

ALON KEINAN – CURRICULUM VITAE

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Cornell University
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ACADEMIC POSITIONS

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

EDUCATION

- Ph.D. in Computer Science, *with distinction*** Tel Aviv, Israel
2005
School of Computer Science, Tel Aviv University
Thesis advisors: Dr. Eytan Ruppin (School of Computer Science and School of Medicine) and
Dr. Isaac Meilijson (Department of Statistics and Operations Research)
- B.Sc. in Computer Science, Statistics, and Operations Research, *Summa Cum Laude*** 1997
School of Mathematical Sciences, Tel Aviv University

RELATED PROFESSIONAL EXPERIENCE

Involvement in several companies

- Consultation, advising, and speaking engagements
- Spanning the areas of population genetics, personal genomics, statistical genetics, genomic technology, precision medicine, and nutrigenomics
- Including guiding the commercialization of own research output

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

- Initiated, planned, and designed the development of a large-scale data and knowledge management system for hundreds of end-users within the intelligence community
- Recruited and led 15-20 software engineers in implementing the system
- Managed all aspects of the project, including budget (\$12M equivalent)

Team leader

1998 – 1999

Programmer

1997 – 1998

AWARDS & HONORS

Ellison Medical Foundation New Scholar Award 2012-2017
The Ellison Medical Foundation

Edward Mallinckrodt, Jr. Foundation Award 2013-2016

Robert N. Noyce Assistant Professorship in Life Science and Technology 2011-2014
Noyce Foundation (awarded by Provost, Cornell University)

Sloan Research Fellowship 2011-2013
Alfred P. Sloan Foundation

Research and Extension Award for Early Achievement 2013
College of Agriculture and Life Sciences, Cornell University
awarded to one Assistant or Associate professor during their first ten years as a faculty

Stellar Abstract Award 2008
Emerging Quantitative Issues in Parallel Sequencing Annual Meeting

Outstanding Trainee Research Award Finalist 2008
The American Society of Human Genetics Annual Meeting

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|---|-----------|
| Postdoctoral Travel Grant Harvard University <i>awarded in the inaugural cycle to 10 postdocs from across Harvard University</i> | 2008 |
| Rothschild Postdoctoral Fellowship “Yad Hanadiv” Foundation <i>awarded to 10 young Israeli scholars from across all areas of science for outstanding merit</i> | 2005-2006 |
| Dan David Prize Scholarship <i>awarded based on merit to 10 Ph.D. students and postdocs in predetermined fields</i> | 2004-2005 |
| Wolf Award for Ph.D. Students Wolf Foundation <i>known as Israel’s most prestigious graduate student award</i> | 2004-2005 |
| Marcel Adams Award for Best Publications of the Year Adams Super Center for Brain Studies, Tel Aviv University | 2003 |
| Award for achievements towards Ph.D. School of Computer Science, Tel Aviv University <i>awarded to one Ph.D. student</i> | 2003 |
| Training grant for Ph.D. students The Aharon Katzir Center, Weizmann Institute of Science | 2003 |

GRANT SUPPORT

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

(h-index = 46; i10-index = 75; citation count > 43,000; 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[^]. Crowdsourced genealogies and genomes. *Science* (2018). (*Invited Perspective*.)

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

F. Gao & A. Keinan[^]. 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^{^*} & E. Y. Levanon^{^*}. Clustered mutations in hominid genome evolution are consistent with *APOBEC3G* enzymatic activity. *Genome Research* (2016).

K.S. Kothapalli*, K. Ye*, ... (10 authors) ..., A. Keinan[^] & J. T. Brenna[^]. 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 Consortium¹. 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[^]. Neutral genomic regions refine models of recent rapid human population growth. *PNAS* (2014).

L. Ma, A. G. Clark & A. Keinan[^]. 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[^] & A. G. Clark. Recent explosive human population growth has resulted in an excess of rare genetic variants. *Science* (2012).

D. Chang & A. Keinan[^]. 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[^]. Analyses of X-linked and autosomal genetic variation in population-scale whole genome sequencing. *Nature Genetics* (2011).

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

A. Keinan[^] & 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[^], 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[^], 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[^]. 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 Consortium¹. 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[^]. 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[^]. 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 Consortium¹. 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 Consortium¹. Alignment of 1000 Genomes Project reads to reference assembly GRCh38. *GigaScience* 6, 1-8 (2017).
10. F. Gao & A. Keinan[^]. 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[^]. The genetic history of Cochin Jews from India. *Human Genetics* 135, 1127-1143 (2016).
12. F. Gao & A. Keinan[^]. 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[^]. 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^{^*} & E. Y. Levanon^{^*}. 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[^] & J. T. Brenna[^]. 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**[^]. 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 Consortium¹. 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**[^]. 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**[^]. 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 Consortium¹. A global reference for human genetic variation. *Nature* 526, 68-74 (2015).
23. A. Sams, J. Hawks & **A. Keinan**[^]. 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 Consortium¹. 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**[^]. 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**[^]. 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*[^]. Contrasting X-linked and autosomal diversity across 14 human populations. *American Journal of Human Genetics* 94, 827-844 (2014).
32. *D. Chang & A. Keinan*[^]. Principal component analysis characterizes shared pathogenetics from genome-wide association studies. *PLOS Computational Biology* 10, e1003820 (2014).
33. *F. Gao & A. Keinan*[^]. 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*[^]. 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*^{*^} & Ariel Brautbar^{*^}. 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 Consortium¹. The landscape of human STR variation. *Genome Research* 24, Article number 3934 (2014).
38. O. Delaneau *et al.* with The 1000 Genomes Project Consortium¹. 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*[^]. 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*[^]. 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*[^] & 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*[^]. 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*[^]. 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*^{*^} & A. Brautbar^{*^}. 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*[^]. NRE: A tool for exploring neutral loci in the human genome. *BMC Bioinformatics* 13, paper 301 (2012).

47. The 1000 Genomes Project Consortium¹. 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 Consortium¹. 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 Consortium¹. 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 Consortium¹. 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**[^]. 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).
53. Y. Y. Waldman, T. Tuller, **A. Keinan**^{*^} & E. Ruppin^{*^}. Selection for translation efficiency on synonymous polymorphisms in recent human evolution. *Genome Biology and Evolution* 3, 749-761 (2011).
54. R. D. Hernandez *et al.* with The 1000 Genomes Project Consortium¹. Classic selective sweeps were rare in recent human evolution. *Science* 331, 920-924 (2011).
55. R. E. Mills *et al.* with The 1000 Genomes Project Consortium¹. Mapping copy number variation by population-scale genome sequencing. *Nature* 470, 59-65 (2011).
56. P. Moorjani, N. Patterson, J. N. Hirschhorn, **A. Keinan**, L. Hao, G. Atzmon, E. R. Burns, H. Ostrer, A. Price & D. Reich. The history of African gene flow into Southern Europeans, Levantines and Jews. *PLOS Genetics* 7, e1001373 (2011).
57. S. Gravel *et al.* with The 1000 Genomes Project Consortium¹. Demographic history and rare allele sharing among human populations. *Proceedings of the National Academy of Sciences* 108, 11983-8 (2011).
58. P. Danecek *et al.* with The 1000 Genomes Project Consortium¹. The variant call format and VCFtools. *Bioinformatics* 27, 2156-2158 (2011).
59. **A. Keinan**[^] & D. Reich. Human population differentiation is strongly correlated with local recombination rate. *PLOS Genetics* 6, e1000886 (2010).
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**[^] & 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 Consortium¹. 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 Consortium¹. Diversity of human copy number variation and multicopy genes. *Science* 330, 641-646 (2010).

65. F. M. De La Vega, K. Bryc, J. D. Degenhardt, S. Musharoff, J. M. Kidd, V. Seth, S. Stanley, A. Brisbin, **A. Keinan**, A. Clark & C. D. Bustamante. Genome sequencing and analysis of admixed genomes of African and Mexican ancestry: implications for personal ancestry reconstruction and multi-ethnic medical genomics. *Genome Biology* 11, paper O4 (2010).
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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).
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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**¹, C. C. Hilgetag, I. Meilijson & E. Ruppín. Causal localization of neural function: The Shapley value method. *Neurocomputing* 58-60C, 215-222 (2004).
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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).

¹ **A. Keinan** is a co-author of and contributor to the indicated 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. Ruppin. Identification of effective elements in complex systems. United States Patent #7,130,763 (2006).

TRAINEES AT CORNELL UNIVERSITY

Postdoctoral Researchers

| | |
|---|-------------|
| Dr. Alexandre Lussier (role: research advisor) <i>Continued to a postdoctoral research position, Harvard Medical School</i> | 2018 – 2019 |
| 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&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 Director of Data Science at Valo</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 Principal 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 Associate Director, Think Team, Otsuka Pharmaceutical Companies</i> | 2010 – 2012 |

Graduate Students

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

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| 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 |
| Yingjie Guo (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 |
| Andrea Slavney, Ph.D. (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 |
| Paul Billing-Ross, M.A. (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 |
| Feng Gao, Ph.D. (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 |
| Diana Chang, Ph.D. (role: research advisor and Ph.D. thesis committee chair) <i>Continued to a postdoctoral position at Genentech; Currently Senior Scientist, Genentech</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.)

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| 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 |

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| 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 |
| Dr. 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); graduated</i> | 2014 – 2015 |
| Dr. Arjun Biddanda (role: research advisor) <i>Continued to graduate school at the University of Chicago, Program of Human Genetics (advisor: John Novembre); graduated</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

| | |
|---|---|
| Department of Biological Statistics & Computational Biology, Cornell University | Ithaca, NY |
| Instructor , BTRY 6820/4820: “Statistical Genomics: Coalescent Theory and Human Population Genomics” | Spring 2012; Spring 2013; Spring 2016 |
| Instructor , BTRY 6890: “Topics in Population Genetics and Genomics” | Spring 2012; Spring 2013; Fall 2016 |
| Co-instructor , BTRY 6700: “Applied Bioinformatics and Systems Biology” | Fall 2010; Fall 2011 |
| Instructor , 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 |
| School of Mathematical Sciences and School of Computer Science, Tel Aviv University | Tel Aviv, Israel |
| Instructor , “Neural Networks for Machine Learning” (course) | Spring 2004; Spring 2005 |
| Instructor , “Artificial Life (Evolutionary Computation & Neural Networks)” (workshop) | Spring 2004 |
| Teaching Assistant , multiple courses most semesters | 1997 – 2002 |
| 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. | (7 semesters) |

INTRAMURAL RECENT PROFESSIONAL ACTIVITIES AND SERVICE

- Chair and lead of high-performance computing cluster, including proposal, planning, design, construction, work with stakeholders, purchasing, and leading of support team (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

- Journal Editor:
 - Associate Editor, PLOS Computational Biology (2013 – present)
 - Associate Editor, Frontiers in Evolutionary and Population Genetics (2011 – present)
 - Guest Associate Editor, PLOS Genetics (2018)
- Organizer, 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)
- 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 of
 - papers for scientific 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
 - grant proposals, National Science Foundation
 - grant proposals, U.S.-Israel Binational Science Foundation
 - book proposals, Oxford University Press