

# The geometry of admixture in population genetics: the blessing of dimensionality

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## Abstract

We present a geometry-based interpretation of the  $f$ -statistics framework, commonly used to determine phylogenetic relationships from genetic data. The focus is on the determination of the mixing coefficients in population admixture events subject to post-admixture drift. The interpretation takes advantage of the high dimension of the dataset and analyzes the problem as a dimensional reduction issue. We show that it is possible to think of the  $f$ -statistics technique as an implicit transformation of the genetic data from a phase space into a subspace where the mapped data structure is more similar to the ancestral admixture configuration. The positive effect of the map can be explicitly assessed. The overarching geometric framework provides slightly more general formulas than the  $f$ -formalism by using a different rationale as a starting point. Explicitly addressed are two- and three-way admixtures. The mixture proportions are provided by suitable linear fits in two or three dimensions that can be easily visualized. The developments and findings are illustrated with numerical simulations from real world datasets.

**Keywords:** population admixture;  $f$ -statistics; genetic drift; dimensional reduction

## Introduction

The determination of admixture proportions in hybrid populations is a central topic in population genetics. At large evolutionary time scales, a population admixture event can be thought of as a sudden process in which a new lineage emerges as the genetic weighted combination of two or more donors, in its simplest formulation.

The formalism known as  $f$ -statistics Patterson *et al.* (2012); Haak *et al.* (2015); Lazaridis *et al.* (2016); Peter (2016); Lipson (2020); Eadaoin Harney *et al.* (2021); Peter (2022), which deals with allele-sharing correlations between two, three and four populations, is a commonly used technique to determine the admixture coefficients. Despite their simple computation and definition, the  $f$ -statistics outcome assessment may not be straightforward Lipson (2020). We develop a geometry-based interpretation of  $f$ -statistics intended to deepen understanding of the population admixture problem. Geometric-like methods have already been raised in the past Cavalli-Sforza (1966); Cavalli-Sforza and Piazza (1975); Cavalli-Sforza *et al.* (1994); Long (1991); Oteo-García (PhD thesis, 2020); Agranat-Tamir *et al.* (2021). The strength of our approach is to take advantage of the high dimensionality of the problem, broadening the  $f$ -formalism toolkit.

Whenever the genetic information from the original populations is available, determining the admixture proportions is straightforward. However, the evolutionary history of the original populations manifests itself, for example, in random changes in allele frequencies, a phenomenon known as genetic drift. Although ancient DNA can sometimes aid in estimating admixture proportions by providing better proxies, the time elapsed since

admixture and the possibility that the putative parents themselves are extinct make accurate estimates difficult. Moreover, a population may experience over time continuous, discrete, occasional, or repeated genetic influx from other or multiple others, which makes the issue more challenging. The present study is concerned with the approximation of admixture proportions in populations that are assumed to have evolved in time via genetic drift. A dataset with population allele frequencies corresponding to a large number of Single Nucleotide Polymorphisms (SNPs) is the common starting point for dealing with this question.

The population admixture problem may be posed as a geometric issue in a phase space, the allele frequency space, where each population is represented by a point and each axis corresponds to a SNP in the dataset Oteo-García and Oteo (2021). With only three SNP, Figure 1 outlines the nature of the problem. Populations  $i$ ,  $a'$ ,  $b'$ ,  $x$ ,  $b$ ,  $j$ , are assumed to be related by phylogenetic tree and are located in phase space by their position vectors whose coordinates are given by the allele frequencies in the dataset. At the time of admixture, we have three co-linear points,  $a'$ ,  $x$ ,  $b'$ , with  $a'$  and  $b'$  the donors and  $x$  the hybrid. Then, they describe Brownian-like trajectories because allele frequencies undergo small random changes as a result of genetic drift, resulting in population proxies  $a$ ,  $x$ ,  $b$ .

Populations  $i$  and  $j$ , which appear as spectators in the Figure 1, will be referred to as auxiliary populations and will play an important role. Any population related to the admixture contributors via phylogenetic tree and may be considered as auxiliary. The Brownian-like trajectory depicted from  $b$  to  $j$  is

# The Geometry Of Population Genetics

**Anthony William Fairbank Edwards**



## **The Geometry Of Population Genetics:**

The Geometry of Population Genetics Ethan Akin, 1979-11-01      *Information Geometry and Population Genetics* Julian Hofrichter, Jürgen Jost, Tat Dat Tran, 2017-02-23 The present monograph develops a versatile and profound mathematical perspective of the Wright Fisher model of population genetics This well known and intensively studied model carries a rich and beautiful mathematical structure which is uncovered here in a systematic manner In addition to approaches by means of analysis combinatorics and PDE a geometric perspective is brought in through Amari's and Chentsov's information geometry This concept allows us to calculate many quantities of interest systematically likewise the employed global perspective elucidates the stratification of the model in an unprecedented manner Furthermore the links to statistical mechanics and large deviation theory are explored and developed into powerful tools Altogether the manuscript provides a solid and broad working basis for graduate students and researchers interested in this field      **Population Genetics, Molecular**

**Evolution, and the Neutral Theory** Motoo Kimura, 1994 One of this century's leading evolutionary biologists Motoo Kimura revolutionized the field with his random drift theory of molecular evolution the neutral theory and his groundbreaking theoretical work in population genetics This volume collects 57 of Kimura's most important papers and covers forty years of his diverse and original contributions to our understanding of how genetic variation affects evolutionary change Kimura's neutral theory first presented in 1968 challenged the notion that natural selection was the sole directive force in evolution Arguing that mutations and random drift account for variations at the level of DNA and amino acids Kimura advanced a theory of evolutionary change that was strongly challenged at first and that eventually earned the respect and interest of evolutionary biologists throughout the world This volume includes the seminal papers on the neutral theory as well as many others that cover such topics as population structure variable selection intensity the genetics of quantitative characters inbreeding systems and reversibility of changes by random drift Background essays by Naoyuki Takahata examine Kimura's work in relation to its effects and recent developments in each area      **Theories of Population Variation in Genes and**

**Genomes** Freddy Bugge Christiansen, 2014-12-17 This textbook provides an authoritative introduction to both classical and coalescent approaches to population genetics Written for graduate students and advanced undergraduates by one of the world's leading authorities in the field the book focuses on the theoretical background of population genetics while emphasizing the close interplay between theory and empiricism Traditional topics such as genetic and phenotypic variation mutation migration and linkage are covered and advanced by contemporary coalescent theory which describes the genealogy of genes in a population ultimately connecting them to a single common ancestor Effects of selection particularly genomic effects are discussed with reference to molecular genetic variation The book is designed for students of population genetics bioinformatics evolutionary biology molecular evolution and theoretical biology as well as biologists molecular biologists breeders biomathematicians and biostatisticians Contains up to date treatment of key areas in classical and modern

theoretical population genetics Provides in depth coverage of coalescent theory Discusses genomic effects of selection Gives examples from empirical population genetics Incorporates figures diagrams and boxed features throughout Includes end of chapter exercises Speaks to a wide range of students in biology bioinformatics and biostatistics

**Population Genetics in Forestry** Hans-Rolf Gregorius, 2013-03-13 When we consider the main object of forestry the tree it immediately becomes clear why experimental population geneticists have been so hesitant in making this object a primary concern of their research Trees are very long living organisms with generation intervals frequently exceeding those of their investigators by multiples They virtually exclude therefore application of the classical methods of population genetics since these are based on observing genetic structures over generations This situation where the limits set to observation are so severe particularly requires close cooperation between theory and experiment It also requires careful consideration of results obtained for organisms other than trees in order to gain additional insights by comparing the results for trees with those for other organisms Yet the greatest challenge to population and ecological genetics probably originates from the fact that forests are very likely to be the most complex ecosystems of all even in some cases where they are subject to intense management This complexity which equally comprises biotic and abiotic factors varying both in time and space makes extremely high demands on the adaptational capacity and thus flexibility of the carriers of such an ecosystem Longevity combined with immobility during the vegetative phase however appears to contradict the obvious necessity of adaptational flexibility in forest tree populations when compared with short lived and or mobile organisms

**The Stability Concept of Evolutionary Game Theory** Ross Cressman, 2013-03-09 These Notes grew from my research in evolutionary biology specifically on the theory of evolutionarily stable strategies ESS theory over the past ten years Personally evolutionary game theory has given me the opportunity to transfer my enthusiasm for abstract mathematics to more practical pursuits I was fortunate to have entered this field in its infancy when many biologists recognized its potential but were not prepared to grant it general acceptance This is no longer the case ESS theory is now a rapidly expanding in both applied and theoretical directions force that no evolutionary biologist can afford to ignore Perhaps to continue the life cycle metaphor ESS theory is now in its late adolescence and displays much of the optimism and exuberance of this exciting age There are dangers in writing a text about a theory at this stage of development A comprehensive treatment would involve too many loose ends for the reader to appreciate the central message On the other hand the current central message may soon become obsolete as the theory matures Although the restricted topics I have chosen for this text reflect my own research bias I am confident they will remain the theoretical basis of ESS theory Indeed I feel the adult maturity of ESS theory is close at hand and I hope the text will play an important role in this achievement

*Population Biology* K. Wöhrmann, S.K. Jain, 2012-12-06 Fascinated by the diversity of living organisms humans have always been curious about its origin Darwin was the first to provide the scholarly and persuasive thesis for gradual evolution and speciation under natural selection Although we now have much information

on evolution we still don't understand it in detail. Many questions still remain open due to the complexity and multiplicity of interacting factors. Several approaches mainly arising from population ecology and genetics are presented in this book in order to help understand genetic variation and evolution.

**Hopf Bifurcation in the Two Locus Genetic Model** Ethan Akin, 1983. Hopf bifurcations occur in the class of simple genetic models for the combined effect of selection and recombination. The demonstration of cycling in such models is biologically unexpected. To study this phenomenon we describe the locus of positions at which Hopf bifurcation occurs in the two locus two allele model. The description is given by an explicit computable parametrization which can be used to generate all possible examples. Asymptotic estimates show that limit cycles can occur.

**The Mathematics of Darwin's Legacy** Fabio A. C. Chalub, José Francisco Rodrigues, 2011-06-24. The book presents a general overview of mathematical models in the context of evolution. It covers a wide range of topics such as population genetics, population dynamics, speciation, adaptive dynamics, game theory, kin selection, and stochastic processes. Written by leading scientists working at the interface between evolutionary biology and mathematics, the book is the outcome of a conference commemorating Charles Darwin's 200th birthday and the 150th anniversary of the first publication of his book *On the origin of species*. Its chapters vary in format between general introductory and state of the art research texts in biomathematics, in this way addressing both students and researchers in mathematics, biology, and related fields. Mathematicians looking for new problems as well as biologists looking for rigorous description of population dynamics will find this book fundamental.

**Phylogenetic Inference, Selection Theory, and History of Science** Anthony William Fairbank Edwards, 2018-07-19. Seminal papers by A. W. F. Edwards published together for the first time with commentaries from leading experts to contextualise his contribution.

**Fundamentals of Mathematical Evolutionary Genetics** Yuri M. Svirezhev, V. P. Passekov, 2012-12-06. One service mathematics has rendered the human race. It has put common sense back. Je riserai point à Jules Verne where it belongs on the topmost shelf next to the dusty canister labelled discarded. The series is divergent therefore we may be sense able to do something with it. Eric T. Bell. O Heavieside Mathematics is a tool for thought. A highly necessary tool in a world where both feedback and non linearities abound. Similarly all kinds of parts of mathematics serve as tools for other parts and for other sciences. Applying a simple rewriting rule to the quote on the right above one finds such statements as: One service topology has rendered mathematical physics. One service logic has rendered computer science. One service category theory has rendered mathematics. All arguably true. And all statements obtainable this way form part of the *raison d'être* of this series.

**Population Biology** Simon A. Levin, 1984. Contains lecture notes that were presented at the AMS Short Course on Population Biology held August 6-7 1983 in Albany New York in conjunction with the summer meeting of the American Mathematical Society. This title acquaints the reader with the mathematical ideas that pervade various levels of thinking in population biology.

**New Trends in Dynamic Games and Applications** Jan G. Olsder, 1995-12-01. The theory of dynamic

games is very rich in nature and very much alive. If the reader does not already agree with this statement I hope he/she will surely do so after having consulted the contents of the current volume. The activities which fall under the heading of dynamic games cannot easily be put into one scientific discipline. On the theoretical side one deals with differential games, difference games, the underlying models are described by differential respectively difference equations and games based on Markov chains with deterministic and stochastic games, zero sum and nonzero sum games, two player and many player games, all under various forms of equilibria. On the practical side one sees applications to economics stimulated by the recent Nobel prize for economics which went to three prominent scientists in game theory, biology, management science and engineering. The contents of this volume are primarily based on selected presentations made at the Sixth International Symposium on Dynamic Games and Applications held in St. Jovite, Quebec, Canada, 13-15 July 1994. Every paper that appears in this volume has passed through a stringent reviewing process as is the case with publications for archival technical journals. This conference as well as its predecessor which was held in Grimentz, 1992, took place under the auspices of the International Society of Dynamic Games (ISDG) established in 1990. One of the activities of the ISDG is the publication of these Annals. The contributions in this volume have been grouped around five themes:

**The Dynamics of Physiologically Structured Populations** Johan A. Metz, Odo Diekmann, 2014-03-11

**Evolutionary Theory and Processes: Modern Horizons** Solomon P. Wasser, 2013-03-09

Evolution is the most profound of human ideas integrating all natural phenomena, cosmic, biological and cultural into a continuous universal change. This volume deals with evolutionary observations, experiments and theories contributing to a deeper understanding of the evolutionary process, honoring the 75 birthday of Eviatar Eibi Nevo. I first met Eibi in 1966 when he was a Fellow in the Museum of Comparative Zoology at Harvard University and working mostly on cricket frog vocalization and speciation in the United States. His unique discovery of pipid fossil frogs in the Israeli Early Cretaceous central Negev is possibly the largest world collection of ancient fossil frogs. Our acquaintance developed into mutual friendship and admiration. Since then our long lasting friendship has included a visit to Israel enabling me to follow Eibi's major scientific achievements in particular his founding of the Institute of Evolution in the University of Haifa and now the pending establishment of the International Graduate School of Evolution. The research program of Eibi Nevo in collaboration with numerous colleagues and students in Israel and across the world encompasses diverse perspectives of evolutionary biology and biodiversity of genes, populations, species and ecosystems integrating modern and classical evolutionary approaches, molecular and organismal. They deal with model organisms in all forms from bacteria through plants, fungi, animals and humans conducted over local, regional and global scales.

**Advances In Mathematical Population Dynamics -- Molecules, Cells And Man - Proceedings Of The 4th International Conference On Mathematical Population Dynamics** O. Arino, David E. Axelrod, Marek Kimmel, 1997-12-04

This book presents a new approach to the subject of cosmology. It fully exploits Einstein's theory of general relativity. It is found that the most general formal expression of the theory

replaces the 10 component tensor formalism with a 16 component quaternion formalism This leads to a unified field theory where one field incorporates gravitation and electromagnetism The theory predicts an oscillating universe cosmology with a spiral configuration Dark matter is explained in terms of a sea of particle antiparticle pairs each in a particular derived ground state This leads to an explanation for the separation between matter and antimatter in the universe There is a brief discussion of black holes and pulsars The final chapter delves into philosophical considerations such as the different types of truth positivism versus realism and a discussion of the role of the Mach principle in physics and cosmology a

**Evolutionary Theory and Processes: Modern Horizons** Eviatar Nevo, 2004-01-31 Evolution is the most profound of human ideas integrating all natural phenomena cosmic biological and cultural into a continuous universal change This volume deals with evolutionary observations experiments and theories contributing to a deeper understanding of the evolutionary process th honoring the 75 birthday of Eviatar Eibi Nevo I first met Eibi in 1966 when he was a Fellow in the Museum of Comparative Zoology at Harvard University and working mostly on cricket frog vocalization and speciation in the United States His unique discovery of pipid fossil frogs in the Israeli Early Cretaceous central Negev is possibly the largest world collection of ancient fossil frogs Our acquaintance developed into mutual friendship and admiration Since then our long lasting friendship has included a visit to Israel enabling me to follow Eibi s major scientific achievements in particular his founding of the Institute of Evolution in the University of Haifa and now the pending establishment of the International Graduate School of Evolution The research program of Eibi Nevo in collaboration with numerous colleagues and students in Israel and across the world encompasses diverse perspectives of evolutionary biology and biodiversity of genes populations species and ecosystems integrating modern and classical evolutionary approaches molecular and organismal They deal with model organisms in all forms from bacteria through plants fungi animals and humans conducted over local regional and global scales *Dynamics of Macrosystems* Jean-P. Aubin, Donald Saari, Karl Sigmund, 2013-03-14 Population Genetics and Microevolutionary Theory Alan R. Templeton, 2021-05-04 Population Genetics and Microevolutionary Theory Explore the fundamentals of the biological implications of population genetic theory In the newly revised Second Edition of Population Genetics and Microevolutionary Theory accomplished researcher and author Alan R Templeton delivers a fulsome discussion of population genetics with coverage of exciting new developments in the field including new discoveries in epigenetics and genome wide studies The book prepares students to successfully apply population genetics analytical tools by providing a solid foundation in microevolutionary theory The book emphasizes that population structure forms the underlying template upon which quantitative genetics and natural selection operate and is a must read for future population and evolutionary geneticists and those who wish to work in genetic epidemiology or conservation biology You ll learn about a wide array of topics including quantitative genetics the interactions of natural selection with other evolutionary forces and selection in heterogeneous environments and age structured populations Appendices that cover genetic survey techniques and

probability and statistics conclude the book Readers will also benefit from the inclusion of A thorough introduction to population genetics including the scope of the subject its premises and the Hardy Weinberg Model of Microevolution An exploration of systems of mating including a treatment of the use of runs of homozygosity to show pedigree inbreeding in distant ancestors A practical discussion of genetic drift including the use of effective sizes in conservation biology with a discussion of African rhinos as an example A concise examination of coalescence including a treatment of the infinite sites model Perfect for graduate students in genetics and evolutionary biology programs and advanced undergraduate biology majors Population Genetics and Microevolutionary Theory will also earn a place in the libraries of students taking courses in conservation biology human genetics bioinformatics and genomics

Mathematical and Statistical Approaches to AIDS Epidemiology Carlos Castillo-Chavez, 2013-03-13 The 18 research articles of this volume discuss the major themes that have emerged from mathematical and statistical research in the epidemiology of HIV The opening paper reviews important recent contributions Five sections follow Statistical Methodology and Forecasting Infectivity and the HIV Heterogeneity and HIV Transmission Dynamics Social Dynamics and AIDS and The Immune System and The HIV In each leading experts in AIDS epidemiology present the recent results Some address the role of variable infectivity heterogeneous mixing and long periods of infectiousness in the dynamics of HIV others concentrate on parameter estimation and short term forecasting The last section looks at the interaction between the HIV and the immune system



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