive landscape of a nascent bacterial community. *Nature Communications*, 14: 248 (2023).
17. Dapa, T\*, D.P.G.H.Wong\*, K.S. Vasquez, K.B. Xavier†, K.C. Huang†, and B.H. Good†. Within-host evolution of the gut microbiome. *Current Opinion in Microbiology*, 71: 102258 (2023).
18. Ghosh, O.M. and B.H. Good. Emergent evolutionary forces in spatial models of luminal growth and their application to the human gut microbiota. *Proc. Natl. Acad. Sci. USA* 119(28): e2114931119 (2022).
19. Melissa, M.J., B.H. Good, D.S. Fisher, and M.M. Desai. Population genetics of polymorphism and divergence in rapidly evolving populations. *Genetics* 221(4):iyac053 (2022).

20. Ho, P.Y., B.H. Good<sup>†</sup>, and K.C. Huang<sup>†</sup>. Competition for fluctuating resources reproduces statistics of species abundance over time across wide-ranging microbiotas. *eLife* 11:e75168 (2022).
21. B.H. Good. Linkage disequilibrium between rare mutations. *Genetics* 220(4): iyac004 (2022).
22. Vasquez, K.S., L. Willis, N. Cira, K.M. Ng, M.F. Pedro, A. Aranda-Díaz, M. Ranjendram, F.B. Yu, S. Higginbottom, N. Neff, G. Sherlock, K.B. Xavier, S. Quake, J. Sonnenburg, B.H. Good<sup>†</sup>, and K.C. Huang<sup>†</sup>. Quantifying the interplay between rapid bacterial evolution within the mouse intestine and transmission between hosts. *Cell Host & Microbe* 29(9): 1454-1468.e4 (2021).
23. Roodgar, M.\*, B.H. Good<sup>\*†</sup>, N.R. Garud, S. Martis, M. Avula, W. Zhou, S. Lancaster, H. Lee, A. Babveyh, S. Nesamoney, K.S. Pollard<sup>†</sup>, and M.P. Snyder<sup>†</sup>. Longitudinal linked read sequencing reveals ecological and evolutionary responses of a human gut microbiome during antibiotic treatment. *Genome Research* 31: 1433-1446 (2021).
24. Garud, N.R.\*<sup>†</sup>, B.H. Good<sup>\*†</sup>, O. Hallatschek, and K.S. Pollard. Evolutionary dynamics of bacteria in the gut microbiome within and across hosts. *PLoS Biology* 17(1):e3000102 (2019).
25. Good, B.H.<sup>†</sup> and O. Hallatschek. Effective models and the search for quantitative principles in microbial evolution. *Current Opinions in Microbiology* 45:203-212 (2018).
26. Good, B.H.<sup>†</sup>, S. Martis, and O. Hallatschek. Adaptation limits ecological diversification and promotes ecological tinkering during the competition for substitutable resources. *Proc. Natl. Acad. Sci. USA* 115:E10407–E10416 (2018).
27. Cvijovic, I., B.H. Good, and M.M. Desai. The effect of strong purifying selection on genetic diversity. *Genetics*, 209:1235–1278 (2018).
28. Good, B.H.<sup>\*</sup>, M. J. McDonald<sup>\*</sup>, J. E. Barrick, R. E. Lenski, and M. M. Desai. The Dynamics of Molecular Evolution Over 60,000 Generations. *Nature* 551:45–50 (2017).
29. Good, B. H. and M. M. Desai. Evolution of mutation rates in rapidly adapting asexual populations. *Genetics*, 204:1249–1266 (2016).
30. Cvijovic, I.\*<sup>\*</sup>, B.H. Good<sup>\*</sup>, E.R. Jerison, and M.M. Desai. The fate of a mutation in a fluctuating environment. *Proc. Natl. Acad. Sci. USA* 112:E5021-E5028 (2015).
31. Rice, D. P., B.H. Good, and M.M. Desai. The evolutionarily stable distribution of fitness effects. *Genetics* 200:321–329 (2015).
32. Good, B. H. and M. M. Desai. The impact of macroscopic epistasis on long-term evolutionary dynamics. *Genetics* 199:177–190 (2015).
33. Good, B. H. and M. M. Desai. Deleterious passengers in adapting populations. *Genetics* 198:1183-1208 (2014).
34. Frenkel, E. M., B.H. Good, and M. M. Desai. The fates of mutant lineages and the distribution of fitness effects of beneficial mutations in laboratory budding yeast populations. *Genetics* 196:1217-1226 (2014).
35. Good, B. H., A.M. Walczak, R. A. Neher, and M. M. Desai. Genetic diversity in the interference selection limit. *PLoS Genetics* 10:e1004222 (2014).
36. Good, B. H. and M. M. Desai. Fluctuations in fitness distributions and the effects of weak selection on sequence evolution. *Theoretical Population Biology* 85:86-102 (2013).
37. Smith, D. E., D. K. Foley, and B. H. Good. Unhedgeable shocks and statistical economic equilibrium. *Economic Theory* 52: 187-235 (2013).

38. Good, B. H., I. M. Rouzine, D. J. Balick, O. Hallatschek, and M. M. Desai. Distribution of fixed beneficial mutations and the rate of adaptation in asexual populations. *Proc. Natl. Acad. Sci. USA* 109:4950-4955 (2012).
39. Good, B. H., Y.-A. de Montjoye, and A. Clauset. The performance of modularity maximization in practical contexts. *Phys. Rev. E* 81, 046106 (2010).

## Invited Talks and Seminars

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Philippe Meyer Prize Symposium, Ecole Normale Supérieure, Paris, France, 4/8/25.

Function of Evolving Systems Symposium, Simons Foundation, New York, NY, 12/2/24.

Early Career Keynote, Bay Area Population Genomics XXIII, UC Berkeley, CA, 11/09/24.

Phage Therapy Working Group, Gladstone Institute of Virology, San Francisco, CA, 10/22/24.

Horizontal Gene Transfer and Mobile Elements in Microbial Ecology and Evolution, KITP, Santa Barbara, CA, 7/16/24.

Emerging Directions Workshop. National Institute for Theory in Mathematics and Biology, Chicago, IL, 2/21/24.

CEHG Evolgenome Seminar, Stanford University, CA, 11/29/23.

Microbiome Research in the Bay Area Symposium, UCSF, San Francisco, CA, 11/17/23.

Greater Boston Area Theoretical Chemistry Seminar, MIT/BU/Harvard, Boston, MA, 11/8/23.

International Laboratory for Human Genome Research Seminar, National Autonomous University of Mexico (Virtual), 4/17/23.

Biohub Investigator Meeting, Chan Zuckerberg Biohub, San Francisco, CA, 12/15/22.

Evolutionary Studies Seminar Series, Vanderbilt University, Nashville, TN, 10/26/22.

Stanford Bio-X Talks in English (T.I.E.), Stanford University, CA, 8/22/22.

Bridging Population and Quantitative Genetics, KITP, Santa Barbara, CA, 7/7/22.

Physics & Astronomy Colloquium, Swarthmore College, Swarthmore, PA, 10/29/21.

Fall Symposium, Institute for Systems Biology, Seattle, WA (virtual), 10/15/21

Biophysics Program Retreat (Student Speaker Selection), Stanford University, Stanford, CA, 9/15/21.

The Ecology and Evolution of Microbial Communities, KITP, Santa Barbara, CA, 7/26/21.

Bug Club, Stanford University, Stanford, CA, 5/24/21.

Microbial Population Biology Seminar, Max Plank Institute for Evolutionary Biology, Plön, Germany, 3/23/21.

American Physical Society March Meeting (Virtual), 3/15/21.

qEvo 2021, Institut Henri Poincaré (Virtual), 1/12/21.

Physics Colloquium, Emory University, Atlanta, GA, 9/29/20.

Fall Seminar Series, Carnegie Institution for Science, Stanford, CA, 12/6/19.

Evolution, Ecology, and Behavior Seminar, Indiana University, Bloomington, IN, 10/25/19.

Out-of-Equilibrium Processes in Evolution and Ecology, CMO-BIRS, Oaxaca, Mexico, 8/21/19.

Microbiome Meeting, Cold Spring Harbor Laboratory, Cold Spring Harbor, NY, 7/19/19.

From Molecular Basis to Predictability and Control of Evolution, Nordita Institute, Stockholm, Sweden, 7/15/19.

Miller Lunch Talk, Berkeley, CA, 3/26/19.

American Physical Society March Meeting, Boston, MA, 3/7/19.

Ecology and Evolution Seminar, University of Chicago, Chicago, IL, 3/4/19.

CME Seminar, Arizona State University, Tempe, AZ, 2/18/19.

Mathematics Colloquium, University of Pittsburgh, Pittsburgh, PA, 2/12/19.

Computational Biology Seminar, Cornell University, Ithaca, NY, 2/7/19.

Special Seminar, Cold Spring Harbor Laboratory, Cold Spring Harbor, NY, 1/30/19.

Condensed Matter Physics Seminar, Stanford University, Palo Alto, CA, 1/17/19.

Microbial Eco-Evo Seminar, Stanford University, Palo Alto, CA, 1/17/19.

Phyloseminar (virtual), phyloseminar.org, 6/26/19.

Physics Colloquium, Gettysburg College, Gettysburg PA, 10/19/18.

Condensed Matter and Biological Physics Seminar, Washington University in St. Louis, St. Louis MO, 9/17/18.

Physical Principles Governing the Organization of Microbial Communities, Aspen Center for Physics, Aspen, CO, 6/8/18.

Ecology and Evolution of Microbial Populations, IGC, Lisbon, Portugal, 4/12/18.

*Escherichai coli*: The model microbe. Microbiology Society 2018, Birmingham, UK, 4/10/18.

Special Seminar, KITP, Santa Barbara, CA, 2/15/18.

Biophysics Seminar, Princeton University, Princeton, NJ, 2/5/18.

Eco-Evolutionary Dynamics in Nature and the Lab, KITP, Santa Barbara, CA, 9/11/17.

Eco-Evolutionary Dynamics in Nature and the Lab, KITP, Santa Barbara, CA, 9/5/17.

Probing Microbiome Dynamics, SMCB 2017, Austin, TX, 7/4/17.

qBio Seminar, University of California, San Diego, 10/10/16.

Bay Area Population Genomics XIV, San Francisco State University, 9/17/16.

Evolutionary Dynamics Seminar, PED, Harvard University, 3/22/16.

Populations, Evolution, and Physics, Aspen Center for Physics, 1/3/16

Condensed Matter Theory Kids Seminar, Harvard University, 10/13/15.

Walter M. Fitch Symposium, SMCB 2015, Vienna, Austria, 7/15/15.

Boston Evolutionary Genomics Retreat, Broad Institute, 8/30/13.

FAS Center for Systems Biology Groupmeeting, Harvard University, 7/3/13.

American Physical Society March Meeting, Baltimore, MD, 3/18/2013.

Condensed Matter Theory Kids Seminar, Harvard University, 9/18/2012.

Evolution Ottawa, 7/10/2012.

FAS Center for Systems Biology Groupmeeting, Harvard University, 4/25/12.

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## Teaching Experience

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### Stanford University

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| Applied Physics 237 // Biology 251: Quantitative evolutionary dynamics and genomics | 2020-21, 2023-24 |
| Applied Physics 205 // Biology 126/226: Introduction to Biophysics                  | 2021-2025        |

### Harvard University

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| <i>Teaching Fellow</i> , Applied Math 126 / Physics 141: Statistics and Inference in Biology | 2015 |
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### Swarthmore College

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| <i>Teaching Assistant</i> , Physics 14: Introduction to Quantum Mechanics   | 2010 |
| <i>Teaching Assistant</i> , Physics 7: Introductory Mechanics               | 2009 |
| <i>Lab teaching assistant</i> , Physics 50: Mathematical Methods in Physics | 2009 |

### Gettysburg College

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| <i>Lab teaching assistant</i> , Physics 211: Electricity and Magnetism | 2006 |
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### Guest Lecturer

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| QBio Summer Course: Microbial Interactions, <i>Kavli Institute for Theoretical Physics</i> | 2021       |
| Biophysics 250: Seminar in Biophysics, <i>Stanford University</i>                          | 2019, 2020 |
| Ecology and Evolution of Microbial Populations, <i>IGC, Lisbon</i>                         | 2018       |

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| OEB 230: Comparative and Evolutionary Genomics, <i>Harvard University</i> | 2018 |
| Math 243: Evolutionary Dynamics Seminar, <i>Harvard University</i>        | 2016 |

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## Professional Activities

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Referee for *Cell*, *Nature*, *Nature Ecology & Evolution*, *Nature Microbiology*, *Nature Communications*, *PNAS*, *eLife*, *Current Biology*, *Genetics*, *PLoS Biology*, *PLoS Genetics*, *PLoS Computational Biology*, *The American Naturalist*, *Ecology Letters*, *Evolution*, *Bioinformatics*, *BMC Evolutionary Biology*, *PLoS ONE*, *Physical Review Letters*, *Physical Review E*, *Physical Review X*, *Journal of Statistical Mechanics: Theory and Experiment*, *Journal of Statistical Physics*

Guest Editor for *Physical Review X*, *PLoS Computational Biology*.

Grant referee for US Army Research Office (Microbiology Program), Human Frontier Science Program, European Research Council.

Co-organizer (w/ Allison Carey, Honour McCann, Katie Pollard, and Julia Salzman) for “Horizontal Gene Transfer and Mobile Elements in Microbial Ecology and Evolution” Program, Kavli Institute for Theoretical Physics, Santa Barbara, CA (Summer 2024).

Co-director (w/ Honour McCann) for QBio Summer Course, Kavli Institute for Theoretical Physics, Santa Barbara, CA (Summer 2024).

Co-organizer (w/ Dmitri Petrov) of the Bay Area Population Genomics Conference (Spring 2022).

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## Outreach

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Speaker for Stanford Physics, Identity, and Equity (PIE) Summer Workshop (October 2023, September 2024)

Research supervisor for 3 high-school students in STEM Internship Program at the Neuva School, San Mateo, CA (Summer 2022 and 2023).

Research supervisor for 2 students in STEM Research Program at College Prep High-School, Oakland, CA (Summer 2017 and Summer 2018).

Co-organizer for Harvard Science Weeks public outreach event (4/12/2012).