ALON KEINAN – CURRICULUM VITAE

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POSITIONS

Associate Professor — Ithaca, NY
Department of Biological Statistics & Computational Biology, Cornell University — 11/1/14 – present

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 — 08/26/15 – present

Faculty
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

Postdoctoral Research Fellow — Boston, MA
Department of Genetics, Harvard Medical School — 9/2005 – 8/2009
& Program in Medical and Population Genetics, Broad Institute of MIT and Harvard

EDUCATION

Ph.D. in Computer Science, *with distinction* — Tel Aviv, Israel
School of Computer Science, Tel Aviv University — 2005
Thesis advisors: Professor Eytan Ruppin (School of Computer Science and School of Medicine) and Professor 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
School of Mathematical Sciences, Tel Aviv University — 1997

AWARDS & HONORS

Edward Mallinckrodt, Jr. Foundation Award 2013-2016

Ellison Medical Foundation New Scholar Award 2012-2016
The Ellison Medical Foundation

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

Postdoctoral Travel Grant 2008
Harvard University
awarded in the inaugural cycle to 10 postdocs from across Harvard University

Rothschild Postdoctoral Fellowship 2005-2006
"Yad Hanadiv" Foundation
awarded to 10 Israeli young scholars from across all areas of science for outstanding merit

Dan David Prize Scholarship 2004-2005
awarded based on merit to 10 Ph.D. students and/or postdocs in predetermined fields

Wolf Award for Ph.D. Students 2004-2005
Wolf Foundation
known as Israel's most prestigious graduate student award

Marcel Adams Award for Best Publications of the Year 2003
Adams Super Center for Brain Studies, Tel Aviv University

Award for achievements towards Ph.D. 2003
School of Computer Science, Tel Aviv University
awarded to one Ph.D. student

Training grant for Ph.D. students
The Aharon Katzir Center, Weizmann Institute of Science 2003

CURRENT AND RECENT EXTRAMURAL GRANT SUPPORT

1. NIH/NHGRI R01HG006849 (Role: **PI**). The X-factor of complex disease: From population genetics to GWAS of Chromosome X.
   Award period: 9/9/2013 – 6/30/2017 (NCE)
   Total amount (all to Keinan): $1,136,361

2. Edward Mallinckrodt, Jr. Foundation award (Role: **PI**)
   Award period: 3/1/2013 – 2/28/2017 (NCE)
   Total amount (all to Keinan): $180,000

3. New Scholar Award, The Ellison Medical Foundation (Role: **PI**).
   Award period: 7/1/2012 – 6/30/2016
   Total amount (all to Keinan): $400,000

4. Robert N. Noyce endowed chair, Noyce Foundation (Role: **PI**).
   Award period: 8/1/2011 – 7/31/2014
   Total amount (all to Keinan): $135,000

5. 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 lab: $734,760

6. 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

7. Sloan Research Fellowship, Alfred P. Sloan Foundation (Role: **PI**).
   Award period: 9/15/2011 – 9/15/2013
   Total amount (all to Keinan): $50,000

8. NIH/NHGRI U01HG005715 (Role: **co-PI**; PI: Carlos D. Bustamante). Population structure, admixture and selection across the 1000 Genomes data set.
   Award period: 9/9/2010 – 6/30/2013
   Total amount to Keinan lab: $432,692

Pending

9. 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. (score 18 percentile; pending council review)
   Requested award period: 11/01/2016 – 10/31/2021 (5 years)
   Requested total amount (all to Keinan): $1,878,295.00

PUBLICATIONS

(h-index = 31; i10-index = 51; citation count = 15,578; 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)

2016

1. *F. Gao* **& A. Keinan^.** Explosive genetic evidence for explosive human population growth. *Current Opinion in Genetics & Development*, 41, 130-139 (2016). (*Invited review.*)
2. *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).
3. *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).
4. *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).
5. 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).
6. 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. Caspermeyer. 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 Altmetric score of 727, i.e. within top 2,000 papers out of over 6 million papers with Altmetric score ever published.)
7. *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).
8. 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)
9. *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).

2015

10. *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).
11. *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)
12. 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).

13. 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).
14. *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).
15. *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).
16. 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*, … (70 authors in total) , **A. Keinan**, E. T. Luning Prak, C. Polychronakos, R. N. Baldassano, H. Li, B. J. Keating, H. Hakonarson. Meta-analysis of shared genetic architecture across ten pediatric autoimmune diseases. *Nature Medicine*, 21, 1018-27 (2015).

2014

17. *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).
18. *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).
19. *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).
20. *D. Chang* **& A. Keinan^.** Principal component analysis characterizes shared pathogenetics from genome-wide association studies. *PLOS Computational Biology* 10, e1003820 (2014).
21. *F. Gao* **& A. Keinan^.** High burden of private mutations due to explosive human population growth and purifying selection. *BMC Genomics* 15, 1-7 (2014).
22. *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).
23. *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).
24. *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, E4548-E4550 (2014).

- 2013

25. *L. Ma*, A. G. Clark **& A. Keinan^**. Gene-based testing of interactions in association studies of quantitative traits. *PLOS Genetics* 9, e1003321 (2013).
26. *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).

27. *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.**

28. **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).

29. *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).

30. *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).

31. *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).

32. *L. Arbiza*, *E. Zhong* **& A. Keinan^.** NRE: A tool for exploring neutral loci in the human genome. *BMC Bioinformatics* 13, paper 301 (2012).

33. 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).

34. *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).

35. *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).

36. 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).

37. **A. Keinan^** & D. Reich. Human population differentiation is strongly correlated with local recombination rate. *PLOS Genetics* 6, e1000886 (2010).

38. 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).

39. **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).

40. **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)

41. 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).

42. **A. Keinan^**, 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).

43. 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).
44. **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* 39, 1251-1255 (2007).
45. G. Ayodo, A. L. Price, **A. Keinan**, A. Ajwang, M. F. Otieno, A. S. S. Orago, N. Patterson & D. Reich. Combining evidence of natural selection with association analysis increases power to detect Malaria-resistance variants. *American Journal of Human Genetics* 81, 234-242 (2007).
46. **A. Keinan**, B. Sandbank, C. C. Hilgetag, I. Meilijson & E. Ruppin. Axiomatic scalable neurocontroller analysis via the Shapley value. *Artificial Life* 12, 333-352 (2006).
47. **A. Keinan**, A. Kaufman, C. C. Hilgetag, I. Meilijson & E. Ruppin. 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).
48. K. Saggie-Wexler, **A. Keinan** & E. Ruppin. Neural processing of counting in evolved spiking and McCulloch-Pitts agents. *Artificial Life* 12, 1-16 (2006).
49. Z. Ganon, **A. Keinan** & E. Ruppin. Neurocontroller analysis via evolutionary network minimization. *Artificial Life* 12, 435-448 (2006).
50. A. Kaufman*, **A. Keinan***, I. Meilijson, M. Kupiec & E. Ruppin. Quantitative analysis of genetic and neuronal multi-perturbation experiments. *PLOS Computational Biology* 1, e64 (2005).
51. **A. Keinan**, B. Sandbank, C. C. Hilgetag, I. Meilijson & E. Ruppin. Fair attribution of functional contribution in artificial and biological networks. *Neural Computation* 16, 1887-1915 (2004).
52. **A. Keinan**^, C. C. Hilgetag, I. Meilijson & E. Ruppin. Causal localization of neural function: The Shapley value method. *Neurocomputing* 58-60C, 215-222 (2004).
53. **A. Keinan**, A. Kaufman, N. Sachs, C. C. Hilgetag & E. Ruppin. Fair localization of function via multi-lesion analysis. *Neuroinformatics* 2, 163-168 (2004).
54. **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).
55. K. Saggie, **A. Keinan** & E. Ruppin. Spikes that count: Rethinking spikiness in neurally embedded systems. *Neurocomputing* 58-60C, 303-311 (2004).
56. Z. Ganon, **A. Keinan** & E. Ruppin. Evolutionary network minimization: Adaptive implicit pruning of successful agents. *Advances in Artificial Life* 2801, 319-327 (2003).
57. K. Saggie, **A. Keinan** & E. Ruppin. Solving a delayed response task with spiking and McCulloch-Pitts agents. *Advances in Artificial Life* 2801, 199-208 (2003).
58. **A. Keinan**, I. Meilijson & E. Ruppin. Controlled analysis of neurocontrollers with informational lesioning. *Philosophical Transactions of the Royal Society A* 361, 2123-2144 (2003).

Selected publications by The 1000 Genomes Project Consortium (2010-2016)

(**A. Keinan** is a co-author on and contributor to these publications as a member of both the Analysis group and the Samples and ELSI group; however, the consortium consists of almost 500 co-authors.)

59. Punctuated bursts in human male demography inferred from 1,244 worldwide Y-chromosome sequences. Nature Genetics 48, 593-599 (2016).
60. A global reference for human genetic variation. *Nature* 526, 68-74 (2015).
61. An integrated map of structural variation in 2,504 human genomes. *Nature* 526, 75-81 (2015).

62. Integrating sequence and array data to create an improved 1000 Genomes Project haplotype reference panel. *Nature Communications* 5, Article number 3934 (2014).
63. An integrated map of genetic variation from 1,092 human genomes. *Nature* 491, 56-65 (2012).
64. Classic selective sweeps were rare in recent human evolution. *Science* 331, 920-924 (2011).
65. Mapping copy number variation by population-scale genome sequencing. *Nature* 470, 59-65 (2011).
66. Demographic history and rare allele sharing among human populations. *Proceedings of the National Academy of Sciences* 108, 11983-8 (2011).
67. The variant call format and VCFtools. *Bioinformatics* 27, 2156-2158 (2011).
68. A map of human genome variation from population scale sequencing. *Nature* 467, 1061-1073 (2010).
69. Diversity of human copy number variation and multicopy genes. *Science* 330, 641-646 (2010).

Patent

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

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.
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.

Recent invited talks

1. Upcoming: Mathematical Biology, University of Pennsylvania (March 2017).
2. Upcoming: 5th Annual Epistasis Discovery in Genetics and Epidemiology workshop, Key West (2/9/2017). *Keynote speaker*
3. Upcoming: Center for Vertebrate Genomics, Cornell University (11/8/2016).
4. Department of Genetics, Harvard Medical School (2016).
5. Molecular Biology and Genetics, Cornell University (2015).
6. The American Society of Human Genetics Annual Meeting, San Diego (2014).
7. Institute for Human Genetics, UC San Francisco (2014).
8. AndyFest Symposium: Principals in Population Genetics: A coalescence of community to celebrate Andy Clark, Cornell University (2014).
9. Department of Genetics, School of Medicine, University of Pennsylvania (2014).
10. Department of Genetics and Human Genetics Institute, Rutgers University, New Brunswick (2014).
11. Departments of Biology and Computer Science, University of Maryland, College Park (2014).
12. SNP-SIG Meeting, Annual International Conference on Intelligent Systems for Molecular Biology (2013). *Keynote speaker*

13. Program in Quantitative Genomics, Harvard University (2013).
14. Human Genetics & Genomics Gordon Research Conference (2013).
15. Department of Cell Biology and Molecular Genetics, University of Maryland, College Park (2013).
16. Statistics, Cornell University (2012).
17. Tel Aviv University, Tel Aviv, Israel (2012).
18. Bar-Ilan University, Ramat Gan, Israel (2012).

Selected recent conference abstracts

1. *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.** A tale of two communities - the genetic history of Bene Israel and Cochin Jews. First International Conference on Founder Populations and their contribution to our understanding of Biology and History, Haifa, Israel (2016). *Platform presentation*
2. *A. Madar, D. Chang, F. Gao, A. J. Sams, Y. Y. Y. Waldman*, D. S. Cunninghame-Graham, T. J. Vyse, A. G. Clark **& A. Keinan.** Computational biology as applied to hypersensitivity Dnase analysis. Functional Genomics Workshop, King's college, London, UK (2016). *Platform presentation*
3. **A. Keinan**, *D. Chang, F. Gao, A. J. Sams, Y. Waldman*, D. Cunninghame-Graham, T. Vyse, A. Clark & A. Madar. Leveraging regulatory and genotype-phenotype data to discover and interpret the function of human regulatory DNA in health and disease. The Biology of Genomes, Cold Spring Harbor Laboratory, Cold Spring Harbor, NY (2016).
4. K.S. Kothapalli, M. S. Gadgil, S. E. Carlson, K. O. O'Brien, *K. Ye*, J. Y. Zhang, H. G. Park, K. Ojukwu, J. Zou, S. S. Hyon, K. S. Joshi, **A. Keinan** & J. T. Brenna. A 22 bp *FADS2* Insertion-Deletion (Indel) Polymorphism Influences Arachidonic Acid Status. The Experimental Biology 2016 Meeting, San Diego (2016). (The FASEB Journal 30, 267.4). *Platform presentation*
5. *A. Madar*, *D. Chang*, *F. Gao*, *A. J. Sams*, *Y. Waldman*, A. G. Clark **& A. Keinan.** Resolving regulatory DNA specific to adaptive immune cells allows the robust identification of hundreds of novel loci for autoimmune diseases that lie below the detection power of genome-wide association studies. The 2015 Winter q-bio Meeting, Maui (2015). *Platform presentation*
6. *F. Gao* & **A. Keinan.** Inference of super-exponential human population growth via efficient computation of the site frequency spectrum for generalized models. The American Society of Human Genetics Annual Meeting, Baltimore, MD (2015). *Platform presentation*
7. *A. Madar, D. Chang, F. Gao, A. J. Sams, Y. Y. Y. Waldman*, D. S. Cunninghame-Graham, T. J. Vyse, A. G. Clark **& A. Keinan.** Connecting the regulatory dots at the GWAS discovery phase. The American Society of Human Genetics Annual Meeting, Baltimore, MD (2015). *Platform presentation*
8. **A. Keinan**, on behalf of the XWAS Consortium. The X-factor of complex disease: Methods, software, and extensive application for studying the X chromosome in association studies. The American Society of Human Genetics Annual Meeting, Baltimore, MD (2015). *Platform presentation*
9. *L. Arbiza* **& A. Keinan.** The relative effective population size of chromosome X and the autosomes along distinct branches of the human population tree. The American Society of Human Genetics Annual Meeting, Baltimore, MD (2015).
10. *A. Slavney, L. Arbiza*, A. Clark **& A. Keinan.** Strong evolutionary constraint on human genes escaping X-inactivation is modulated by their expression breadth and level in both sexes. The American Society of Human Genetics Annual Meeting, Baltimore, MD (2015).
11. *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. The American Society of Human Genetics Annual Meeting, Baltimore, MD (2015).

12. *A. J. Sams*, *A. Madar* **& A. Keinan.** Analysis of cell-specific regulatory DNA reveals elevated immune specificity in genomic regions of high Neandertal ancestry. The 84th Annual Meeting of the American Association of Physical Anthropologists, St. Louis, MO (2015). (American Journal of Physical Anthropology 156, 275).

13. *A. Madar*, *D. Chang*, *A. J. Sams*, *F. Gao*, *Y. Waldman*, C. Van Hout, A. G. Clark **& A. Keinan.** A regulatory DNA association study between autoimmune disease risk and variation in regulatory regions that are highly unique to adaptive immune cells. The American Society of Human Genetics Annual Meeting, San Diego (2014). *Platform presentation*

14. *F. Gao* **& A. Keinan.** Human population growth and purifying selection have increased the burden of autosomal and X-linked private mutations. The American Society of Human Genetics Annual Meeting, San Diego (2014).

15. *A. Slavney*, *F. Gao*, A. Clark **& A. Keinan**. Differential purifying and positive selection across genes stratified by X chromosome inactivation status. The American Society of Human Genetics Annual Meeting, San Diego (2014).

16. *P. Billing-Ross*, *K. Ye*, **A. Keinan** & Z. Gu. Quantifying mitochondrial copy number using next-generation sequencing data. The American Society of Human Genetics Annual Meeting, San Diego (2014).

17. **A. Keinan**, *F. Gao, E. Gazave, L. Ma, D. Chang* & A. Clark. The burden of private mutations is greatly affected by recent explosive human population growth. The Annual Meeting of the Society of Molecular Biology and Evolution, San Juan, Puerto Rico (2014).

18. *L. Ma* **& A. Keinan**. Detecting X-linked association with a variance test of X-Inactivation. Plant & Animal Genome XXII Conference, San Diego (2014).

19. **A. Keinan**, *F. Gao*, *L. Ma*, *A. Sams*, *A. Slavney*, *P. Billing-Ross*, *A. Madar*, R. Spritz & *D. Chang*. No eXceptions: Accounting for the X chromosome in GWAS reveals new genes implicated in autoimmune diseases. The Biology of Genomes, Cold Spring Harbor Laboratory, Cold Spring Harbor, NY (2014).

20. *A. Madar*, *D. Chang*, *A. Sams*, *F. Gao*, C. Van Hout, *Y. Waldman*, A. Clark **& A. Keinan.** Integrating autoimmune disease genome wide association studies with DNase-seq data reveals hundreds of functional T cell specific cis regulatory modules. Gene Expression & Signaling in the Immune System, Cold Spring Harbor Laboratory, Cold Spring Harbor, NY (2014).

21. *A. Sams* **& A. Keinan.** Genomic identification and characterization of adaptive introgression from Neandertals. The 83rd Annual Meeting of the American Association of Physical Anthropologists, Calgary, Canada (2014). (American Journal of Physical Anthropology 153, 228)

22. *R. Blekhman*, J. K. Goodrich, **A. Keinan**, R. E. Ley, D. Gevers & A. G. Clark. A role for host-bacteria interactions in shaping patterns of genetic variation across human populations. The 83rd Annual Meeting of the American Association of Physical Anthropologists, Calgary, Canada (2014). (American Journal of Physical Anthropology 153, 80). *Platform presentation*

23. **A. Keinan** & *D. Chang*. Characterizing shared pathogenetics from genome-wide association studies via principal component analysis. The American Society of Human Genetics Annual Meeting, Boston (2013). *Platform presentation*

24. *L. Ma*, C. Ballantyne, A. Brautbar **& A. Keinan.** Evidence from multiple genome-wide association studies of a hub of gene-gene interactions affecting human HDL cholesterol levels. The American Society of Human Genetics Annual Meeting, Boston (2013). *Platform presentation*

25. *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. A role for host-bacteria interactions in shaping patterns of genetic variation across human populations. The American Society of Human Genetics Annual Meeting, Boston (2013). *Platform presentation*

26. **A. Keinan**, *E. Gazave*, A. Coventry, *S. Gottipati*, *D. Chang*, *L. Ma*, D. Muzny, E. Boerwinkle, C. Sing, R. Gibbs & A. G. Clark. Rare genetic variants in deep sequencing of neutral regions from a homogeneous

population refine models of recent explosive human population growth. The American Society of Human Genetics Annual Meeting, San Francisco (2012). *Platform presentation*

27. *L. Ma*, A. Brautbar, E. Boerwinkle, C. F. Sing, A. G. Clark **& A. Keinan.** Gene-based epistasis analysis in genome-wide association studies. The American Society of Human Genetics Annual Meeting, San Francisco (2012). *Platform presentation*.

28. **A. Keinan**, *L. Ma*, A. Brautbar, E. Boerwinkle, C. Sing & A. G. Clark. Knowledge-driven analysis identified a gene-gene interaction affecting High-Density Lipoprotein Cholesterol levels in multi-ethnic populations. Fourth International Conference of Quantitative Genetics: Understanding Variation in Complex Traits, Edinburgh, Scotland, UK (2012). *Platform presentation*

29. **A. Keinan**, *S. Gottipati*, A. Siepel, A. Clark & *L. Arbiza*. Contrasting human X-linked and autosomal variation in population-scale whole genome sequencing. International Congress of Human Genetics and the American Society of Human Genetics Annual Meeting, Montreal, Canada (2011). *Platform presentation*

30. A. Coventry, L. Bull-Otterson, **A. Keinan**, X. Liu, A. Clark, T. Maxwell, J. Hixson, T. Rea, A. Templeton, D. Muzny, L. Lewis, D. Villasana, E. Boerwinkle, R. Gibbs & C. Sing. "Peeking near the peaks" for large-effect rare variants. International Congress of Human Genetics and the American Society of Human Genetics Annual Meeting, Montreal, Canada (2011). *Platform presentation*

TRAINEES AT CORNELL UNIVERSITY

Postdoctoral Researchers

Dr. Kaixiong Ye (role: research advisor) 2015 – present

Dr. Leonardo Arbiza (role: research advisor; initially jointly with Adam Siepel); 2010 – present
From 2013, Research Associate in my group alone and serves in the capacity of a Programmer

Dr. Aviv Madar (role: research advisor; jointly with Andrew Clark) 2013 – 2016
Continued to an Investigator II position, Novartis, Cambridge, MA

Dr. Yedael Waldman (role: research advisor) 2014 – 2016
Continued to a position of Computational Biologist at NRGene
(while waiting for paper publication in order to go on the academic job market)

Dr. Aaron Sams (role: research advisor) 2013 – 2015
Currently a Bioinformatics Research Scientist, Embark Veterinary (at Cornell University)

Dr. Li Ma (role: research advisor; jointly with Dr. Andrew Clark) 2010 – 2013
Continued to a tenure-track faculty position, University of Maryland College Park
(Department of Animal and Avian Sciences; Also Visiting Scientist, Animal Genomics and Improvement Lab at USDA ARS)

Dr. Elodie Gazave (role: research advisor) 2010 – 2013
Currently a Research Associate at Cornell University, School of Integrative Plant Science, Plant Breeding and Genetics Section (working with Michael Gore)

Dr. Ran Blekhman (role: secondary research advisor and mentor) 2010 – 2013
Continued to a tenure-track faculty position, University of Minnesota Twin Cities (Department of Genetics; Department of Ecology, Evolution, and Behavior; Also Member, Microbial and Plant Genomics Institute, Bioinformatics and Computational Biology Graduate Program; Principal Investigator, Minnesota Supercomputing Institute; Program Member, Cancer Center)

Dr. Srikanth Gottipati (role: research advisor; jointly with Dr. Andrew Clark) 2010 – 2012
Currently Sr. Manager, Translational Medicine and Think team, Otsuka Pharmaceutical Commercialization and Development, Inc. Princeton, NJ

Graduate Students

(including rotations; **bold** indicates conducting graduate research in my group)
*not included are students for whom I merely served/serving on their Ph.D. thesis committee.

Jens Sannerud (role: rotation advisor and NSF proposal advisor)	2016 – present
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) *Returned to her home university (Harbin Institute of Technology, School of Computer Science and Technology) in Sep 2016 in order to finalize PhD (expected graduation: July 2017)*	2014 – 2016
Andrea Slavney (role: research advisor and Ph.D. committee chair; jointly with Andrew Clark) *PhD candidate (A-exam passed on 8/27/2014)*	2013 – present
Paul Billing-Ross (role: secondary research advisor to Zhenglong Gu) *After passing A-exam, decided to graduate with an M.A. and continued to being a Software Developer, the Stanford School of Medicine.*	2013 – 2015
Feng Gao (role: research advisor and Ph.D. thesis committee chair) *PhD candidate (A-exam passed on 8/28/2014); B-exam planned for Dec 2016.*	2012 – present
Diana Chang (role: research advisor and Ph.D. thesis committee chair) *Currently Associate Scientist at Genentech, after a short postdoctoral position there*	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

(**bold** indicates conducting research in my group, which is the case for students who have spent at least two semesters of independent study with me; *continued position indicated for those*)

David Wang (role: research advisor)	2016 – present
Edward Li (role: research advisor)	2016 – present
Yuhuan Qiu (role: research advisor)	2016 – present
Lauren Lo (role: research advisor)	2016 – present
Liang Zhang (role: research advisor, both as undergraduate and for M.Eng thesis) *Continued to a position of Analyst at BlackRock, NY, NY*	2015 – 2016
Liam Bui (role: independent reading advisor)	2015
Zilu Zhou (role: research advisor) *Continued to graduate school at the University of Pennsylvania, program of Genomics and Computational Biology, Perelman School of Medicine (advisor: Nancy Zhang)*	2014 – 2015
Arjun Biddanda (role: research advisor) *Continued to graduate school at the University of Chicago, program of Human Genetics (advisor: John Novembre)*	2013 – 2015
Elaine Zhong (role: research advisor) *Continued to medical school, Columbia University (from online search only: currently MD and a practicing physician out of Columbia University)*	2010 – 2011
Beverly Anderson (role: independent reading advisor)	2011
Elena Chen (role: independent reading advisor)	2010

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 or master thesis courses:	
CS 5999: Master of Engineering Project	Spring 2016
CS 4999: "Independent Reading & Research"	Fall 2015; Spring 2016; Fall 2016
BIOG 4990: "Independent Undergraduate Research in Biology"	Spring 2010; Spring 2011; Fall 2011; Spring 2014; Fall 2014; Spring 2015
BIOG 2990: "Introduction to Research Methods in Biology"	Fall 2013; Spring 2015
BTRY 4990: "Independent Undergraduate Research"	Fall 2011; Fall 2014; Fall 2015
School of Mathematical Sciences and School of Computer Science, Tel Aviv University	Tel Aviv, Israel
Instructor, "Introduction to Neural Networks" (course)	Fall 2004; Fall 2005
Instructor, "Artificial Life" (workshop)	Fall 2004
Teaching Assistant, many Computer Science, Statistics and Mathematics courses (7 semesters)	1997 – 2002

OTHER RECENT PROFESSIONAL ACTIVITIES AND SERVICE

At Cornell University

- Committee member, proposal for NSF Workshop on Sharing Sensitive Data (2016 – present)
- Committee member, NSF Big Data Hubs (2015 – present)
- Senator, CALS Faculty Senate (2015 – present)
- Chair, planning, construction, development, and maintenance of High Performance Computing resource for Computational Biology (2013 – present)
- Member, Task force for Campus-Wide Research Support and Teaching in Computational Biology (2014 – 2015)
- Member, Faculty Search Committee in Computational Genomics, Department of Molecular Biology and Genetics (2014 – 2015)
- Member, Priming Grant review committee, Cornell Center for Comparative and Population Genomics (2014)
- Member, Faculty Search Committee in Computational Biology, Department of Biological Statistics & Computational Biology (2012 – 2013)
- 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, Faculty Search Committee, Department of Plant Breeding & Genetics (2011 – 2012)
- Participation in 3 NSF IGERT proposals (2010 – 2012)

- Participation in Training Grant T32 and its extension, Tri-Institutional Training Program in Computational Biology and Medicine (2009 – present)
- 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)
- Member, Ithaca Admissions Committee of Graduate Fields of Computational Biology and Computational Biology and Medicine (2009 – 2010)
- Advising 38 undergraduate students in the Biometry & Statistics major (2009 – present)

Other

- 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)
- Associate Editor, PLOS Computational Biology (2013 – present; Editor of ~15 manuscripts)
- Member, International Society for Computational Biology (2013 – present)
- Associate Editor, Frontiers in Evolutionary and Population Genetics (2011 – present)
- Faculty Member, 'FACULTY of 1000' (2011 – present)
- 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 – present)
- 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:
  Science, PNAS, PLOS Genetics, Nature Reviews Genetics, American Journal of Human Genetics, PLOS Computational Biology, Genetics, Molecular Biology and Evolution, Genome Biology, Bioinformatics, Artificial Life, Theoretical Population Biology, Molecular Ecology, Human Genetics