

Curriculum Vitae

Benjamin Allen

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Google Scholar Citations:

<http://scholar.google.com/citations?hl=en&user=3MBv8rIAAAAJ>

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Education

Boston University, Mathematics, Ph.D., 2010
Bryn Mawr College, Mathematics, M.A., 2002
Haverford College, Mathematics, B.A., 2002

Professional Experience

2018-present Associate Professor, Department of Mathematics, Emmanuel College.
2012-2018 Assistant Professor, Department of Mathematics, Emmanuel College.
2014-2015 Visiting Scholar, Center for Mathematical Sciences and Applications, Harvard University.
2012-2014 Research Associate, Program for Evolutionary Dynamics, Harvard University.
2010-2012 Research Scientist, Program for Evolutionary Dynamics, Harvard University.
2006-2010 Graduate Teaching Associate, Boston University.
Summer 2009 Research Fellow, Young Scientists Summer Program, International Institute for Applied Systems Analysis, Austria.
Summer 2008 Teaching Assistant, PROMYS for Teachers, Boston University.
Summer 2007 Instructor, Calculus for Social and Life Sciences, Boston University.
2004-2005 Mathematics Teacher, East Boston High School, Boston, MA.
2002-2004 Mathematics Teacher, Austin High School, Chicago, IL (through Teach for America).

Research Interests

I use mathematical modeling to investigate theoretical questions in evolutionary biology. Using simple, abstract models of evolution, as well as axiomatically-defined classes of models, my research aims to formalize general principles of evolution as mathematical theorems.

I am particularly interested in how population structure (spatial layout, social networks, etc.) can promote or inhibit the evolution of cooperative behavior. On the more empirically-motivated side, I use branching process models to study the somatic evolution of cancer and the emergence of resistance to targeted cancer therapies.

Beyond evolutionary dynamics, I am interested in the power of information theory to quantify structure and diversity in complex physical, biological, and social systems. This thread of my research ranges from the concrete (developing information-theoretic measures of biodiversity) to

the abstract (formalizing a multiscale approach to information theory in which information applies at particular scales).

Grants and Funding

- 2012-2014 National Philanthropic Trust (sponsored by John Templeton Foundation)
Foundational Questions in Evolutionary Biology Grant #RFP-12-02
Evolution of cooperation and complexity in structured populations
PI Martin A. Nowak, Co-PI's Benjamin Allen and Oliver Hauser
- 2017-2020 National Science Foundation
Division of Mathematical Sciences Award #1715315
RUI: The rate of evolution in structured populations
PI Benjamin Allen, Co-PI Christine Sample

Peer-reviewed research publications

- Fotouhi, B., Momeni, N., Allen, B., & Nowak, M. A. (2018) “Conjoining uncooperative societies facilitates evolution of cooperation” *Nature Human Behavior*, in press
- Allen, B., Kon, M. A. (2017). The Marr Conjecture and Uniqueness of Wavelet Transforms. *Annals of Mathematical Sciences and Applications*, in press.
- Allen, B., Lippner, G., Chen, Y. T., Fotouhi, B., Momeni, N., Yau, S. T., & Nowak, M. A. (2017). Evolutionary dynamics on any population structure. *Nature*, **544**(7649):227-230.
- Allen, B., Stacey, B. C. and Bar-Yam, Y. (2017). Multiscale Information Theory and the Marginal Utility of Information. *Entropy*, **19**(6):273.
- Nowak, M. A., McAvoy, A., Allen, B., & Wilson, E. O. (2017). The general form of Hamilton's rule makes no predictions and cannot be tested empirically. *Proceedings of the National Academy of Sciences*, **114**(22):5665–5670.
- Sample, C., & Allen, B. (2017). The limits of weak selection and large population size in evolutionary game theory. *Journal of Mathematical Biology*, online ahead of print.
- Stacey, B. C., Allen, B., & Bar-Yam, Y. (2017). Multiscale information theory for complex systems: Theory and applications. In M. Burgin, C. S. Calude (Ed.) *Information and Complexity* (pp. 176-199) Hackensack, NJ, USA: World Scientific.
- van Veelen, M., Allen, B., Hoffman, M., Simon, B., & Veller, C. (2017). Hamilton's rule. *Journal of Theoretical Biology*, **414**:176-230.
- Makohon-Moore, A. P., Zhang, M., Reiter, J. G., Bozic, I., Allen, B., Kundu, D., Chatterjee, K., Wong, F., Jiao, Y., Kohutek, Z., Hong, J., Attiyeh, M., Javier, B., Wood, L., Hruban, R., Nowak, M. A., Papadopolous, N., Kinzler, K. W., Vogelstein, B., Iacobuzio-Donahue, C.

- A. (2017). Limited heterogeneity of known driver gene mutations among the metastases of individual patients with pancreatic cancer. *Nature Genetics*, **49**:358-366.
- Cooney, D., Allen, B., & Veller, C. (2016) Assortment and the evolution of cooperation in a Moran process with exponential fitness. *Journal of Theoretical Biology* **409**:38-46.
- Olejarz, J. W., Allen, B., Veller, C., Gadagkar, R., & Nowak, M. A. (2016). Evolution of worker policing. *Journal of Theoretical Biology*, **399**:103-116.
- Allen, B., Sample, C., Dementieva, Y., Medeiros, R. C., Paoletti, C., & Nowak, M. A. (2015). The molecular clock of neutral evolution can be accelerated or slowed by asymmetric spatial structure. *PLoS Computational Biology*, **11**(2):e1004108.
- Allen, B., & Nowak, M. A. (2015). Games among relatives revisited. *Journal of Theoretical Biology*, **378**:103-116.
- Olejarz, J. W., Allen, B., Veller, C., & Nowak, M. A. (2015). The evolution of non-reproductive workers in insect colonies with haplodiploid genetics. *eLife* **4**:e08918.
- Szabó, G., Bodó, K. S., Allen, B., & Nowak, M. A. (2015). Four classes of interactions for evolutionary games. *Physical Review E*, **92**(2):022820.
- Vukov, J., Varga, L., Allen, B., Nowak, M. A., & Szabó, G. (2015). Payoff components and their effects in a spatial three-strategy evolutionary social dilemma. *Physical Review E*, **92**(1):012813.
- Allen, B. and M. A. Nowak (2014). Games on graphs. *EMS Surveys in Mathematical Sciences* **1**:113-151.
- Allen, B. and C. E. Tarnita (2014). Measures of success in a class of evolutionary models with fixed population size and structure. *Journal of Mathematical Biology*, **68**:109-143.
- Jeong, H. C., S. Y. Oh, B. Allen, and M. A. Nowak (2014). Optional games on cycles and complete graphs. *Journal of Theoretical Biology* **356**:98-112.
- Rosenbloom, D. I. S. and B. Allen (2014). Frequency-dependent competition can lead to the evolution of high mutation rates. *American Naturalist* **183**: E131-E153.
- Szabó, G., Bodó, K. S., Allen, B., & Nowak, M. A. (2014). Fourier decomposition of payoff matrix for symmetric three-strategy games. *Physical Review E*, **90**:042811.
- Allen, B., J. Gore, and M. A. Nowak (2013). Spatial dilemmas of diffusible public goods. *eLife* **2**:e01169.
- Allen, B., M. A. Nowak, and E. O. Wilson (2013). Limitations of inclusive fitness. *Proceedings of the National Academy of Sciences*, **110**:20135-20139.

- Allen, B., M. A. Nowak, and U. Dieckmann (2013). Adaptive dynamics with interaction structure. *The American Naturalist* **181**:E139-E163.
- Dickinson, B. C., A. M. Leconte, B. Allen, K. M. Esvelt, and D. R. Liu (2013). Experimental interrogation of the path dependence and stochasticity of protein evolution using phage-assisted continuous evolution. *Proceedings of the National Academy of Sciences* **110**:9007-9012.
- Leconte, A. M., B. C. Dickinson, D. D. Yang, I. A. Chen, B. Allen, and D. R. Liu (2013). A population-based experimental model for protein evolution: effects of mutation rate and selection stringency on evolutionary outcomes. *Biochemistry* **52**:1490-1499.
- Bozic, Ivana, J. G. Reiter, B. Allen, T. Antal, K. Chatterjee, P. Shah, Y. S. Moon et al (2013). Evolutionary dynamics of cancer in response to targeted combination therapy. *Elife* **2**:e00747.
- Reiter, J. G., I. Bozic, B. Allen, K. Chatterjee, and M. A. Nowak (2013). The effect of one additional driver mutation on tumor progression. *Evolutionary Applications* **6**:34-45.
- Allen, B. and M. A. Nowak (2012). Evolutionary shift dynamics on a cycle. *Journal of Theoretical Biology* **311**:28-39.
- Allen, B. and D. I. S. Rosenbloom (2012). Mutation rate evolution in replicator dynamics. *Bulletin of Mathematical Biology* **74**:2650-2675.
- Allen, B., A. Traulsen, C. E. Tarnita, and M. A. Nowak (2012). How mutation affects evolutionary games on graphs. *Journal of Theoretical Biology* **299**:97-105.
- Bozic, I., B. Allen, and M. A. Nowak (2012). Dynamics of targeted cancer therapy. *Trends in Molecular Medicine* **18**:311-316.
- Diaz Jr, L. A., R. T. Williams, J. Wu, I. Kinde, J. R. Hecht, J. Berlin, B. Allen, I. Bozic, J. G. Reiter, and M. A. Nowak (2012). The molecular evolution of acquired resistance to targeted EGFR blockade in colorectal cancers. *Nature* **486**:537-540.
- Allen, B., M. Kon, and Y. Bar-Yam (2009). A new phylogenetic diversity measure generalizing the Shannon index and its application to phyllostomid bats. *The American Naturalist* **174**:236-243.

Scholarly commentary (book reviews, opinion, etc.)

- Allen, B. (2016). Statistical Inference Is Not Needed When the Solution Is Already Known. *BioScience*, **66**(3):186-186.

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- Allen, B., & Nowak, M. A. (2016). There is no inclusive fitness at the level of the individual. *Current Opinion in Behavioral Sciences*, **12**:122-128.
- Allen, B. (2015). Inclusive Fitness Theory Becomes an End in Itself. *BioScience*, **65**(11), 1103-1104.
- Nowak M. A. and Allen, B. (2015) Inclusive Fitness Theorizing Invokes Phenomena That Are Not Relevant for the Evolution of Eusociality. *PLoS Biology* **13**(4):e1002134.
- Allen, B. and M. A. Nowak (2013). O brave new world with such games. *Science* **341**:844.
- Allen, B. and M. A. Nowak (2013). Cooperation and the fate of microbial societies. *PLoS Biology* **11**:e1001549.
- Anton, B. P., Chang, Y. C., Brown, P., Choi, H. P., Faller, L. L., Guleria, J., et al. (2013). The COMBREX project: design, methodology, and initial results. *PLoS Biology*, **11**(8):e1001638.

General-Audience Publications

- Allen, B. (2017, September 5) Global cooperation depends on the strength of local connections. *Aeon*, retrieved from <https://aeon.co/ideas/global-cooperation-depends-on-the-strength-of-local-connections>. Also published as Allen B. (2017, September 6) A mathematical model of altruism. *The Atlantic*, retrieved from <https://www.theatlantic.com/science/archive/2017/09/cooperation-networks/538842>.

Awards and Honors:

- 2010 Foundational Questions in Evolutionary Biology prize fellowship, John Templeton Foundation.
- 2009 Young Scientists Summer Program fellowship, International Institute for Applied Systems Analysis, Austria.
- 2009 Outstanding Teaching Fellow award, Boston University.
- 2005 NSF GAANN fellowship.

Professional Activities:

- Member, Scientific Committee, “The Mathematics of Biodiversity” research program, Centre de Recerca Matemàtica, Barcelona, June 18-July 20, 2012.
- Author, PLEKTIX blog on complex systems, <http://plektix.fieldofscience.com>.
- Reviewed manuscripts for *American Naturalist*, *Biology Letters*, *BMC Evolutionary Biology*, *Discrete Dynamical Systems*, *Ecological Modeling*, *Journal of Mathematical Biology*, *Journal of Theoretical Biology*, *Physica A*, *Physical Review Letters*, *PLoS Computational Biology*, *PLoS ONE*, *Proceedings of the Royal Society A: Mathematical and Physical Sciences*, and *Proceedings of the Royal Society B: Biological Sciences*

Invited and Conference Talks:

- 2018 Biophysics Seminar, Boston University, Boston MA, “Evolutionary dynamics on any population structure”
- 2018 Models, Inference & Algorithms Seminar, Broad Institute, Cambridge MA, “Evolutionary dynamics on any population structure”
- 2017 Mathematical Models in Ecology and Evolution, City University of London, “Evolutionary games on any graph”
- 2017 Applied & Interdisciplinary Mathematics Seminar, Northeastern University, Boston MA, “Evolutionary dynamics on any population structure”
- 2016 Seminar on *Discrete Dynamical Systems in Biology*, Diego Portales University, Santiago, Chile, “Evolutionary dynamics on any population structure”.
- 2016 Symposium on *Cooperation from cells to humans: Theoretical, empirical and philosophical perspectives on inclusive fitness*, Cambridge University, Cambridge, UK, “ ‘Testing’ Hamilton’s Rule”.
- 2016 Mathematical Biology Seminar, University of Edinburgh, “Neutral Drift and Weak Selection on Graphs”
- 2015 Workshop on *Conflict, Competition, Cooperation and Complexity*, Max Planck Institute for Evolutionary Biology, Plön, Germany “Death-Birth Dynamics on Heterogeneous Graphs”
- 2014 Brandeis University IGERT: *Geometry and Dynamics* Program “An Information-Theoretic Formalism for Multiscale Structure in Complex Systems”
- 2014 Advances in Interdisciplinary Statistics and Combinatorics, University of North Carolina-Greensboro, “Asymmetric Spatial Structure Alters the Molecular Clock”
- 2013 Workshop on *Biodiversity and Environment: Viability and Dynamic Games Perspectives*, Center for Research in Mathematics, Montreal, Canada “Mathematically general approaches to the evolution of cooperation”
- 2013 Brandeis University IGERT: *Geometry and Dynamics* Program “Evolutionary games in structured populations”
- 2013 MERCK Science Seminar, Emmanuel College, Boston, “Evolution of cooperation by diffusible public goods”
- 2013 MERCK Science Seminar, Emmanuel College, Boston, “Mathematical modeling of targeted cancer therapy”
- 2012 Exploratory Conference on *The Mathematics of Biodiversity*, Centre de Recerca Matemàtica, Barcelona, Spain, “Hill Numbers: Interpretations and Generalizations”
- 2011 IGERT *Program in Evolutionary Modeling* at Washington State University, “How interaction structure influences the evolution of social behavior”
- 2011 International Conference on Complex Systems, “A formalism for multiscale variety in complex systems”
- 2011 International Conference on Complex Systems, “Population structure and the evolution of social behavior”
- 2011 Harvard University Program in Evolutionary Dynamics Seminar Series, “How useful and general is Hamilton’s rule?”
- 2011 Santa Fe Institute Seminar, “Evolution in structured populations”

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- 2010 Max Planck Institute for Evolutionary Biology Seminar, Plön, Germany, “How mutation affects the evolution of cooperation on graphs”
- 2010 Haverford & Bryn Mawr Mathematics Colloquium, “Evolutionary game theory in structured populations”
- 2010 Boston University Probability and Statistics Seminar, “Edge detection and the Marr Conjecture”
- 2009 Boston University Computer Science Theory Seminar; “Evolutionary game theory.”
- 2009 Young Scientists Summer Program Late Summer Workshop, IIASA, Austria; “Adaptive dynamics of cooperation in structured populations.”
- 2008 Boston University Computer Science Theory Seminar; “The category-theoretic arithmetic of communication.”