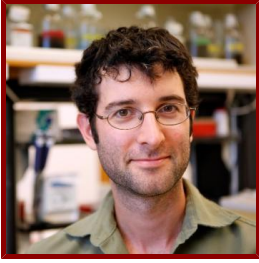


Stanford



Hunter Fraser

Professor of Biology

 Curriculum Vitae available Online

Bio

ACADEMIC APPOINTMENTS

- Professor, Biology
- Member, Bio-X
- Member, Maternal & Child Health Research Institute (MCHRI)
- Member, Stanford Cancer Institute
- Member, Wu Tsai Neurosciences Institute

LINKS

- Fraser Lab: <https://web.stanford.edu/group/fraserlab/>

Research & Scholarship

CURRENT RESEARCH AND SCHOLARLY INTERESTS

We study the evolution of complex traits by developing new experimental and computational methods.

Our work brings together quantitative genetics, genomics, epigenetics, and evolutionary biology to achieve a deeper understanding of how genetic variation shapes the phenotypic diversity of life. Our main focus is on the evolution of gene expression, which is the primary fuel for natural selection. Our long-term goal is to be able to introduce complex traits into new species via genome editing.

Teaching

COURSES

2025-26

- The Science and Ethics of Personalized Genomic Medicine: BIO 4N (Win)

2024-25

- The Science and Ethics of Personalized Genomic Medicine: BIO 4N (Win)

2023-24

- Evolutionary Genomics: BIO 191, BIO 332 (Win)
- The Science and Ethics of Personalized Genomic Medicine: BIO 4N (Win)

STANFORD ADVISEES

Doctoral Dissertation Reader (AC)

Joel Erberich, Ellen Morgan

Postdoctoral Faculty Sponsor

Deshan Perera

Doctoral Dissertation Advisor (AC)

Zhenzhen Ma, Alex Starr

Undergraduate Major Advisor

Daria Gusarova

GRADUATE AND FELLOWSHIP PROGRAM AFFILIATIONS

- Biology (School of Humanities and Sciences) (Phd Program)
- Biomedical Data Science (Phd Program)

Publications

PUBLICATIONS

- **Disentangling cell-intrinsic and cell-extrinsic factors underlying evolution.** *Cell genomics*
Starr, A. L., Nishimura, T., Igarashi, K. J., Funamoto, C., Nakauchi, H., Fraser, H. B.
2025: 100891
- **Primate cell fusion disentangles gene regulatory divergence in neurodevelopment.** *Nature*
Agoglia, R. M., Sun, D. n., Birey, F. n., Yoon, S. J., Miura, Y. n., Sabatini, K. n., Paşca, S. P., Fraser, H. B.
2021
- **Human-chimpanzee fused cells reveal cis-regulatory divergence underlying skeletal evolution.** *Nature genetics*
Gokhman, D. n., Agoglia, R. M., Kinnebrew, M. n., Gordon, W. n., Sun, D. n., Bajpai, V. K., Naqvi, S. n., Chen, C. n., Chan, A. n., Chen, C. n., Petrov, D. A., Ahituv, N. n., Zhang, et al
2021
- **Detecting selection with a genetic cross.** *Proceedings of the National Academy of Sciences of the United States of America*
Fraser, H. B.
2020
- **The somatic mutation landscape of the human body.** *Genome biology*
Garcia-Nieto, P. E., Morrison, A. J., Fraser, H. B.
2019; 20 (1): 298
- **Fine-mapping cis-regulatory variants in diverse human populations.** *eLife*
Tehranchi, A., Hie, B., Dacre, M., Kaplow, I., Pettie, K., Combs, P., Fraser, H. B.
2019; 8
- **Tissue-Specific cis-Regulatory Divergence Implicates *eloF* in Inhibiting Interspecies Mating in *Drosophila*.** *Current biology : CB*
Combs, P. A., Krupp, J. J., Khosla, N. M., Bua, D., Petrov, D. A., Levine, J. D., Fraser, H. B.
2018
- **Functional Genetic Variants Revealed by Massively Parallel Precise Genome Editing** *CELL*
Sharon, E., Chen, S. A., Khosla, N. M., Smith, J. D., Pritchard, J. K., Fraser, H. B.
2018; 175 (2): 544+
- **Pooled ChIP-Seq Links Variation in Transcription Factor Binding to Complex Disease Risk** *CELL*
Tehranchi, A. K., Myrthil, M., Martin, T., Hie, B. L., Golan, D., Fraser, H. B.

2016; 165 (3): 730-741

- **Dissecting the Genetic Basis of a Complex cis-Regulatory Adaptation.** *PLoS genetics*
Naranjo, S., Smith, J. D., Artieri, C. G., Zhang, M., Zhou, Y., Palmer, M. E., Fraser, H. B.
2015; 11 (12)
- **Genetic conflict reflected in tissue-specific maps of genomic imprinting in human and mouse.** *Nature genetics*
Babak, T., Deveale, B., Tsang, E. K., Zhou, Y., Li, X., Smith, K. S., Kukurba, K. R., Zhang, R., Li, J. B., van der Kooy, D., Montgomery, S. B., Fraser, H. B.
2015; 47 (5): 544-549
- **Gene expression drives local adaptation in humans** *GENOME RESEARCH*
Fraser, H. B.
2013; 23 (7): 1089-1096
- **In silico genome transplants and the cis-regulatory basis of biodiversity.** *Trends in genetics : TIG*
Starr, A. L., Palmer, M. E., Fraser, H. B.
2025
- **A General Principle of Neuronal Evolution Reveals a Human-Accelerated Neuron Type Potentially Underlying the High Prevalence of Autism in Humans.** *Molecular biology and evolution*
Starr, A. L., Fraser, H. B.
2025; 42 (9)
- **Massively parallel experimental interrogation of natural variants in ancient signaling pathways reveals both purifying selection and local adaptation.** *bioRxiv : the preprint server for biology*
Aguilar-Rodríguez, J., Vila, J., Chen, S. A., Razo-Mejia, M., Ghosh, O., Fraser, H. B., Jarosz, D. F., Petrov, D. A.
2024
- **A general principle governing neuronal evolution reveals a human-accelerated neuron type potentially underlying the high prevalence of autism in humans.** *bioRxiv : the preprint server for biology*
Starr, A. L., Fraser, H. B.
2024
- **Cell-type-specific cis-regulatory divergence in gene expression and chromatin accessibility revealed by human-chimpanzee hybrid cells.** *eLife*
Wang, B., Starr, A. L., Fraser, H. B.
2024; 12
- **Chromatin activity identifies differential gene regulation across human ancestries.** *Genome biology*
Pettie, K. P., Mumbach, M., Lea, A. J., Ayroles, J., Chang, H. Y., Kasowski, M., Fraser, H. B.
2024; 25 (1): 21
- **Cell type-specific cis-regulatory divergence in gene expression and chromatin accessibility revealed by human-chimpanzee hybrid cells.** *bioRxiv : the preprint server for biology*
Wang, B., Starr, A. L., Fraser, H. B.
2023
- **Allele-specific expression reveals genetic drivers of tissue regeneration in mice.** *Cell stem cell*
Mack, K. L., Talbott, H. E., Griffin, M. F., Parker, J. B., Guardino, N. J., Spielman, A. F., Davitt, M. F., Mascharak, S., Downer, M., Morgan, A., Valencia, C., Akras, D., Berger, et al
2023
- **Gene-by-environment interactions are pervasive among natural genetic variants.** *Cell genomics*
Chen, S. A., Kern, A. F., Ang, R. M., Xie, Y., Fraser, H. B.
2023; 3 (4): 100273
- **Widespread epistasis among beneficial genetic variants revealed by high-throughput genome editing.** *Cell genomics*
Ang, R. M., Chen, S. A., Kern, A. F., Xie, Y., Fraser, H. B.
2023; 3 (4): 100260

- **Evolution of spatial and temporal cis-regulatory divergence in sticklebacks.** *Molecular biology and evolution*
Mack, K. L., Square, T. A., Zhao, B., Miller, C. T., Fraser, H. B.
2023
- **Accounting for cis-regulatory constraint prioritizes genes likely to affect species-specific traits.** *Genome biology*
Starr, A. L., Gokhman, D., Fraser, H. B.
2023; 24 (1): 11
- **Existing methods are effective at measuring natural selection on gene expression.** *Nature ecology & evolution*
Fraser, H. B.
2022
- **Bacterial Retrons Enable Precise Gene Editing in Human Cells**
Zhao, B.
CELL PRESS.2022: 102
- **Transcriptome diversity is a systematic source of variation in RNA-sequencing data.** *PLoS computational biology*
García-Nieto, P. E., Wang, B., Fraser, H. B.
2022; 18 (3): e1009939
- **Bacterial Retrons Enable Precise Gene Editing in Human Cells.** *The CRISPR journal*
Zhao, B., Chen, S. A., Lee, J., Fraser, H. B.
1800
- **cis-Regulatory changes in locomotor genes are associated with the evolution of burrowing behavior.** *Cell reports*
Hu, C. K., York, R. A., Metz, H. C., Bedford, N. L., Fraser, H. B., Hoekstra, H. E.
2022; 38 (7): 110360
- **Divergent patterns of selection on metabolite levels and gene expression.** *BMC ecology and evolution*
Kern, A. F., Yang, G. X., Khosla, N. M., Ang, R. M., Snyder, M. P., Fraser, H. B.
2021; 21 (1): 185
- **GRINS: Genetic elements that recode assembly-line polyketide synthases and accelerate their diversification.** *Proceedings of the National Academy of Sciences of the United States of America*
Nivina, A., Herrera Paredes, S., Fraser, H. B., Khosla, C.
2021; 118 (26)
- **The cis-regulatory effects of modern human-specific variants.** *eLife*
Weiss, C. V., Harshman, L., Inoue, F., Fraser, H. B., Petrov, D. A., Ahituv, N., Gokhman, D.
2021; 10
- **Lineage-specific selection and the evolution of virulence in the Candida clade.** *Proceedings of the National Academy of Sciences of the United States of America*
Singh-Babak, S. D., Babak, T. n., Fraser, H. B., Johnson, A. D.
2021; 118 (12)
- **Molecular mechanisms of coronary disease revealed using quantitative trait loci for TCF21 binding, chromatin accessibility, and chromosomal looping.** *Genome biology*
Zhao, Q. n., Dacre, M. n., Nguyen, T. n., Pjanic, M. n., Liu, B. n., Iyer, D. n., Cheng, P. n., Wirka, R. n., Kim, J. B., Fraser, H. B., Quertermous, T. n.
2020; 21 (1): 135
- **Fine-mapping cis-regulatory variants in diverse human populations** *ELIFE*
Tehranchi, A., Hie, B., Dacre, M., Kaplow, I., Pettie, K., Combs, P., Fraser, H. B.
2019; 8
- **Improving Estimates of Compensatory cis-trans Regulatory Divergence** *TRENDS IN GENETICS*
Fraser, H. B.
2019; 35 (1): 3-5
- **Tissue-Specific cis-Regulatory Divergence Implicates eloF in Inhibiting Interspecies Mating in Drosophila** *CURRENT BIOLOGY*

- Combs, P. A., Krupp, J. J., Khosla, N. M., Bua, D., Petrov, D. A., Levine, J. D., Fraser, H. B.
2018; 28 (24): 3969-+
- **Comparative expression profiling reveals widespread coordinated evolution of gene expression across eukaryotes.** *Nature communications*
Martin, T., Fraser, H. B.
2018; 9 (1): 4963
 - **Behavior-dependent cis regulation reveals genes and pathways associated with bower building in cichlid fishes** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*
York, R. A., Patil, C., Abdilleh, K., Johnson, Z. V., Conte, M. A., Genner, M. J., McGrath, P. T., Fraser, H. B., Fernald, R. D., Streebman, J.
2018; 115 (47): E11081-E11090
 - **Spatially varying cis-regulatory divergence in *Drosophila* embryos elucidates cis-regulatory logic.** *PLoS genetics*
Combs, P. A., Fraser, H. B.
2018; 14 (11): e1007631
 - **Improving Estimates of Compensatory cis-trans Regulatory Divergence.** *Trends in genetics : TIG*
Fraser, H. B.
2018
 - **High-resolution mapping of cis-regulatory variation in budding yeast** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*
Kita, R., Venkataram, S., Zhou, Y., Fraser, H. B.
2017; 114 (50): E10736–E10744
 - **Worldwide patterns of human epigenetic variation** *NATURE ECOLOGY & EVOLUTION*
Carja, O., Maclsaac, J. L., Mah, S. M., Henn, B. M., Kobor, M. S., Feldman, M. W., Fraser, H. B.
2017; 1 (10): 1577–83
 - **Cis-regulatory evolution in prokaryotes revealed by interspecific archaeal hybrids** *SCIENTIFIC REPORTS*
Artieri, C. G., Naor, A., Turgeman-Grott, I., Zhou, Y., York, R., Gophna, U., Fraser, H. B.
2017; 7: 3986
 - **Local Adaptation of Sun-Exposure-Dependent Gene Expression Regulation in Human Skin.** *PLoS genetics*
Kita, R., Fraser, H. B.
2016; 12 (10)
 - **Genetic variation in MHC proteins is associated with T cell receptor expression biases.** *Nature genetics*
Sharon, E., Sibener, L. V., Battle, A., Fraser, H. B., Garcia, K. C., Pritchard, J. K.
2016; 48 (9): 995-1002
 - **Disentangling Sources of Selection on Exonic Transcriptional Enhancers.** *Molecular biology and evolution*
Agogli, R. M., Fraser, H. B.
2016; 33 (2): 585-590
 - **A pooling-based approach to mapping genetic variants associated with DNA methylation** *GENOME RESEARCH*
Kaplou, I. M., Maclsaac, J. L., Mah, S. M., McEwen, L. M., Kobor, M. S., Fraser, H. B.
2015; 25 (6): 907-917
 - **Common variants spanning *PLK4* are associated with mitotic-origin aneuploidy in human embryos** *SCIENCE*
McCoy, R. C., Demko, Z., Ryan, A., Banjevic, M., Hill, M., Sigurjonsson, S., Rabinowitz, M., Fraser, H. B., Petrov, D. A.
2015; 348 (6231): 235-238
 - **Discordance of DNA Methylation Variance Between two Accessible Human Tissues.** *Scientific reports*
Jiang, R., Jones, M. J., Chen, E., Neumann, S. M., Fraser, H. B., Miller, G. E., Kobor, M. S.
2015; 5: 8257-?
 - **Accounting for biases in riboprofiling data indicates a major role for proline in stalling translation** *GENOME RESEARCH*
Artieri, C. G., Fraser, H. B.
2014; 24 (12): 2011-2021

- **Transcript Length Mediates Developmental Timing of Gene Expression Across *Drosophila*** *MOLECULAR BIOLOGY AND EVOLUTION*
Artieri, C. G., Fraser, H. B.
2014; 31 (11): 2879-2889
- **Evolution at two levels of gene expression in yeast.** *Genome research*
Artieri, C. G., Fraser, H. B.
2014; 24 (3): 411-421
- **A Novel Test for Selection on cis-Regulatory Elements Reveals Positive and Negative Selection Acting on Mammalian Transcriptional Enhancers.** *Molecular biology and evolution*
Smith, J. D., McManus, K. F., Fraser, H. B.
2013; 30 (11): 2509-2518
- **Ancient cis-regulatory constraints and the evolution of genome architecture** *TRENDS IN GENETICS*
Irimia, M., Maeso, I., Roy, S. W., Fraser, H. B.
2013; 29 (9): 521-528
- **The molecular mechanism of a cis-regulatory adaptation in yeast.** *PLoS genetics*
Chang, J., Zhou, Y., Hu, X., Lam, L., Henry, C., Green, E. M., Kita, R., Kobor, M. S., Fraser, H. B.
2013; 9 (9)
- **Cell-cycle regulated transcription associates with DNA replication timing in yeast and human** *GENOME BIOLOGY*
Fraser, H. B.
2013; 14 (10)
- **Differences in enhancer activity in mouse and zebrafish reporter assays are often associated with changes in gene expression** *BMC GENOMICS*
Ariza-Cosano, A., Visel, A., Pennacchio, L. A., Fraser, H. B., Luis Gomez-Skarmeta, J., Irimia, M., Bessa, J.
2012; 13
- **Extensive conservation of ancient microsynteny across metazoans due to cis-regulatory constraints** *GENOME RESEARCH*
Irimia, M., Tena, J. J., Alexis, M. S., Fernandez-Minan, A., Maeso, I., Bogdanovic, O., de la Calle-Mustienes, E., Roy, S. W., Gomez-Skarmeta, J. L., Fraser, H. B.
2012; 22 (12): 2356-2367
- **Factors underlying variable DNA methylation in a human community cohort** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*
Lam, L. L., Emberly, E., Fraser, H. B., Neumann, S. M., Chen, E., Miller, G. E., Kobor, M. S.
2012; 109: 17253-17260
- **Polygenic cis-regulatory adaptaion in the evolution of yeast pathogenicity** *GENOME RESEARCH*
Fraser, H. B., Levy, S., Chavan, A., Shah, H. B., Perez, J. C., Zhou, Y., Siegal, M. L., Sinha, H.
2012; 22 (10): 1930-1939
- **Population-specificity of human DNA methylation** *GENOME BIOLOGY*
Fraser, H. B., Lam, L. L., Neumann, S. M., Kobor, M. S.
2012; 13 (2)
- **Genome-wide approaches to the study of adaptive gene expression evolution Systematic studies of evolutionary adaptations involving gene expression will allow many fundamental questions in evolutionary biology to be addressed** *BIOESSAYS*
Fraser, H. B.
2011; 33 (6): 469-477
- **Systematic Detection of Polygenic cis-Regulatory Evolution** *PLOS GENETICS*
Fraser, H. B., Babak, T., Tsang, J., Zhou, Y., Zhang, B., Mehrabian, M., Schadt, E. E.
2011; 7 (3)
- **Genetic validation of whole-transcriptome sequencing for mapping expression affected by cis-regulatory variation** *BMC GENOMICS*
Babak, T., Garrett-Engle, P., Armour, C. D., Raymond, C. K., Keller, M. P., Chen, R., Rohl, C. A., Johnson, J. M., Attie, A. D., Fraser, H. B., Schadt, E. E.

2010; 11

- **Evidence for widespread adaptive evolution of gene expression in budding yeast** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*
Fraser, H. B., Moses, A. M., Schadt, E. E.
2010; 107 (7): 2977-2982
- **The Quantitative Genetics of Phenotypic Robustness** *PLOS ONE*
Fraser, H. B., Schadt, E. E.
2010; 5 (1)
- **Common polymorphic transcript variation in human disease** *GENOME RESEARCH*
Fraser, H. B., Xie, X.
2009; 19 (4): 567-575
- **Ab initio construction of a eukaryotic transcriptome by massively parallel mRNA sequencing** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*
Yassour, M., Kapan, T., Fraser, H. B., Levin, J. Z., Pfiffner, J., Adiconis, X., Schroth, G., Luo, S., Khrebtukova, I., Gnirke, A., Nusbaum, C., Thompson, D., Friedman, et al
2009; 106 (9): 3264-3269
- **Confirmation of organized modularity in the yeast interactome** *PLOS BIOLOGY*
Bertin, N., Simonis, N., Dupuy, D., Cusick, M. E., Han, J. J., Fraser, H. B., Roth, F. P., Vidal, M.
2007; 5 (6): 1206-1210
- **Assessing the determinants of evolutionary rates in the presence of noise** *MOLECULAR BIOLOGY AND EVOLUTION*
Plotkin, J. B., Fraser, H. B.
2007; 24 (5): 1113-1121
- **Using protein complexes to predict phenotypic effects of gene mutation** *GENOME BIOLOGY*
Fraser, H. B., Plotkin, J. B.
2007; 8 (11)
- **Coevolution, modularity and human disease** *CURRENT OPINION IN GENETICS & DEVELOPMENT*
Fraser, H. B.
2006; 16 (6): 637-644
- **Codon usage and selection on proteins** *JOURNAL OF MOLECULAR EVOLUTION*
Plotkin, J. B., Dushoff, J., Desai, M. M., Fraser, H. B.
2006; 63 (5): 635-653
- **Estimating selection pressures from limited comparative data** *MOLECULAR BIOLOGY AND EVOLUTION*
Plotkin, J. B., Dushoff, J., Desai, M. M., Fraser, H. B.
2006; 23 (8): 1457-1459
- **Aging and gene expression in the primate brain** *PLOS BIOLOGY*
Fraser, H. B., Khaitovich, P., Plotkin, J. B., Paabo, S., Eisen, M. B.
2005; 3 (9): 1653-1661
- **Sum1p, the origin recognition complex, and the spreading of a promoter-specific repressor in *Saccharomyces cerevisiae*** *MOLECULAR AND CELLULAR BIOLOGY*
Lynch, P. J., Fraser, H. B., Sevastopoulos, E., Rine, J., Rusche, L. N.
2005; 25 (14): 5920-5932
- **Functional genomic analysis of the rates of protein evolution** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*
Wall, D. P., Hirsh, A. E., Fraser, H. B., Kumm, J., Giaever, G., Eisen, M. B., Feldman, M. W.
2005; 102 (15): 5483-5488
- **Modularity and evolutionary constraint on proteins** *NATURE GENETICS*
Fraser, H. B.

2005; 37 (4): 351-352

- **Adjusting for selection on synonymous sites in estimates of evolutionary distance** *MOLECULAR BIOLOGY AND EVOLUTION*
Hirsh, A. E., Fraser, H. B., Wall, D. P.
2005; 22 (1): 174-177
- **Conservation and evolution of cis-regulatory systems in ascomycete fungi** *PLOS BIOLOGY*
Gasch, A. P., Moses, A. M., Chiang, D. Y., Fraser, H. B., Berardini, M., Eisen, M. B.
2004; 2 (12): 2202-2219
- **Coevolution of gene expression among interacting proteins** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*
Fraser, H. B., Hirsh, A. E., Wall, D. P., Eisen, M. B.
2004; 101 (24): 9033-9038
- **Noise minimization in eukaryotic gene expression** *PLOS BIOLOGY*
Fraser, H. B., Hirsh, A. E., Giaever, G., Kumm, J., Eisen, M. B.
2004; 2 (6): 834-838
- **Evolutionary rate depends on number of protein-protein interactions independently of gene expression level** *BMC EVOLUTIONARY BIOLOGY*
Fraser, H. B., Hirsh, A. E.
2004; 4
- **Detecting selection using a single genome sequence of M-tuberculosis and P-falciparum** *NATURE*
Plotkin, J. B., Dushoff, J., Fraser, H. B.
2004; 428 (6986): 942-945
- **Detecting putative orthologs** *BIOINFORMATICS*
Wall, D. P., Fraser, H. B., Hirsh, A. E.
2003; 19 (13): 1710-1711
- **A simple dependence between protein evolution rate and the number of protein-protein interactions** *BMC EVOLUTIONARY BIOLOGY*
Fraser, H. B., Wall, D. P., Hirsh, A. E.
2003; 3
- **Evolutionary rate in the protein interaction network** *SCIENCE*
Fraser, H. B., Hirsh, A. E., Steinmetz, L. M., Scharfe, C., Feldman, M. W.
2002; 296 (5568): 750-752
- **Explaining mortality rate plateaus** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*
Weitz, J. S., Fraser, H. B.
2001; 98 (26): 15383-15386
- **Protein dispensability and rate of evolution** *NATURE*
Hirsh, A. E., Fraser, H. B.
2001; 411 (6841): 1046-1049