PART IIA/IIB

Paper BAN6 - Evolution within our species

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Lecturers:
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Structure

Please note:
The content of courses and timetables are always subject to change. We will endeavour to inform you of any changes as they occur but please always refer to the online version of this syllabus for the most up-to-date information.

Course documents are available on Moodle: [link to be provided by Undergraduate administrator] Timetables are available on Moodle and the University Online Timetabling system: [links to be provided by Undergraduate administrator]

Structure

Lectures: 2 hours each week (Michaelmas and Lent)
Supervisions: 3 supervisions in Michaelmas and 3 supervisions in Lent

Mode of examination

Undergraduates: For the mode of examination for this paper please see the Form & Conduct Notice for papers in Biological Anthropology online [http://www.bioanth.cam.ac.uk/current/undergraduates.html].

MPhils: For the mode of examination for this paper please see outline of papers in Biological Anthropology online [http://www.bioanth.cam.ac.uk/current/graduates.html].

Aims of the course:
This paper investigates the mechanisms which have driven the genetic and phenotypic variation within our species. We investigate models which explain the origin and maintenance of variation, the role of dispersals and major cultural transitions in shaping human diversity, and the interaction between cultural change, natural environments and the biology of our species. This includes consideration of the roles of plasticity, developmental biology, life history, natural selection and neutral mechanisms in shaping human diversity and its variation in time and space.

BAN6 Evolution within our species - is comprised of 4 modules, 2 of which will be taught in Michaelmas and 2 in Lent. These are as follows:

Module M1: Human Diversity, Evolutionary Theory, and Culture (8 lectures)
Module M2: Plasticity and Human Adaptability (8 lectures)
Module L1: Understanding the sources of genetic variation within our species: 9 lectures
Module L2: Impact of recent changes in life-style on our genetic diversity: 7 lectures

Learning outcomes:
On the successful completion of BAN6 students will be able produce high quality written work that demonstrates an informed and critical understanding of the mechanisms which drive intraspecific variation, with particular emphasis on our species. Students will be able to critically evaluate the relationship between cultural and biological variation, with an emphasis on interaction and mechanisms of change in adaptive systems, and the relationship between our Anthropological understanding of human diversity relative to the biological and social sciences more broadly.
Supervisions:
There are three supervisions each term. Supervision topics and reading lists will be
circulated during lectures and uploaded on Moodle. As a rough guide, supervision
essays should be between 1500 and 2000 words (excluding bibliography), line
spacing at least 1.5. Concision is one of the most important skills in scientific writing,
and it will be evaluated in the essays. As such, essays longer than 2000 words will
only be read and evaluated up to the word limit. Please provide a word count
(excluding bibliography) with your essay.

General readings:
Below is a list of texts which provide a good introduction to the material covered in
the course. Throughout the course, you will be provided with specific references and
sources for the topics covered in lectures, supervisions and practicals, and you are
strongly encouraged to go beyond the textbooks and explore the original scientific
literature.

Academic Press.
Jablonka, E., Lamb, M. 2006. Evolution in four dimensions: Genetic, Epigenetic,
Behavioural and Symbolic Variation in the History of Life. The MIT Press.

Lectures:
Lectures will be held at 09.00am on Mondays and 11am on Fridays of each week. The
Michaelmas term will cover themes of the history and philosophy of science as it
regards human diversity, mechanisms that drive phenotypic variation in our species,
and how they relate to underlying cultural and biological process, and evidence for
recent cultural influences on human phenotypes. The Lent term will cover genetic
evidence of differentiation among human populations and the key mechanisms of
genic change including dispersals, admixture and adaptation.
Module M1: Human Diversity, Evolutionary Theory, and Culture (4 lectures)

Module Co-ordinator: Jay Stock

Lecturers: Jay Stock

Objectives of module
This module will cover the historical context of our understanding of human diversity and adaptability. Emphasis will be placed on the development of the culture paradigm and differing views of evolutionary theory as it applies to human variation. Various attempts to ‘unite the human sciences’ will be considered, including those of E.O. Wilson and Stephen Jay Gould, as well as critiques of the evolutionary paradigm.

Background reading
Below is a list of fundamental background reading. Further reading will be provided for each individual lecture.


Lecture 1.
The scope of human adaptability – mechanisms, history, culture

This lecture will cover historical perspectives on human diversity, with an overall emphasis on means of understanding variation, and the relationship of variability to the natural environment. The political context of human diversity will be considered to the extent that it informs the history of academic disciplines such as Anthropology and Biology. The origin of the concept of culture will also be discussed, with particular emphasis on the impact of
'culture' on the discipline of Anthropology, and our understanding of human diversity. The political context of the 'culture paradigm' will be considered in historic context, to investigate how theoretical perspectives on human diversity shaped inquiry in the discipline.


Lecture 2.

**Battles over evolutionary theory and the nature of science**

Evolutionary theory, as it applies to humans, has been controversial. Here we consider how differing views of evolution apply to our understanding of human diversity, and how they relate to broader political and intellectual trends of the past 60 years. Emphasis will be placed on the contrast between adaptationist and ‘exceptionalist’ perspectives, and how these theoretical perspectives have influenced Anthropology. The lecture will also consider opposing views of science, as typified by the work of Karl Popper and Thomas Kuhn, and situate debates about human variation within the context of broader issues in the philosophy of science.


Lecture 3.

**Cultural Evolution, Adaptability, and Neutral Theory**

Clinal variation in human cultural and biological phenotypes are often thought to reflect adaptation to environmental conditions. This lecture considers the mechanisms that can lead to geographic variation in variation, and attempts to determine whether variation is ‘neutral’ or ‘adaptive’. Emphasis will be placed on neutral theory, dispersal history (contingency) and demography as mechanisms which can drive clinal variation and lead researchers to falsely identify human adaptation.
Lecture 4.

Darwin, Metaphysics and the Mind - uniting the human sciences

JTS

The discipline of Anthropology can be seen as divided with respect to the paradigms through which we understand human diversity. This lecture considers central aspects of this debate, and attempts to ‘unite’ the human sciences, most notably by E.O. Wilson and Stephen Jay Gould, as well as approaches to cultural evolution. Critical emphasis will be placed on whether cultural change occurs through Darwinian mechanisms, and the implications of this cultural change on human phenotypic variation. Through critique of these approaches, this lecture will consider the challenges of a theoretically unified anthropology.


Module supervision topics

1. Critically evaluate the challenges (philosophical or practical) in the interpretation of either: a) cultural; b) biological; or c) 'dual inheritance' models of human evolution.

Readings for the individual lectures will be informative here, as well as the more general sources below


Richerson, P. 2017. Recent critiques of Dual Inheritance Theory. Evolutionary Studies in Imaginative Culture. DOI: 10.26613/esic/1.1.27

Module M2: Plasticity and Human Adaptability (8 lectures)

Module Co-ordinator: Jay Stock

Lecturers: Jay Stock, Alison Macintosh

Objectives of module
This module will consider intergenerational, developmental and physiological mechanisms that underpin human variation, with an emphasis on those that provide accommodation to environmental stress. These mechanisms of plasticity will be considered relative to broader patterns of human adaptability and energetics. While the underlying interaction of genes and development are complex, this module will conclude by considering several aspects of human variation with an emphasis on identifying different sources of variation through the life course.

Background reading
Below is a list of fundamental background reading. Further reading will be provided for each individual lecture.


Lecture 5.
**Plasticman: avoiding the costs of adaptation**

Phenotypic plasticity is the ability of one genotype to produce more than one phenotype when exposed to different environments. Through plasticity, organisms can modify their biology to accommodate environmental stress, and can lead to the illusion of adaptation by natural selection. This lecture considers the importance of plasticity to human biology and our understanding of human adaptability.

Lecture 6.
**Canalisation, modularity and development**

Canalisation a measure of the ability to produce the same phenotype regardless of variability of its environment or genotype. When combined with developmental modularity, it can lead to phenotypic stability in a range of traits, linked by developmental pathways. The importance of these mechanisms in underpinning human variation, and in particular variation associated with neutral population history, will be considered.


Lecture 7.
**Growth, Epigenetics and Developmental Systems**

Growth and development of the organisms provides a means of adapting physiology and metabolism in response to environmental stress encountered during life. The underlying mechanisms may often be epigenetic, but outcomes of modified developmental trajectories may underpin some aspects of human phenotypic variation. Oyama’s Developmental Systems Theory attempts to cast evolutionary theory in the context of development. Does this provide a basis for understanding the origins of human diversity?


Lecture 8.
**Towards an integrated understanding of human adaptability**

Towards an integrated understanding of human adaptability
Our species accommodates environmental stress through a variety of potentially adaptive systems, including culture and technology, physiology and development, and genetic variation by natural selection. A considerable amount of human phenotypic variation, however, may be non-adaptive. Is it possible to reconcile these approaches to develop an integrated understanding of human diversity?

Lecture 9.

**Bone growth trajectories and body size/shape: Integration and flexibility
AM**

Growth of the body, in size and shape, is based upon skeletal growth. Human variation in body size and shape is largely driven by skeletal growth. By considering bone growth as a model system, this lecture considers evidence for both the integration and plasticity of skeletal growth between individuals and populations.


Lecture 10.

**Culture, climate, and the growing skeleton
AM**

Growth trajectories are both genetically influenced and plastic in response to environmental stress. This lecture considers variation in growth in relation to both natural and cultural environments to illustrate how they interact to drive variation in human phenotypes.


Lecture 11.

**Mechanical loading, bone biomechanics, and functional adaptation
AM**

Bone is highly responsive to mechanical loading throughout the lifespan, but particularly during growth and development. That being said, skeletal tissue also follows tightly controlled and well understood developmental trajectories. In this context, it is an excellent example of how genes, the natural environment and even human behaviour can influence
phenotypic outcomes. This lecture will consider the impact of lifestyle and activity on bone development within our species.

Macintosh et al. 2016. Early life conditions and physiological stress following the transition to farming in Central/Southeast Europe: Skeletal growth impairment and 6000 years of gradual recovery. PLoS ONE 11(2):e0148468
Ruff et al. 2015. Gradual decline in mobility with the adoption of food production in Europe. PNAS 112:7147-7152.

Lecture 12.
The hidden life of soft tissue: The evolutionary importance of muscle and fat
AM

In addition to bone, the soft tissues of muscle and fat have many roles within the body. Consideration of the biology of fat and muscle illustrates how the body balances various physiological and adaptive needs throughout the lifespan.

Module supervision topics
To what extent is ‘plasticity’ a new paradigm in our understanding of human adaptability?

How does human culture and technology influence our phenotype and skeletal morphology?

Readings:
Module M3: Energetics, Life History, and Human Adaptability (4 lectures)

Module Co-ordinator: Jay Stock

Lecturers: Daniel Longman

Objectives of module
This module will consider the role of phenotypic plasticity in adaptation to a changing environment.

Life history theory predicts the existence of trade-offs between competing physiological functions relating to reproduction, maintenance, growth and storage under conditions of limited environmental resources. Individuals that have developed effective mechanisms for both acquisition and optimal allocation of energy in their particular ecological niche are thereby advantaged. This module uses the conceptual framework provided by life history theory to consider reproduction, growth and senescence.

Background reading
Below is a list of fundamental background reading. Further reading will be provided for each individual lecture.


Lecture 13.
Energetics and Human Evolution

DL

“… the fundamental object of contention in the life-struggle, in the evolution of the organic world, is available energy” – Lotka, 1922.

The significant role played by energy in the process of evolution has long been recognised. This lecture will discuss the energetic considerations of two defining traits of human evolution: the development of an enlarged brain, and bipedal locomotion.


Lecture 14.

**Life History Theory: Reproduction**

**DL**

Life history theory seeks to explain how natural selection shapes an organism to maximise fitness. In doing so, it visualises the life of an organism as an evolutionary solution to an ecological problem. The energetic cost of reproduction is central to life history trade-offs. Although reproduction is only one of the key functions described by life history theory, the other processes are only of value from a fitness perspective in that combined they increase opportunities for reproduction in the future.


Lecture 15.

**Life History Theory: Growth**

**DL**

This lecture will consider the second area described by life history theory, growth. The human life cycle, as well as the growth rates of different sexes and tissues, will be discussed.


**Lecture 16.**

**Life History Theory: Senescence**

*Lecture*

**Senescence** has been defined as the post-maturation decline in survivorship and fecundity that accompanies advancing ages (Rose & Charlesworth, 1980). Senescence is the result of investment in maintenance being below a level that would enable indefinite survival. This lecture will consider why senescence persists, and ways in which some believe ageing is a problem that can be solved.


http://www.theguardian.com/science/2015/jan/11/-sp-live-forever-extend-life-calico-google-longevity

**Module supervision topics**

How do environmental conditions influence reproduction?

**Reading:**


**BAN6: Lent 2018**

*Mondays 9-10 am, Fridays 11-12 noon. Fitzwilliam Street Lecture Theatre*

The module structure of Lent Term BAN6 lectures

The Lent Term lectures are organized by two modules, L1 and L2. These will be preceded by a general introduction lecture that covers the background information on the neutral and adaptive mechanisms of genetic differentiation that will be referred to in the L1 and L2 modules.

**Lecture 1.**  
*Introduction: Neutral and adaptive mechanisms of genetic differentiation*

The first lecture introduces general terminology and principles of genetic change at species and population level relevant for this module. What is a founder effect and what do we mean by genetic bottleneck, genetic drift, and genetic load? Do different types of selection necessarily lead to different outcomes and what are the key
methods to detect selection in action? The lecture will highlight the key challenges for untangling the neutral and adaptive mechanisms from empirical data.


**Module L1: Understanding the sources of genetic variation within our species**

*Module Co-ordinator: Toomas Kivisild*

*Lecturers: Toomas Kivisild, Christiana Scheib*

**Objectives of module**
The Lent term module L1 will cover genetic evidence of variation within our species that is apportioned among major population groups at continental level. Models explaining observed patterns of genetic differentiation will be discussed in terms of major dispersal events, introgression, and also evolution by natural selection.

**Background reading**
Fundamental background reading for modules L1 and L2 is provided below after the lecture descriptions of both modules. Further reading will be provided for each individual lecture.

**Lecture 2.**
*Why do humans have so low genetic diversity?*

*TK*

Compared to other species human populations show low levels of genetic differentiation. Most genetic diversity is observed within populations and only minor proportion of differences is among groups. This lecture reviews the evidence of human genetic variation at genome scale in populations from across the world and contextualizes this with evidence from other primate species. How old is our species and what do gene coalescent times and population split dates really mean?


Lecture 3.

*Out of Africa model with archaic introgression*

*TK*

Which model best explains the fact that Africans have the highest level of genetic diversity and how does this model cope with the fact that populations outside Africa share more genetic variation with the Neanderthals? The lecture will give a brief background to the historical debate on the models and will then consider recent genome scale evidence for archaic introgression. Have some of the Neanderthal genes persisted because of their positive adaptive value?


Lecture 4.

*Genetic structure of human populations: race vs ancestry*

*TK*
Using a few hundred genetic loci geographic ancestry of individuals can be predicted at continental scale. Further improvements in accuracy can be made when increasing the number of markers. This is because genetic and geographic distances among human populations are correlated. Genetic ancestry components can be argued to be not compatible with the 19th cc anthropological concept of race because they do not support (a) their independent origins, (b) descent from original unadmixed pure sources, nor (c) the superiority/inferiority in behaviour that would be caused by fixed adaptive differences.

http://cehg.stanford.edu/letter-from-population-geneticists/


Lecture 5.
Peopling of Australia and the Old World and the origins of populations characterized by short stature

A bulk of genetic evidence suggests that anatomically modern humans spread out of Africa and colonized Eurasia and Australia in a single wave. However, a small proportion of Oceanian genetic ancestry derives from admixture with Denisovans and another small proportion may arguably derive from a separate out of Africa dispersal that preceded the main dispersal event by few tens of thousands of years. African and Oceanian pygmy populations have evolved their short stature likely independently. Furthermore, Southeast Asian and Papuan pygmy groups are more similar to their non-pygmy neighbours than to each other suggesting that pygmy phenotype may have more than a single origins there.


Lecture 6.
Genetic differentiation of Eurasian populations and adaptations to different environments

TK/CS

Ancient DNA evidence suggests that genetic differentiation of Eurasian populations started to occur at around 45 kya. This lecture will review the genetic differences detected among regional populations of Eurasia, the scale of differentiation within and among populations in light of dispersal models and adaptation, including cases of genetic adaptation to extreme environments, such as cold and high altitude.


Bigham AW. 2016 Genetics of human origin and evolution: high-altitude adaptations. Curr Opin Genet Dev. 41:8-13


Lecture 7.
Peopling of the New World

TK/CS

Living Native Americans draw their genetic ancestry from multiple continents and the intercontinental admixture can be distinctly different when looking at genetic markers from sex chromosomes or autosomes. Multiple lines of evidence suggest that Siberia has been the ultimate source of Native American genetic variation that existed in Americas before the colonial period. It seems likely that all dispersal events had their source in or around Beringia and involved elements of the same gene pool sampled at different times.


Lecture 8.
*Ancient DNA and the research ethics in dealing with ancient human remains*

**TK/CS**

Ancient DNA has dramatically changed the debate on Native American origins by revealing previously hidden aspects of past genetic variation as well as opening new debates about the genetic identity and its role in assessing ancient human remains. The Beringian gene pool would have drawn, as suggested by the analyses of the 24 thousand year old Mal’ta boy’s genome, part of its ancestry from the East and part from the West Eurasian pools. It is plausible that before the later dispersal events occurred, the (circum-) Beringian gene pool had been enriched by additional gene flow from other Siberian populations that had meanwhile set foot in the neighborhood.


Lecture 9.
*Complex models of Native American ancestry*

**TK/CS**

Genetic data support the hypothesis of (at least) three independent waves of dispersal into the Americas from a Beringian source and reveal the similarity of most American populations to one another and their distinction from the rest of the world. The majority of Native Americans trace their ancestry solely to the first dispersal event ~20–15 KYA whereas the Na-Dene and Eskimo-Aleutian populations draw their genetic diversity from a mixture of the first and later dispersal waves. However, the genetic ancestry ascribed to the first dispersal is also complex.<Reading>


**Module L2: Impact of recent changes in life-style on our genetic diversity**

*Module Co-ordinator: Toomas Kivisild*

*Lecturers: Toomas Kivisild*

**Objectives of module**

The objectives of the Lent term module L2 will be to learn about the nature and extent of genetic differentiation that has been associated with the changes of human life-style, shift to farming and settled way of life.

**Lecture 10.**

Agricultural expansions and gene flow

TK

The shifts from hunter-gatherer to sedentary life style in the past >8 thousand years correlate with growth of global population and geographic expansions at local continental scales. These shifts were likely protracted in time rather than revolutionary and involved many rather than just handful of centres of domestication. Genetic variation in Europe is correlated with geography (rather than with ethnicity or language). Phylogeographic analyses based on modern variation of mtDNA and Y haplogroups have suggested high levels of local continuity whereas ancient DNA studies have revealed that Neolithic was a period of large scale genetic changes.


Lecture 11.
Genetic evidence of population changes in Europe during the last 10 thousand years

At least three distinct ancestry components have been inferred from the combined analysis of modern and ancient DNA data to explain genetic variation in Europe. Gimbutas’ Kurgan model is supported by new ancient DNA evidence. It remains less clear, however, whether the genetic contributions from Yamnaya to Corded Ware people were associated with major linguistic changes in Europe< Reading>


Haak et al. 2015 Massive migration from the steppe was a source for Indo-European languages in Europe. Nature. 522(7555):207-11.

Lecture 12.
Sex-specific aspects of population histories

What happens when populations meet? Admixture can be sex-specific and can lead to diverse patterns of population structure across space. This lecture reviews firstly the approaches that one can take to detect and measure the extent of sex-specific gene flow among populations and presents then cases for a number of regional examples where sex-specific admixture has been detected from modern and ancient DNA evidence.


Lecture 13.
Evidence of recent purifying and positive selection in human populations

Similarly to changes in environment that dispersing human populations faced when colonizing different parts of the world changes in life-style can lead to changes in allele frequency by positive or purifying selection. Analyses of whole genome sequences enable us to compare populations also by load of deleterious mutations. These differences in genetic load can be expressed differently by functional classes of genes. This lecture looks at population-specific differences in genes affected by natural selection. Examples include evidence on pigmentation, height and immunity genes.


Lecture 14.
Evidence for diet related genetic adaptations

Recent changes in life-style and shifts to settled way of life have dramatically changed our diet and genes coding for proteins involved in metabolism of carbohydrates and fatty acids have been implicated as targets of recent positive selection. This lecture critically reviews the current evidence on examples including LCT and AMY cluster of genes.


**Lecture 15.**
*Agricultural expansions elsewhere in the world TK*

Bantu and Austronesian expansions represent examples of recent co-expansion of genes, languages, material culture and life-style. Both show the evidence of sex-specific patterns of admixture between the farmers and local hunter-gatherers, even though the directions are opposite: Bantu correlates more with Y, Austronesian with mtDNA. Express Train and Slow Boat two competing models to explain Austronesian dispersal and both linguistic evidence and mtDNA are in support of Taiwanese origins while Y chromosome suggests strong Melanesian contribution. Autosomal evidence in both cases intermediate consistent with less than 20% of admixture with Melanesians in case of Austronesians. Dispersal routes of domesticates generally support Asian source of Austronesian expansion with extensive maritime connections.


**Lecture 16.**
*Summary: Are we still evolving? TK*

The final lecture/seminar will recapitulate on the material covered in the Lent term modules. Discussion will focus on the extent to which genetics can inform us about our ancestry and to what extent our phenotypic variation may reflect genetic adaptations that have arisen recently in the scope of the last few tens of thousands of years.


**General background reading for both modules:**


**Module L1 and L2 supervision topics**

1. How do we explain the low level of genetic differentiation observed among human continental populations?
2. Do we know whether archaic introgression was sex- or gene-specific?
3. What are the main insights into the history of Native American populations that we would not know about if we did not have genome scale evidence from ancient DNA studies?
4. What impact have genetic studies had on our understanding of the neolithization process in Europe?
5. Have recent shifts to settled way of life left the same or different signatures on the genomes of populations from different depending on their environment?
6. Has the role of genetic adaptation increased or decreased over time as human populations have expanded while inhabiting different parts of the world?