

# JOSHUA B. PLOTKIN

University of Pennsylvania  
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## EDUCATION

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- 1999–2003 Princeton University, *Ph.D.* in Applied and Computational Mathematics  
Advisor: Simon Levin  
1994–1999 Harvard University, *A.B. summa cum laude* in Mathematics  
1997–1998 Oxford University, Visiting student in Mathematics  
1988–1994 The Roxbury Latin School

## SCIENTIFIC POSITIONS

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- 2014– Professor of Biology, Mathematics, Computer & Information Science, U. Pennsylvania  
2011–2014 Associate Professor of Biology, Computer & Information Science, U. Pennsylvania  
2009–2011 Martin Meyerson Assistant Professor of Interdisciplinary Studies, U. Pennsylvania  
2007–2011 Assistant Professor of Biology and Computer Science, University of Pennsylvania  
2002–2007 Junior Fellow of the Harvard Society of Fellows  
1999–2003 Member, Institute for Advanced Study, Princeton, NJ  
1998–2011 Adjunct research faculty, Institute for Defense Analyses, Princeton, NJ  
1997, 1998 Cryptographic research mathematician, US National Security Agency, Fort Meade, and  
(summers) Government Communications HQ, England (top-secret/SCI clearance)

## AWARDS AND FELLOWSHIPS

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- 2015 Akira Okubo Prize of the Society for Mathematical Biology and the Japanese SMB  
2009–2014 David and Lucile Packard Fellowship in Science and Engineering  
2009–2011 Alfred P. Sloan Foundation Research Fellowship  
2005–2010 Burroughs Wellcome Fund Career Award at the Scientific Interface  
2002–2007 Junior Fellow of the Harvard Society of Fellows  
2002–2003 Porter Ogden Jacobus Award of Princeton University  
2001–2003 Burroughs Wellcome Fund training fellowship  
2001–2002 Teresa Heinz Scholarship for Environmental Research  
1999–2002 National Science Foundation graduate fellowship in mathematics  
1999–2002 Princeton University merit fellowship in the natural sciences and mathematics  
1999 *A.B. summa cum laude*, Harvard University  
1998 *Phi Beta Kappa*, Harvard University  
1995–1999 John Harvard scholarship  
1994 Detur Prize, Harvard University  
1989–1994 Eight ACL national Latin and Greek Exam awards

## EDITORIAL BOARD SERVICE

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- 2012– Board of Reviewing Editors, *Science* (AAAS)  
2011– Editorial Board, *Cell Reports*  
2013– Guest Editor, *Proceedings of the National Academy of Sciences*  
2006–2013 Associate Editor, *Journal of Molecular Evolution*

## FUNDING HISTORY

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- 2017–2020 Army Research Office W911NF-17-1-0083  
*Inferring the role of epistasis in molecular evolution*  
PI Plotkin
- 2016–2020 Defense Advanced Research Projects Agency (DARPA) D17AC00005  
*The Statistical Mechanics of Crowds: predictive modeling in the social sciences*  
PI Plotkin, with five co-investigators
- 2012–2016 Defense Advanced Research Projects Agency (DARPA) D12AP00025  
*Biochronicity: Time, Evolution, Networks and Function*  
Co-PIs Plotkin and Hogenesch (U. Penn portion)
- 2012–2015 Army Research Office  
*Inferring Microbial Fitness Landscapes*  
PIs Plotkin and Epstein
- 2012–2014 National Philanthropic Trust  
*An explanatory framework for the evolution of complexity*  
PI Plotkin
- 2009–2016 David and Lucile Packard Fellowship in Science and Engineering  
*Towards a quantitative understanding of molecular evolution*  
PI Plotkin
- 2009–2011 NIAID 3U54AI057168  
*Predicting the antigenic future of influenza A: a computational approach*  
Co-I Plotkin
- 2009–2011 Alfred P. Sloan Foundation Research Fellowship  
PI Plotkin
- 2009–2010 National Academy of Sciences Keck Futures Initiative  
*Population dynamics of language evolution*  
PI Plotkin
- 2009–2010 University of Pennsylvania Research Foundation  
PI Plotkin
- 2008–2013 James S. McDonnell Foundation  
*Robustness and adaptability in evolving viral populations*  
PI Plotkin
- 2008–2012 NIGMS R01GM085226-01  
*Methods for evolutionary analysis of eukaryotic transcriptional regulation*  
PI Hannenhalli, Co-I Plotkin
- 2009–2012 Defense Advanced Research Projects Agency (DARPA) HR0011-05-1-0057  
*Fundamental laws in biology*  
Co-PIs Plotkin and Epstein (U. Penn portion)
- 2005–2010 Burroughs Wellcome Fund, Career Award at the Scientific Interface  
*Novel methods to compute selection pressures on proteins at the genome-wide scale*  
PI Plotkin
- 2005–2012 United Nations Development Program UNOSP INT95R71  
*Conservation of Biodiversity Through Improved Forest Planning*  
Co-PIs Plotkin, Bossert, Davies

## MENTORSHIP

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### Post-doctoral Fellows

- 2017– Arunas Radzvilavicius (PhD, UCL, Applied Mathematics)  
2017– Andrew Tilman (PhD, Princeton, Ecology & Evolutionary Biology)  
2017– Colin Twomey (PhD, Princeton, Ecology & Evolutionary Biology)  
2013– Davorka Gulisija (PhD, University of Wisconsin Madison, Zoology)  
2012– Jakub Otwinowski (PhD, Emory University, Physics)  
2013–2017 Oana Carja (PhD, Stanford, Biology)  
currently tenure-track Assistant Professor at Carnegie Mellon University (Jan 2019)  
2012–2016 David McCandlish (PhD, Duke University, Biology)  
currently a tenure-track Assistant Professor at Cold Spring Harbor Laboratories  
2011–2015 Premal Shah (PhD, University of Tennessee, Biology)  
currently a tenure-track Assistant Professor at Rutgers University  
2010–2015 Alexander Stewart (PhD, University College London, Applied Mathematics)  
currently a Royal Society Research Fellow at University College London  
2010–2013 Ricky Der (PhD, University of Pennsylvania, Mathematics)  
2011–2013 David Bostick (PhD, UNC Chapel Hill, Physics)  
2011–2013 Etienne Rajon (PhD, University of Lyon, Ecology)  
currently a tenure-track Assistant Professor at *Université de Lyon*  
2008–2012 Jeremy Draghi (PhD, Yale University, Biology)  
currently tenure-track Assistant Professor at City University New York  
2007–2011 Todd Parsons (PhD, University of Toronto, Mathematics)  
currently a permanent scientist of *CNRS* at *Université Pierre et Marie Curie*  
2009–2011 Helene Morlon (PhD, University of Bordeaux, Biology)  
currently a permanent scientist of *CNRS* at *École Normale Supérieure*  
2008–2010 Gasper Tkacik (PhD, Princeton University, Applied Mathematics) joint with P. Nelson  
currently a tenure-track Asst. Professor at Inst. of Science and Technology, Austria  
2007–2010 Sergey Kryazhimskiy (PhD, Princeton University, Applied Mathematics)  
currently a tenure-track Assistant Professor at UCSD  
2007–2010 Michael Levy (PhD, Emory University, Biology)  
currently an Associate Professor at U. Pennsylvania, Dept. of Biostatistics  
2008–2010 Anchal Vishnoi (PhD, Nehru University, Biology) joint with S. Hannenhalli  
currently a Lecturer at Nehru University  
2005–2007 Grzegorz Kudla (PhD, University of Warsaw, Biology)  
currently a Senior Scientist of the MRC, at the University of Edinburgh

### Graduate Students

- 2012–2017 Mitchell Johnson, PhD student in Biology, currently in the Michigan Society of Fellows and Assistant Professor of Complex Systems at University of Michigan (Sep 2018)  
2014–2015 Koji Noshita, Visiting PhD student from Kyushu University, Japan  
2010–2015 Yang Ding, PhD student in Biology, currently at post-doc with B. Palsson (UCSD)  
2007–2010 Ricky Der, PhD student in Mathematics, joint with C. Epstein  
2008–2010 Serena Rezny, MA student in Applied Mathematics  
2009 Lena Gieschen, visiting PhD student from University of Kiel

### Undergraduate Students

- 2012–2013 Krishna Kaliannan, undergraduate researcher  
2008–2012 Alison Feder, undergraduate researcher, currently a PhD student at Stanford  
2008–2010 Sebastian Akle, undergraduate researcher, currently a PhD student at Harvard  
2007–2009 Daril Vilhena, undergraduate researcher, subsequently a PhD student at U. Washington  
2007–2008 Bo Zhou, undergraduate researcher, subsequently a PhD student at Harvard

## TEACHING EXPERIENCE

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- 2009– Advanced Evolution (BIOL 410), University of Pennsylvania  
2008– Statistics for Biologists (BIOL 446), University of Pennsylvania  
2003 Biological Dynamics (APC 514) Princeton University, with E. Cox, W. Bialek

## INVITED LECTURES

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- 2018 University of Chicago, Department of Ecology and Evolutionary Biology, Chicago IL  
2016 Princeton University, Department of Ecology and Evolutionary Biology, Princeton NJ  
2016 Temple University, Institute for Genomics and Evolutionary Medicine, Philadelphia PA  
2015 Okubo Prize Lecture, Society for Mathematical Biology, Atlanta, GA  
2015 Okubo Prize Lecture, Japanese Society for Mathematical Biology, Kyoto, Japan  
2015 Keynote Address, Mathematical Models in Ecology and Evolution, Paris, France  
2015 Stanford University, Department of Biology, Palo Alto, CA  
2015 Session Chair, Society for Molecular Biology and Evolution, Vienna, Austria  
2014 University of Maryland, Computational Biology Program student-invited speaker  
2013 Rockefeller University, Center for Physics and Biology  
2013 Rutgers University, 110th Statistical Physics Conference  
2012 American Society for Microbiology Bio-defense Conference, Washington DC  
2012 Institute for Systems Biology, Seattle WA, student-invited speaker  
2012 Academia Sinica, Institute of Physics, Taipei, Taiwan  
2012 New York University, Department of Biology  
2012 Duke University, Department of Mathematics  
2012 National Institute for Mathematical and Biological Synthesis, Knoxville TN  
2012 University of Pennsylvania, Friday Research Discussion  
2011 California Institute of Technology, Biophysics Lecture Series  
2011 Princeton University, Colloquium in Applied Mathematics  
2011 Yale University, Department of Ecology & Evolutionary Biology  
2011 Cold Spring Harbor Laboratories, Quantitative Biology Seminar Series  
2010 Duke University, Biology and Mathematics joint colloquium  
2010 Packard Fellows Annual Meeting, Monterey CA  
2010 UC Berkeley, Departments of Mathematics and Integrative Biology  
2010 University of Chicago, Department of Ecology and Evolution  
2010 Georgia Tech, Department of Biology  
2009 Science/AAAS Webinar, Washington DC  
2009 33<sup>rd</sup> Penn Linguistics Colloquium, University of Pennsylvania  
2008 Kavli Institute for Theoretical Physics, Santa Barbara CA  
2007 Mathematics colloquium, Penn State University  
2007 National Academy of Sciences USA, US-Japan Frontiers of Science, Kanagawa, Japan  
2006 Keck Graduate Institute, Claremont CA  
2005 NIH Twinbrook Distinguished Lecture Series, Rockville MD  
2004 The Fields Institute, Toronto ON  
2004 Santa Fe Institute Workshop on Diversity Scaling, Czech Natl. Acad. Sci., Prague  
2004 Gordon Conference on Theoretical Biology & Biomathematics, Tilton NH  
2003 Gordon Conference on Evolutionary and Ecological Genomics, New London NH  
2002 First European Influenza Conference, St. Juliens, Malta  
2001 *Laboratoire d' Ecologie Terrestre, CNRS, Toulouse, France*  
2001 Polish Academy of Sciences, Stefan Banach International Mathematics Centre, Warsaw  
2000 Imperial College of Science, Technology and Medicine, Silwood Park, England  
2000 Smithsonian Tropical Research Institute Annual Meeting, Singapore  
1998 Mathematics Institute, Oxford University, Oxford, England

## PUBLICATIONS ([google scholar](#))

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1. **Otwinowski J, McCandlish D, Plotkin JB.**  
Inferring the shape of global epistasis.  
*bioRxiv* 10.1101/2728630
2. **Carja O, Plotkin JB.**  
Phenotypic plasticity can facilitate evolutionary rescue.  
*bioRxiv* 10.1101/092718
3. **Newberry MG, Ahern C, Clark R, Plotkin JB\***.  
Evolutionary forces in language change.  
*Nature* 551: 223-226 (2017)
4. **Gulisija D, Plotkin JB.**  
Phenotypic plasticity promotes recombination and gene clustering in periodic environments.  
*Nature Communications* 8: 2041 (2017)
5. **Plotkin JB.**  
No escape from the tangled bank.  
*Nature* 551: 42-43 (2017)
6. **Carja O, Xing T, Wallace EW, Plotkin JB, Shah P.**  
riboviz: analysis and visualization of ribosome profiling datasets.  
*BMC Bioinformatics* 10.1186/s12859-017-1873-8 (2017)
7. **Carja O, Plotkin JB.**  
The evolutionary advantage of heritable phenotypic heterogeneity.  
*Scientific Reports* 7: 5090 (2017)
8. **Stewart A, Parsons T, Plotkin JB.**  
Evolutionary consequences of behavioral diversity.  
*Proceedings of the National Academy of Sciences USA* 113: 7003-7009 (2016)
9. **Newberry M, McCandlish D, Plotkin JB.**  
Assortative mating can impede or facilitate fixation of underdominant alleles.  
*Theoretical Population Biology* 112: 14-21 (2016)
10. **Nourmohammad A, Otwinowski J, Plotkin JB.**  
Host-pathogen co-evolution and the emergence of broadly neutralizing antibodies in chronic infections.  
*PLOS Genetics* 12: 1006171 (2016)
11. **Stewart A, Plotkin JB.**  
Small groups and long memories promote cooperation.  
*Scientific Reports* 6: 26899 (2016)
12. **McCandlish D, Shah P, Plotkin JB.**  
Epistasis and the dynamics of reversion in molecular evolution.  
*Genetics* 203: 1335-1351 (2016)
13. **Gulisija D, Kim Y, Plotkin JB.**  
Phenotypic plasticity promotes balanced polymorphism in periodic environments by a genomic storage effect.  
*Genetics* 202: 1437-1448 (2016)

14. **McCandlish D, Plotkin JB\***.  
Transcriptional errors and the drift barrier.  
*Proceedings of the National Academy of Sciences USA* 113: 3136-3138 (2016)
15. Weinberg DE<sup>#</sup>, **Shah P<sup>#</sup>**, Eichhorn SW, Hussmann JA, **Plotkin JB**, Bartel DP.  
Improved ribosome-footprint and mRNA measurements provide insights into dynamics and regulation of yeast translation.  
*Cell Reports* 14:1-13 (2016)
16. **McCandlish M, Otwinowski J, Plotkin JB**.  
Detecting epistasis from an ensemble of adapting populations.  
*Evolution* 69: 2359-2380 (2015)
17. Neverov AD, **Kryazhimskiy S, Plotkin JB**, Bazykin GA.  
Coordinated evolution of Influenza A surface proteins.  
*PLoS Genetics* 11: 1005404 (2015)
18. **Stewart A, Plotkin JB**.  
The evolvability of cooperation under local and non-local mutations.  
*Games* 6:231-250 (2015)
19. **McCandlish D, Epstein C, Plotkin JB**.  
Formal properties of the probability of fixation: identities, inequalities and approximations.  
*Theoretical Population Biology* 99:98-113 (2015)
20. Schulte MB, **Draghi JA, Plotkin JB**, Andino R.  
Experimentally guided models reveal replication principles that shape the mutation distribution of RNA viruses.  
*eLife* 4:3753 (2015)
21. Kumar S, **Plotkin JB**, Hannenhalli S.  
Regulated CRISPR modules exploit a dual defense strategy of restriction and abortive infection in a model of prokaryote-phage coevolution.  
*PLoS Computational Biology* 11: 1004603 (2015)
22. **Shah P, McCandlish M, Plotkin JB\***.  
Historical contingency and entrenchment in protein evolution under purifying selection.  
*Proceedings of the National Academy of Sciences USA* 112:3226–3235 (2015)
23. **Stewart A, Plotkin JB\***.  
The collapse of cooperation in evolving games.  
*Proceedings of the National Academy of Sciences* 111: 17558-17563 (2014)
24. **Otwinowski J, Plotkin JB\***.  
Inferring fitness landscapes by regression produces biased estimates of epistasis.  
*Proceedings of the National Academy of Sciences USA* 111:2301-2309 (2014)
25. **Der R, Plotkin JB**.  
The equilibrium allele frequency distribution for a population with reproductive skew.  
*Genetics* 196: 1199-1216 (2014)
26. **McCandlish D, Epstein C, Plotkin JB**.  
The inevitability of unconditionally deleterious substitutions during adaptation.  
*Evolution* 68:1351-1365 (2014)
27. **Stewart A, Plotkin JB\***.  
From extortion to generosity, evolution in the Iterated Prisoner's Dilemma.  
*Proceedings of the National Academy of Sciences USA* 110: 15348-15353 (2013)

28. **Shah P, Ding Y, Niemczyk M, Kudla G, Plotkin JB\***.  
Rate-limiting steps in yeast protein translation.  
*Cell* 153: 1589-1601 (2013)
29. **McCandlish D, Rajon E, Shah P, Ding Y, Plotkin JB\***.  
The role of epistasis in protein evolution.  
*Nature* 497: E1-E2 (2013)
30. **Feder A, Kryazhimskiy S, Plotkin JB\***.  
Identifying signatures of selection in genetic time series.  
*Genetics* 196: 509-522 (2013)
31. **Draghi J, Plotkin JB**.  
Selection biases the prevalence and type of epistasis along adaptive trajectories.  
*Evolution* 67: 3120–3131 (2013)
32. Lipsitch M, Fisman D, **Plotkin JB**, Simonsen L.  
Ferret H7N9 flu model questioned.  
*Nature* 501: 33 (2013)
33. Li Y, **Bostick D**, Sullivan C, Myers J, Griesemer S, St. George K, **Plotkin JB\***, Hensley S\*.  
Single Hemagglutinin mutations that alter both antigenicity and receptor-binding avidity.  
*Journal of Virology* 87: 9904-9910 (2013)
34. Li Y, Myers J, **Bostick D**, Sullivan C, Madara J, Linderman S, Liu Q, Carter D, Wranmert J, Esposito S, Principi N, **Plotkin JB**, Ross T, Ahmed R, Wilson P, Hensley S.  
Immune history shapes specificity of pandemic H1N1 Influenza antibody responses.  
*Journal of Experimental Medicine* 210: 1493-1500 (2013)
35. **Stewart A, Plotkin JB\***.  
The evolution of complex gene regulation by low-specificity binding sites.  
*Proceedings of The Royal Society B* 280: 20131313 (2013)
36. **Rajon E, Plotkin JB**.  
The evolution of genetic architectures underlying quantitative traits.  
*Proceedings of The Royal Society B* 280: 20131552 (2013)
37. Harrison RD, Tan S, **Plotkin JB**, Slik F, Detto M, Brenes T, Itoh A, Davis SJ.  
Consequences of defaunation for a tropical tree community.  
*Ecology Letters* 16: 687–694 (2013).
38. **Stewart A, Hannenhalli S, Plotkin JB\***.  
Why transcription factor binding sites are ten nucleotides long.  
*Genetics* 192: 973-985 (2012)
39. **Stewart A, Seymour R, Pomiankowski A\*, Plotkin JB\***.  
The population genetics of cooperative gene regulation.  
*BMC Evolutionary Biology* 12: 173 (2012)
40. **Ding Y, Shah P, Plotkin JB\***.  
Weak 5' mRNA structure in short eukaryotic genes.  
*Genome Biology and Evolution* 4: 1046-1053 (2012)
41. **Stewart A, Plotkin JB\***.  
Extortion and cooperation in the Prisoner's Dilemma.  
*Proceedings of the National Academy of Sciences USA* 109: 10134-10135 (2012)

42. Lipsitch M, **Plotkin JB**, Simonsen L, Bloom B.  
Evolution, safety, and highly pathogenic Influenza viruses.  
*Science* 336: 1529-1531 (2012)
43. **Der R**, Epstein C, **Plotkin JB**\*.  
The dynamics of neutral and selected alleles when the offspring distribution is skewed.  
*Genetics* 191:1331-1344 (2012)
44. **Stewart A**, **Parsons T**, **Plotkin JB**\*.  
Environmental robustness and the adaptability of populations.  
*Evolution* 66: 1598-1612 (2012)
45. **Toll-Riera M**, **Bostick D**, Alba M\*, **Plotkin JB**\*.  
Structure and age jointly influence rates of protein evolution  
*PLoS Computational Biology* 8:1002542 (2012)
46. **Morlon H**, Kempes B, **Plotkin JB**, Brisson D.  
Explosive radiation of a bacterial species group.  
*Evolution* 66: 2577–2586 (2012)
47. Walczak AM, Nicolaisen LE, **Plotkin JB**, Desai MM.  
The structure of genealogies in the presence of purifying selection: a fitness-class coalescent.  
*Genetics* 190: 753-779 (2012)
48. Desai MM, Nicolaisen LE, Walczak AM, **Plotkin JB**\*.  
The structure of allelic diversity in the presence of purifying selection.  
*Theoretical Population Biology* 8: 144-157 (2012)
49. **Draghi J**, **Plotkin JB**.  
A network of paths towards innovation.  
*BioEssays* 34: 518–520 (2012)
50. **Kryazhimskiy S**, **Draghi J**, **Plotkin JB**\*.  
In evolution, the sum is less than its parts.  
*Science* 332: 1160-1161 (2011)
51. **Draghi J**, **Plotkin JB**\*.  
Hidden diversity sparks adaptation.  
*Nature* 474: 45-46 (2011)
52. **Der R**, Epstein C, **Plotkin JB**.  
Generalized population models and the nature of genetic drift.  
*Theoretical Population Biology* 80: 80-99 (2011)
53. **Plotkin JB**.  
The lives of proteins.  
*Science* 331: 683-684 (2011)
54. **Vishnoi A**, Sethupathy P, Simola D, **Plotkin JB**\*, Hannehalli S\*.  
Genome-wide survey of natural selection on functional, structural, and network properties of polymorphic sites in *Saccharomyces paradoxus*.  
*Molecular Biology and Evolution* 28: 2615-2627 (2011)
55. **Levy M**, Small D, **Vilhena D**, Bowman N, Kawai V, Carpio J, Codova E, Gilman R, **Plotkin JB**.  
Retracing micro-epidemics of Chagas disease using epicenter regression.  
*PLoS Computational Biology* 7: 1002146 (2011)



56. **Draghi J, Parsons T, Plotkin JB.**  
Epistasis increases the rate of conditionally neutral substitution in an adapting population.  
*Genetics* 187: 1139–1152 (2011)
- Morlon H, Parsons T, Plotkin JB.**  
Reconciling molecular phylogenies with the fossil record.  
*Proceedings of the National Academy of Sciences USA* 108: 16327-332 (2011, cover article)
57. **Plotkin JB\***, Kudla G.  
Synonymous but not the same: the causes and consequences of codon bias.  
*Nature Reviews Genetics* 12: 32-42 (2011)
58. **Kryazhimskiy S**, Dushoff J, Bazykin G, **Plotkin JB\***.  
Prevalence of epistasis in the evolution of Influenza A surface proteins.  
*PLoS Genetics* 7: 1001301 (2011)
59. **Draghi J, Parsons T**, Wagner G, **Plotkin JB\***.  
Mutational robustness can facilitate adaptation.  
*Nature* 426: 353-355 (2010)
60. **Morlon H\***, Potts M, **Plotkin JB\***.  
Inferring the dynamics of diversification: a coalescent approach.  
*PLoS Biology* 8: 1000493 (2010)
61. **Vishnoi A**, Kryazhimskiy S, Bazykin G, Hannenhalli S\*, **Plotkin JB\***.  
Young proteins experience more variable selection pressures than old proteins.  
*Genome Research* 20: 1574-1581 (2010)
62. Cao K, Chen-Plotkin AS, **Plotkin JB**, Wang LS.  
Age-correlated gene expression in normal and neurodegenerative human brain tissues.  
*PLoS One* 5: 13098 (2010)
63. Toole J, Eagle N, **Plotkin JB**.  
Spatiotemporal correlations in criminal offense records.  
*ACM Transactions on Intelligent Systems and Technology* 2:38 (2010)
64. Salguero-Gomez R, **Plotkin JB**.  
The effects of dimensionality on demographic studies using projection matrices.  
*The American Naturalist* 176:710-722 (2010)
65. **Levy MZ**, Malaga F, Cornejo del Carpio JG, **Vilhena D**, McKenzie FE, **Plotkin JB**.  
Rational strategies for eliminating a Chagas disease vector.  
*Proceedings of the Royal Society Interface* 7: 1061-1070 (2010)
66. Toole J, Eagle N, **Plotkin JB**.  
Quantifying behavioral data sets of criminal activity.  
*AAAI Spring Symposium SS-10-01: 91-96* (2010)
67. Ndifon W, **Plotkin JB**, Dushoff J.  
Environmental impact on the evolutionary accessibility of adaptive phenotypes of a bacterial metabolic network.  
*PLoS Computational Biology* 5: 1000472 (2009)
68. **Plotkin JB**.  
Transcriptional regulation is only half the story.  
*Molecular Systems Biology* 6: 406 (2010)

69. Roy S, Vandenberghe L, **Kryazhimskiy S**, Grant R, Calcedo R, Yuan X, Keough M, Sandhu A, Wang Q, Medina-Jaszek C, **Plotkin JB**, Wilson JM.  
Isolation and characterization of Adenoviruses persistently shed from the gastrointestinal tract of non-human primates.  
*PLoS Pathogens* 5: 1000503 (2009)
70. Goldstein E, Dushoff J, Ma J, **Plotkin JB**, Earn DJ, Lipsitch M.  
Reconstructing influenza incidence by de-convolution of daily mortality time series.  
*Proceedings of the National Academy of Sciences USA* 106: 21825-21829 (2009)
71. **Kryazhimskiy S**, **Tkacik G**, **Plotkin JB**\*.  
The dynamics of adaptation on correlated fitness landscapes.  
*Proceedings of the National Academy of Sciences USA* 106:18638-18643 (2009)
72. **Kudla G**, Murray AW, Tollervey D, **Plotkin JB**\*.  
Coding-sequence determinants of gene expression in *Escherichia coli*.  
*Science* 324: 255-258 (2009)
73. **Levy MZ**, Bowman NM, Kawai V, **Plotkin JB**, Waller LA, Cabrera L, Steurer F, Seitz AE, Cancino VV, Cornejo del Carpio JG, Cordova BE, McKenzie F, Maguire J, Gilman RH, Bern C.  
Spatial patterns in discordant diagnostic test results for Chagas disease: links to transmission hotspots.  
*Clinical Infectious Diseases* 48:1104-1106 (2009)
74. **Kryazhimskiy S**, **Plotkin JB**\*.  
The population genetics of dN/dS.  
*PLoS Genetics* 4: 1000304 (2008)
75. Desai MM, **Plotkin JB**\*.  
The polymorphism frequency spectrum of finitely many sites under selection.  
*Genetics* 180: 2175-2191 (2008)
76. **Kryazhimskiy S**, Basykin GA, **Plotkin JB**, Dushoff J.  
Directionality in the evolution of Influenza A Hemagglutinin.  
*Proceedings of the Royal Society B* 275: 2455-2464 (2008)
77. **Parsons T**, Quince C, **Plotkin JB**.  
Absorption and fixation times for neutral and quasi-neutral populations with density dependence.  
*Theoretical Population Biology* 74: 302-310 (2008)
78. Sethupathy P, Giang H, **Plotkin JB**, Hannenhalli S.  
Genome-wide analysis of natural selection on human cis-elements.  
*PLoS One* 3: 3137- (2008)
79. Wu M, Li J, Engleka K, Zhou B, Lu M, **Plotkin JB**, Epstein JA.  
Persistent expression of Pax3 in neural crest causes cleft palate and defective osteogenesis.  
*Journal of Clinical Investigation* 118: 2076-2078 (2008)
80. Chen-Plotkin AS, Geser F, **Plotkin JB** et al.  
Variations in the progranulin gene affect global gene expression in frontotemporal lobar degeneration.  
*Human Molecular Genetics* 17: 1349-1362 (2008)
81. Lucks J, **Kudla G**, Nelson D, **Plotkin JB**\*.  
Genome landscapes and bacteriophage codon usage.  
*PLoS Computational Biology* 4:1 (2008)

82. Fraser HB, **Plotkin JB**.  
Using protein complexes to predict phenotypic effects of gene mutation.  
*Genome Biology* 8:252 (2007)
83. Green JL, **Plotkin JB**\*.  
A statistical theory for sampling species abundances.  
*Ecology Letters* 10: 1037-1045 (2007)
84. **Plotkin JB**\*, Fraser HB.  
Assessing the determinants of evolutionary rates in the presence of noise.  
*Molecular Biology and Evolution* 24: 1113-1121 (2007)
85. Dushoff J, **Plotkin JB**, Viboud C, Simonesen L, Miller M.  
Vaccinating to protect a vulnerable subpopulation.  
*PLoS Medicine* 4:174 (2007)
86. Seidler T, **Plotkin JB**\*.  
Seed dispersal and spatial pattern in tropical trees.  
*PLoS Biology* 4: 344 (2006)
87. **Plotkin JB**\*, Dushoff J, Desai MM, Fraser HB.  
Codon usage and selection on proteins.  
*Journal of Molecular Evolution* 63: 635-553 (2006)
88. **Plotkin JB**\*, Dushoff J, Desai MM, Fraser HB.  
Estimating selection pressures from limited comparative data.  
*Molecular Biology and Evolution* 23: 1457-1459 (2006)
89. Dushoff J, **Plotkin JB**, Viboud C, Earn JD, Simonsen L.  
Mortality due to influenza in the US – an annualized approach to estimation using multiple-cause mortality data.  
*American Journal of Epidemiology* 163: 181-187 (2006)
90. Ng K, Soon LL, Saw LG, **Plotkin JB**, Koh CL.  
Spatial structure and genetic diversity of three tropical tree species with different habitat preferences.  
*Tree Genetics and Genomes* 2: 121-131 (2006)
91. HB Fraser, P Khaitovich, **JB Plotkin**, S Paabo, MB Eisen.  
Aging and gene expression in the primate brain.  
*PLoS Biology* 3: 274- (2005)
92. Lukhtanov V, Kandul N, **Plotkin JB**, Dantchenko A, Haig D, Pierce N.  
Reinforcement of pre-zygotic isolation and karyotype evolution in *Agrodiaetus* butterflies.  
*Nature* 436: 385-389 (2005)
93. **Plotkin JB**\*, Dushoff J, Fraser HB.  
Codon bias and selection on single genomes – reply.  
*Nature* 433 E7-E8 (2005)
94. Dushoff J, **Plotkin JB**, Levin SA, Earn DE.  
Dynamic resonance can explain the seasonality of influenza incidence.  
*Proceedings of the National Academy of Sciences USA*, 101: 16915-16916 (2004)
95. **Plotkin JB**\*, Robins H, Levine A.  
Tissue specific codon usage and the expression of human genes.  
*Proceedings of the National Academy of Sciences USA* 101: 12588-12591 (2004)

96. **Plotkin JB\***, Dushoff J, Fraser HB.  
Detecting selection using a single genome sequence of *M. tuberculosis* and *P. falciparum*.  
*Nature* 428: 942-945 (2004)
97. Levin SA, Dushoff J, **Plotkin JB**.  
Evolution and persistence of Influenza A and other diseases.  
*Mathematical Biosciences* 188: 12-28 (2004)
98. **Plotkin JB\***, Muller-Landau H.  
Sampling the species composition of a landscape.  
*Ecology* 83: 3344-3356 (2002)
99. **Plotkin JB\***, Nowak MA.  
The different effects of apoptosis and DNA repair on tumorigenesis.  
*Journal of Theoretical Biology* 214: 453-467 (2002)
100. Krakauer D, **Plotkin JB**.  
Principles and parameters of molecular robustness.  
In *Robust Design*, ed. Erica Jen, Santa Fe Press (2002)
101. **Plotkin JB\***, Chave J, Ashton PS.  
Cluster analysis of spatial patterns in Malaysian tree species.  
*The American Naturalist* 160: 629-644 (2002)
102. Potts MD, Ashton PS, Kaufman LS, **Plotkin JB**.  
Habitat patterns in tropical rain forests: a comparison of 105 plots in Northwest Borneo.  
*Ecology* 83: 2782-2797 (2002)
103. **Plotkin JB\***, Dushoff J.  
Codon bias and frequency-dependent selection on the Hemagglutinin epitopes of Influenza A virus.  
*Proceedings of the National Academy of Sciences USA* 100: 7152-7157 (2003)
104. **Plotkin JB\***, Dushoff J, Levin SA.  
Hemagglutinin sequence clusters and the antigenic evolution of Influenza A virus.  
*Proceedings of the National Academy of Sciences USA* 99: 6263-6268 (2002)
105. Krakauer D, **Plotkin JB**.  
Redundancy, anti-redundancy, and the stability of genomes.  
*Proceedings of the National Academy of Sciences USA* 99: 1405-1409 (2002)
106. **Plotkin JB\***, Levin SA.  
The spatial distribution and abundances of species: Lessons from tropical forests.  
*Comments on Theoretical Biology* 6: 251-278 (2001)
107. **Plotkin JB\***, Nowak MA.  
Major transitions in language evolution.  
*Entropy* 4: 227-246 (2001)
108. Potts MD, **Plotkin JB**, Lee HS, Manokaran N.  
Sampling biodiversity: effects of plot shape.  
*The Malaysian Forester* 64: 29-34 (2001)
109. **Plotkin JB\***, Nowak MA.  
Language evolution and information theory.  
*Journal of Theoretical Biology* 205: 147-159 (2000)

110. **Plotkin JB**<sup>\*</sup>, Potts M, Leslie N, Manokaran N, LaFrankie J, Ashton P.  
Species-area curves, spatial aggregation, and habitat specialization in tropical forests.  
*Journal of Theoretical Biology* 207:81-99 (2000)
111. **Plotkin JB**<sup>\*</sup>, Potts M, Yu D, Bunyavejchewin S, Condit R, Foster R, Hubbell S, LaFrankie J,  
Manokaran N, Seng L, Sukumar R, Nowak MA, Ashton PS.  
Predicting species diversity in tropical forests.  
*Proceedings of the National Academy of Sciences USA* 97, 10850-10854 (2000)
112. Nowak M, **Plotkin JB**, Jansen V.  
The evolution of syntactic communication.  
*Nature* 404: 495-498 (2000)
113. Nowak MA, **Plotkin JB**, Krakauer D.  
The evolutionary language game.  
*Journal of Theoretical Biology* 200: 147-162 (1999)

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Plotkin research group members in **bold**.

#### **CLASSIFIED PUBLICATIONS**

114. **Plotkin JB**.  
Classified research paper on cryptography and number theory.  
Institute for Defense Analyses internal peer-reviewed journal (1998)
115. **Plotkin JB**.  
Classified research paper on cryptography and number theory  
Institute for Defense Analyses internal peer-reviewed journal (1998)
116. **Plotkin JB**.  
Classified research paper on cryptography and number theory  
U.S. National Security Agency internal R51 journal (1997)