

Julien F. Ayroles, Ph.D.

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Research Scope: My group studies the biological basis for individual variation. We seek to understand how genes interact with each other and their environment to shape variation between individuals. To that end we develop cutting-edge experimental and analytical approaches aimed at improving our understanding of the biological forces that drive variation in complex traits and their evolution.

APPOINTMENTS

2016-present	Assistant professor Princeton University, Princeton, NJ Department of Ecology and Evolutionary Biology and Lewis-Sigler Institute for Integrative Genomics
2011-2015	Harvard Junior Fellow Cambridge, MA Harvard Society of Fellows, Harvard University
2003-2005	Research and Field Assistant Champaign, IL (Under Dr. Ken Paige) University of Illinois, Department of Zoology

EDUCATION

2011	Ph.D. in Genetics North Carolina State University, Raleigh, Department of Genetics Title: <i>A Systems Genetics Approach to the Dissection of Complex Traits in Drosophila melanogaster</i> .
2005	Master of Sciences in Natural Resources and Environmental Sciences University of Illinois, Urbana-Champaign, Department of Animal Behavior
2002	Maîtrise (equivalent B.S.) in Organismal and Population Biology with honors Paul Sabatier Université, Toulouse, France (Exchange program TASSEP)
2001	General degree in Biological Sciences (DEUG) with honors Paul Sabatier Université, Toulouse, France

PUBLICATIONS

Submitted	59	2023	Sadowski M, Thompson M, Mefford J, Haldar T, Oni-Orisan A, Pharm.D., Richard Border R, Pazokitoroudi A, Ayroles JF , Sankararaman S., Dahl A, (2023). Genetics modulates the impact of widely-used drugs on outcomes and side effects (under review at New England Journal of Medicine).
Preprints	58	2023	Forsberg* S.K.G, Melo* D, Wolf S, Grenier JK, Tang M, Henry LP, Pallares LF, Clark AG, and Ayroles JF . (2023). Longitudinal sequencing reveals polygenic and epistatic nature of genomic response to selection.
	57	2023	Lea AJ, Caldas IV, Garske K, J Echwa, M Gurven, C Handley, J Kamau, M Kiboi, P Kinyua, F Lotukoi, A Lopurudo, S Lowasa, R Mallarino, D Martins, P Messer, CMiano, B Muhoya, J Peng, T Phung, R Siford, A Stone, A Taravella Oill, SMathew, M Wilson, JF Ayroles (2022) Adaptations to heat and pastoralism in the Turkana of northwest Kenya. <i>bioRxiv</i> (Under revision at <i>Science</i>)
	56	2023	Melo, D., Pallares, L. F., & Ayroles, J. F. (2023). Reassessing the modularity of gene co-expression networks using the Stochastic Block Model. <i>bioRxiv</i> , 2023-05. (Under review at <i>Plos Computational Biology</i>)
	55	2023	Pallares LF, Melo D, Wolf S, Cofer EM, Abhyankar V, Peng J Ayroles JFA. (2023) Saturating the eQTL map in <i>Drosophila melanogaster</i>: genome-wide patterns of cis and trans

regulation of transcriptional variation in outbred populations *bioRxiv* (under review at *Genome Research*)

- 54 2023 Wolf, S., Abhyankar, V., Melo, D., Ayroles, J. F., & Pallares, L. F. (2023). **From GWAS to signal validation: An approach for estimating genetic effects while preserving genomic context.** *bioRxiv*. (under revision [PeerJ](#))
- 53 2023 Pettie, KP, Mumbach, M, Lea, AJ, **Ayroles, JF**, Chang, HY, Kasowski, M, & Fraser, HB. (2023). **Chromatin activity identifies differential gene regulation across human ancestries.** *Genome Biology*, *in press*.
- 52 2022 Henry, L. P., Fernandez, M., Wolf, S., & **Ayroles, JF**. (2022). **Wolbachia interacts with the microbiome to shape fitness-associated traits during seasonal adaptation in *Drosophila melanogaster*.** *bioRxiv* (under revision at [mBio](#))
- 51 2022 Henry L, Fernandez M, **Ayroles JF**. (2022) **The environment modulates the effects of the microbiome on host adaptive potential.** *bioRxiv* doi.org/10.1101/2020.09.21.306779 (under revision [ISME](#))
- 50 2022 Akhund-Zade J, Yoon D, Bangerter A, Polizos N, Campbell M, Soloshenko A, Zhang T, Wice E, Albright A, Narayanan A, Schmidt P, Saltz J, **Ayroles JF**, Klein M, Bergland B, de Bivort B. (2022) **Wild flies hedge their thermal preference bets in response to seasonal fluctuations.** *bioRxiv*. (under revision [Evolution](#))
- Published
- 49 2023 Bruijning M, **Ayroles JF.**, Henry LP, Koskella B., Meyer KM, Metcalf JM. (2023). **Relative abundance data can misrepresent heritability of the microbiome.** *BMC microbiology*, 11(1), 222.
- 48 2023 Lea A, Clark A, Dahl A, Devinsky O, Garcia A, Golden C, Kamau J, Kraft T, Martins D, Mogoi D, Pajukanta P, Perry G, Pontzer H, Trumble B, Urlacher S, Venkataraman V, Wallace I, Gurven M, Lieberman D, **Ayroles, JF**. (2022). **Applying an evolutionary mismatch framework to understand disease susceptibility.** *Plos Biology*, 21(9), e3002311.
- 47 2023 Wolf, S*, Melo, D*, Garske, KM, Pallares, LF, & **Ayroles, JF**. (2023). **Characterizing the landscape of gene expression variance in humans.** *Plos Genetics*, 19(7), e1010833.
- 46 2022 Golden, C. D.*, **Ayroles, JF.***, Eurich, J. G., Gephart, J. A., Seto, K. L., Sharp, M. K., ... & Timeon, E. (2022) **Study Protocol: Interactive dynamics between coral reef fisheries and the nutrition transition in Kiribati.** *Frontiers in Public Health*, 1639. (*equal contribution)
- 45 2022 Golden, C. D.*, **Ayroles, JF.***, Eurich, J. G., Gephart, J. A., Seto, K. L., Sharp, M. K., ... & Timeon, E. (2022) **Study Protocol: Interactive dynamics between coral reef fisheries and the nutrition transition in Kiribati.** *Frontiers in Public Health*, 1639. (*equal contribution)
- 44 2022 Lea, AJ, Peng, J, & **Ayroles, JF**. (2022). **Diverse environmental perturbations reveal the evolution and context-dependency of genetic effects on gene expression levels.** *Genome Research*, 32(10), 1826-1839.
- 43 2022 Henry, LP, & **Ayroles, JF**. (2022). ***Drosophila melanogaster* microbiome is shaped by strict filtering and neutrality along a latitudinal cline.** *Molecular ecology*, 31(22), 5861-5871.
- 42 2022 Lea AJ, Garcia A, Arevalo J, **Ayroles JF**, Buetow K, Cole SW, Rodriguez DE, Gutierrez M, Highland HM, Hooper P, Justice A, Kraft T, North KE, Stieglitz J, Kaplan H, Trumble BC, Gurven MD. (2022) **Natural selection of immune and metabolic genes associated with health in two lowland Bolivian populations.** *PNAS* 120 (1) e2207544120.

- 41 2022 Pallares LF, Lea AJ, Han C, Filippova EV, Andolfatto P, **Ayroles JF**. (2022) **Diet unmasks genetic variants that regulate lifespan in outbred Drosophila**. *Nature Genetics* 55, 123–129.
- 40 2022 de Bivort, B, Buchanan, S, Skutt-Kakaria, K, Gajda, E, **Ayroles, JF**, O’Leary, C, & Smith, M. A. Y. (2022). **Precise quantification of behavioral individuality from 80 million decisions across 183,000 flies**. *Frontiers in Behavioral Neuroscience*, 16.
- 39 2021 Bruijning M, Henry LP, Forsberg SK, Metcalf CJ, **Ayroles JF**. (2021) **When the microbiome defines the host phenotype: selection on vertical transmission in varying environments**. *Nature ecology & evolution*, 1-11.
- 38 2021 Henry LP, and **Ayroles JF**, 2021. **Meta-analysis suggests the microbiome responds to Evolve and Resequencing experiments in Drosophila melanogaster**. *BMC microbiology*, 21(1):1-14.
- 37 2021 Choi JY, Dai X, Peng JZ, Rughani P, Hickey S, Harrington E, Juul S, **Ayroles JF**, Purugganan M, Stacy E. (2020) **Selection on ancient variations drives the adaptive radiation of *Metrosideros* across the Hawaiian archipelago**. *Proceedings of the National Academy of Sciences* 118(37)
- 36 2021 Lea, A.J., Waigwa, C., Muhoya, B., Lotukoi, F., Peng, J., Henry, L., Abhyankar, V., Kamau, J., Martins, D., Gurven, M. and **Ayroles, J.F.** (2021). **Socioeconomic status effects on health vary between rural and urban Turkana**. *Evolution, medicine, and public health* 9 (1), 406-419.
- 35 2021 Werkhoven Z, Bravin A, Skutt-Kakaria K, Reimers P, Pallares LF, **Ayroles JF**, De Bivort BL*. (2020) **The structure of behavioral variation within a genotype**. *eLife* 10, p.e64988.
- 34 2021 Akhund-Zade, J., Lall, S., Gajda, E., Yoon, D., **Ayroles, J.F.**, & de Bivort, B. L. (2021). **Genetic basis of offspring number-body weight tradeoff in Drosophila melanogaster**. *G3 Genesl Genomesl Genetics*.
- 33 2020 Rau CD, Gonzales NM, Bloom JS, Park D, **Ayroles J.F.**, Palmer AA, Lusia AJ, Zaitlen N. (2020) **Modeling Epistasis in Mice and Yeast Using the Proportion of Two or More Distinct Genetic Backgrounds: Evidence for Polygenic Epistasis**. *Plos Genetics* 16(10), e1009165.
- 32 2020 Lea AJ., Martins D., Kamau, J., Gurven, M., **Ayroles, J.F.** (2020). **Urbanization and market integration have strong, nonlinear effects on cardiometabolic health in the Turkana**. *Science advances*, 6(43), eabb1430
- 31 2020 Bruijning, M., Metcalf, C. J. E., Jongejans, E., & **Ayroles, J. F.** (2020). **The evolution of variance control**. *Trends in ecology & evolution*, 35(1), 22-33.
- 30 2020 Pallares LF, Picard S, **Ayroles J.F.** (2020) **TM3’seq: a tagmentation-mediated 3’sequencing approach for improving scalability of RNAseq experiments**. *G3: Genes, Genomes, Genetics* 10(1), 143-150
- 28 2020 Henry LP., Bruijning M., Forsberg KGS., **Ayroles JF**. (2020). **The microbiome extends host evolutionary potential** *Nature Communications* 12(1), 1-13.
- 27 2019 Lea AJ, Subramaniam M, A Ko, T Lehtimäki, E Raitoharju, MikaKähönen, I Seppälä, N Mononen, O Raitakari, M Ala-Korpela, P Pajukanta, N Zaitlen, **Ayroles JF**. (2019). **Genetic and environmental perturbations lead to regulatory decoherence**. *eLife* 8, e40538
- 26 2019 Musharoff S, Park DS, A Dahl, JM Galanter, X Liu, S Huntsman, C Eng, Burchard EG, **Ayroles JF ***, Zaitlen N* (2019) **Existence and implications of population variance structure**. bioRxiv, 439661 (in revision to *AJHG*). (*equal contribution)

- 25 2018 Schrider DR, **Ayroles JF**, Matute DR, AD Kern AD. (2018). **Supervised machine learning reveals introgressed loci in the genomes of *Drosophila simulans* and *D. sechellia***. *PLoS genetics* 14 (4), e1007341
- 24 2018 Dumitrascu B, Darnell G, **Ayroles JF**, Engelhardt BE. (2018). **Statistical tests for detecting variance effects in quantitative trait studies**. *Bioinformatics* 35(2): 200-210.
- 23 2015 Zwarts L, Broeck LV, Cappuyns E, **Ayroles JF**, Magwire MM, Vulsteke V, Clements J, Mackay TF, Callaerts P. (2015) **The genetic basis of natural variation in mushroom body size in *Drosophila melanogaster***. *Nature communications* 11(6).
- 22 2015 **Ayroles JF**, Buchanan SM, O'Leary C, Skutt-Kakaria K, Grenier JK, Clark AG, Hartl DL, de Bivort BL. (2015). **Behavioral idiosyncrasy reveals genetic control of phenotypic variability**. *Proceedings of the National Academy of Sciences* 112(21): 6706-11
- 21 2014 Matute DR*, **Ayroles JF***. (2014) **Hybridization occurs between *Drosophila simulans* and *D. sechellia* in the Seychelles archipelago**. *Journal of evolutionary biology*. 27(6):1057-68
- 20 2013 Corbett-Detig RB, Zhou J, Clark AG, Hartl DL, **Ayroles JF** . (2013). **Genetic Incompatibilities Within Species are Widespread**. *Nature* 504, 135–137. *Faculty of 1000, Biology*
- 19 2012 Huang W, Richards S, Carbone MA, Zhu D, Anholt RRH, **Ayroles JF**, et al. (2012) **Epistasis Dominates The Genetic Architecture Of *Drosophila* Quantitative Traits**. *Proceedings of the National Academy of Sciences* 109:15553-15559
- 18 2012 Massouras A, Waszak SM, Albarca M, Hens K, Holcombe K, **Ayroles JF**, Dermitzakis ET, Eric A Stone EA, Jensen J D, Mackay T.F.C, Deplancke B. (2012) **Genomic Variation And Its Impact On Gene Expression In *Drosophila Melanogaster***. *Plos Genetics* 8 (11): e1003055
- 17 2012 Mackay TFC*, Richards S*, Barbadilla A *, Stone EA*, **Ayroles JF***, Zhu D, Sònia Casillas. et. al. (2012) **The *Drosophila* Genetics Reference Panel:A Community Resource for Analysis of Population Genomics and Quantitative Traits**. *Nature* 482(7384):173-8. *Faculty of 1000, Biology*
- 16 2011 Ober U, **Ayroles JF**, Stone EA, Richards S, Zhu D, Gibbs RA, Stricker C, Gianola D, Schlather M, Mackay TFC, Simianer H. (2011) **Using Whole Genome Sequence Data to Predict Quantitative Trait Phenotypes in *Drosophila melanogaster***. *PLoS Genetics* 8(5): e1002685. *Faculty of 1000, Biology*
- 15 2011 Rowe K, Singhal S, MacManes M, **Ayroles JF**, Morelli TL, Rubidge E, Bi K, Moritz C (2012). **Museum Genomics: Low Cost And High Accuracy Genetic Data From Historical Specimens**. *Molecular Ecology Ressources* 11(6): 1082–1092
- 14 2011 **Ayroles JF**, Laflamme B, Wolfner MA, Mackay TFC. (2011) **Sifting Through The Data: Identifying Top Candidates For Novel seminal Protein Genes From *Drosophila* Whole Genome Expression Data**. *Genetics Research* 93(6): 387-395
- 13 2010 Jumbo-Lucioni P*, **Ayroles JF***, Chambers MM, Jordan KW, Leips J, Mackay TF, De Luca M. (2010) **Systems Genetics Analysis Of Body Weight And Energy Metabolism Traits In *Drosophila Melanogaster***. *BMC Genomics* 11(11): 297. (* Contributed equally)
- 12 2009 Edwards, A, **Ayroles JF**, Stone EA, Mackay TFC. (2009) **A Transcriptional Network Associated With Natural Variation In *Drosophila* Aggressive Behavior**. *Genome Biology* 10(7): R76.
- 11 2009 Mackay TFC, Stone EA, **Ayroles JF**. (2009) **Quantitative Genetics: Prospects And Challenges**. *Nature Review Genetics* 10(8): 565-577

- 10 2009 Morozova TV*, Ayroles JF*, Jordan KW, Duncan LH, Carbone MA, Lyman RF, Stone EA, Govindaraju DR, Ellison RC, Mackay TF, Anholt RR. (2009) Alcohol Sensitivity In *Drosophila*: Translational Potential Of Systems Genetics. *Genetics* 183(2): 733-745 (* Contributed equally)
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- 8 2009 Ayroles JF, Carbone MA, Stone EA, Jordan KW, Lyman RF, Magwire MM, Rollman SM, Duncan LH, Lawrence F, Anholt RH, Mackay TFC. (2009) **Systems genetics of complex traits in *Drosophila melanogaster*.** *Nature Genetics* 41(3): 299-307. [Faculty of 1000, Biology](#)
- 7 2009 Kocher SD, Ayroles JF, Stone EA, Grozinger CM. (2009) **Genomics Of Pheromone Response: Cooperation And Conflict In Honey Bees.** *Plos ONE* 5(2): e9116
- 6 2009 Stone EA, Ayroles JF. (2009) **Modulated Modularity Clustering As An Exploratory Tool For Functional Genomic Inference.** *PLoS Genetics* 5(5): e1000479
- 5 2009 Ayroles JF, Hughes KA, Reedy MM, Rodriguez-Zas SL, Drnevich JM, Rowe KC, Cáceres CE, Paige KN. (2009) **Genome-Wide Assessment Of Inbreeding Depression In *Drosophila Melanogaster*.***Conservation Biology* 23(4): 920-930
- 4 2009 Carbone MA, Ayroles JF, Yamamoto A, Morozova TV, West SA, Magwire MM, Mackay TF, Anholt RR. (2009) **Overexpression Of Myocilin In The *Drosophila* Eye Activates The Unfolded Protein Response: Implications For Glaucoma.** *PLoS ONE* 4(1): e4216
- 3 2006 Ayroles JF, Gibson G. (2006) **Analysis Of Variance Of Microarray Data.** *Methods Enzymol* 411: -33
- 2 2006 Ayroles JF, Hughes KA, Reedy MM, Drnevich JM, Rowe KC, Ruedi EA, Cáceres CE, Paige KN. (2006) **Segregating Variation In The Transcriptome: Cis Regulation And Additivity Of Effects.** *Genetics* 173(3): 1347-1355.
- 1 2005 Dejean A, Solano PJ, Ayroles JF, Corbara B, Orivel J. (2005) **Insect Behaviour: Arboreal Ants Build Traps to Capture Prey.** *Nature* (434):973

BOOK CHAPTER

- 2020 Metcalf CJE*, Ayroles JF*. (2020). Chapter: **"Why does intra-genotypic variance persist?"** In book titled "Unsolved Problems in Ecology". Princeton University Press. (*equal contribution)

GRANTS

- 2022-2027 **NIH- NIGMS R35** - A path to personalized phenotypic prediction: unlocking the context-dependency of allelic effects.
- 2022-2024 **Catalysis initiative** - A new paradigm to dissect the genetic basis of addictive behavior.
- 2022-2024 **HMEI Grand Water Challenge** - Characterizing the health, cultural and ecological impact of borehole water dependence in Pastoralist communities.
- 2021-2023 **PCI** - Surviving at the extreme: Studying human adaptation to extreme environments to identify novel avenues for therapeutics targets and treatments
- 2018 - 2023 **NIH NIEHS - R01**- Improved methods for inference of genotype-specific response to environmental toxins
- 2020-2023 **Chan Zuckerberg Initiative DAF** - How does a western lifestyle modify immune response the Turkana people.

2017-2022	NIH- NIGMS R35 - A path to personalized phenotypic prediction: unlocking the context-dependency of allelic effects.
2019 - 2021	Mpala Funds - Evolutionary functional genomics of the Turkana: signatures of past selection and responses to modern urbanization.
2019	San Diego Zoo Exploration funds
2017	New Ideas in the Natural Sciences, Princeton University
2015	Banff International Research Station
2015	Foundation les Treilles
2014	3CPG – Cornell University
2014	Broad Institute SPARC
2012	Milton Research Award

TEACHING

2020 - 2022	EEB309 "Introduction to Evolutionary Biology"
2020 - 2023	EEB521 "Tropical Ecology" (graduate Students)
2020 - 2022	EEB388 "Genomics in the wild"
2019	EEB380 "Ecology & Conservation of Africa"
2017	EEB409 "The evolution of adaptive systems"
2016 - 2021	ISC326 "Past, present and future of the human genome"

SELECTED INVITED PRESENTATIONS

2023	<u>University of British Columbia</u> : From individual variation to the genetic basis of environmental sensitivity
2023	<u>NHGRI workshop</u> : Advances in the Genetic Architecture of Complex Human Traits
2023	<u>Princeton University</u> : Leveraging Evolutionary Mismatches to Study G-by-E Interactions
2023	<u>Stanford University</u> : Leveraging Evolutionary Mismatches to Study G-by-E Interactions
2023	<u>Brown University</u> : Applying an evolutionary mismatch framework to understand genotype-by-environment interactions.
2023	<u>North Carolina State University</u> : The genetics of disruption: studying the genetic basis of environmental sensitivity.
2023	<u>University of Pennsylvania</u> : Leveraging Evolutionary Mismatches to Study G-by-E Interactions
2022	<u>Population, Evolutionary and Quantitative Genetics Meeting</u> : Dietary stress unmasks cryptic genetic variation regulating lifespan in outbred <i>Drosophila</i> .
2022	<u>Biology of Genomes CSHL</u> : Studying adaptation to desert living and pastoralism in the Turkana.
2022	<u>UCLA</u> (Bioinformatics seminar): Leveraging Evolutionary Mismatches to Study G-by-E Interactions.
2020	<u>Harvard/MIT Evolutionary Genomics seminar series</u> : Leveraging Evolutionary Mismatches to Study Genotype by Environment Interactions
2020	<u>Cornell</u> : Leveraging Evolutionary Mismatches to Study Genotype by Environment Interactions
2019	<u>EEFG Gordon Conference</u> : A Novel, Massively Parallel Mapping Framework to Unlock Genotype-Dependent Environmental Response
2019	<u>Vienna Veterinärmedizinische Universität</u> : The genetics of disruption: studying the genetic basis of environmental sensitivity.

2018	<u>Duke University</u> : From individual variation to the genetic basis of environmental sensitivity
2018	<u>UT Austin</u> : From individual variation to the genetic basis of environmental sensitivity
2018	<u>Uppsala University</u> : The complex Genetics of Complex Traits
2017	<u>Penn State</u> : Heritability and Prediction in Human Genetics
2017	<u>Workshop</u> : Latin-American School on Evolution (Sao Paolo)
2017	<u>UCLA (Human Genetics)</u> : The genetics of disruption: studying the genetic basis for phenotypic covariance
2017	<u>Foundation les Treilles (organizer)</u>
2016	<u>Banff International Research Station</u>
2016	<u>American Society for Human Genetics</u>
2016	<u>Broad Institute</u> : Behavioral individuality reveals genetic control of phenotypic variability

POSTDOCTORAL RESEARCHERS MENTORED

2021 – Present	Dr Kristina Garke	<u>Mentee Awards</u> : NIH NRSA fellowship (F32)
2020 - Present	Dr Diogo Melo	<u>Mentee Awards</u> : Princeton Presidential Fellow
2018 - 2022	Dr Amanda Lea	<u>Current</u> : Assistant Professor (Research), Vanderbilt University. <u>Mentee Awards</u> : Helen Hay Whitney, NSF postdoctoral Fellowship
2018 - 2021	Dr Marjolein Bruijning	<u>Current</u> : Assistant Professor (Research), Amsterdam University. <u>Mentee Awards</u> : Dutch NWO Rubicon fellowship
2017 - 2021	Dr Luisa Pallares	<u>Current</u> : Group Leader at the Max Plank Institute, tübingen. <u>Mentee Awards</u> : The International Human Frontier Science Foundation Program
2016 - 2020	Dr Simon Frosberg	<u>Current</u> : Senior Data Scientist at Olink Proteomics. <u>Mentee Awards</u> : EMBO Fellowship and Swedish Research Council (VR)

GRADUATE STUDENTS MENTORED

2023 – Present	Emma Gerlinger	QCB
2021 – Present	Benjamin Muhoya	EEB
2021 – Present	Emmanuel D’Agustino	EEB - <u>Mentee Awards</u> : NSF-GRSP
2017 – Present	Scott Wolf	QCB - <u>Mentee Awards</u> : NSF-GRSP
2016 – 2022	Lukas Henry	EEB - <u>Mentee Awards</u> : NSF-GRSP <u>Current</u> : Postdoctoral fellow at NYU