

# ALON KEINAN – CURRICULUM VITAE

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## POSITIONS

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<b>Associate Professor of Computational Biology</b> (with tenure) Department of Biological Statistics & Computational Biology, Cornell University (Starting 2019, in newly-formed Department of Computational Biology, Cornell University)	Ithaca, NY 11/1/14 – present
<b>Robert N. Noyce Assistant Professor in Life Science and Technology</b> Cornell University	8/1/11 – 10/31/14
<b>Assistant Professor</b> Department of Biological Statistics & Computational Biology, Cornell University	8/17/09 – 10/31/14
<b>Faculty Member</b> Cornell Center for Comparative and Population Genomics (3CPG), Cornell University Center for Vertebrate Genomics (CVG), Cornell University Center for Enervating NeuroImmune Disease	10/12/09 – present 8/26/15 – present 10/25/16 – present
<b>Faculty</b> Graduate Field of Computational Biology and Medicine, Tri-Institutional program of Cornell University, Weill Cornell Medical College, and Sloan-Kettering Institute	8/17/09 – present
Graduate Field of Computational Biology, Cornell University	8/17/09 – present
Graduate Field of Applied Mathematics, Cornell University	8/18/09 – present
Graduate Field of Genetics, Genomics, and Development, Cornell University	12/18/09 – present
Graduate Field of Computer Science, Cornell University	4/21/12 – present
Graduate Field of Statistics, Cornell University	12/17/12 – present
<b>Postdoctoral Research Fellow</b> Department of Genetics, Harvard Medical School & Program in Medical and Population Genetics, Broad Institute of MIT and Harvard Mentor: Dr. David Reich	Boston, MA 9/2005 – 8/2009
<b>Instructor</b> School of Mathematical Sciences & School of Computer Science Tel Aviv University	Tel Aviv, Israel 3/2004 – 7/2005
<b>Teaching Assistant</b> School of Mathematical Sciences & School of Computer Science	1997 – 2002

## EDUCATION

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**Ph.D. in Computer Science, *with distinction*** Tel Aviv, Israel  
2005  
School of Computer Science, Tel Aviv University  
Thesis advisors: Dr. Eytan Ruppim (School of Computer Science and School of Medicine) and  
Dr. Isaac Meilijson (Department of Statistics and Operations Research)  
Thesis title: Localization of function via multi-perturbation analysis: Theory and applications  
for the analysis of neural networks

**B.Sc. in Computer Science, Statistics, and Operations Research, *Summa Cum Laude*** Tel Aviv, Israel  
1997  
School of Mathematical Sciences, Tel Aviv University

## RELATED PROFESSIONAL EXPERIENCE

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**R&D unit, Intelligence Corps, Israel Defense Forces (Mandatory Military Service)** Israel  
2002 – 2004

***Chief R&D Officer***

- Led research of algorithms, statistical methods, and products for military intelligence information and knowledge management
- Developed specialized data mining algorithms to address unique challenges faced by the intelligence community

***Project Manager***

1999 – 2002

- Initiated, planned, and designed a large-scale project for the development of an information technology, knowledge management system for hundreds of end-users within the intelligence community
- Recruited and led several teams of about 15-20 software engineers, combined, in implementing the software
- Managed all aspects of the project, including the budget (\$12M equivalent), project planning, the interactions with representatives of the end-users, hiring, reporting, etc.

***Team leader***

1998 – 1999

- Analyzed and designed new versions of an information technology, knowledge management application for the intelligence community
- Led a team of 3 software engineers in implementing the application

***Programmer and Systems Analyst***

1997 – 1998

- Participated in the development of an information technology application
- Analyzed and designed components of the application

**CTC**

Kfar Saba, Israel

***Programmer***

1996 – 1997

- Designed and developed components of a software for room design that involved Computer Graphics algorithms (part time)
- Worked with a furniture stores chain to tailor software and optimize usability

## AWARDS & HONORS

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<b>Edward Mallinckrodt, Jr. Foundation Award</b>	2013-2016
<b>Ellison Medical Foundation New Scholar Award</b> The Ellison Medical Foundation	2012-2017
<b>Robert N. Noyce Assistant Professorship in Life Science and Technology</b> Noyce Foundation (awarded by Provost, Cornell University)	2011-2014
<b>Sloan Research Fellowship</b> Alfred P. Sloan Foundation	2011-2013
<b>Research and Extension Award for Early Achievement</b> College of Agriculture and Life Sciences, Cornell University <i>awarded to one Assistant or Associate professor during their first ten years as a faculty</i>	2013
<b>Stellar Abstract Award</b> Emerging Quantitative Issues in Parallel Sequencing Annual Meeting	2008
<b>Outstanding Trainee Research Award Finalist</b> The American Society of Human Genetics Annual Meeting	2008
<b>Postdoctoral Travel Grant</b> Harvard University <i>awarded in the inaugural cycle to 10 postdocs from across Harvard University</i>	2008
<b>Rothschild Postdoctoral Fellowship</b> “Yad Hanadiv” Foundation <i>awarded to 10 young Israeli scholars from across all areas of science for outstanding merit</i>	2005-2006
<b>Dan David Prize Scholarship</b> <i>awarded based on merit to 10 Ph.D. students and postdocs in predetermined fields</i>	2004-2005
<b>Wolf Award for Ph.D. Students</b> Wolf Foundation <i>known as Israel’s most prestigious graduate student award</i>	2004-2005
<b>Marcel Adams Award for Best Publications of the Year</b> Adams Super Center for Brain Studies, Tel Aviv University	2003
<b>Award for achievements towards Ph.D.</b> School of Computer Science, Tel Aviv University <i>awarded to one Ph.D. student</i>	2003
<b>Training grant for Ph.D. students</b> The Aharon Katzir Center, Weizmann Institute of Science	2003

## CURRENT AND RECENT GRANT SUPPORT

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1. NIH/NHGRI 2R01HG006849 (Role: **PI**). The X-factor of complex disease: Development, implementation, and extensive application of methods for analysis of the X chromosome in GWA, sequence-based association, and eQTL studies.  
Award period: 9/1/2017 – 6/30/2022  
Total amount (all to Keinan): \$1,517,147
2. NIH/NHGRI R01HG006849 (Role: **PI**). The X-factor of complex disease: From population genetics to GWAS of Chromosome X.  
Award period: 9/9/2013 – 8/31/2017  
Total amount (all to Keinan): \$1,136,361
3. NIH/NIGMS R01GM108805 (Role: **PI**; as part of Multiple Principal Investigators with John Novembre, Yun S. Song and Andrew G. Clark). Population genetic consequences of recent explosive population growth in humans.  
Award period: 5/10/2014 – 4/30/2018  
Total amount to Keinan: \$510,180 (total budget: 2,163,000)
4. New Scholar Award, The Ellison Medical Foundation (Role: **PI**).  
Award period: 7/1/2012 – 6/30/2017  
Total amount (all to Keinan): \$400,000
5. Edward Mallinckrodt, Jr. Foundation award (Role: **PI**)  
Award period: 3/1/2013 – 2/28/2016  
Total amount (all to Keinan): \$180,000
6. Robert N. Noyce endowed chair, Noyce Foundation (Role: **PI**).  
Award period: 8/1/2011 – 7/31/2014  
Total amount (all to Keinan): \$135,000
7. Hutchins Family Foundation (Role: **co-PI**; PI: Maureen Hanson). Mitochondrial Genomes in CFS/ME  
Award period: 7/1/2014 – 6/30/2015  
Total amount: \$120,929
8. Sloan Research Fellowship, Alfred P. Sloan Foundation (Role: **PI**).  
Award period: 9/15/2011 – 9/15/2013  
Total amount (all to Keinan): \$50,000
9. NIH/NHGRI U01HG005715 (Role: **PI**; as part of Multiple Principal Investigators with Andrew G. Clark and Carlos D. Bustamante). Population structure, admixture and selection across the 1000 Genomes data set.  
Award period: 9/9/2010 – 6/30/2014  
Total amount to Keinan: \$432,692 (total budget: 1,074,255)

### **Intramural support** (Discretionary funds to Keinan)

10. College Start-up Funds  
Award period: 08/17/2009 – present
11. Supplemental Start-up Funds from Cornell Center for Comparative and Population Genomics  
Award period: 08/17/2009 – present
12. College Retention Funds  
Award period: 07/01/2013 – present
13. College Funds for High-Performance Computing.  
Award period: 07/1/2014 – 06/30/2019 (annually)

## PUBLICATIONS

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(h-index = 44; i10-index = 70; citation count > 35,000; updated citation information and publication list on Google Scholar page ([link](#)));

*Italics* indicate trainees in A. Keinan's group at Cornell University; ^corresponding author; \*equal contribution

### **Selected publications**

A. A. Lussier & A. Keinan<sup>^</sup>. Crowdsourced genealogies and genomes. *Science* (2018). (*Invited Perspective*.)

K. Ye, F. Gao, D. Wang, O. Bar-Yosef & A. Keinan<sup>^</sup>. Dietary adaptation of *FADS* genes in Europe varied across time and geography. *Nature Ecology & Evolution* (2017).

F. Gao & A. Keinan<sup>^</sup>. Explosive genetic evidence for explosive human population growth. *Current Opinion in Genetics & Development* (2016). (*Invited review*.)

Y. Pinto, O. Gabay, L. Arbiza, A. J. Sams, A. Keinan<sup>^\*</sup> & E. Y. Levanon<sup>^\*</sup>. Clustered mutations in hominid genome evolution are consistent with *APOBEC3G* enzymatic activity. *Genome Research* (2016).

K.S. Kothapalli\*, K. Ye\*, ... (10 authors) ..., A. Keinan<sup>^</sup> & J. T. Brenna<sup>^</sup>. Positive selection on a regulatory insertion-deletion polymorphism in *FADS2* influences apparent endogenous synthesis of arachidonic acid. *Molecular Biology and Evolution* (2016).

The 1000 Genomes Project Consortium<sup>1</sup>. A global reference for human genetic variation. *Nature* (2015).

E. Gazave, L. Ma, D. Chang, A. Coventry, F. Gao, D. Muzny, E. Boerwinkle, R. Gibbs, C. F. Sing, A. G. Clark & A. Keinan<sup>^</sup>. Neutral genomic regions refine models of recent rapid human population growth. *PNAS* (2014).

L. Ma, A. G. Clark & A. Keinan<sup>^</sup>. Gene-based testing of interactions in association studies of quantitative traits. *PLOS Genetics* (2013).

L. Arbiza, I. Gronau, B. A. Aksoy, M. J. Hubisz, B. Gulko, A. Keinan & A. Siepel. Genome-wide inference of natural selection on human transcription factor binding sites. *Nature Genetics* (2013).

A. Keinan<sup>^</sup> & A. G. Clark. Recent explosive human population growth has resulted in an excess of rare genetic variants. *Science* (2012).

D. Chang & A. Keinan<sup>^</sup>. Predicting signatures of “synthetic associations” and “natural associations” from empirical patterns of human genetic variation. *PLOS Computational Biology* (2012).

S. Gottipati, L. Arbiza, A. Siepel, A. Clark & A. Keinan<sup>^</sup>. Analyses of X-linked and autosomal genetic variation in population-scale whole genome sequencing. *Nature Genetics* (2011).

Y. Y. Waldman, T. Tuller, A. Keinan<sup>^\*</sup> & E. Ruppin<sup>^\*</sup>. Selection for translation efficiency on synonymous polymorphisms in recent human evolution. *Genome Biology and Evolution* (2011).

A. Keinan<sup>^</sup> & D. Reich. Human population differentiation is strongly correlated with local recombination rate. *PLOS Genetics* (2010).

**The International HapMap3 Consortium.** Integrating common and rare genetic variation in diverse human populations. *Nature* (2010). (A. Keinan is Leader, Population analysis group & Member, Low frequency variation analysis group)

A. Keinan<sup>^</sup>, J. C. Mullikin, N. Patterson & D. Reich. Accelerated genetic drift on chromosome X during the human dispersal out of Africa. *Nature Genetics* (2009).

A. Keinan<sup>^</sup>, J. C. Mullikin, N. Patterson & D. Reich. Measurement of the human allele frequency spectrum demonstrates greater genetic drift in East Asians than in Europeans. *Nature Genetics* (2007).

A. Keinan, B. Sandbank, C. C. Hilgetag, I. Meilijson & E. Ruppin. Fair attribution of functional contribution in artificial and biological networks. *Neural Computation* (2004).

## All Publications

1. Y. Guo, C. Wu, M. Guo, Q. Zou, X. Liu & **A. Keinan**<sup>^</sup>. Combining Sparse Group Lasso and Linear Mixed Model improves power for finding genetic variants underlying quantitative traits. *Frontiers in Genetics* 10 (2019). (Also in eBook: *Machine Learning Advanced Dynamic Omics Data Analysis for Precision Medicine*.)
2. R. Fragoza, J. Das, S. D. Wierbowski, J. Liang, T. N. Tran, S. Liang, J. F. Beltran, C. A. Rivera-Erick, K. Ye, T. Wang, L. Yao, M. Mort, P. D. Stenson, D. Cooper, X. Wei, **A. Keinan**, J. C. Schimenti, A. G. Clark, & H. Yu. Extensive disruption of protein interactions by genetic variants across the allele frequency spectrum in human populations. *Nature communications* 10, 1-15 (2019).
3. E. Lowy-Gallego *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. Variant calling on the GRCh38 assembly with the data from phase three of the 1000 Genomes Project. *Wellcome Open Research* 4, 50 (2019)
4. A. A. Lussier & **A. Keinan**<sup>^</sup>. Crowdsourced genealogies and genomes. *Science* 360, 153-154 (2018). (*Invited Perspective*.)
5. Y. Guo, C. Wu, M. Guo, X. Liu & **A. Keinan**. Gene-based nonparametric testing of interactions using distance correlation coefficient in case-control association studies. *Genes* 9, 608 (2018).
6. K. Ye, F. Gao, D. Wang, O. Bar-Yosef & **A. Keinan**<sup>^</sup>. Dietary adaptation of *FADS* genes in Europe varied across time and geography. *Nature Ecology & Evolution* 1, 0167 (2017).
7. F. D'Amico, E. Skarmoutsou, L. J. Lo, M. Granata, C. Trovato, G. A. Rossi, C. Bellocchi, M. Marchini, R. Scorza, M. C. Mazzarino, & **A. Keinan**. Association between rs2294020 in X-Linked *CCDC22* and susceptibility to autoimmune diseases with focus on systemic lupus erythematosus. *Immunology Letters* 181, 58-62 (2017).
8. J. Gardner *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. The Mobile Element Locator Tool (MELT): population-scale mobile element discovery and biology. *Genome Research*, 27, 1916-1929 (2017).
9. X. Zheng-Bradley *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. Alignment of 1000 Genomes Project reads to reference assembly GRCh38. *GigaScience* 6, 1-8 (2017).
10. F. Gao & **A. Keinan**<sup>^</sup>. Explosive genetic evidence for explosive human population growth. *Current Opinion in Genetics & Development* 41, 130-139 (2016). (*Invited review*.)
11. Y. Y. Waldman, A. Biddanda, M. Dubrovsky, C. L. Campbell, C. Oddoux, E. Friedman, G. Atzmon, E. Halperin, H. Ostrer & **A. Keinan**<sup>^</sup>. The genetic history of Cochin Jews from India. *Human Genetics* 135, 1127-1143 (2016).
12. F. Gao & **A. Keinan**<sup>^</sup>. Inference of super-exponential human population growth via efficient computation of the site frequency spectrum for generalized models. *Genetics* 202, 235-245 (2016).
13. A. Slavney, L. Arbiza, A. G. Clark & **A. Keinan**<sup>^</sup>. Strong constraint on human genes escaping X-inactivation is modulated by their expression level and Breadth in both sexes. *Molecular Biology and Evolution* 33, 384-393 (2016).
14. Y. Pinto, O. Gabay, L. Arbiza, A. J. Sams, **A. Keinan**<sup>^\*</sup> & E. Y. Levanon<sup>^\*</sup>. Clustered mutations in hominid genome evolution are consistent with *APOBEC3G* enzymatic activity. *Genome Research* 26: 579-587 (2016). (Cover Article.) **Featured in a News item in Science**: E. Pennisi. Virus fighter may have played a key role in human evolution. *Science* (2016).
15. K.S. Kothapalli\*, K. Ye\*, M. S. Gadgil, S. E. Carlson, K. O. O'Brien, J. Y. Zhang, H. G. Park, K. Ojukwu, J. Zou, S. S. Hyon, K. S. Joshi, Z. Gu, **A. Keinan**<sup>^</sup> & J. T. Brenna<sup>^</sup>. Positive selection on a regulatory insertion-deletion polymorphism in *FADS2* influences apparent endogenous synthesis of arachidonic acid. *Molecular Biology and Evolution* 33, 1726-1739 (2016). (On the cover.) **Highlighted by the journal**: J. Caspermeier. Are we what we eat? Evidence of a vegetarian diet permanently shaping the human genome to change individual risk of cancer and heart disease. *Molecular Biology and Evolution* 33, 1887-8 (2016). (**Numerous additional journal and press coverages**, leading to Oxford's Altmetric score in the 99.98%).

16. Y. Y. Waldman, A. Biddanda, N. R. Davidson, P. Billing-Ross, M. Dubrovsky, C. L. Campbell, C. Oddoux, E. Friedman, G. Atzmon, E. Halperin, H. Ostrer & **A. Keinan**<sup>^</sup>. The Genetics of Bene Israel from India Reveals Both Substantial Jewish and Indian Ancestry. *PLOS ONE* 11: e0152056 (2016).
17. J. L. Rodriguez-Flores, K. Fakhro, F. Agosto-Perez, M. D. Ramstetter, L. Arbiza, T. L. Vincent, A. Robay, J. A. Malek, K. Suhre, L. Chouchane, R. Badii, A. Al-Nabet Al-Marri, C. Abi Khalil, M. Zirie, A. Jayyousi, J. Salit, **A. Keinan**, A. G. Clark, R. G. Crystal & Jason G. Mezey. Indigenous Arabs are descendants of the earliest split from ancient Eurasian populations. *Genome Research* 26, 151-162 (2016). (Cover Article)
18. P. Billing-Ross, A. Germain, K. Ye, **A. Keinan**, Z. Gu & M. R. Hanson. Mitochondrial DNA variants correlate with symptoms in myalgic encephalomyelitis/chronic fatigue syndrome. *Journal of Translational Medicine* 14, 19 (2016).  
And related Commentary: M.R. Hanson, Z. Gu, **A. Keinan**, K. Ye, A. Germain & P. Billing-Ross. Association of mitochondrial DNA variants with myalgic encephalomyelitis/chronic fatigue syndrome (ME/CFS) symptoms. *Journal of Translational Medicine* 14:342 (2016).
19. G. D. Poznik *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. Punctuated bursts in human male demography inferred from 1,244 worldwide Y-chromosome sequences. *Nature Genetics* 48, 593-599 (2016).
20. L. Ma, G. Hoffman & **A. Keinan**<sup>^</sup>. X-inactivation informs variance-based testing for X-linked association of a quantitative trait. *BMC Genomics* 16, 241 (2015).
21. F. Gao, D. Chang, A. Biddanda, L. Ma, Y. Guo, Z. Zhou & **A. Keinan**<sup>^</sup>. XWAS: A software toolset for genetic data analysis and association studies of the X Chromosome. *Journal of Heredity*, 106: 666-671 (2015)
22. The 1000 Genomes Project Consortium<sup>1</sup>. A global reference for human genetic variation. *Nature* 526, 68-74 (2015).
23. A. Sams, J. Hawks & **A. Keinan**<sup>^</sup>. The utility of ancient human DNA for improving allele age estimates, with implications for demographic models and tests of natural selection. *Journal of Human Evolution* 79, 64-72 (2015).
24. R. Blekhman, J. K. Goodrich, K. Huang, Q. Sun, R. Bukowski, J. T. Bell, T. D. Spector, **A. Keinan**, R. E. Ley, D. Gevers & A. G. Clark. Host genetic variation impacts microbiome composition across human body sites. *Genome Biology* 16, 191 (2015).
25. F. Yu, J. Lu, X. Liu, E. Gazave, D. Chang, S. Raj, H. Hunter-Zinck, R. Blekhman, L. Arbiza, C. Van Hout, A. Morrison, A. D. Johnson, J. Bis, L. Cupples, B. M. Psaty, D. Muzny, J. Yu, R. A. Gibbs, **A. Keinan**, A. G. Clark, E. Boerwinkle. Population genomic analysis of 962 whole genome sequences of humans reveals natural selection in non-coding regions. *PLOS ONE* 10, e0121644 (2015).
26. L. Ma, **A. Keinan** & A. G. Clark. Biological Knowledge-Driven Analysis of Epistasis in Human GWAS with Application to Lipid Traits. In J. H. Moore, S. M. Williams (Eds.), *Epistasis, Methods in Molecular Biology*. Springer, NY (2015).
27. Y. R. Li, J. Li, S. D. Zhao, J. P. Bradfield, F. D. Mentch, S. Melkorka Maggadottir C. Hou, D. J. Abrams, D. Chang, F. Gao, ... , **A. Keinan**, E. T. Luning Prak, C. Polychronakos, R. N. Baldassano, H. Li, B. J. Keating, H. Hakonarson (70 authors in total). Meta-analysis of shared genetic architecture across ten pediatric autoimmune diseases. *Nature Medicine* 21, 1018-27 (2015).
28. P. H. Sudmant *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. An integrated map of structural variation in 2,504 human genomes. *Nature* 526, 75-81 (2015).
29. E. Gazave, L. Ma, D. Chang, A. Coventry, F. Gao, D. Muzny, E. Boerwinkle, R. Gibbs, C. F. Sing, A. G. Clark & **A. Keinan**<sup>^</sup>. Neutral genomic regions refine models of recent rapid human population growth. *Proceedings of the National Academy of Sciences* 11, 757-762 (2014).
30. D. Chang, F. Gao, A. Slavney, L. Ma, Y. Y. Waldman, A. J. Sams, P. Billing-Ross, A. Madar, R. Spritz & **A. Keinan**<sup>^</sup>. Accounting for eXentricities: Analysis of the X chromosome in GWAS reveals X-linked genes implicated in autoimmune diseases. *PLOS ONE* 10, e113684 (2014).

31. *L. Arbiza, S. Gottipati, A. Siepel & A. Keinan*<sup>^</sup>. Contrasting X-linked and autosomal diversity across 14 human populations. *American Journal of Human Genetics* 94, 827-844 (2014).
32. *D. Chang & A. Keinan*<sup>^</sup>. Principal component analysis characterizes shared pathogenetics from genome-wide association studies. *PLOS Computational Biology* 10, e1003820 (2014).
33. *F. Gao & A. Keinan*<sup>^</sup>. High burden of private mutations due to explosive human population growth and purifying selection. *BMC Genomics* 15, 1-7 (2014).
34. *L. Ma, C. Ballantyne, A. Brautbar & A. Keinan*<sup>^</sup>. Analysis of multiple association studies provides evidence of an expression QTL hub in gene-gene interaction network affecting HDL cholesterol levels. *PLOS ONE* 9, e92469 (2014).
35. *F. Gao, C. Ballantyne, L. Ma, S. Virani, A. Keinan*<sup>\*^</sup> & Ariel Brautbar<sup>\*^</sup>. Rare *LPL* gene variants attenuate triglyceride reduction and HDL cholesterol increase in response to fenofibric acid therapy in individuals with mixed dyslipidemia. *Atherosclerosis* 234, 249–253 (2014).
36. *K. Ye, J. Lu, F. Ma, A. Keinan & Z. Gu*. Extensive pathogenicity of mitochondrial heteroplasmy in healthy human individuals. *Proceedings of the National Academy of Sciences*, 111, 10654-10659 (2014). **Highlighted by the journal editors; Featured in several other journals, including:** K. B. Gerber. Mixed Up. *American Journal of Human Genetics* 95, 129 (2014).  
Also: *K. Ye, J. Lu, F. Ma, A. Keinan & Z. Gu*. Reply to Just et al.: Mitochondrial DNA heteroplasmy could be reliably detected with massively parallel sequencing technologies. *Proceedings of the National Academy of Sciences* 111, 1894-1904 (2014).
37. T. Willems *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. The landscape of human STR variation. *Genome Research* 24, Article number 3934 (2014).
38. O. Delaneau *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. Integrating sequence and array data to create an improved 1000 Genomes Project haplotype reference panel. *Nature Communications* 5, Article number 3934 (2014).
39. *L. Ma, A. G. Clark & A. Keinan*<sup>^</sup>. Gene-based testing of interactions in association studies of quantitative traits. *PLOS Genetics* 9, e1003321 (2013).
40. *L. Arbiza, I. Gronau, B. A. Aksoy, M. J. Hubisz, B. Gulko, A. Keinan & A. Siepel*. Genome-wide inference of natural selection on human transcription factor binding sites. *Nature Genetics* 45, 723–729 (2013). **Featured in Nature Reviews Genetics:** H. Stower. Adaptive human regulatory variation. *Nature Reviews Genetics* (2013).
41. *E. Gazave, D. Chang, A. G. Clark & A. Keinan*<sup>^</sup>. Population growth inflates the per-individual number of deleterious mutations and reduces their mean effect. *Genetics* 195, 969-978 (2013). **Highlighted by the journal editors.**
42. *A. Keinan*<sup>^</sup> & A. G. Clark. Recent explosive human population growth has resulted in an excess of rare genetic variants. *Science* 336, 740-743 (2012). **Featured in many journals, including in a News article in Nature:** E. Check Hayden. Humans riddled with rare genetic variants. *Nature* (2012).
43. *L. Ma, A. Brautbar, E. Boerwinkle, C. F. Sing, A. G. Clark & A. Keinan*<sup>^</sup>. Knowledge-driven analysis identifies a gene-gene interaction affecting High-Density Lipoprotein Cholesterol levels in multi-ethnic populations. *PLOS Genetics* 8, e1002714 (2012).
44. *D. Chang & A. Keinan*<sup>^</sup>. Predicting signatures of “synthetic associations” and “natural associations” from empirical patterns of human genetic variation. *PLOS Computational Biology* 8, e1002600 (2012).
45. *L. Ma, C. Ballantyne, J. Belmont, A. Keinan*<sup>\*^</sup> & A. Brautbar<sup>\*^</sup>. Interaction between SNPs in the *RXRA* and near *ANGPTL3* gene region inhibits apoB reduction after statin-fenofibric acid therapy in individuals with mixed dyslipidemia. *Journal of Lipid Research* 53, 2425-2428 (2012).
46. *L. Arbiza, E. Zhong & A. Keinan*<sup>^</sup>. NRE: A tool for exploring neutral loci in the human genome. *BMC Bioinformatics* 13, paper 301 (2012).



47. The 1000 Genomes Project Consortium<sup>1</sup>. An integrated map of genetic variation from 1,092 human genomes. *Nature* 491, 56-65 (2012).
48. Y. Xue *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. Deleterious- and disease-allele prevalence in healthy individuals: Insights from current predictions, mutation databases, and population-scale resequencing. *Science* 335, 823-828 (2012).
49. J. M. Kidd, S. Gravel, J. Byrnes, A. Moreno-Estrada, S. Musharoff, K. Bryc, J. D. Degenhardt, A. Brisbin, V. Sheth, R. Chen, S. F. McLaughlin, H. E. Peckham, L. Omberg, C. A. Bormann Chung, S. Stanley, K. Pearlstein, E. Levandowsky, S. Acevedo-Acevedo, A. Auton, **A. Keinan**, V. Acuna-Alonzo, R. Barquera-Lozano, S. Canizales-Quinteros, C. Eng, E. G. Burchard, A. Russell, A. Reynolds, A. G. Clark, M. G. Reese, S. E. Lincoln, A. J. Butte, F. M. De La Vega & C. D. Bustamante. Population genetic inference from personal genome data: impact of ancestry and admixture on human genomic variation. *American Journal of Human Genetics* 91, 660-671 (2012).
50. D. MacArthur *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. A systematic survey of loss-of-function variants in human protein-coding genes. *Science* 335, 823-828 (2012).
51. L. Clarke *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. The 1000 Genomes Project: data management and community access. *Nature Methods* 9, 459-462 (2012).
52. S. Gottipati, L. Arbiza, A. Siepel, A. Clark & **A. Keinan**<sup>^</sup>. Analyses of X-linked and autosomal genetic variation in population-scale whole genome sequencing. *Nature Genetics* 43, 741-743 (2011). **Featured in a News article in Science**: A. Gibbons. X-tra diversity for Africans. *Science* 334, 582-583 (2011).
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57. S. Gravel *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. Demographic history and rare allele sharing among human populations. *Proceedings of the National Academy of Sciences* 108, 11983-8 (2011).
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60. K. E. Lohmueller, J. D. Degenhardt & **A. Keinan**. Sex-averaged recombination and mutation rates on the X chromosome. *American Journal of Human Genetics* 86, 978-981 (2010).
61. **A. Keinan**<sup>^</sup> & D. Reich. Can a sex-biased human demography account for the reduced effective population size of chromosome X in non-Africans? *Molecular Biology and Evolution* 27, 2312-2321 (2010).
62. **The International HapMap3 Consortium**. Integrating common and rare genetic variation in diverse human populations. *Nature* 467, 52-58 (2010). (**A. Keinan** is Leader, Population analysis group & Member, Low frequency variation analysis group)
63. The 1000 Genomes Project Consortium<sup>1</sup>. A map of human genome variation from population-scale sequencing. *Nature* 467, 1061-1073 (2010).
64. P. H. Sudmant *et al.* with The 1000 Genomes Project Consortium<sup>1</sup>. Diversity of human copy number variation and multicopy genes. *Science* 330, 641-646 (2010).

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66. **A. Keinan**<sup>1</sup>, J. C. Mullikin, N. Patterson & D. Reich. Accelerated genetic drift on chromosome X during the human dispersal out of Africa. *Nature Genetics* 41, 66-70 (2009). **Featured in a News and Views article:** C. D. Bustamante & S. Ramachandran. Evaluating signatures of sex-specific processes in the human genome. *Nature Genetics* (2009).
67. F. Yu, **A. Keinan**, H. Chen, R. J. Ferland, R. S. Hill, A. A. Mignault, C. A. Walsh & D. Reich. Detecting natural selection by empirical comparison to random regions of the genome. *Human Molecular Genetics* 18, 4853-4867 (2009).
68. **A. Keinan**<sup>1</sup>, J. C. Mullikin, N. Patterson & D. Reich. Measurement of the human allele frequency spectrum demonstrates greater genetic drift in East Asians than in Europeans. *Nature Genetics* 39, 1251-1255 (2007).
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71. **A. Keinan**, A. Kaufman, C. C. Hilgetag, I. Meilijson & E. Ruppín. Who does what: Taking measures. In M. J. Wegner, C. Schuster (Eds.), *Statistical and process models for cognitive neuroscience and aging*. Mahwah, NJ: Erlbaum (2006).
72. K. Saggie-Wexler, **A. Keinan** & E. Ruppín. Neural processing of counting in evolved spiking and McCulloch-Pitts agents. *Artificial Life* 12, 1-16 (2006).
73. Z. Ganon, **A. Keinan** & E. Ruppín. Neurocontroller analysis via evolutionary network minimization. *Artificial Life* 12, 435-448 (2006).
74. A. Kaufman\*, **A. Keinan**\*, I. Meilijson, M. Kupiec & E. Ruppín. Quantitative analysis of genetic and neuronal multi-perturbation experiments. *PLOS Computational Biology* 1, e64 (2005).
75. **A. Keinan**, B. Sandbank, C. C. Hilgetag, I. Meilijson & E. Ruppín. Fair attribution of functional contribution in artificial and biological networks. *Neural Computation* 16, 1887-1915 (2004).
76. **A. Keinan**<sup>1</sup>, C. C. Hilgetag, I. Meilijson & E. Ruppín. Causal localization of neural function: The Shapley value method. *Neurocomputing* 58-60C, 215-222 (2004).
77. **A. Keinan**, A. Kaufman, N. Sachs, C. C. Hilgetag & E. Ruppín. Fair localization of function via multi-lesion analysis. *Neuroinformatics* 2, 163-168 (2004).
78. **A. Keinan**. Analyzing evolved fault-tolerant neurocontrollers. *Proceedings of the Ninth International Conference on the Simulation and Synthesis of Living Systems (ALIFE)*, 557-562 (2004).
79. K. Saggie, **A. Keinan** & E. Ruppín. Spikes that count: Rethinking spikiness in neurally embedded systems. *Neurocomputing* 58-60C, 303-311 (2004).
80. Z. Ganon, **A. Keinan** & E. Ruppín. Evolutionary network minimization: Adaptive implicit pruning of successful agents. *Advances in Artificial Life* 2801, 319-327 (2003).
81. K. Saggie, **A. Keinan** & E. Ruppín. Solving a delayed response task with spiking and McCulloch-Pitts agents. *Advances in Artificial Life* 2801, 199-208 (2003).
82. **A. Keinan**, I. Meilijson & E. Ruppín. Controlled analysis of neurocontrollers with informational lesioning. *Philosophical Transactions of the Royal Society A* 361, 2123-2144 (2003).

<sup>1</sup> **A. Keinan** is a co-author of and contributor to these publications as a member of both the Analysis group and the Samples and ELSI group of the 1000 Genomes Project Consortium.

## **Development and Maintenance of Publicly Available Research Software**

(all available at <http://keinanlab.cb.bscb.cornell.edu/>)

1. XWAS (chromosome X-Wide Analysis toolSet): Toolset for genetic data analysis and association studies of the X chromosome. Multiple releases from 2013 - present
2. EGGS (Efficient computation of Generalized-Growth demographic models' summary Statistics).
3. disPCA (disease Principal Component Analysis): Method for genome-wide characterization of shared and distinct risk factors between and within disease classes based on data from genome-wide association studies.
4. NRE (Neutral Regions Explorer): Web server for filtering, extraction, and population genetic analysis of regions from the human genome that meet user-specified criteria.
5. MSA (Multi-perturbation Shapley value Analysis): Software package for deducing causal function localization from experiments of multiple perturbations based on concepts from game theory.

## **Patent**

**A. Keinan**, I. Meilijson & E. Ruppim. Identification of effective elements in complex systems. United States Patent #7,130,763 (2006).

## **SELECTED INVITED TALKS**

1. 5th Annual Epistasis Discovery in Genetics and Epidemiology workshop, Key West (2017). *Keynote speaker*
2. Braun School of Public Health and Community Medicine, The Hebrew University of Jerusalem (2017).
3. NRGene (“The World's Leading Genomic Big Data Solutions Company”), Ness Ziona, Israel (2017).
4. The Mina and Everard Goodman Faculty of Life Sciences, Bar-Ilan University (2017).
5. Genoox (“Translate complex genetic data into clinical results”), Tel Aviv, Israel (2017).
6. Center for Vertebrate Genomics, Cornell University (2016).
7. Department of Genetics, Harvard Medical School (2016).
8. Molecular Biology and Genetics, Cornell University (2015).
9. The American Society of Human Genetics Annual Meeting, San Diego (2014).
10. Institute for Human Genetics, UC San Francisco (2014).
11. AndyFest Symposium: Principals in Population Genetics: A coalescence of community to celebrate Andy Clark, Cornell University (2014).
12. Department of Genetics, School of Medicine, University of Pennsylvania (2014).
13. Department of Genetics and Human Genetics Institute, Rutgers University, New Brunswick (2014).
14. Departments of Biology and Computer Science, University of Maryland, College Park (2014).
15. SNP-SIG Meeting, Annual International Conference on Intelligent Systems for Molecular Biology (2013).  
*Keynote speaker*
16. Program in Quantitative Genomics, Harvard University (2013).
17. Human Genetics & Genomics Gordon Research Conference (2013).
18. Department of Cell Biology and Molecular Genetics, University of Maryland, College Park (2013).
19. Statistics, Cornell University (2012).
20. Tel Aviv University, Tel Aviv, Israel (2012).
21. Bar-Ilan University, Ramat Gan, Israel (2012).

## TRAINEES AT CORNELL UNIVERSITY

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### Postdoctoral Researchers

Dr. Alexandre Lussier (role: research advisor)	2018 – present
Dr. Kaixiong Ye (role: research advisor) <i>Continued to a tenure-track faculty position, University of Georgia (Assistant Professor of Human Genetics, Department of Genetics)</i>	2015 – 2018
Dr. Leonardo Arbiza (role: research advisor; initially jointly with Adam Siepel); <i>From 2013, Research Associate in the capacity of a Programmer only in the group. Continued to an R&amp;D Scientist, Bioinformatics position at Twist Bioscience, San Francisco, CA</i>	2010 – 2017
Dr. Aviv Madar (role: research advisor; jointly with Andrew Clark) <i>Continued to an Investigator II position, Novartis, Cambridge, MA; currently Investigator III, Novartis Institutes for BioMedical Research</i>	2013 – 2016
Dr. Yedael Waldman (role: research advisor) <i>Continued to a research position as Computational Biologist at NRGene, Israel</i>	2014 – 2016
Dr. Aaron Sams (role: research advisor) <i>Currently Senior Scientist, Embark Veterinary (at Cornell University)</i>	2013 – 2015
Dr. Li Ma (role: research advisor; jointly with Dr. Andrew Clark) <i>Continued to a tenure-track faculty position, Department of Animal and Avian Sciences, University of Maryland College Park; promoted in 2019 to Associate Professor with tenure</i>	2010 – 2013
Dr. Ran Blekhman (role: secondary research advisor and mentor) <i>Continued to a tenure-track faculty position, University of Minnesota Twin Cities (Department of Genetics; Department of Ecology, Evolution, and Behavior; promoted in 2019 to Associate Professor with tenure</i>	2010 – 2013
Dr. Elodie Gazave (role: research advisor) <i>Continued to a Research Associate position, School of Integrative Plant Science, Cornell University; Currently Communications Specialist, Institute of Biotechnology, Cornell University</i>	2010 – 2013
Dr. Srikanth Gottipati (role: research advisor; jointly with Dr. Andrew Clark) <i>Currently Sr. Manager, Translational Medicine and Think team, Otsuka Pharmaceutical Commercialization and Development, Inc. Princeton, NJ</i>	2010 – 2012

### Graduate Students

(including rotations; **bold** indicates conducting graduate research in the group)

Madhav Mantri (role: rotation advisor)	2018
Runxi Shen (role: rotation advisor)	2018
Weilin Xu (role: rotation advisor)	2017 – 2018
Siddharth Avadhanam (role: rotation advisor)	2017 – 2018
Zhilu Zhang (role: rotation advisor)	2016
Jens Sannerud (role: rotation advisor and NSF proposal advisor)	2016
Gideon Dresdner (role: rotation advisor and “launch committee” chair)	2015 – 2016
Ying Qiao (role: rotation advisor)	2015 – 2016
Alexander Gorelick (role: rotation advisor)	2015 – 2016
<b>Yingjie Guo</b> (Visiting Student from China for two years; role: research advisor) <i>Returned to her home university (Harbin Institute of Technology, School of Computer Science and Technology) in Sep 2016 to finalize her Ph.D.</i>	2014 – 2016

<b>Andrea Slavney, Ph.D.</b> (role: research advisor and Ph.D. committee chair; jointly with Andrew Clark) <i>Continued to a position of Bioinformatics Scientist at Embark Veterinary</i>	2013 – 2018
<b>Paul Billing-Ross, M.A.</b> (role: secondary research advisor to Zhenglong Gu) <i>After becoming a Ph.D. candidate (passing A-exam), graduated with an M.A. Continued to a position of Bioinformatics Software Developer at Stanford University School of Medicine</i>	2013 – 2015
<b>Feng Gao, Ph.D.</b> (role: research advisor and Ph.D. thesis committee chair) <i>Continued to a position of Research Scientist in a healthcare AI startup at Seattle, WA</i>	2012 – 2016
<b>Diana Chang, Ph.D.</b> (role: research advisor and Ph.D. thesis committee chair) <i>Currently Scientist at Genentech, after a postdoctoral position there</i>	2010 – 2014
Natalie Davidson (role: rotation advisor and “launch committee” chair)	2013 – 2014
Lauren Fairchild (role: rotation advisor and “launch committee” member)	2012
Eyal Nitzany (role: rotation advisor)	2010
Mark Carty (role: rotation advisor)	2009

### **Undergraduate Researchers**

(selected list of undergraduate students who conducted research in the group, which is the case for students who have spent at least two semesters—often more—in the group.)

Rosa Ma (role: research advisor & honors thesis advisor) <i>Continued to graduate school at Stanford University, program of Genetics, Stanford Medicine</i>	2017 – 2018
Lauren Lo (role: research advisor) <i>Stayed in the group in a Programmer position after graduation; Then continued to a position of Software Engineer at Google</i>	2016 – 2018
David Wang (role: research advisor & honors thesis advisor) <i>Continued to graduate school at the University of Pennsylvania, program of Genomics and Computational Biology, Perelman School of Medicine</i>	2016 – 2018
Edward Li (role: research advisor) <i>Continued to a position of Software Engineer at Facebook, Seattle WA</i>	2016 – 2017
Yuhuan Qiu (role: research advisor) <i>Continued to a position of Software Engineer at Facebook, Seattle WA</i>	2016 – 2017
Liang Zhang, M.Eng. (roles: research advisor; then master thesis research advisor) <i>Currently Associate at BlackRock, NY, NY, after first continuing to an Analyst position there.</i>	2015 – 2016
Zilu Zhou (role: research advisor) <i>Continued to graduate school at the University of Pennsylvania, program of Genomics and Computational Biology, Perelman School of Medicine (advisor: Nancy Zhang)</i>	2014 – 2015
Arjun Biddanda (role: research advisor) <i>Continued to graduate school at the University of Chicago, Program of Human Genetics (advisor: John Novembre)</i>	2013 – 2015
Elaine Zhong (role: research advisor) <i>Continued to medical school, Columbia University; currently a practicing physician and house staff member at New York Presbyterian Hospital-Weill Cornell Medicine</i>	2010 – 2011

## TEACHING EXPERIENCE

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<b>Department of Biological Statistics &amp; Computational Biology, Cornell University</b>	Ithaca, NY
<b>Instructor</b> , BTRY 6820/4820: “Statistical Genomics: Coalescent Theory and Human Population Genomics”	Spring 2012; Spring 2013; Spring 2016
<b>Instructor</b> , BTRY 6890: “Topics in Population Genetics and Genomics”	Spring 2012; Spring 2013; Fall 2016
<b>Co-instructor</b> , BTRY 6700: “Applied Bioinformatics and Systems Biology”	Fall 2010; Fall 2011
<b>Instructor</b> , independent undergraduate research and master thesis courses:	
CS 5999: Master of Engineering Project	Spring 2016
CS 4999: “Independent Reading & Research”, Computer Science	Fall 2015; Spring 2016; Fall 2016; Spring 2017; Fall 2017; Spring 2018
BIOG 4990: “Independent Undergraduate Research in Biology”	Spring 2010; Spring 2011; Fall 2011; Spring 2014; Fall 2014; Spring 2015; Spring 2017; Fall 2017; Spring 2018
BIOG 2990: “Introduction to Research Methods in Biology”	Fall 2013; Spring 2015; Fall 2017
BTRY 4990: “Independent Undergraduate Research”, Biometry and Statistics	Fall 2011; Fall 2014; Fall 2015
<b>School of Mathematical Sciences and School of Computer Science, Tel Aviv University</b>	Tel Aviv, Israel
<b>Instructor</b> , “Neural Networks for Machine Learning” (course)	Spring 2004; Spring 2005
<b>Instructor</b> , “Artificial Life (Evolutionary Computation & Neural Networks)” (workshop)	Spring 2004
<b>Teaching Assistant</b> , multiple courses most semesters	1997 – 2002 (7 semesters)
An array of Computer Science, Statistics and Mathematics courses, ranging from introductory courses in all these fields to graduate-level courses in Computer Science such as machine learning.	
<b>R&amp;D unit, Intelligence Corps, Israel Defense Forces</b>	Israel
Designed and co-taught courses on the .Net framework, object oriented programming, C#, and their potential for developing applications for military Intelligence	2002 – 2003

## **INTRAMURAL RECENT PROFESSIONAL ACTIVITIES AND SERVICE**

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- Chair and lead of new High-Performance Computing resource for Computational Biology, including initial proposal, planning, design, construction, work with stakeholder and the Bioinformatics Facility, development, obtaining intramural funding, purchasing, negotiation, additional building and design improvements over time, and high-level testing and maintenance (2013 – 2018)
- College of Agriculture and Life Sciences Curriculum Committee (2017 – 2018)
- Committee member, proposal for NSF Workshop on Sharing Sensitive Data (2016)
- Committee member, NSF Big Data Hubs (2015 – 2016)
- Senator, College of Agriculture and Life Sciences Faculty Senate (2015 – 2016)
- Member, Task force for Campus-Wide Research Support and Teaching in Computational Biology (2014 – 2015)
- Member, Priming Grant review committee, Cornell Center for Comparative and Population Genomics (2014)
- Chair, Ithaca Admissions Committee of Graduate Fields of Computational Biology and Computational Biology and Medicine, Tri-Institutional program of Cornell University, Weill Cornell Medical College, and Sloan-Kettering Institute (2011 – 2012)
- Member of several Faculty Search Committees, both in the Department (Department of Biological Statistics & Computational Biology) and in other departments, including Department of Plant Breeding & Genetics, and Department of Molecular Biology and Genetics (2011 – present)
- Participation in 3 NSF IGERT proposals (2010 – 2012)
- Participation in Training Grant T32 and its extension, graduate field of Genetics, Genomics, and development (2009 – present)
- Chair, Cornell Center for Comparative and Population Genomics Seminar Series (2010 – 2011)
- Participation in Training Grant T32 and its extension, Tri-Institutional Training Program in Computational Biology and Medicine (2009 – 2018)
- Member, Admissions Committee of Graduate Fields of Computational Biology and Computational Biology and Medicine (most years spanning 2009 - 2018)
- Advising dozens of undergraduate students in the Biometry & Statistics major (2009 – 2018)

## **EXTRAMURAL RECENT PROFESSIONAL ACTIVITIES AND SERVICE**

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- Journal Editor:  
Associate Editor, PLOS Computational Biology (2013 – present; editor of ~15 manuscripts)  
Associate Editor, Frontiers in Evolutionary and Population Genetics (2011 – present)  
Guest Associate Editor, PLOS Genetics (2018)
- Proposer, moderator, and speaker, Invited Session entitled “The X-factor of complex disease: From evolution to association studies of the X chromosome”, American Society of Human Genetics Annual Meeting (2014). Highlighted in several places, including: Cristy Gelling, GSA Communications Director, ASHG Meeting Report: The X-factor in complex disease ([link](#))
- Member, American Association for the Advancement of Science (2018 – present)
- Member, Genetics Society of America (2016 – present)
- Member, International Society for Computational Biology (2013 – present)
- Faculty Member, ‘FACULTY of 1000’ (2011 – present; 14 published Recommendations)
- Merit reviewer, U.S.-Israel Binational Science Foundation (2011 – 2012)
- Book proposal reviewer, Oxford University Press (2012)
- Merit reviewer, National Science Foundation (2009 – 2011)
- Member, Analysis Group, The 1000 Genomes Project Consortium (2008 – 2015)
- Member, American Society of Human Genetics (2006 – present)
- Member, The International HapMap3 Consortium (2008 – 2011)
- Member, Society of Molecular Biology and Evolution (2008 – 2009; 2014 – present)
- Reviewer for manuscripts submitted to peer-reviewed journals, including:  
Science, Nature Genetics, Nature Reviews Genetics, Scientific Reports, Genome Biology, Molecular Biology and Evolution, American Journal of Human Genetics, PLOS Genetics, PNAS, PLOS Computational Biology, Genetics, Bioinformatics, Molecular Ecology, Human Genetics, Artificial Life, Theoretical Population Biology