UNIVERSITY OF TARTU
Faculty of Science and Technology
Institute of Technology

Katrīna Ducena

Evolution of genetic variation underpinning human personality reflects changing lifestyle and environments in the European Holocene

Bachelor's Thesis (12 ECTS)

Curriculum Science and Technology

Supervisor(s):
Associate Professor, PhD Jon Anders Eriksson

Tartu 2024

Evolution of genetic variation underpinning human personality reflects changing lifestyle and environments in the European Holocene

Abstract:

This paper describes the analysis of the evolution of personality traits in the European Holocene.

The constantly changing environment, having risks and rewards shift alongside culture and technology, requires humans to adapt their behaviour for survival and efficient use of resources in the environment, thus leading to a lifestyle switch and personality adjustment.

The thesis examines how within different time periods and geographic locations human genetic architecture of personality has evolved due to the changing environment. It analyses the main human personality dimensions across six time periods: hunter-gatherer, Neolithic, Chalcolithic, Bronze Age, Iron Age, and Modern-day period. The results demonstrate how the polygenic scores for these traits have shifted, which populations according to these scores are genetically more related, and what traits are more expressed in specific regions and times. The findings of genetic variation of personality traits suggest that these modifications might be potentially adaptive to the changing lifestyles and environments in the European Holocene.

Keywords:

Evolution, behaviour, personality traits, environment, lifestyle, polygenic scores, genome-wide association studies

CERCS:

B220, B100, S260

Pealkiri eesti keeles (title in Estonian)

Geneetilise mitmekesisuse evolutsioon, mis toetab inimeste isiksust, peegeldab muutuvat eluviisi ja keskkonda Euroopa holotseenis.

Lühikokkuvõte:

Käesolev töö kirjeldab isiksuseomaduste evolutsiooni analüüsi Euroopa holotseenis. Pidevalt muutuv keskkond, kus riskid ja hüved muutuvad koos kultuuri ja tehnoloogiaga, nõuab inimestelt oma käitumise kohandamist ellujäämiseks ja keskkonna ressursside tõhusaks kasutamiseks, mis viib elustiili muutumiseni ja isiksuse kohandumiseni.

Lõputöö uurib, kuidas erinevatel ajaperioodidel ja geograafilistes asukohtades on inimese isiksuse geneetiline arhitektuur muutunud tänu muutuvale keskkonnale. See analüüsib peamisi inimisiksuse mõõtmeid kuue ajaperioodi vältel: kütt-korilane, neoliitikum, kalkoliitikum, pronksiaeg, rauaaeg ja kaasaegne periood. Tulemused näitavad, kuidas nende omaduste polügeensed skoorid on muutunud, millised populatsioonid on nende skooride järgi geneetiliselt lähedasemad ja millised omadused on teatud piirkondades ja aegadel rohkem väljendunud. Isiksuseomaduste geneetilise varieerumise tulemused viitavad sellele, et need muutused võivad olla potentsiaalselt kohanemisvõimelised muutuvate elustiilide ja keskkondadega Euroopa holotseenis.

Võtmesõnad:

Evolutsioon, käitumine, isiksuseomadused, keskkond, elustiil, polügeensed skoorid, kogu genoomi hõlmavad assotsiatsiooniuuringud

CERCS:

B220, B100, S260

TABLE OF CONTENTS

TERMS, ABBREVIATIONS AND NOTATIONS

Polygenic score - a genetic predictor for a phenotype that is computed by summing the genetic variants carried by an individual, weighted by their estimated effect size

Single nucleotide polymorphism (SNP) – a germline substitution of a single nucleotide at a specific position in the genome

Complex traits – traits that are affected by two or more genes and do not follow Mendel's Law of Dominance, with both - genetic and environmental factors - having an impact on the variation in expression

Linkage disequilibrium – a measure of non-random association between segments of DNA, due to the phenomenon that genes lying close together tend to be inherited together

Meta-analysis – a statistical process that combines the data of multiple studies to find common results and to identify overall trends

GWAS - an approach to compare the genomes of many different people to find genetic markers associated with a particular phenotype or risk of disease.

INTRODUCTION

Throughout history, humans have adapted their behaviour to take advantage of resources in the environment and protect themselves from dangers (Larsen, 2023). Natural selection is one of the factors having a major effect on behaviour (Donahoe, 2012). There are plenty of examples that show how the environment a population has inhabited has a strong effect on behavioural adaptation to enable a more prosperous life in various climates and a smarter use of the local resources, such as planting crops that thrive under certain climate conditions or using tools made of new material (Brown et al., 2011).

Although genetically highly similar, humans have individual differences in their behaviour and these differences are heritable (Martin et al., 2023). Complex behavioural traits are controlled by many small-effect genetic variants (Jasinska & Freimer, 2009). These variants interact with each other and the environment, complicating the process of finding causal variants. Mutations like single nucleotide polymorphisms disrupt ancestral behaviours and lead to the evolution of behaviour (Sheehan et al., 2018a). In the past, behavioural novelties appear to have happened rarely and have mostly been disadvantageous, since complex behavioural phenotypes are persistent and decay over a considerably long period of time (Rayner et al., 2022). Behaviour not only varies in timescale but also across geographic regions, as different environments favour distinct behaviours (Vernon et al., 1997).

The human lifestyle has greatly changed from the hunter-gatherer period to the present day. Indirect evidence from archaeology demonstrates these adaptations from the various ways of obtaining food, such as hunting and gathering or farming, to the tools that we operate with (Tryon et al., 2010). The constantly changing environment, with risks and rewards changing alongside culture and technology, demands from humans an altering behaviour, leading to a lifestyle switch (Vernon et al., 1997). As personality encapsulates innate tendencies that systematically shape behaviour, from an individual's social interactions to cognitive and emotional responses (Stangor & Walinga, 2014), such far-reaching behavioural changes would also put evolutionary pressure on any heritable aspects of personality.

This research aims to explore the extent to which human personality has varied over time and across space, and whether any environmental and cultural factors are related to the variation between different ancient populations. Focusing on the European Holocene, this was done by combining ancient and present-day genetic data with information from genome-wide association studies (GWAS) on the genetic basis of key personality traits to estimate population-level variation polygenic scores for the personality traits in a wide range of Holocene populations and performing statistical analyses to test the hypothesis that personality change occurred in response to shifts in lifestyle and environmental factors.

1 LITERATURE REVIEW

1.1 EVOLUTION OF HUMAN BEHAVIOUR

Homo sapiens started to inhabit the Earth more than 200,000 years ago (*Homo Sapiens | Meaning, Characteristics, & Evolution*, 2024). The environment and climate in all parts of the Earth have changed countless times throughout this period (*Climate Effects on Human Evolution*, 2024). Changes in the environment promote behavioural adjustments, however, the regulation of complex behavioural traits happens over long time periods (Rayner et al., 2022).

Heritable changes in behaviour might include adjustments in sensory systems, in the brain or anatomical switches in some structures responsible for behaviour (Sheehan et al., 2018). In the broad sense, changes in the sensory perception or processing of stimuli, the motivation to respond to these stimuli, the template for behavioural response and morphological or physiological structures required to perform a behaviour lead to behaviour evolution.

Genetic behaviour novelties are typically unfavourable, they appear and become permanent only rarely (Foster, 1999). On the other hand, ancestral behavioural shifts tend to occur more frequently, since they can be disrupted by mutations, although these phenotypes decay over considerably long periods when under relaxed selection. An example of such a trait is the behaviour of predator avoidance, that is learned in early life. These behaviours are generally learned in high-risk environments and can affect the future boldness level of an animal (Foster, 1999). The main goal of researchers studying the evolution of behaviour is to discover links between disruptive mutations and complex behavioural phenotypes (Sheehan et al., 2018). Genetic data from various populations suggests that the evolution of adaptive behavioural traits is constrained. Tuning the frequency of expression of a behavioural trait leads to differentiation, for example, human populations with a history of migration have a greater frequency of alleles encoding the gene for dopamine D4 receptor (DRD4), related to sensation-seeking, than sedentary populations do (Chen et al., 1999). These differences are the products of evolutionary pressures.

Several well-known evolutionary mechanisms explain the heritable variation in behaviour. Firstly, the variation is maintained via the accumulation of mutations that do not influence survival or reproductive success (Weiss, 2018a). Secondly, it is affected by a balancing selection. The role of a trait and whether it is needed for survival depends on the environment, time period and the stage in life of an individual. And lastly, there can be differences in the life-history strategies that are affected by the level of risk in an environment. Individual life history strategy is a compromise adapted between conflicting goals. Life-history strategy choice affects mating, the number of children, longevity of relationships, and environment change (Nettle, 2005).

There are three fundamental trade-offs in life history theory: current versus future reproduction, quantity versus quality of offspring, and mating versus parenting effort (Foster, 1999). The best fitness-related phenotype from the perspective of evolution is usually a compromise since the goal for all living organisms is to maximize their long-term genetic input to future generations (Bolund, 2020). Usually, there is a presence of a trade-off for this strategy, which means that being at a higher level for one trait, for example, extraversion, prevents one from being at a high level for another trait, such as neuroticism (Bolund, 2020).

There is also an incredibly large variation in the life history traits between different human populations, which is affected by the highly diverse environments that humans inhabit (Bolund, 2020). For the life-history traits and other behavioural traits, both environmental and genetic factors, and their interactions, are important in shaping the phenotypic variation (Santostefano et al., 2021).

The local environmental conditions have a significant effect on human phenotypes. Changes in these conditions are reflected in an individual's personality and lifestyle (Hopwood et al., 2021). A strong increase in social complexity throughout time, the Neolithic revolution and the process of urbanisation and occupational specialisation are possible contributors to the improved intelligence scores for our evolutionary advantage (Kuijpers et al., 2022).

To study the evolution of behaviour, one ought to conduct studies of the development of genetically controlled behaviours, to discover the underlying genetic basis of adaption of behaviour and how and which quantitative trait loci affect neural development (Sheehan et al., 2018).

In this thesis, the behavioural traits are compared across six time periods in the European Holocene, spanning approximately 20,000 years ago to the present day, with individual ancient DNA data. These time periods include Mesolithic hunter-gatherers, the Neolithic, Chalcolithic, Iron Age, Bronze Age, and Modern-day populations.

European Mesolithic hunter-gatherers were characterised by high mobility, a lack of permanent settlements, and a subsistence strategy based on hunting, fishing, and collecting a wide range of edible plants (Bayliss-Smith, 2004). They lived in small groups of 10-100 people (Boyd et al., 2014). Each group had quite a large territory to obtain enough food, necessitating high mobility (Venkataraman et al., 2017). The mobile lifestyle in smaller groups contributed to lower risks of acute, epidemic diseases (Page et al., 2018). The hunter-gatherer lifestyle has been studied by anthropologists in the few hunter-gatherer societies that still exist around the world. These studies highlight that hunter-gatherers are fully or semi-nomadic, usually divide the work by gender, and have animistic religions (Ember, 2020). In regions where the temperature is warmer, societies engage more in gathering and less in hunting as a result of higher plant biomass.

Looking into the behavioural patterns in this time period, research states that hunter-gatherers required high levels of adaptability and resilience to survive in unpredictable environments, favouring personality traits such as conscientiousness (Charles, 2020). Compared to other periods, childhood in hunter-gatherer societies seems to be more relaxed, possibly due to fewer chores assigned to them, with children receiving more affection from their parents (Ember, 2020).

Some studies show that a highly influential historical period, determining continuous evolutionary processes afterwards was the Neolithic period, since the Neolithic revolution had a high impact on human lifestyle and health (Kuijpers et al., 2022).

There was a gradual transition to a more settled lifestyle starting around 10 – 12,000 years ago and ending with the transition to the Neolithic (*Hunter-gatherer | Definition, Societies, & Facts*, 2024). Due to this, some hunter-gatherer groups switched to more permanent living establishments. A few hunter-gatherer groups in parts of Europe, and North and South America, however, remained with the lifestyle long after this revolution.

The Neolithic populations lived in densely built settlements of 50 to 300 people. Towards the end of the Neolithic time, pottery appeared. This historical period is known for the beginning of farming and domestication of animals (Bowles & Choi, 2019). Populations learned to grow crops, cultivate cereal grains and keep livestock. Early farmers and later farming populations, in addition to farming, engaged in hunting (*Neolithic | Definition & Facts*, 2024). More advanced stone tools were being made, by polishing harder rocks. The early farmers raised barley and wheat and kept goats and sheep, latte pigs and cattle as well. The Neolithic lifestyle began in the Middle East and spread north across Turkey and Greece into central Europe. In the Neolithic time emerged a social division of labour, with individuals specialising in specific tasks (Vásárhelyi & Scheuring, 2018). This specialisation in specific fields might give rise to new genetic polymorphisms. Some groups, in contrast to others, mimicked hunter-gatherers (Vásárhelyi & Scheuring, 2018).

Some studies show an increase in physical violence between the early farmers of Northwestern Europe (Fibiger et al., 2023). It is thought that the violence occurred due to an increase in competition between already established communities and those still growing, fighting for the land. Another reason for increased violence could be the emergence of stable settlements where resources, such as domesticated animals and harvested grains, were kept and could be stolen. The higher competition is due to a higher demographic density which is associated with a slower rate of migration of farmers, which hinders the spread of agriculture (Svizzero, n.d.).

The Chalcolithic or copper-stone period is considered as the beginning of the Bronze Age. This period marked the start of copper metallurgy (*Bronze Age | Definition, History, Inventions, Tools, & Facts*, 2024). Craft specialisation emerged, long-distance exchange networks became more popular and complex societal structures increased (Golden, 2008). Importantly, extramural cemeteries and corporate cave tombs appeared. It has also been suggested that, perhaps, new religious practices arose (Golden, 2008). The Chalcolithic culture varied depending on the region, as it developed from the local Neolithic traditions.

The Bronze Age indicates the time when people started to replace stone with bronze made from melting tin and copper for creating tools and weapons (Onion, 2023). During the Bronze Age, were introduced the first writing systems in some areas. The Bronze Age started at separate times in different regions. In Greece and China, it started before 3000 BCE, whereas in some countries, such as the United Kingdom, it started considerably later – at about 1900 BCE (*Bronze Age | Definition, History, Inventions, Tools, & Facts*, 2024). During this time, larger societies with leaders, such as kingdoms like Mesopotamia and Ancient Greece emerged. These kingdoms engaged in trading activities with each other. Important shifts happened in the fields of culture, ideology and technology, perhaps due to trade with non-local people (Kneisel et al., 2019). Evidence shows cycles of demographic fluctuations during this period. A growth of population could have been caused by new agricultural techniques and crops.

The Iron Age period followed the Stone and Bronze Age times. This period signifies the use of tools and weapons from iron and steel in regions of Europe, Asia and Africa (Onion, 2023). Research highlights the Iron Age societies as interactive societies with overall similarities and key local differences, changing through time and influences (Thurston, 2009).

For some states, such as Ancient Greece, a cultural decline happened within this time due to losing trade routes and a literacy decline. Towards the end of the Iron Age in Greece, once its economy had recovered, a period of the famous Greek drama, democracy and philosophers began (Onion, 2023). In the regions of Europe, agricultural and rural life dominated, there were mostly still farmers in small villages using iron tools for farming.

1.2 QUANTIFYING HUMAN PERSONALITY TRAITS

Personality refers to an individuals way of feeling, thinking and behaving (Holzman, 2024). It includes inherent and acquired behavioural patterns that can be observed by one's interactions with others and the environment. These behavioural consistencies can be explained by the underlying genetic architecture of personality traits (Lacombe et al., 2022).

This research focuses on the evolution of personality traits; therefore, this section presents an overview of the process of measuring the genetic data of personality traits. The advances in computational abilities over the last century and the larger datasets such as the UK Biobank have made it possible for the behavioural genetics field to evolve rapidly.

When it comes to personality traits, their analysis involves additional complications, not present when dissecting genetic data of physical characteristics, since physical traits are more under direct biological control (Abdellaoui & Verweij, 2021a).

In the process of investigating the genetic portion of variation in a phenotype, one should estimate the heritability of a trait. There are various ways to estimate it, a few of them include family, twin and adoption studies (Sallis et al., 2018a). Using genome-wide genotyping arrays to calculate the heritability contribution of a trait is also an effective tool that enables one to capture the relatively common variants across the entire genome. Additionally, one can use single nucleotide polymorphism (SNP) heritability calculation methods (Barry et al., 2022). These methods attempt to capture genetic variants that might be associated with a phenotype of interest. For this approach are used genome-wide association studies.

One must choose carefully the population to conduct the study with. Conducting studies with participants from different geographic regions can cause population stratification effects (Sallis et al., 2018a). Risk alleles might occur in different frequencies across the populations, leading to falsified correlations between a genetic variant and a phenotype, which are merely associations due to population substructure. Population stratification can be caused by ancestral differences or population structure (Hellwege et al., 2017). One way to overcome this issue is by performing principal component analysis to cluster populations considering the variation caused by population differences.

Complex traits are known to be influenced by many individual DNA sequence variants that travel through many cascades of bidirectional biological processes and interact with the environment (Abdellaoui & Verweij, 2021a). Due to such high complexity studies on these behavioural traits are usually done over narrower geographic dimensions or within families. Studying different populations reveals the significant heritable variation of complex behaviours (Nettle, 2005). The notable variation is maintained by mutations, since complex traits, having many genes of effect, provide many targets for mutations in every generation. In different environments and times, the optimal value of a trait varies (Nettle, 2005).

Personality is affected both by genetic and environmental components and is correlated with mental health (Kang et al., 2023). Nowadays, a common method of researching personality involves using meta-analysis, which merges the findings of multiple studies. To determine the correlation between personality traits is calculated the linkage disequilibrium (LD) score (Ni et al., 2018). The LD score shows the relationship between two traits, indicating if their relationship cannot be merely coincidental. To avoid any biases, LD scores ought to be replicated in other studies. A good-quality LD score is replicable in multiple studies, showing consistent effects (Abdellaoui & Verweij, 2021a).

When performing analysis using genetic data of complex traits, it is crucial to take into account the other aspects that might be underlying the detected signal. Furthermore, it should be examined whether someone participating in a study is a heritable behavioural trait (Abdellaoui & Verweij, 2021a). To improve the accuracy of data, increasing sample sizes is helpful.

For quantifying personality traits commonly are used genome-wide association studies (GWASs). GWASs use a hypothesis-free method to find genetic variants which are associated with a phenotype (Sallis et al., 2018a). GWAS, contrary to linkage studies, uses unrelated participants to conduct research with, enabling the possibility of capturing smaller regions with an effect on the phenotype (Sanchez-Roige et al., 2018). Each SNP in the dataset is analysed, ensuring that all the causal SNPs are captured or tagged by other SNPs. Additionally, GWAS creates a regression model for each variant with the genotype at the specific SNP and other covariates that account for the variation in phenotype, not via the SNP (Uffelmann et al., 2021).

In the process of measuring personality traits, a crucial step is finding the single nucleotide polymorphisms (SNPs) with the highest effect, so-called 'peaks'. These peaks are found by looking at the Bonferroni corrected p-value (-log10(p)) (Weiss, 2018a). The smaller the p-value, the higher the significance of the genetic variant, thus the association between the SNP and the personality trait is stronger. The SNP is considered statistically significant if it is below the GWAS threshold of $p = 5 * 10^{-8}$ (Uffelmann et al., 2021). The discovered SNPs should be replicated to test whether their directionality is consistent.

1.3 GWAS STUDIES ON THE "FIVE FACTOR MODEL" TRAITS AND RISK-TAKING

According to trait theory, people differ from each other based on the strength of basic trait dimensions (Weiss, 2018b). This research focuses on the evolution of six specific personality traits, that capture different major dimensions of human personality.

Five of the behavioural traits are taken from the Five Factor Model (FFM) of personality or "the Big Five". This taxonomic model over the last century has been frequently used to measure individual differences in personalities (Lo et al., 2017a). "The Big Five" covers the main personality domains. *Extraversion* signals high activity level, talkativeness, seeking out stimulation and is associated with the experience of positive emotions (De Moor et al., 2012a). *Agreeableness* reflects compassion and cooperativeness; *neuroticism* measures the experience of negative emotions, such as emotional instability, vulnerability to stress, depression and anxiety. *Openness to experience* denotes intellectual curiosity, active imagination and creativity. Lastly, *conscientiousness* captures diligence, carefulness, organization and an individual's self-discipline (Weiss, 2018a).

These traits are typically assessed using questionnaires such as the 'Neo Five-Factor Inventory' (NEO-FFI) with 60 statements, 12 per trait (such as 'Tries new foods' or 'Enjoys playing with theories' to assess the openness to experience trait) (Costa & McCrae, 1992).

Additionally, this thesis explores the complex behavioural trait of risk-taking. Measuring risk-taking behaviour is of high significance to the public health sector, although not much is known about the genetic architecture of this trait.

A study "Meta-analysis of genome-wide association studies for personality" combined ten genome-wide association studies (GWAS) and discovered multiple genetic variants that are associated with the FFM personality traits (De Moor et al., 2012a). The research explained that conscientiousness is highly associated with an intronic variant in the gene *KATNAL2* on chromosome 18q2.1, furthermore, openness to experience had genetic variants signalling in *RASA1* and *PTPRD* genes (De Moor et al., 2012a). *RASA1* gene encodes for GTPase activating regulatory protein, that is involved in cellular proliferation, differentiation and and intracellular signalling (De Moor et al., 2012b). The *KATNAL2* gene encodes a protein widely expressed in the CNS and is thought to play a role in neuronal migration, dendritic pruning and axonal growth (De Moor et al., 2012b). This suggests that the *KATNAL2* gene has an important role in neurodevelopment. Later studies with a larger number of participants have found new single nucleotide polymorphisms that are linked to neuroticism. UK Biobank studies discovered that genetic variants with the highest association with neuroticism are in the subregion of 8p23.1, covering about 4 Megabases (Johannesson et al., 2016). However, few of the chromosomal regions associated with the behavioural traits have been consistently reported in multiple studies (Sanchez-Roige et al., 2018).

One study performed GWAS of self-reported risk-taking behaviour with the European UK Biobank study participants (Clifton et al., 2018). They identified 26 genome-wide significant loci. 24 of these loci were novel and enriched in the GABA receptor pathway. GABA is the dominant inhibitory neurotransmitter in the mammalian CNS (*GABAergic Synapse Pathway - Creative Diagnostics*, n.d.)

Some of these behavioural traits have been associated with mental health disorders. Neuroticism is well-known to be correlated with major depressive disorder (MDD) as well as other anxiety and mood disorders. On the contrary, conscientiousness is inversely correlated with MDD (De Moor et al., 2012a). A locus rich with variants linked to extraversion was found to be on the 12q23.3 region within the gene *WSCD2* (Lo et al., 2017a). This locus has been previously denoted as a significant locus for alleles related to temperament and personality from bipolar disorder studies.

Furthermore, a study analysing genetic variants influencing neuroticism found that around 75% of single nucleotide polymorphisms for neuroticism overlap with the MDD (Luciano et al., 2018), but their biological function is not very well understood except in general terms: the research demonstrated that these SNPs are located in genes that contribute to metabolic and cellular processes, encode for transcription factors and nucleic acid binding, and play a role in the catalytic activity of molecular functioning. The underlying genetic architecture of neuroticism is potentially clinically relevant, as genes that affect neuroticism reveal pathways of currently prescribed antidepressant action.

Risk-taking has been found to be positively correlated with some mental health diseases like ADHD, schizophrenia and neuroticism (Karlsson Linnér et al., 2019). Research has reported several positive genetic correlations between risk-taking and childhood obesity, ever-smoking, ADHD, schizophrenia and waist-hip ratio (Strawbridge et al., 2018). The risky behaviour could stem from neglecting long-term outcomes and following one's impulses. (Clifton et al., 2018).

Activity in the pre-frontal cortex is associated with the behavioural measures of risk-taking, the hippocampus is known to play a role in behavioural inhibition, the anterior cingulate cortex is involved in the training of task performance control and the hypothalamus participates in the processing of innate and learned fear. The fear might include pain, aggression or predators (Clifton et al., 2018).

Some studies have endeavoured to explain the correlations between the FFM traits. Neuroticism has been proven to be inversely correlated with the other traits and all the other traits to have a positive correlation (Lo et al., 2017b). The highest correlations are reported to be between conscientiousness, agreeableness and extraversion. Personality traits are often correlated due to one trait inducing the other or via having a common causal component (Kandler et al., 2017).

Complex behavioural trait expression tends to vary on environmental factors. Neuroticism has been shown to have a significantly higher expression in more dangerous, less predictable and less resource-rich environments. It has also been reported to increase with age (Weiss, 2018b). Genetic signals of complex traits usually reveal polygenicity (Maier et al., 2017). These signals could reflect other factors, such as correlation with other traits, environmental effects being linked to polygenic effects, and biases created by the study participants. However, the recruitment of participants to such studies may have systematic biases as individuals being more prone to mental health disorders are not so likely to engage in data collection for such behavioural trait studies (Abdellaoui & Verweij, 2021b). It has been shown that candidates for these research studies tend to be more educated, healthier and financially stable. Participants with disorders are prone to underreporting their alcohol intake, leading to confounding results between a complex trait and alcohol use (Abdellaoui & Verweij, 2021b).

To predict and measure personality traits, GWAS often use calculations of polygenic scores (PGS). These scores are obtained using GWAS single nucleotide polymorphism (SNP) accumulative effect size information to allow for the prediction of the genetic basis for a complex trait (Schultz et al., 2022). The analysis of PGS is rapidly increasing, due to the expansion of GWAS availability and analytical methods to obtain the scores (Ma & Zhou, 2021). PGS can help to assess the evolution of personality traits with a comparison of GWAS summary data and the ancient DNA data. The discoveries of evolutionary trends facilitate the process of finding lifestyle factors and environmental changes that promote personality trait evolution (Piffer & Kirkegaard, 2024).

There are always certain limitations present in conducting studies in behavioural genetics. Some caveats that might affect the studies reporting genetic correlations include sample size - even if it is relatively large, it could be too small to capture the majority of SNPs associated with the traits due to the relatively strict GWAS threshold (Lo et al., 2017b).

The literature on behavioural genetics stresses that a lot more research is needed to be done in this field since often even large-scale studies with huge sample sizes cannot identify the genetic variants that have an impact on complex behavioural traits. Mostly variants with large effect are rare and predominantly common variants with small effect size are underlying the phenotypic variation (Sallis et al., 2018b). The detection of even small effect size variants helps to understand the biological processes that describe an individual's personality, social and health behaviour as well the psychiatric diseases that might be linked with these personality traits (Uffelmann et al., 2021).

2 THE AIMS OF THE THESIS

The thesis has three main aims:

1. To analyse how personality trait expression varies between different geographical locations.

The first aim consists of analysing different European population regions to test whether behavioural traits are expressed at varied levels based on the latitude and longitude the population has inhabited and to evaluate the effect of the local environment on behavioural trait adaption.

2. To test whether changes in average personality traits are statistically significant and compatible with expectations from natural selection.

The second aim incorporates testing whether the data supports the hypothesis of behavioural trait adaption throughout time and making quantitative estimates for these adaptations. Additionally, the aim is to study whether different selection pressures have favoured some complex behavioural phenotypes over others at certain time points.

3. To draw conclusions about possible environmental and cultural factors that could be linked to variation between different ancient populations.

The last aim encompasses determining whether certain environmental and cultural factors are selecting for specific behavioural phenotypes for species continuation and survival and examining how changes in societal structures and lifestyles affect the key personality traits.

3 EXPERIMENTAL PART

3.1 MATERIALS AND METHODS

3.1.1 Genetic data from human fossils (ancient DNA)

To obtain the ancient DNA information, sample data was downloaded from the published Allen Ancient DNA Resource genotype database, which is available on the David Reich Lab website: https://reich.hms.harvard.edu/allen-ancient-dna-resource-aadr-downloadable-genotypes-present-day-and-ancient-dna-data. The dataset version used was *v54.1*. The website provided a file with information about the location (longitude and latitude), date, etc. for each sample. Samples for all six time periods were selected based on their geographic location criteria for longitude being less than 60 degrees, to focus on the regions of Europe. Only variants present in both the ancient data and the GWAS datasets were maintained.

3.1.2 Tools used in the thesis

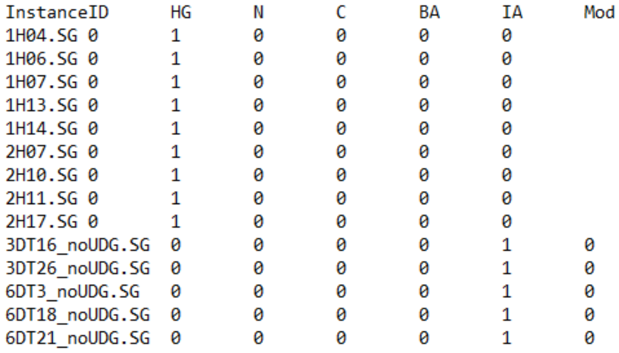
Processing of ancient DNA data files was done using PLINK version 1.90 beta (Purcell et al., 2007, https://www.cog-genomics.org/plink/). PLINK 1.90 is Shaun Purcell's command-line programme, which was developed by Christopher Chang. Custom Bash scripts were developed by the author to filter the data and extract genotype information.

'Bcftools' allow for the usage of Variant Call Format (VCF) and Binary Call Format (BCF) files. The variant call format provides efficient and robust storage of GWAS summary statistics (Lyon et al., 2020). Bcftools were used to process the summary statistics files for the personality trait GWASs used in this thesis.

Matlab (R2023a, R2024a) was used for numerical and statistical analyses, using built-in functions and custom scripts developed by the author.

3.1.3 Selection of study populations

Upon obtaining the ancient DNA (aDNA) genotype file, all the instance IDs - unique identifiers assigned to each individual - were filtered to separate them into different time periods, by looking at the date range indicated in the data. The six time periods analysed are Neolithic, hunter-gatherer, Bronze Age, Iron Age, Chalcolithic and Modern-day.



```
InstanceID      HG      N       C       BA      IA      Mod
1H04.SG 0       1       0       0       0       0
1H06.SG 0       1       0       0       0       0
1H07.SG 0       1       0       0       0       0
1H13.SG 0       1       0       0       0       0
1H14.SG 0       1       0       0       0       0
2H07.SG 0       1       0       0       0       0
2H10.SG 0       1       0       0       0       0
2H11.SG 0       1       0       0       0       0
2H17.SG 0       1       0       0       0       0
3DT16_noUDG.SG  0       0       0       0       1       0
3DT26_noUDG.SG  0       0       0       0       1       0
6DT3_noUDG.SG   0       0       0       0       1       0
6DT18_noUDG.SG  0       0       0       0       1       0
6DT21_noUDG.SG  0       0       0       0       1       0
```

Figure 1. Instance IDs of samples. *With "1" denoted an individual belonging to the specific time period, with "0" denoted the lack of an individual belonging to that time period. HG- hunter-gatherer, N- Neolithic, C – Chalcolithic, BA – Bronze Age, IA – Iron Age and Mod – modern-day.*

The created text file (Figure 1) was then uploaded in MATLAB and matched for the sequence of individuals within the *v54.1* file. The MATLAB operations excluded individuals with missing longitude data and included samples with longitude that is lower than 60 degrees, to focus on individuals in Europe and some parts of Asia. Afterwards, there were selected only those instance IDs of individuals belonging to the specific historical period.

The next step involved performing principal component analysis. Principal component analysis (PCA) is a statistical method that allows for the visualisation of multiple variables by reducing the dimensions of a high-dimensional data table and analysing the variable relationships through the coordinates of data points within the principal component (PC) new axis coordinate system (Lever et al., 2017). The analysis simplifies the data but is designed to maximally explain the variation of all the variables (Lever et al., 2017). The first principal component explains most of the variance. In genetic association studies, PCA allows for the exploration of the possible effects of confounders, such as age, sex and population on the PRS. In this thesis, PCA was used to examine the effects of population stratification.

A major challenge in using PCA with ancient DNA is the variable (and often) large amounts of missing data, stemming from poor preservation conditions and typically resulting in low DNA yields and sequencing errors. As standard principal component calculation methods require complete data, it is common practice to either replace missing genotype data with the average genotype and/or to project samples using available data onto PCs of genetic variation of present-day populations. However, both of these approaches come with potential biases that may influence the interpretation of the patterns. Therefore, was used a different approach, in which PCs are estimated self-consistently. Such approaches have previously been shown to be unbiased down to very low coverage levels of <1% (Meisner et al., 2021). The lead 20 principal components were estimated with a fixed-point method, implemented as a Matlab script. PLINK 1.9 was used to identify individuals with <99% missing data and to identify unlinked loci (with flags --geno 0.4 --maf 0.05 --indep 50 5 2).

For the initial analysis, the mean frequencies for each locus were estimated and then used to predict allele dosage at missing loci. Then, an allele dosage variance-covariance matrix between individuals was calculated. This was used to estimate the singular value decomposition (SVD) for the top 20 singular values (and thereby also the top 20 PCs). Missing allele frequencies were predicted using the SVD approximation and the estimated average allele frequencies (restricted to the interval [0,1]). Using this data, the SVD for the top 20 singular values was re-calculated. This process was repeated until the PCs converged.

Each historical time period analysed was then divided into clusters based on the principal component analysis. A trade-off was applied to create bigger clusters of more individuals by merging multiple clusters, meanwhile ensuring that the distances between individuals in the PCA would not be too big. The individuals per each historical period were divided into three to five clusters, based on the geographical closeness of countries and clustering within the principal components. A list of unique countries from all the individuals' data was obtained.

The trends and patterns created by PCA were used to cluster individuals according to their data point coordinates. The coordinate system of principal component 2 against principal component 3 was used to evaluate the data points, visualise what countries group together etc. For some countries, the coordinates of the data points exhibited a wide range of locations in the coordinate system, therefore they were separated by selecting limited ranges on the principal component axes and dividing these individuals from the same countries into different clusters. Exceptional data points that did not cluster with any of the groups were excluded. Clusters that were represented by too few individuals were merged with bigger clusters close by. Together were created 27 clusters from all of the time periods.

After all of the clusters were created, they were merged into one text file, collecting the Instance IDs, Plink FIDs, and Cluster IDs of all the individuals. The Cluster ID corresponds to the name of the cluster an individual belongs to.

The created file with all the clusters was then filtered using PLINK 1.90 to remove any duplicates or triplets in the data. After cleaning the data file, there remained 3810 individuals. Using PLINK 1.90, the *v54.1* files were subsetted to keep the individuals within the cleaned clusters and those having no more than 40% missingness.

Additionally was generated a plot indicating the geographic coordinates of latitude and longitude for all the countries included in the clusters used for the analysis.

3.1.4 Selection of GWAS for personality traits to include in the study

The data used for the complex trait information was taken from biobanks. Biobanks contain phenotypic data, such as lifestyle factors, data from health questionnaires and usually also genetic data for a large sample of participants (Weissenkampen et al., 2019). These biorepositories can be created with the data of patients from hospitals or the general population.

The source of the GWAS (genome-wide association study) summary statistics is the 'IEU open GWAS projects' webpage with more than 50 thousand GWAS summary datasets (*Browse the IEU OpenGWAS Project*, n.d.). For this thesis were chosen datasets of behavioural traits with available summary statistics, preferably larger sample size and SNP count, as well as more up-to-date studies. One of the traits studied is risk-taking (*Trait: Risk Taking - IEU OpenGWAS Project*, n.d.).

The research study that measured this complex trait surveyed participants with a question "Would you describe yourself as someone who takes risks?” (*Data-Field 2040*. (n.d.). https://biobank.ctsu.ox.ac.uk/crystal/field.cgi?id=2040). The possible answers include "Yes/No/Do not know/Prefer not to answer". The number of single nucleotide polymorphisms (SNPs) they detected is 9,851,867 with a sample size of 446,279 of European population. The study was done in 2018.

The five other complex traits analysed in this thesis are taken from a study "Meta-analysis of genome-wide association studies for personality" (De Moor et al., 2012a). Utilizing datasets from a single study allowed for a better comparison of the obtained trait results. The study measured the personality scores for the five factors - Neuroticism, Extraversion, Openness to Experience, Agreeableness, and Conscientiousness - based on 60 items of the NEO Five-Factor Inventory (NEO-FFI) (12 items per factor) (Costa & McCrae, 1992). The items were answered on a 5-point Likert-type scale ranging from strongly disagree (0) to strongly agree (4) (De Moor et al., 2012a). Some examples of the items include statements such as "Feels helpless'" for the neuroticism factor and "Likes having many people around" for the extraversion factor (*Table 1 Item Content of the NEO-FFI. Item Numbering in the Parentheses. . .*, n.d.). The sample size of this study is 17,375 individuals of European populations, the SNP number they have reported per each trait is around 2,305,000. The study was done in the year of 2012.

GWAS summary statistics files for all six complex traits were downloaded in the VCF format *(explained in section 3.1.1)*. Using 'Bcftools' the necessary columns for further analysis were extracted: chromosome, position (of genetic variant), reference allele, alternative allele, effect size and Lp value ((-log10(p-value)).

3.1.5 Polygenic score calculation

Firstly, matching positions within the filtered aDNA *v54.1* and the GWAS summary statistics were found. The reference and alternative alleles at these positions were compared. Afterwards, the inflation factor was calculated to assess the deviation of the distribution of the observed test statistic against the distribution of the expected test statistic. The inflation factor was necessary for the choice of threshold for selecting variants for further analysis. A threshold of the 'Lp value' was chosen, where the observed '–log10p' value began to deviate from the expected '–log10p' value. This step was done to choose the peak variants with the highest association with the trait. This process allows one to narrow down the number of causal variants.

Due to the fact that some variants from GWASs are not causal, the genetic variants that surpass the 'Lp value' are filtered. Genetic variants in close proximity to the actual causal variant might surpass the Lp threshold due to linkage disequilibrium – variants that have been inherited together are linked, causing them to have higher p-values (Weissenkampen et al., 2019). Therefore, starting at the most significant variant, all variants within 500 kilobases of that variant were excluded.

Using PLINK 1.90 were obtained the frequencies of those peak variants that were present also in the file with filtered ancient DNA variants that match the positions of GWAS variants for the individuals within the obtained clusters.

From a file with the filtered matching ancient and GWAS positions of peak genetic variants, for each trait were extracted the columns denoting 'rsIDs' of SNPs, minor allele frequencies, number of chromosomes for the individuals with the genetic variants, as well as alternative and reference alleles. The numbers in the column of chromosome count were divided by half to obtain the number of individuals. For those genetic variants with frequency being reported for the major allele, the number was subtracted from one, to obtain the minor allele frequency.

The 27 clusters of populations were filtered for those that have at least ten individuals for each one of the peak variants of the trait. Those populations with less than ten individuals were excluded. The number of populations remaining slightly varied between the personality traits.

Afterwards, the polygenic scores (PGS) were calculated. The following formula was used for PGS calculation: 2* (MAF * ES), where 'MAF' indicates the minor allele frequency of a genetic variant and 'ES' – the effect size of a genetic variant.

3.1.6 Cluster analyses of PGS

The PGS for all the traits were then normalised to perform principal component analyses on the obtained PGS scores. PCA was done to visualise how closely related are the selected populations based on their PGS scores for all of the six behavioural traits analysed. For this analysis, only the clusters that had sufficient data for all of the traits were chosen, in total 19 clusters. The clusters were analysed by comparing PC1 against PC2, PC1 against PC3 and PC2 against PC3. Furthermore, the six complex traits were analysed with PCA. Performing this PCA allowed to see the correlation between the traits.

Additionally, was done linkage analysis with the Matlab 'ward' method that measures the inner squared distance between clusters and visualizes the results in a dendrogram. To create the dendrogram was used a Matlab function 'linkage' that returns a matrix encoding a tree containing hierarchical clusters of the rows of the input data matrix - the normalised PGS score matrix (*Agglomerative Hierarchical Cluster Tree - MATLAB Linkage*, n.d.).

A heatmap of normalised PGS scores was created in Matlab. For each trait, the scores across all of the populations were averaged to zero. The normalisation of the scores allows for an accurate comparison with a common scale for all the traits. The heatmap provides a visual of polygenic scores across all clusters and all traits. Increasing polygenic scores are illustrated with changing colours on the map.

3.1.7 Temporal and Statistical Analyses of PGS

To ascertain the accuracy of the calculated PGS was used a statistical method of bootstrapping. Bootstrapping allows one to repeat the experiment without the need for a new sample by mimicking the sampling process. It randomly resamples with replacement the original values.

Firstly, the genotypes of the SNP positions were recoded using PLINK 1.90. With the flag – 'recode12' the A2 (major alleles) were encoded as '2', the A1 (minor alleles) were encoded as '1', but the missing genotypes as '0' (*Data Management - PLINK 1.9*, n.d.).

The genotype and plink FID files were then loaded into Matlab. The variable indicating the genotypes was modified to count the numbers indicating the alleles of the genotype and subtracting 2 from the sum, thus '-2' indicated missing data, '0' indicated the presence of two A1 alleles in the genotype and '2' showed for two A2 alleles. With the newly obtained genotypes, were calculated the new frequencies to check for the previous PGS accuracy. The frequencies for each population and peak variant for a trait were iterated over 1000 times, resulting in 1000 new sets of frequencies per trait.

For each bootstrapped set of frequencies were then calculated the PGS scores. Since the bootstrapped frequencies were for the A2 (major allele), before PGS calculation, the minor allele frequencies were obtained by subtracting from 1 the major allele frequencies. Having created 1000 new sets of PGS per trait, containing PGS for each population with each SNP, the mean PGS from all 1000 sets were calculated and compared to the original PGS.

For each population analysed, to visualize PGS changes within a timescale, a polygon in Matlab was created. The polygon y-axis boundaries are the 30th and 70th percentiles of the mean bootstrapped PGS. The polygon x-axis limits are the time point ranges of the historical period to which the cluster belongs, based on the sample date information. Inside each polygon was drawn a line in a slightly darker colour than the polygon itself, representing the mean value of the corresponding cluster and the cluster name. A figure of the population polygons was created, the figure consists of four subplots, indicating the geographic location of the clusters – east, west, north or south. Clusters with two directions mentioned in their name, such as 'east-south' were included in both of the corresponding subplots.

Furthermore, t-tests comparing two independent means were done to check whether the obtained bootstrapped mean PGS values signal of possible significant differences with the transitions of the time periods.

3.2 RESULTS

In the first section of this chapter are presented the results of filtering the individuals from ancient DNA datasets and evaluating how they cluster together within principal component analysis. In the second section are demonstrated the results from the fine mapping of GWAS genetic variants for the personality traits and intersecting the data with ancient DNA. This section describes how many peak genetic variants have surpassed the significance threshold for all of the traits. The final results section illustrates the correlations between the clusters and the traits based on the polygenic scores obtained.

3.2.1 Ancient DNA filtering results

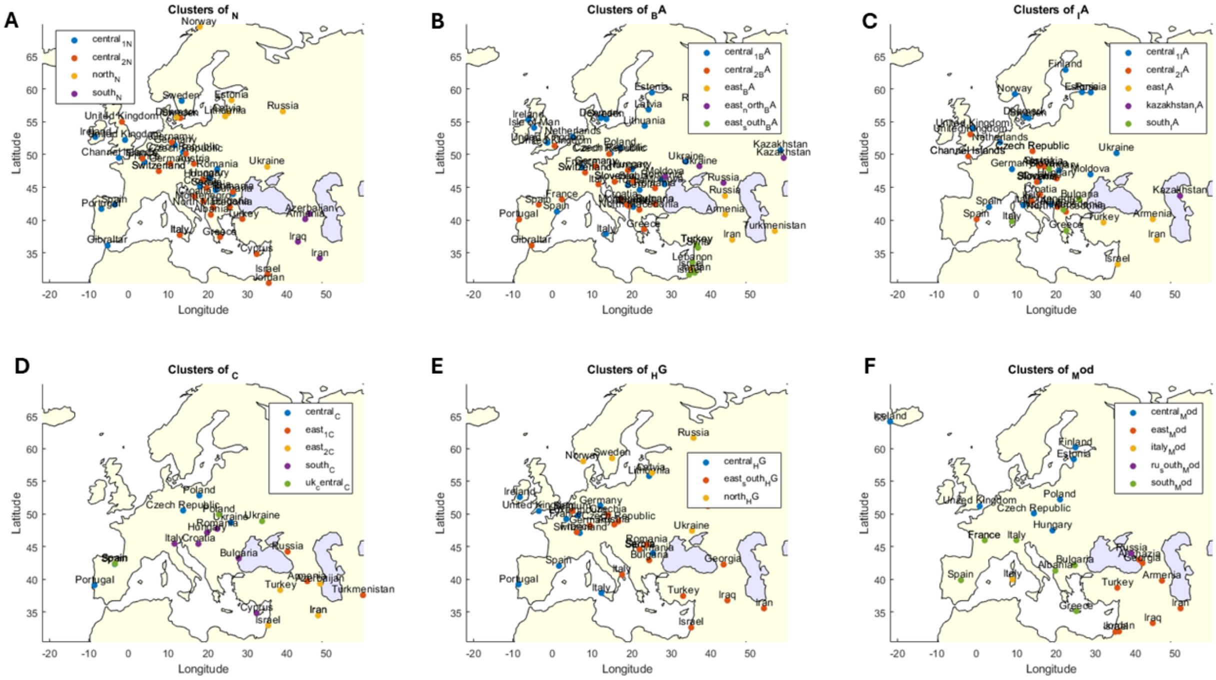


Figure 2. The longitude and latitude information for countries included in each cluster *(A - clusters of Neolithic populations, B - clusters of Bronze Age populations, C - clusters of Iron Age populations, D - clusters of Chalcolithic populations, E - clusters of hunter-gatherers, F - clusters of modern-day populations)*

The figure above depicts the countries that are represented by the individuals included in the clusters analysed. Each subplot is dedicated to a specific time period. The top row represents the Neolithic, Bronze Age and Iron Age geographic coordinates. The bottom row represents the Chalcolithic, hunter-gatherer and Modern-age individual geographic coordinates.

Each time period was divided into clusters based on principal component analysis. The periods were grouped into an average of three to five clusters.

The hunter-gatherers were divided into three groups: North cluster, central cluster and East-South cluster. The North cluster incorporates Sweden, Norway, Ukraine, Latvia and Russia with 47 individuals. The central cluster contains 106 individuals from Belgium, the United Kingdom, Luxembourg, France, Montenegro, Switzerland, Ireland, Italy, Germany, Lithuania, Denmark, Hungary, Serbia, Romania, Spain and Portugal. And lastly, the East-South cluster with 45 individuals includes Georgia, Iran, Iraq, Israel, Turkey, Bulgaria, Czech Republic, Austria, Russia, Serbia, Germany, Belgium, Romania, France and Italy. The corresponding countries for each of the clusters can also be seen in **Figure 2**.

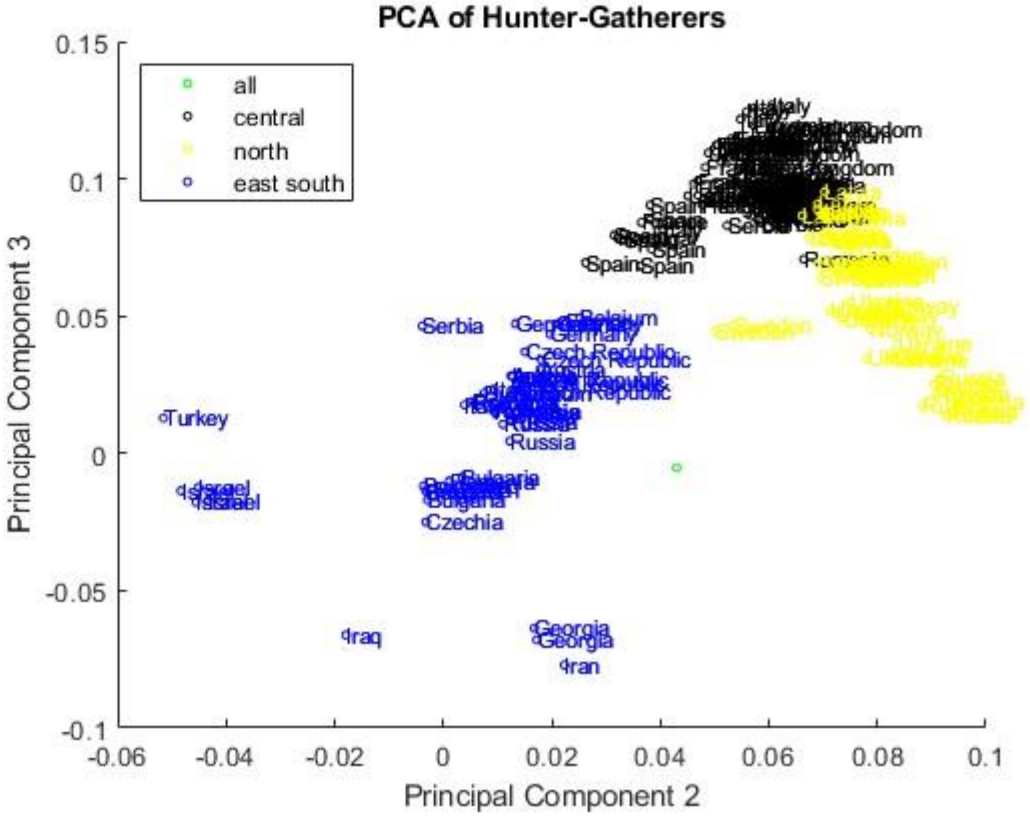


Figure 3. Principal component analysis of the hunter-gatherer populations (PC2 vs PC3)

The hunter-gatherer individuals allowed for a relatively simple division in clusters due to the lower number of individuals belonging to this period. The samples from these clusters are approximately within the time range of 42,000 to 5600 years BCE.

The Neolithic period was divided into four clusters: a North, two central-western region clusters and a South region cluster. The 63 North cluster individuals include the countries of

Latvia, Estonia, Lithuania, Norway, Lithuania, Ukraine, Russia, Denmark and Poland. Both of the central region clusters correspond to the countries of the United Kingdom, France, Channel Islands, Montenegro, Germany, Czech Republic, Austria, Sweden, Switzerland, Ireland, Portugal, Spain, Bulgaria, Italy, Gibraltar, Jordan, Turkey, Israel, Greece, Cyprus, Croatia, North Macedonia, Serbia, Hungary, Albania and Romania. The first central cluster is represented by 506 individuals, the second – 365 individuals. The last cluster of the southern regions consists of 26 individuals from Armenia, Azerbaijan, Iran and Iraq.

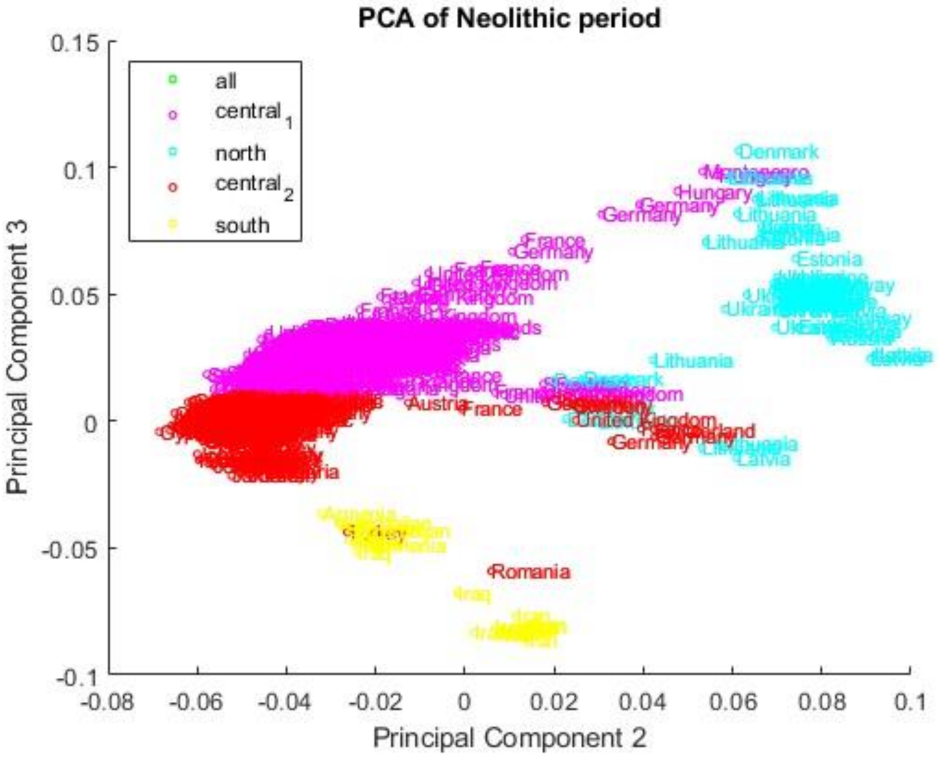


Figure 4. Principal component analysis of Neolithic populations (PC2 vs PC3)

The clustering of Neolithic individuals implied a few complications as the individuals from the same country often were more spread across the principal component axis. Therefore, the countries present in multiple clusters were divided based on the individual clustering within the principal components. Setting the principal component limits allowed for the separation of these individuals. The Neolithic samples date back to the date range of approximately 12,000 to 3000 years BCE.

The Chalcolithic period was grouped into five clusters: 'Uk-central', 'central', 'south', 'east 1' and 'east 2'. The UK-Central cluster contains 63 individuals from the United Kingdom, Poland, Spain and Ukraine. The central cluster is comprised of 229 individuals from the Czech

Republic, Poland, Spain, Portugal, Azerbaijan, Armenia, Iran, Russia, Turkmenistan and Ukraine. South cluster includes 158 individuals from Bulgaria, Serbia, Hungary, Albania, Romania, Cyprus, Croatia and Italy. 'East 1' and 'East 2' clusters encompass the countries of Turkey, Israel, Azerbaijan, Armenia, Iran, Russia, Turkmenistan and Ukraine. The 'East 1' cluster is comprised of 32 individuals, the 'East 2' cluster – 86.

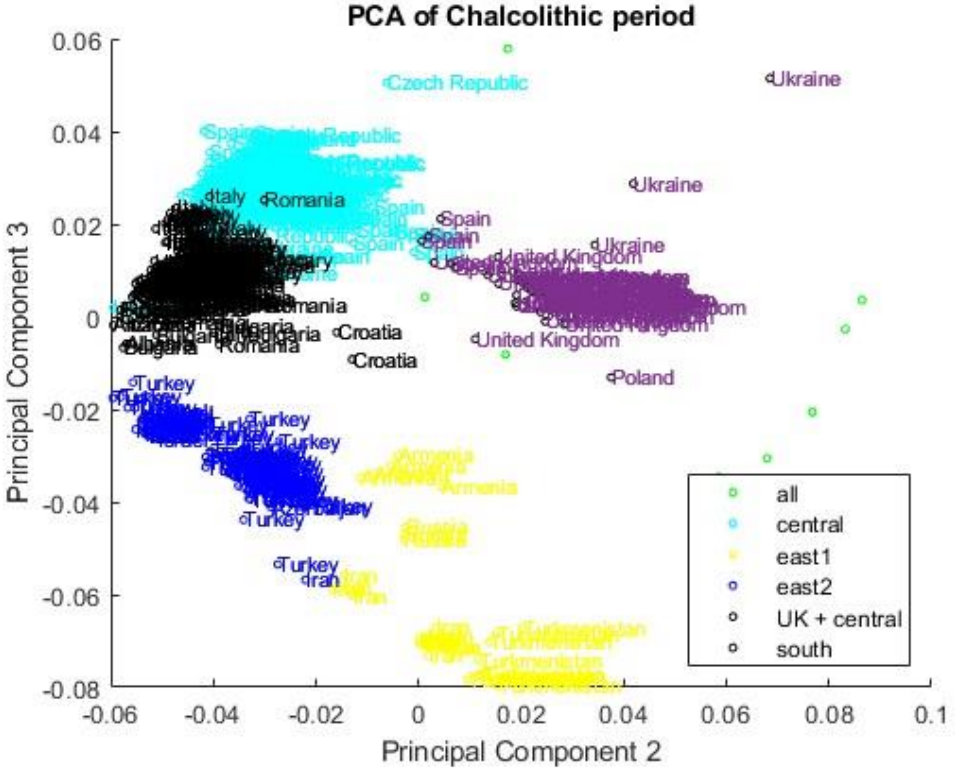


Figure 5. Principal component analysis of Chalcolithic period representing individuals (PC2 vs PC3)

The clusters of the Chalcolithic period were separated based on principal component 3, to allow for the division of the central and southern clusters. The other clusters are comprised of a slightly lower number of individuals, though they are more distinctively separated by the principal components. The samples are in the age range of 4700 to 2300 BCE.

The Bronze Age individuals were split into five clusters: 'east-north', 'east', 'east-south', 'central 1' and 'central 2'. The East-North cluster includes 48 individuals from Russia, Romania, Ukraine, Kazakhstan and Moldova, the East cluster - 176 individuals from Turkey, Syria, Israel, Iran, Armenia, Kazakhstan, Turkmenistan, and Russia. The cluster of East-South parts contains 152 individuals from countries of Turkey, Syria, Israel, Lebanon, Jordan and Iran. The 'central 1' cluster holds 666 individuals from Moldova, Romania, Kazakhstan, Czech Republic, United

Kingdom, Kazakhstan, Netherlands, Poland, Latvia, Estonia, Lithuania, Denmark, Germany, Ireland, Isle of Man, Norway, Sweden, Russia, Ukraine, Spain, Bulgaria, Croatia, North Macedonia, Serbia, Hungary, Albania, Montenegro, Slovenia, Italy, Switzerland, France, Gibraltar, Greece, Portugal. The 'central 2' cluster is composed of the same countries; however, it has a different PC axis range. This cluster includes 419 individuals.

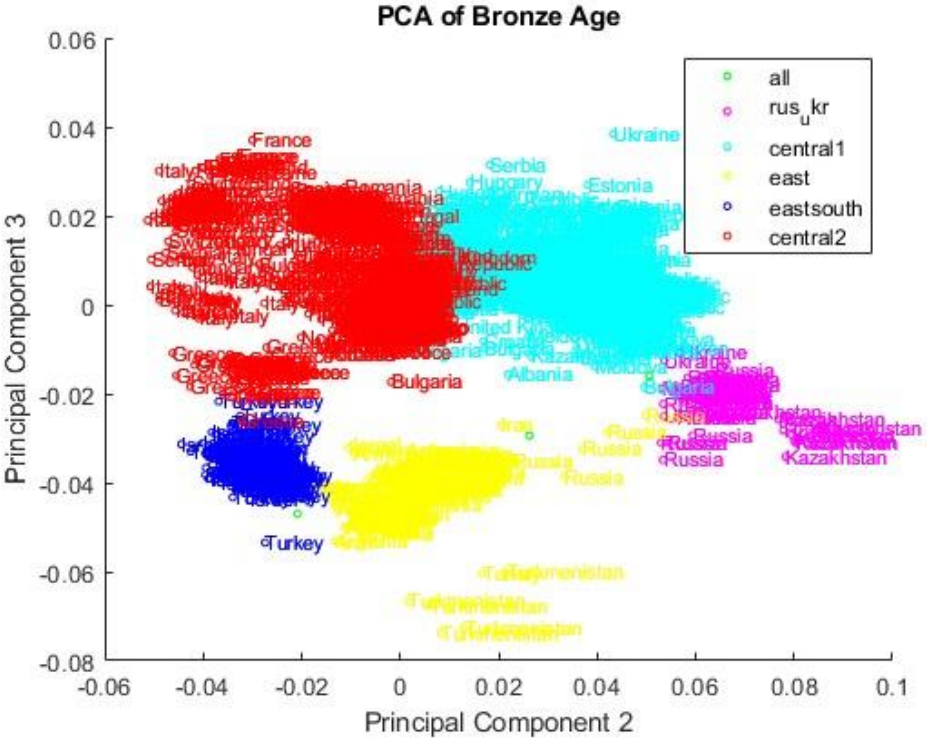


Figure 6. Principal component analysis of Bronze Age representing individuals (PC2 vs PC3)

The two central clusters of the Bronze Age period, depicted in red and light blue are separated by their values on the principal component 2 (x-axis), those with a lower score were included in the 'central_2' cluster in red and those with a higher value are in the 'central_1' cluster in light blue. The other three clusters were clearly distinct, therefore allowing for easier grouping. The Bronze Age samples date back to 3600 to 1200 BCE.

The individuals of the Iron Age were split into five clusters: an East cluster, a cluster of Kazakhstan individuals, 2 separate clusters of central regions, and a cluster of South regions. The East cluster incorporates 137 individuals from Armenia, Iran, Turkey and Israel. Both central region clusters contain individuals from Ukraine, Russia, Montenegro, Sweden, Norway, United Kingdom, Netherlands, Estonia, Finland, Denmark, Germany, Czech Republic, Austria, Slovakia, Hungary, Slovenia, Croatia, North Macedonia, Albania, Moldova, Italy, Spain and the Channel Islands. The individuals from these countries were separated into 2 clusters, based on the data point location in the principal component analysis. The first central cluster consists of 477 individuals, but the second one of 143 individuals.

The South cluster embodies Bulgaria, Greece, Italy, North Macedonia and Slovakia, together having 39 individuals.

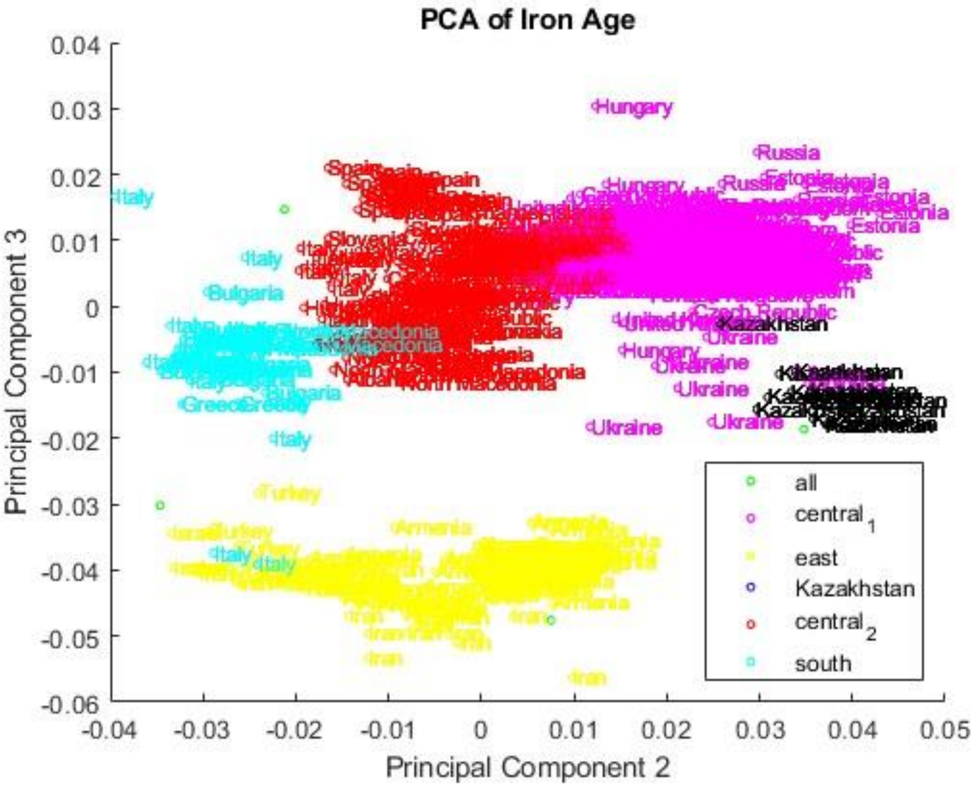


Figure 7. Principal component analysis of Iron Age representing individuals (PC2 vs PC3)

The largest clusters of Iron Age populations - 'central_1' and 'central_2' were separated by the second principal component limits. A smaller cluster of the Kazakhstan individuals was created as it formed a distinct group, however, in further analysis, it didn't pass the set threshold levels for the number of individuals having the peak genetic variants for the selected phenotypes. These samples date back to approximately 1200 to 350 BCE.

The last group of the Modern Age populations was divided into five clusters: a distinct cluster of a group of individuals from Russia, being apart from the other individuals of Russia in the PCA, a cluster of individuals from Italy regions, a cluster of central countries, a cluster of South regions and a cluster of East regions.

The central cluster includes 106 individuals from the countries: Finland, Estonia, Russia, Iceland, Czech Republic, Poland, United Kingdom, Hungary, Bulgaria, Spain, France, Greece, Albania and Italy. The South cluster consists of 212 people, representing the countries of Bulgaria, Spain, France, Greece, Albania and Italy. The East cluster describes the 137 individuals from Israel, Jordan, Iraq, Abkhazia, Armenia, Georgia, Iran, Jordan and Turkey.

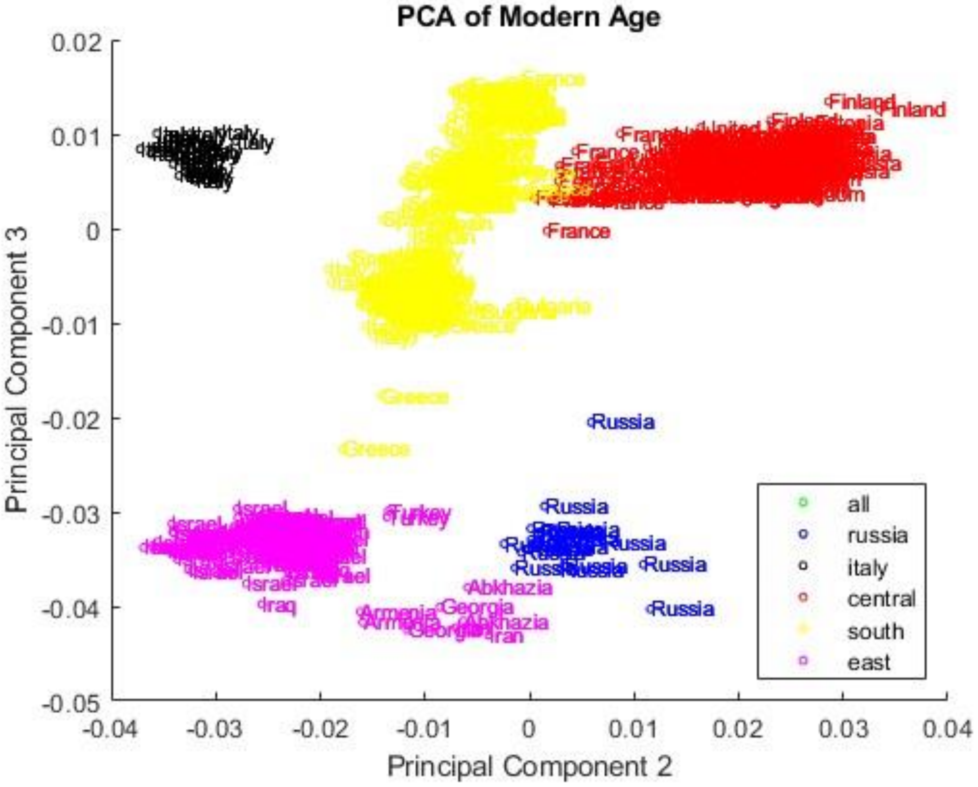


Figure 8. Principal component analysis of Modern-day populations (PC2 vs PC3)

The clustering of modern-day populations resulted in five clearly distinct groups, as the principal component analysis above reflects.

In total 27 clusters were created, the number of individuals per cluster varying. The linkage analysis and PCA of all the traits was performed based on the retained 19 clusters filtered for those that have at least 10 individuals with data for all the peak genetic variant positions of all the personality traits.

3.2.2 Personality trait PGS in Holocene populations

This section presents the results from the fine mapping of the personality traits. Firstly, a threshold for significance level was determined, followed by filtering the surroundings of the variants with the highest association.

The threshold was chosen based on the inflation factor lambda, indicating a diversion from the expected and observed statistic (explained in Methods 3.1.3). For filtering the genetic variants associated with agreeableness, the 'Lp' value threshold chosen was 3.5. After removing the surrounding variants within 500 kilobases, there remained 70 peak variants.

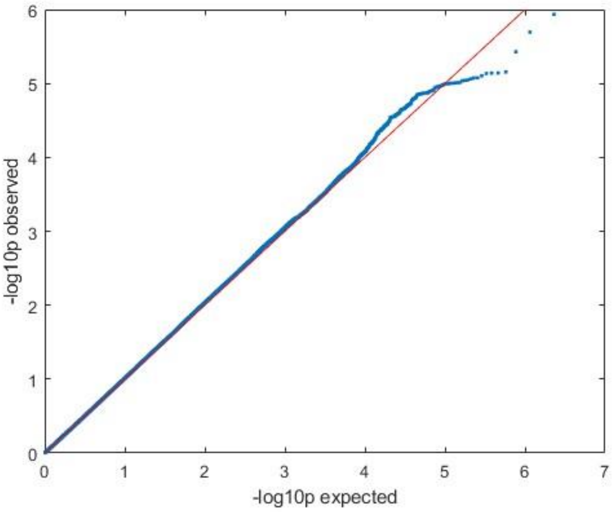
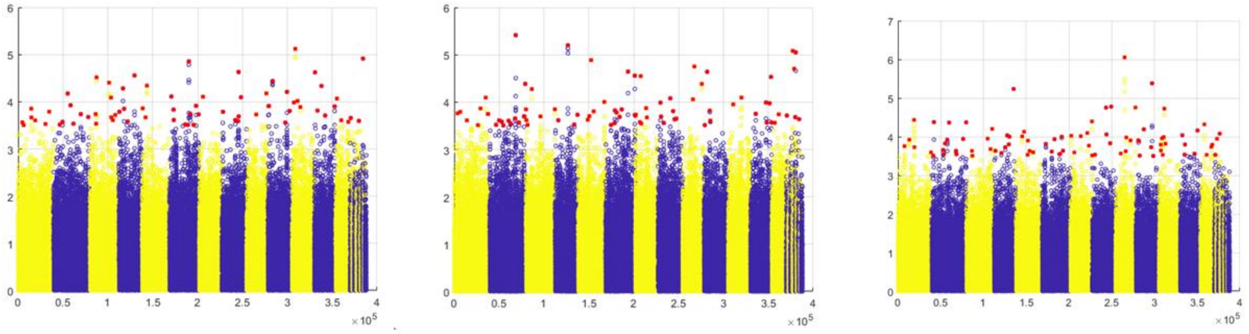
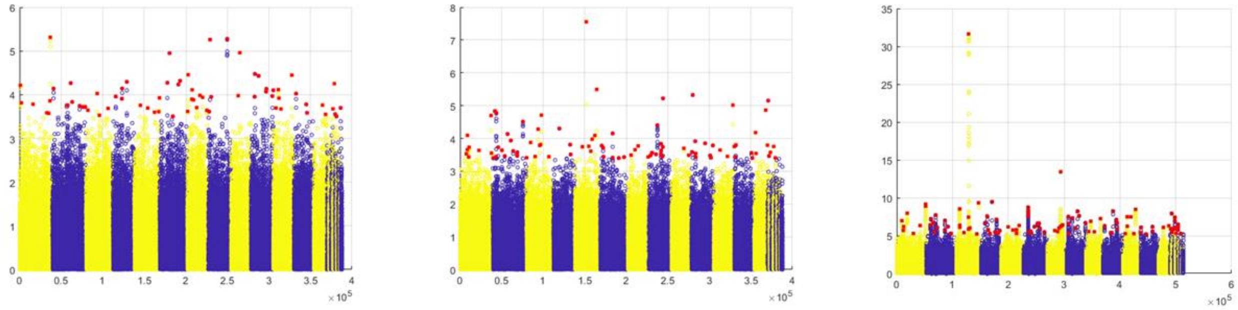


Figure 9. Q-Q plot of expected vs observed trend for agreeableness trait

For the conscientiousness trait, the 'Lp' value threshold chosen was also 3.5 with 80 peak variants remaining, for extraversion and neuroticism the same threshold was applied with 85 peaks and 70 peaks detected for the traits.



Agreeableness **Conscientiousness** **Extraversion**



Neuroticism **Openness to experience** **Risk-taking**

Figure 10. Fine mapping results for the personality traits. *The peak genetic variants that surpass the threshold for significance are displayed in red. The colours of the chromosomes alternate to indicate the start of the next chromosome. The y-axis corresponds to the –log10(p-value)*

For the behaviour of openness to experience the 'Lp' threshold was chosen slightly lower – 3.4, due to an earlier deviation of the observed data from the expected. 88 peak variants were selected. The risk-taking data included more genetic variants, therefore the 'Lp' threshold chosen was considerably higher – 5.2, resulting in 110 peak variants for further analysis.

3.2.3 PGS clustering analyses

The selected peak variants were used in the calculations of polygenic scores of the traits. For the trait of risk-taking, the PGS range across different populations was relatively small contrary to the range observed for the other personality dimensions. Some traits exhibited negative scores, with larger deviations from zero, such as openness to experience, others resulted in positive PGS, with smaller or bigger deviations from zero, for example, extraversion and neuroticism.

A negative mean PGS indicates that the combined effects of the peak genetic variants affecting the trait are associated with a lower relative value of the trait and the phenotype being less expressed compared to the general population (Sud et al., 2023). The higher the value of the

PGS, the greater the genetic predisposition to the trait. A larger negative value of the PGS signifies a more reduced susceptibility to a trait (*Polygenic Risk Scores*, n.d.).

Afterwards, the obtained PGS scores were used to assess the relationships between the populations and the complex behavioural traits.

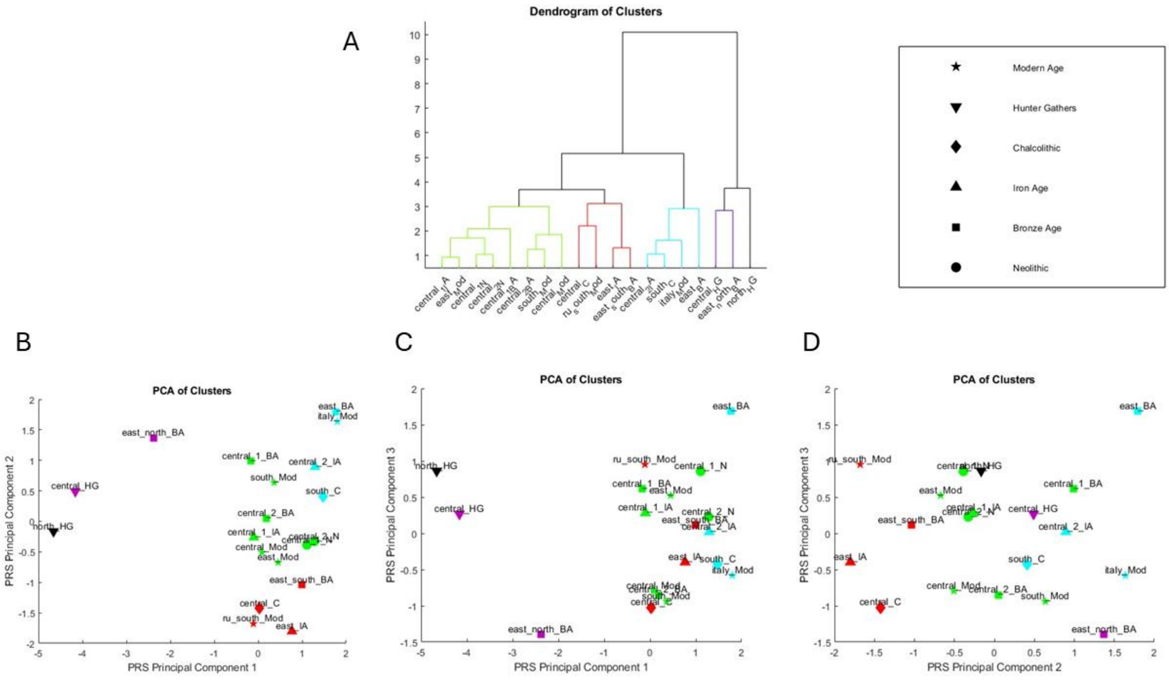


Figure 11. Principal component and linkage analysis of the clusters *(A – linkage analysis, B (PC1 vs PC2), C (PC1 vs PC3), D (PC2 vs PC3) - principal component analysis)*

The dendrogram depicted in panel A (Figure 11 A) separates the clusters into five groups. The length of the branches indicates how closely related are the clusters. The biggest group in the dendrogram, with branches of green colour, largely consists of central-western regions from various time periods from the Neolithic to modern-day clusters. The second cluster group of branches highlighted in red, is predominantly a group of East-South location clusters from the periods of the Chalcolithic to Modern-age. The third group in light blue is comprised of 4 clusters of southern Chalcolithic, Modern-day Italian individuals, central-western Iron Age and eastern Bronze Age individuals. The two smallest groups, displayed on the right of the dendrogram, reflect the outliers. The outliers are both the central and northern hunter-gatherer clusters, as well as the eastern-northern Bronze Age cluster.

The panels below (Figure 11 B, C, D) show the results of cluster analyses for the personality traits. The different time periods are depicted with distinct symbols. The same colours of the branches in the dendrogram were used for the corresponding clusters in the PCA. The first principal component separates the two outlier groups from the rest of the clusters, the second principal component separates the other groups. The second cluster group, highlighted in red, reflect populations with lower principal component two values, the group of lighter blue branches, has higher principal component two values. The largest group of central-western clusters with green branches has PC2 values residing in the middle of the axis.

The Modern Age clusters, indicated with a star symbol show an increase in the PC2 value for the southern populations, similar to the Chalcolithic clusters. For the Iron Age period, the PC2 is higher for the central/western regions than for the eastern regions. Evidently, the Neolithic, Iron Age and Bronze Age, as well as the Modern Age central clusters are predominantly located in closer proximity to each other similar to the dendrogram.

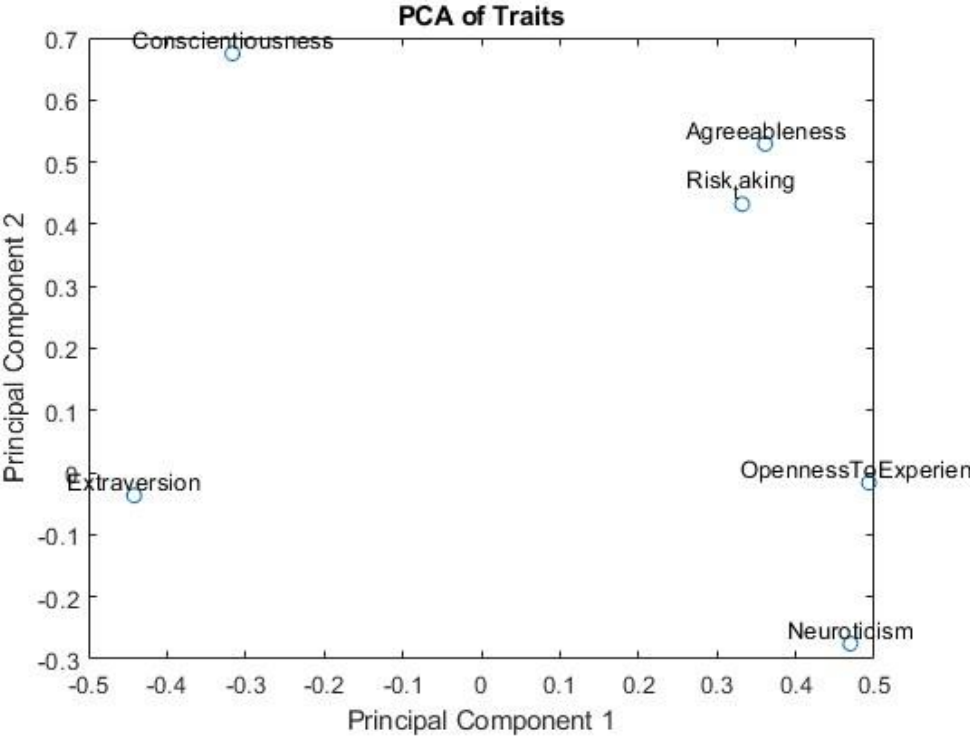


Figure 12. Principal component analysis of the personality traits (PC1 vs PC2)

The principal component analysis of the personality traits separates the traits into four groups. Group one consisting of neuroticism and openness to experience traits, group two – agreeableness and risk-taking, and groups three and four are formed from the traits of conscientiousness and extraversion. The closest related traits according to this analysis are agreeableness and risk-taking. The least correlated ones are neuroticism and conscientiousness.

The key trends in the personality trait shifts and the main outlier populations are presented in the heatmap (Figure 13). On the heatmap, one can also observe which trait expression is more varied between the populations and which ones are relatively similarly expressed.

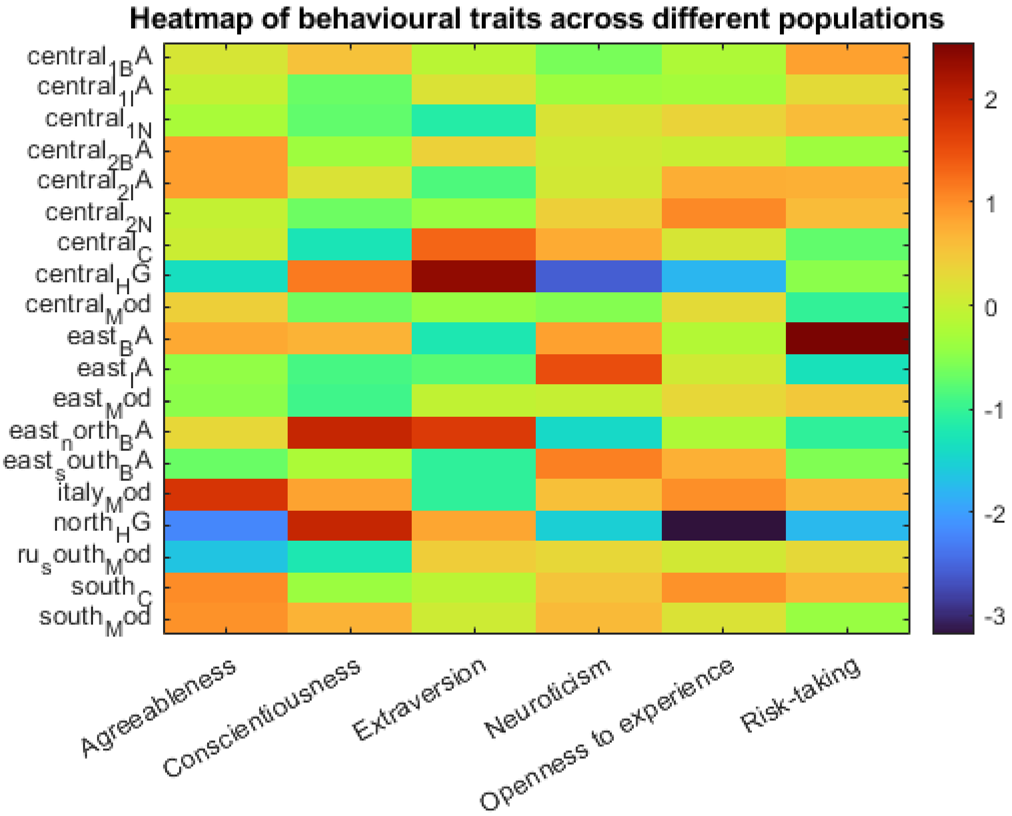


Figure 13. Heatmap of the expression of complex behavioural phenotypes in different populations (based on their normalized PGS scores). The scores below zero (fields in blue and green) indicate a lower susceptibility to the trait, and scores above zero (fields in orange and red) indicate a higher predicted genetic predisposition to the trait.

One of the first details that stands out is the relatively lower score in openness to experience for the northern and central hunter-gatherer populations. The highest score for this trait belongs to the central-western Neolithic cluster 'central - 2'. Within the agreeableness column, the relatively highest score is indicated for the Modern-day population of Italy, followed by the central populations of the Bronze Age and Iron Age, as well as the Modern Age southern cluster and the south Chalcolithic cluster. The lowest agreeableness score is indicated for the North hunter-gatherer cluster.

Looking at the conscientiousness column, the East-North Bronze Age and the North hunter-gatherer populations score the highest. The central hunter-gatherer population has also obtained a relatively high score. The lowest score is for the central Chalcolithic cluster. Evaluating the trait of extraversion, central hunter-gatherers stand out in the heatmap as ranking highest across the populations, with the central Chalcolithic and East-North Bronze age populations being at the top as well. The Bronze Age East cluster has obtained the relatively lowest mean PGS value in comparison to the other clusters. For the neuroticism trait, the East Iron Age populations reflect the strongest susceptibility to the trait, however the central hunter-gatherers – the lowest. The relative difference in mean PGS for neuroticism is quite large. For the last trait of risk-taking, the relatively highest PGS is for the East Bronze Age cluster. The mean PGS for this cluster is considerably larger compared to all of the other populations. The northern hunter-gatherers have obtained the relatively lowest score for risk-taking.

Figures 14 - 19 show the polygenic scores for the six personality traits in Holocene populations throughout time, with separate panels in each figure for different geographical regions (for clarity). Each population and trait is represented as a box where the horizontal range corresponds to the time span of the individuals in the population and the vertical range corresponds to the bootstrapped distribution of trait PGS (see Materials and Methods for details).

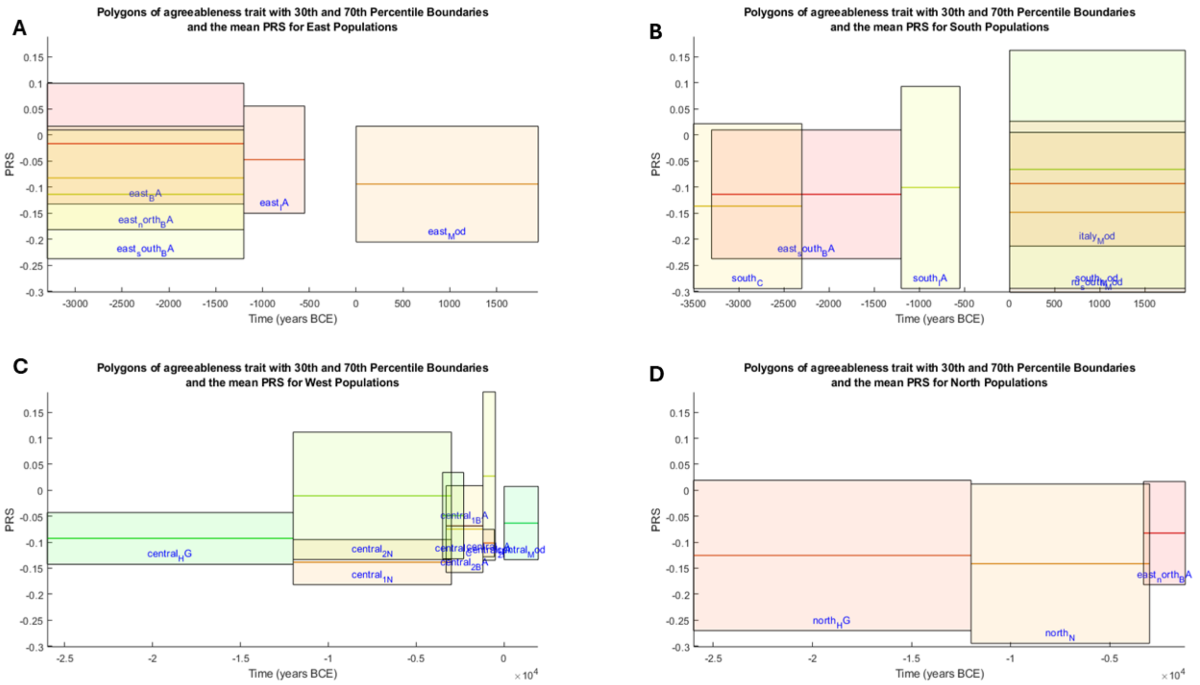


Figure 14. Polygenic score changes over time in different populations for agreeableness trait (*A – East populations, B - South populations, C – West populations, D – North populations)*

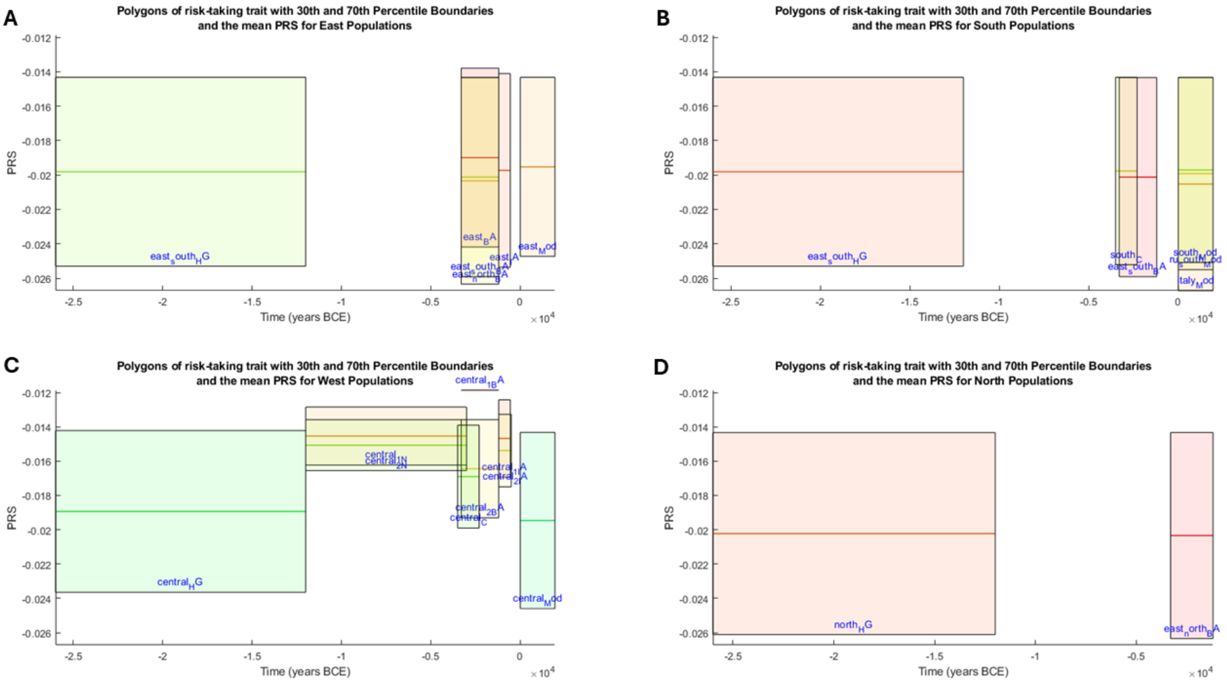


Figure 15. Polygenic score changes over time in different populations for risk-taking (*A – East populations, B - South populations, C – West populations, D – North populations)*

The results from the t-tests performed indicate significant shifts in the PGS for the personality traits across most of the time periods. Each one of the traits was separately analysed for changes within all of the transitional periods.

Starting from the agreeableness trait, the central Neolithic regions and the central hunter-gatherer populations highly differ in their mean PRS for agreeableness. According to the results, there is a significant increase in the agreeableness trait when transitioning to the Neolithic period. Moreover, the results of PGS show a continuation of the significant increase in the agreeableness trait afterwards in the Chalcolithic populations compared to the Neolithic. The comparison of Bronze Age and Chalcolithic individual scores in agreeableness reveals again an increase in the central and western regions. From the the Bronze Age onwards, transitioning into the Iron Age, the agreeableness seems to significantly increase in many central and eastern regions, however, some regions of Europe show a decrease in the trait during the Iron Age. After the Iron Age, the data shows varied results based on population geographic location. In the eastern regions, there seems not to be a significant change, in the southern regions a significant increase is detected, in the western and central regions the changes are significant, with some regions showing an increase in the trait, but others – a decline.

When analysing the shifts in PGS for the behaviour of risk-taking was observed an increase in the trait in the Neolithic populations after hunter-gatherers in central and western regions. The increase in the Neolithic period is followed by a decrease in the Chalcolithic time. The score of risk-taking is comparatively higher in the southern Chalcolithic cluster. The Bronze Age central clusters signal of higher risk-taking behaviour, even higher in the eastern cluster. The Iron Age and Bronze Age scores vary across the regions. The highest risk-taking scores among all the clusters are for the eastern Bronze Age and southern modern-day clusters.

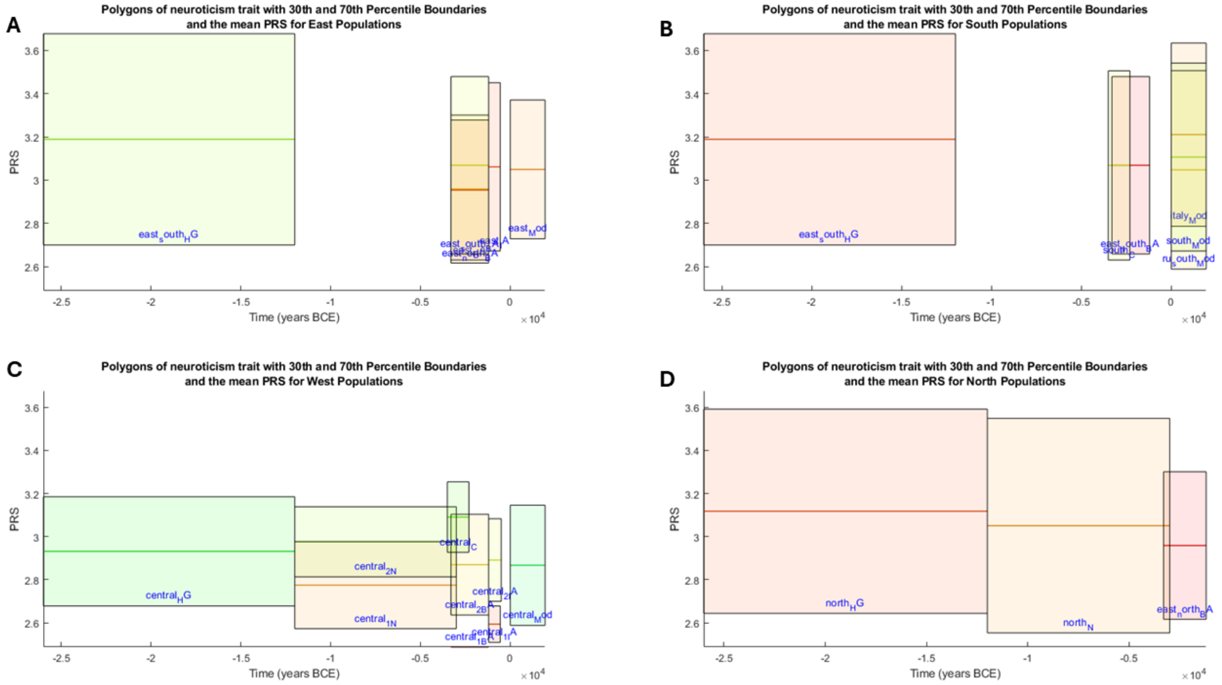


Figure 16. The PGS changes over time in different populations for neuroticism trait (*A – East populations, B - South populations, C – West populations, D – North populations*)

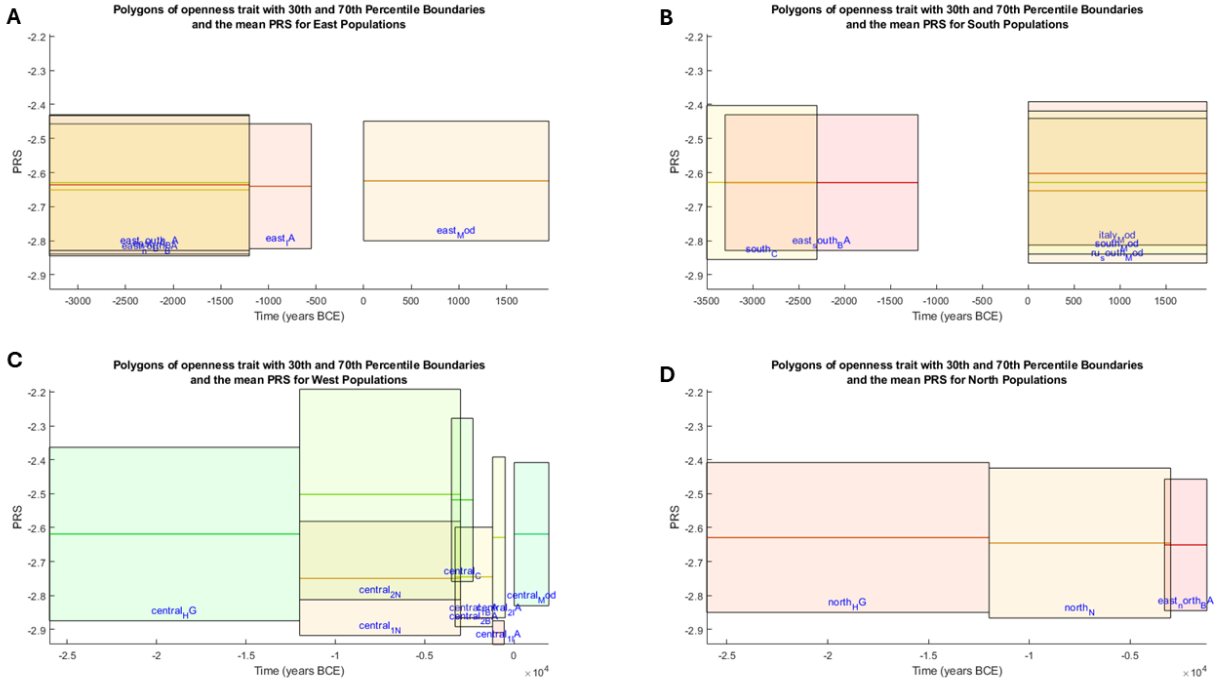
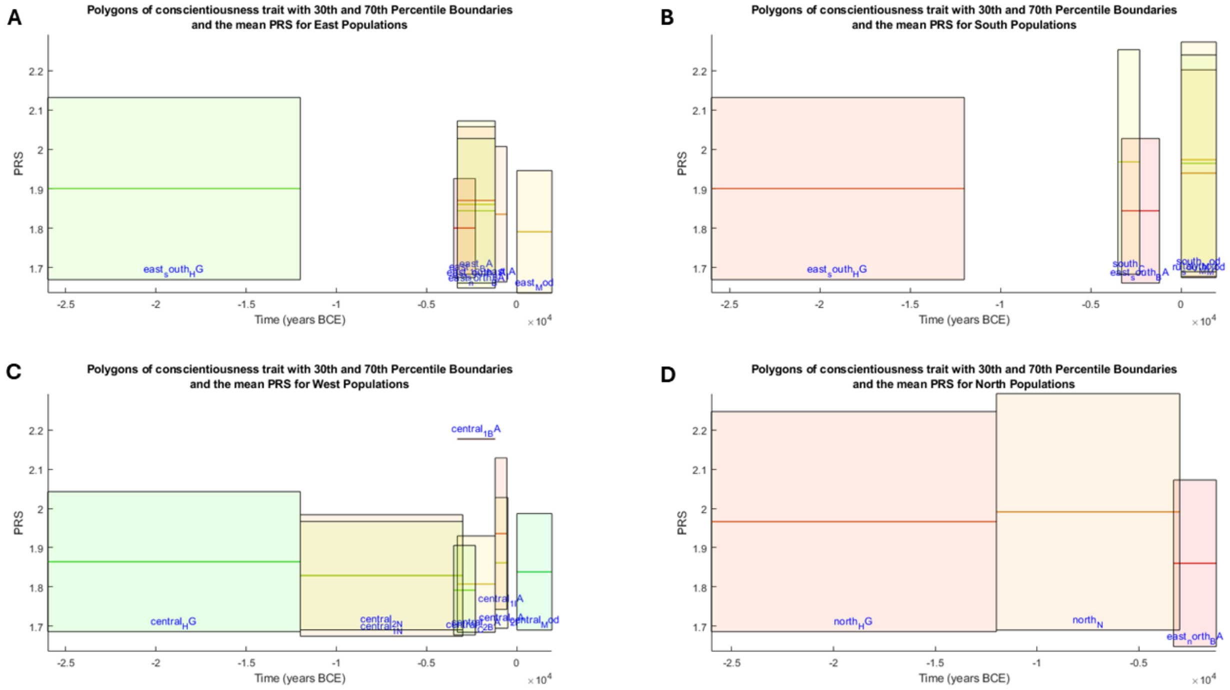


Figure 17. The PGS changes over time in different populations for openness to experience (*A – East populations, B - South populations, C – West populations, D – North populations*)

A relatively very low level of neuroticism was detected in the central and western hunter-gatherer populations, compared to the other clusters. In the t-tests, a massive increase in the trait was observed with the Neolithic transition. A contrasting result was obtained for the northern regions. The North hunter-gatherer cluster exhibits higher levels of neuroticism compared to the North Neolithic. A significant increase in the trait further was seen in the Chalcolithic period when analysing the central-western regions. The Bronze Age scores within the same regions are significantly lower than those of Chalcolithic. The shift in Iron Age is not that significant – the neuroticism scores remain approximately the same, except for the eastern region, where a significant increase is detected. In the modern-day individual results, the neuroticism scores are lower than in the Iron Age in the central, western and eastern regions.

The central hunter-gatherer populations show a significantly lower openness to experience than Neolithic. The North hunter-gatherer populations obtained the lowest score in the trait across all of the clusters, as seen in the heatmap as well (Figure 13). With the transition from the Neolithic to the Chalcolithic period the openness to experience significantly declined. However, the South Chalcolithic cluster shows a higher openness to experience score. The Bronze Age PGS show an even further decrease in this trait after the Chalcolithic period within the central and western regions. The PGS in the Bronze and Iron Age show a variation between different region clusters. The East-South cluster reflects the highest openness to experience behaviour within the Bronze Age. The Iron Age scores are not significantly different from the Bronze Age. There is a slight overall increase in the Modern Age populations.



A

Polygons of conscientiousness trait with 30th and 70th Percentile Boundaries and the mean PRS for East Populations

B

Polygons of conscientiousness trait with 30th and 70th Percentile Boundaries and the mean PRS for South Populations

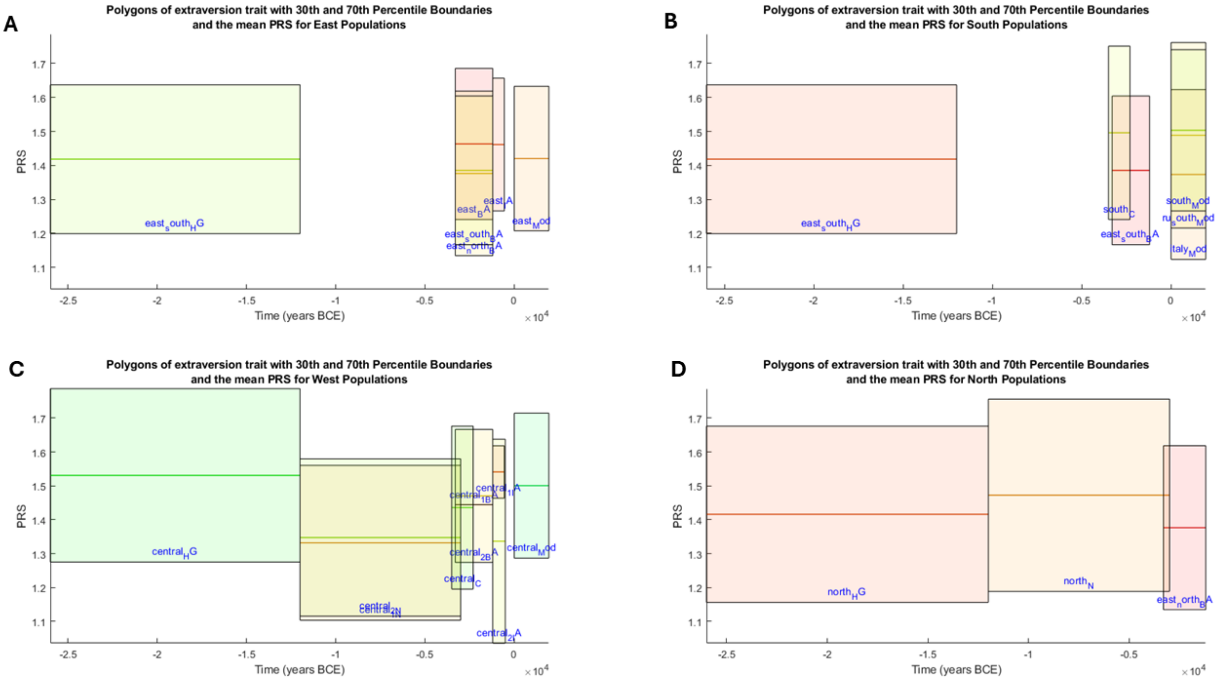
C

Polygons of conscientiousness trait with 30th and 70th Percentile Boundaries and the mean PRS for West Populations

D

Polygons of conscientiousness trait with 30th and 70th Percentile Boundaries and the mean PRS for North Populations

Figure 18. Polygenic score changes over time in different populations for conscientiousness trait (*A – East populations, B - South populations, C – West populations, D – North populations*)



A

Polygons of extraversion trait with 30th and 70th Percentile Boundaries and the mean PRS for East Populations

B

Polygons of extraversion trait with 30th and 70th Percentile Boundaries and the mean PRS for South Populations

C

Polygons of extraversion trait with 30th and 70th Percentile Boundaries and the mean PRS for West Populations

D

Polygons of extraversion trait with 30th and 70th Percentile Boundaries and the mean PRS for North Populations

Figure 19. Polygenic score changes over time in different populations for extroversion (*A –East populations, B - South populations, C – West populations, D – North populations*)

The results for the conscientiousness trait show a significant decline in the trait PGS with the transition from the Mesolithic period to the Neolithic period in the central and western regions. In the northern parts, however, there is an increase in conscientiousness in the Neolithic populations. The transition to Chalcolithic populations shows again a decline in the conscientiousness trait. However, in the Bronze Age within the analysed east, central and western regions, there is a significant increase. Afterwards, a variation between regions is observed. In some of the central regions, there is a decrease in conscientiousness PGS, in some – an increase, but in eastern parts a decline in the Iron Age period. When comparing the Modern Age scores with the Iron Age scores, the Iron Age shows higher values in conscientiousness, however, not in all regions they were significantly different.

The data shows a highly significant decrease in the extroversion trait from the central and western hunter-gatherer regions to central Neolithic. In the northern regions, the shift is not significant. A significant increase in extraversion was observed after the Neolithic period with the transition to the Chalcolithic period, the increase is mostly seen in the central and western regions. Furthermore, the scores for extraversion fluctuate between time periods. A decline in the PGS is detected in the Bronze Age and an increase in most regions in the Iron Age. These fluctuations are statistically significant. In some western and central regions, an increase in extraversion in the Modern Age is seen, in others – a decline. A highly significant decrease in extraversion was observed in the eastern cluster.

3.3 DISCUSSION

In this section, the results derived from the data analysis are discussed in the context of the main research objectives of the thesis. The linkage analysis resulted in the separation of the samples into five main groups. Two of the groups, being on a separate lead branch from the others, formed the outliers – northern, central hunter-gatherer and East-North Bronze Age clusters. Two of the outlier clusters are partially in the northern regions and the central-western European populations mainly cluster together, indicating a possibility of genetic variability in some personality traits based on the geographical location of the country.

The t-test results signal significant changes in polygenic scores between time periods, supporting the hypothesis of complex behavioural trait adaption throughout time. The results show a clear difference in the polygenic scores for the outlier hunter-gatherer populations. A significant shift is seen with the Mesolithic hunter-gatherer to Neolithic transition. Compared to the Neolithic populations, hunter-gatherers appear to be less agreeable, less open to experience and risk-taking, however more conscientious and extraverted. Some of these personality trait changes, such as an increase in agreeableness and risk-taking, seem to be compatible with a transition from a more individualistic to a more collective lifestyle.

Potential underlying factors of the hunter-gatherers being lower in the agreeableness score include the Neolithic transition to living in bigger agricultural communities, having different social dynamics and division of labour (*Neolithic | Definition & Facts*, 2024). The development of hierarchical structures could promote an increase in the expression of agreeableness trait. With higher pressure from society, the skill of cooperation is of higher value (Vásárhelyi & Scheuring, 2018). As the agreeableness trait PGS are increasing even more afterwards, the causes of the continuous increase could be the development of more complex societies with economic and cultural shifts as well as the bigger networks of trade (Golden, 2008). In the Bronze Age - the advancements in technology, the belief system changes and trades with non-locals might promote an increase in the agreeableness behaviour (Kneisel et al., 2019). The further development of the communities varies between regions; thus, the polygenic score changes onwards could differ based on the geographical locations. Perhaps, there was more stability in some regions after the Bronze Age, therefore, the selection pressure favouring this behavioural phenotype, not anymore as strong.

Evaluating the results of conscientiousness trait, the hunter-gatherers show higher conscientiousness levels, perhaps, due to the resilience and adaptability required in order to obtain food (Charles, 2020). With less hierarchical structures, more responsibility could be placed on every individual for the survival of the group. Comparing to the other time periods, the Neolithics might have a higher polygenic score for conscientiousness phenotype because of the pressure for agricultural shift and animal domestication.

The hunter-gatherers, living in smaller and closer groups, likely needed to socially interact with each other for their survival, which might be the cause of their higher score in extraversion compared to the Neolithics. The closeness of the group might enhance their survival and hunting and gathering activities. They probably shared the resources within the groups, indicating aspects of extraversion. The hunter-gatherer adaptability to changing environments could also contribute to their higher score. Perhaps the Neolithic communities had fewer social interactions, having more stratified populations. The larger societies and with more complex networks might have contributed to the Chalcolithic higher score in extraversion compared to the Neolithic. While the Neolithics lived in more settled agricultural communities, Chalcolithic individuals' settlements varied more with the emergence of towns, facilitating more opportunities for social interactions (Golden, 2008). With urbanization in the Iron Age and the advancement in technology and culture sectors, an increase in a more extroverted behaviour could be apparent.

The central and western hunter-gatherer populations score incredibly lower in neuroticism compared to the other clusters. This might be due to close-knit relationships within their groups, the lack of hierarchy and competition and a deeper connection with nature. The Neolithics were more dependent on their crop yields, potential conflicts of the lands between growing and already established communities as well as weather unpredictability which might be the underlying factors to their higher neuroticism score (Fibiger et al., 2023). The shift of values to more materialistic things and status could also have contributed to neuroticism increase. As more stable communities were established with time and living conditions improved, the resulting neuroticism polygenic scores were slightly lower and stabilized in the Bronze Age. With the transition to the Modern Age, the neuroticism scores lowered. Perhaps, the improvements in health systems, technology and education could have facilitated the decrease.

The significantly lower score in openness to experience for the northern hunter-gathers might be due to the harsh northern environmental conditions, where certain practised routines might be preferred over exploration. The Neolithics engaged in trading with other people from various locations, thus receiving a more diverse cultural exposure (*Neolithic | Definition & Facts*, 2024). The Chalcolithic period shows a decline in openness to experience, possibly due to the Chalcolithic being more focused on specific copper metallurgy skills, rather than exploring new approaches. Perhaps, other environmental and cultural factors, such as specific traditions and belief systems contributed to the lack of openness to experience as well.

The risk-taking phenotype results indicated a rise in the polygenic scores during the Neolithic transition in the central-western regions. Possibly, some experimentation was required with the start of agricultural technologies and animal domestication. Selection might have favoured the behaviour of risk-taking in this period because innovative practices could benefit the survival as the crop yields depended also on the weather and other environmental factors (Bowles & Choi, 2019). The change to living a more settled lifestyle demands more long-term planning, which involves some uncertainties and risks. During the Chalcolithic period, certain farming techniques had been already established and become more reliable, perhaps facilitating the decrease in risk-taking during this time. With the rise of bronze metallurgy, stronger weapons could be made used in the conflicts, promoting warfare (*Bronze Age | Definition, History, Inventions, Tools, & Facts*, 2024). This could be one of the factors underlying the risk-taking increase during the Bronze Age.

Some cluster pairs, such as the East Bronze Age and Italy Modern-day cluster, are located closely in principal component space (Figure 11), however, they vary in some trait mean polygenic scores. The Italian populations' predicted scores are higher for mean agreeableness, conscientiousness and extraversion. A similar case is observed between the clusters of eastern Modern-day and central-western Modern-day individuals, with the second cluster signalling for higher extraversion, agreeableness and lower neuroticism and risk-taking. These findings are suggestive of natural selection, although this is not a formal test. The effects of natural selection on personality traits perhaps should be considered more directly in the future.

These results indicate that personality changes might be potentially adaptive, and they vary based on the geographical location. Some traits show more genetic variation throughout time, such as agreeableness, extraversion and neuroticism, although others, for example, risk-taking do not show as large variation. The results are, undoubtedly, affected by the number of genetic variants in the GWAS repositories used for the analysis. Risk-taking summary statistics included the highest number of SNPs, allowing the capturing of more positions from aDNA variants. One of the main challenges of this thesis has been finding good quality GWASs, therefore, if larger and better studies are published in the future it may be possible to get an even better insight into how complex traits have evolved.

The findings also signal complex trait variability due to environmental factors, such as the location a population has inhabited. As discussed in this chapter, the clusters in northern regions reflect contrasting personality trait adaptations to those populations in southern regions. One can conclude that the selection pressures in different environments and time periods vary, leading to an increase or decrease in certain behavioural trait expressions.

SUMMARY

This thesis explores how personality trait expression varies between different regions of Europe. The obtained polygenic scores indicate that changes in the evolution of personality traits are affected by the populations' location, as there are differences in the genetic scores across the clusters of the same time period but different parts of Europe. Six time periods were compared, and an observation was made that within most of the transitions of these periods, the shifts in the average personality traits were significant. This points out to some complex behavioural traits being favoured over others at certain time points, such as the increase of agreeableness trait throughout time. Certain environmental and cultural factors have driven these adaptations. The results show that the emergence of more complex societies, changes in the size of communities, technological advancements and cultural shifts could have influenced the key personality traits.

REFERENCES

Abdellaoui, A., & Verweij, K. J. H. (2021a). Dissecting polygenic signals from genome-wide association studies on human behaviour. In *Nature Human Behaviour* (Vol. 5, Issue 6, pp. 686–694). Nature Research. https://doi.org/10.1038/s41562-021-01110-y

Abdellaoui, A., & Verweij, K. J. H. (2021b). Dissecting polygenic signals from genome-wide association studies on human behaviour. In *Nature Human Behaviour* (Vol. 5, Issue 6, pp. 686–694). Nature Research. https://doi.org/10.1038/s41562-021-01110-y

Agglomerative hierarchical cluster tree - MATLAB linkage. (n.d.). https://www.mathworks.com/help/stats/linkage.html

Barry, C. J. S., Walker, V. M., Cheesman, R., Davey Smith, G., Morris, T. T., & Davies, N. M. (2022, November 25). How to estimate heritability: a guide for genetic epidemiologists. *International Journal of Epidemiology*, *52*(2), 624–632. https://doi.org/10.1093/ije/dyac224

Bayliss-Smith, T. (2004, January 1). *Hunting and Gathering Societies, Energy Flows in*. Elsevier eBooks. https://doi.org/10.1016/b0-12-176480-x/00003-6

Bolund, E. (2020). The challenge of measuring trade-offs in human life history research. *Evolution and Human Behavior*, *41*(6), 502–512. https://doi.org/10.1016/j.evolhumbehav.2020.09.003

Boyd, R., Schonmann, R. H., & Vicente, R. (2014, May). Hunter–Gatherer population structure and the evolution of contingent cooperation. *Evolution and Human Behavior*, *35*(3), 219–227. https://doi.org/10.1016/j.evolhumbehav.2014.02.002

Bowles, S., & Choi, J. K. (2019, October). The Neolithic Agricultural Revolution and the Origins of Private Property. *Journal of Political Economy*, *127*(5), 2186–2228. https://doi.org/10.1086/701789

Bronze Age | Definition, History, Inventions, Tools, & Facts. (2024, May 14). Encyclopedia Britannica. https://www.britannica.com/event/Bronze-Age

Brown, G. R., Dickins, T. E., Sear, R., & Laland, K. N. (2011). Evolutionary accounts of human behavioural diversity. In *Philosophical Transactions of the Royal Society B: Biological*

Sciences (Vol. 366, Issue 1563, pp. 313–324). Royal Society. https://doi.org/10.1098/rstb.2010.0267

Browse the IEU OpenGWAS project. (n.d.). https://gwas.mrcieu.ac.uk/datasets/

Charles, D. K. (2020, April 29). Hunter-Gatherer Adaptation and Resilience: A Bioarchaeological Perspective. DANIEL H. TEMPLE and CHRISTOPHER M. STOJANOWSKI, editors. 2019. Cambridge University Press, Cambridge. x + 395 pp. $99.99 (cloth), ISBN 978-1-107-18735-1. *American Antiquity*, *85*(3), 618–619. https://doi.org/10.1017/aaq.2020.31

Chen, C., Burton, M., Greenberger, E., & Dmitrieva, J. (1999, September). Population Migration and the Variation of Dopamine D4 Receptor (DRD4) Allele Frequencies Around the Globe. *Evolution and Human Behavior*, *20*(5), 309–324. https://doi.org/10.1016/s1090-5138(99)00015-x

Clifton, E. A. D., Perry, J. R. B., Imamura, F., Lotta, L. A., Brage, S., Forouhi, N. G., Griffin, S. J., Wareham, N. J., Ong, K. K., & Day, F. R. (2018). Genome–wide association study for risk taking propensity indicates shared pathways with body mass index. *Communications Biology*, *1*(1). https://doi.org/10.1038/s42003-018-0042-6

Climate Effects on Human Evolution. (2024, March 6). The Smithsonian Institution's Human Origins Program. https://humanorigins.si.edu/research/climate-and-human-evolution/climate-effects-human-evolution

Costa, P. T., Jr., & McCrae, R. R. (1992). Revised NEO Personality Inventory (NEO-PI-R) and NEO Five-Factor Inventory (NEO-FFI) professional manual. Odessa, FL: Psychological Assessment Resources.

Data management - PLINK 1.9. (n.d.). https://www.cog-genomics.org/plink/1.9/data#recodel

Donahoe, J. W. (2012, March). REFLECTIONS ON BEHAVIOR ANALYSIS AND EVOLUTIONARY BIOLOGY: A SELECTIVE REVIEW OF EVOLUTION SINCE DARWIN—THE FIRST 150 YEARS. EDITED BY M. A. BELL, D. J. FUTUYAMA, W. F. EANES, & J. S. LEVINTON. *Journal of the Experimental Analysis of Behavior*, *97*(2), 249–260. https://doi.org/10.1901/jeab.2012.97-249

De Moor, M. H. M., Costa, P. T., Terracciano, A., Krueger, R. F., De Geus, E. J. C., Toshiko, T., Penninx, B. W. J. H., Esko, T., Madden, P. A. F., Derringer, J., Amin, N., Willemsen, G., Hottenga, J. J., Distel, M. A., Uda, M., Sanna, S., Spinhoven, P., Hartman, C. A., Sullivan, P., … Boomsma, D. I. (2012a). Meta-analysis of genome-wide association studies for personality. *Molecular Psychiatry*, *17*(3), 337–349. https://doi.org/10.1038/mp.2010.128

De Moor, M. H. M., Costa, P. T., Terracciano, A., Krueger, R. F., De Geus, E. J. C., Toshiko, T., Penninx, B. W. J. H., Esko, T., Madden, P. A. F., Derringer, J., Amin, N., Willemsen, G., Hottenga, J. J., Distel, M. A., Uda, M., Sanna, S., Spinhoven, P., Hartman, C. A., Sullivan, P., … Boomsma, D. I. (2012b). Meta-analysis of genome-wide association studies for personality. *Molecular Psychiatry*, *17*(3), 337–349. https://doi.org/10.1038/mp.2010.128

Ember, C. R. (2020). *Hunter-Gatherers (Foragers)*.

Fibiger, L., Ahlström, T., Meyer, C., & Smith, M. (2023). Conflict, violence, and warfare among early farmers in Northwestern Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(4). https://doi.org/10.1073/pnas.2209481119

GABAergic Synapse Pathway - Creative Diagnostics. (n.d.). https://www.creative-diagnostics.com/gabaergic-synapse-pathway.htm

Golden, J. M. (2008). Asia, west: Southern levant, chalcolithic cultures. *Encyclopedia of Archaeology*, 900–903. https://doi.org/10.1016/B978-012373962-9.00051-0

Hellwege, J. N., Keaton, J. M., Giri, A., Gao, X., Velez Edwards, D. R., & Edwards, T. L. (2017, October). Population Stratification in Genetic Association Studies. *Current Protocols in Human Genetics*, *95*(1). https://doi.org/10.1002/cphg.48

Holzman, P. S. (2024, April 4). *Personality | Definition, Types, Nature, & Facts*. Encyclopedia Britannica. https://www.britannica.com/topic/personality

Homo sapiens | Meaning, Characteristics, & Evolution. (2024, May 9). Encyclopedia Britannica. https://www.britannica.com/topic/Homo-sapiens/Origin

Hopwood, C. J., Schwaba, T., Milfont, T. L., Sibley, C. G., & Bleidorn, W. (2021, May 17). Personality change and sustainability attitudes and behaviors. *European Journal of Personality*, *36*(5), 750–770. https://doi.org/10.1177/08902070211016260

Hunter-gatherer | Definition, Societies, & Facts. (2024, April 3). Encyclopedia Britannica. https://www.britannica.com/topic/hunter-gatherer

Jasinska, A. J., & Freimer, N. B. (2009). The complex genetic basis of simple behavior. *Journal of Biology*, *8*(8), 71. https://doi.org/10.1186/jbiol172

Johannesson, M., Laibson, D. I., Medland, S. E., Meyer, M. N., Pickrell, J. K., Esko, T., Krueger, R. F., Beauchamp, J. P., Koellinger, P. D., Benjamin, D. J., Bartels, M., Cesarini, D., Okbay, A., Baselmans, B. M. L., De Neve, J. E., Turley, P., Nivard, M. G., Fontana, M. A., Meddens, S. F. W., . . . Hofman, A. (2016, April 18). *Genetic variants associated with subjective well-being, depressive symptoms, and neuroticism identified through genome-wide analyses*. Nature Genetics. https://doi.org/10.1038/ng.3552

Kandler, C., Richter, J., & Zapko-Willmes, A. (2017, January 1). *Genetic Basis of Traits*. Springer eBooks. https://doi.org/10.1007/978-3-319-28099-8_1473-1

Kang, W., Steffens, F., Pineda, S., Widuch, K., & Malvaso, A. (2023, May 1). Personality traits and dimensions of mental health. *Scientific Reports*, *13*(1). https://doi.org/10.1038/s41598-023-33996-1

Karlsson Linnér, R., Biroli, P., Kong, E., Meddens, S. F. W., Wedow, R., Fontana, M. A., Lebreton, M., Tino, S. P., Abdellaoui, A., Hammerschlag, A. R., Nivard, M. G., Okbay, A., Rietveld, C. A., Timshel, P. N., Trzaskowski, M., Vlaming, R. de, Zünd, C. L., Bao, Y., Buzdugan, L., … Wagner, G. G. (2019). Genome-wide association analyses of risk tolerance and risky behaviors in over 1 million individuals identify hundreds of loci and shared genetic influences. *Nature Genetics*, *51*(2), 245–257. https://doi.org/10.1038/s41588-018-0309-3

Kneisel, J., Dörfler, W., Dreibrodt, S., Schaefer-Di Maida, S., & Feeser, I. (2019). Cultural change and population dynamics during the Bronze Age: Integrating archaeological and palaeoenvironmental evidence for Schleswig-Holstein, Northern Germany. *Holocene*, *29*(10), 1607–1621. https://doi.org/10.1177/0959683619857237

Kuijpers, Y., Domínguez-Andrés, J., Bakker, O. B., Gupta, M. K., Grasshoff, M., Xu, C. J., Joosten, L. A. B., Bertranpetit, J., Netea, M. G., & Li, Y. (2022). Evolutionary Trajectories of Complex Traits in European Populations of Modern Humans. *Frontiers in Genetics*, *13*. https://doi.org/10.3389/fgene.2022.833190

Lacombe, A., Dumper, K., Lovett, M., Perlmutter, M., Spielman, R. M., & Jenkins, W. (2022, August 1). *Personality and Behavior*. Pressbooks. https://louis.pressbooks.pub/intropsychology/chapter/personality-and-behavior/

Larsen, C. S. (2023, January 17). The past 12,000 years of behavior, adaptation, population, and evolution shaped who we are today. *Proceedings of the National Academy of Sciences*, *120*(4). https://doi.org/10.1073/pnas.2209613120

Lever, J., Krzywinski, M., & Altman, N. (2017). Points of Significance: Principal component analysis. In *Nature Methods* (Vol. 14, Issue 7, pp. 641–642). Nature Publishing Group. https://doi.org/10.1038/nmeth.4346

Lo, M. T., Hinds, D. A., Tung, J. Y., Franz, C., Fan, C. C., Wang, Y., Smeland, O. B., Schork, A., Holland, D., Kauppi, K., Sanyal, N., Escott-Price, V., Smith, D. J., O'Donovan, M., Stefansson, H., Bjornsdottir, G., Thorgeirsson, T. E., Stefansson, K., McEvoy, L. K., … Chen, C. H. (2017a). Genome-wide analyses for personality traits identify six genomic loci and show correlations with psychiatric disorders. *Nature Genetics*, *49*(1), 152–156. https://doi.org/10.1038/ng.3736

Luciano, M., Hagenaars, S. P., Davies, G., Hill, W. D., Clarke, T. K., Shirali, M., Harris, S. E., Marioni, R. E., Liewald, D. C., Fawns-Ritchie, C., Adams, M. J., Howard, D. M., Lewis, C. M., Gale, C. R., McIntosh, A. M., & Deary, I. J. (2018). Association analysis in over 329,000 individuals identifies 116 independent variants influencing neuroticism. *Nature Genetics*, *50*(1), 6–11. https://doi.org/10.1038/s41588-017-0013-8

Lyon, M., Andrews, S. J., Elsworth, B., Gaunt, T. R., Hemani, G., & Marcora, E. (2020, May 30). *The variant call format provides efficient and robust storage of GWAS summary statistics*. bioRxiv (Cold Spring Harbor Laboratory). https://doi.org/10.1101/2020.05.29.115824

Ma, Y., & Zhou, X. (2021, November 1). *Genetic prediction of complex traits with polygenic scores: a statistical review*. Trends in Genetics. https://doi.org/10.1016/j.tig.2021.06.004

Martin, J. S., Jaeggi, A. V., & Koski, S. E. (2023, January 1). *The social evolution of individual differences: Future directions for a comparative science of personality in social behavior*. Neuroscience & Biobehavioral Reviews/Neuroscience and Biobehavioral Reviews. https://doi.org/10.1016/j.neubiorev.2022.104980

Maier, R. M., Visscher, P. M., Robinson, M. R., & Wray, N. R. (2017, August 29). Embracing polygenicity: a review of methods and tools for psychiatric genetics research. *Psychological Medicine*, *48*(7), 1055–1067. https://doi.org/10.1017/s0033291717002318

Meisner, J., Liu, S., Huang, M., & Albrechtsen, A. (2021, January 18). *Large-scale inference of population structure in presence of missingness using PCA*. Bioinformatics. https://doi.org/10.1093/bioinformatics/btab027

Neolithic | Definition & Facts. (2024, May 21). Encyclopedia Britannica. https://www.britannica.com/event/Neolithic

Nettle, D. (2005). An evolutionary approach to the extraversion continuum. *Evolution and Human Behavior*, *26*(4), 363–373. https://doi.org/10.1016/J.EVOLHUMBEHAV.2004.12.004

Ni, G., Moser, G., Wray, N. R., Lee, S. H., Ripke, S., Neale, B. M., Corvin, A., Walters, J. T., Farh, K. H., Holmans, P. A., Lee, P., Bulik-Sullivan, B., Collier, D. A., Huang, H., Pers, T. H., Agartz, I., Agerbo, E., Albus, M., Alexander, M., . . . O'Donovan, M. C. (2018, June). Estimation of Genetic Correlation via Linkage Disequilibrium Score Regression and Genomic Restricted Maximum Likelihood. *The American Journal of Human Genetics*, *102*(6), 1185–1194. https://doi.org/10.1016/j.ajhg.2018.03.021

Onion, A. (2023, June 13). *Iron Age*. HISTORY. https://www.history.com/topics/pre-history/iron-age

Onion, A. (2023, August 10). *Bronze Age*. HISTORY. https://www.history.com/topics/pre-history/bronze-age

Page, A. E., Minter, T., Viguier, S., & Migliano, A. B. (2018, January). Hunter-gatherer health and development policy: How the promotion of sedentism worsens the Agta's health outcomes. *Social Science & Medicine*, *197*, 39–48. https://doi.org/10.1016/j.socscimed.2017.12.002

Piffer, D., & Kirkegaard, E. O. W. (2024, March 6). Evolutionary Trends of Polygenic Scores in European Populations From the Paleolithic to Modern Times. *Twin Research and Human Genetics*, 1–20. https://doi.org/10.1017/thg.2024.8

Polygenic Risk Scores. (n.d.). Genome.gov. https://www.genome.gov/Health/Genomics-and-Medicine/Polygenic-risk-scores

Rayner, J. G., Sturiale, S. L., & Bailey, N. W. (2022, February 26). The persistence and evolutionary consequences of vestigial behaviours. *Biological Reviews*, *97*(4), 1389–1407. https://doi.org/10.1111/brv.12847

Sallis, H., Smith, G. D., & Munafò, M. R. (2018a). Genetics of biologically based psychological differences. In *Philosophical Transactions of the Royal Society B: Biological Sciences* (Vol. 373, Issue 1744). Royal Society Publishing. https://doi.org/10.1098/rstb.2017.0162

Sallis, H., Smith, G. D., & Munafò, M. R. (2018b). Genetics of biologically based psychological differences. In *Philosophical Transactions of the Royal Society B: Biological*

Sciences (Vol. 373, Issue 1744). Royal Society Publishing. https://doi.org/10.1098/rstb.2017.0162

Sanchez-Roige, S., Gray, J. C., MacKillop, J., Chen, C. H., & Palmer, A. A. (2018). The genetics of human personality. In *Genes, Brain and Behavior* (Vol. 17, Issue 3). Blackwell Publishing Ltd. https://doi.org/10.1111/gbb.12439

Santostefano, F., Allegue, H., Garant, D., Bergeron, P., & Réale, D. (2021). Indirect genetic and environmental effects on behaviors, morphology, and life-history traits in a wild Eastern chipmunk population. *Evolution*, *75*(6), 1492–1512. https://doi.org/10.1111/evo.14232

Schultz, L. M., Merikangas, A. K., Ruparel, K., Jacquemont, S., Glahn, D. C., Gur, R. E., Barzilay, R., & Almasy, L. (2022, April). Stability of polygenic scores across discovery genome-wide association studies. *Human Genetics and Genomics Advances*, *3*(2), 100091. https://doi.org/10.1016/j.xhgg.2022.100091

Sheehan, M. J., Miller, C. H., Vogt, C. C., & Ligon, R. A. (2018a). Behavioral Evolution: Can You Dig It? In *Current Biology* (Vol. 28, Issue 1, pp. R19–R21). Cell Press. https://doi.org/10.1016/j.cub.2017.11.016

Sheehan, M. J., Miller, C. H., Vogt, C. C., & Ligon, R. A. (2018b). Behavioral Evolution: Can You Dig It? In *Current Biology* (Vol. 28, Issue 1, pp. R19–R21). Cell Press. https://doi.org/10.1016/j.cub.2017.11.016

Stangor, C., & Walinga, J. (2014, October 17). *12.1 Personality and Behaviour: Approaches and Measurement*. Pressbooks. https://opentextbc.ca/introductiontopsychology/chapter/11-1-personality-and-behavior-approaches-and-measurement/

Strawbridge, R. J., Ward, J., Cullen, B., Tunbridge, E. M., Hartz, S., Bierut, L., Horton, A., Bailey, M. E. S., Graham, N., Ferguson, A., Lyall, D. M., Mackay, D., Pidgeon, L. M., Cavanagh, J., Pell, J. P., O'Donovan, M., Escott-Price, V., Harrison, P. J., & Smith, D. J. (2018, February 2). Genome-wide analysis of self-reported risk-taking behaviour and cross-disorder genetic correlations in the UK Biobank cohort. *Translational Psychiatry*, *8*(1). https://doi.org/10.1038/s41398-017-0079-1

Sud, A., Horton, R. H., Hingorani, A. D., Tzoulaki, I., Turnbull, C., Houlston, R. S., & Lucassen, A. (2023, February 28). Realistic expectations are key to realising the benefits of polygenic scores. *BMJ*, e073149. https://doi.org/10.1136/bmj-2022-073149

Svizzero, S. (n.d.). *Farmers' spatial behaviour, demographic density dependence and the spread of Neolithic agriculture in Central Europe*. https://doi.org/10.4312/dp.42.8ï

Table 1 Item content of the NEO-FFI. Item numbering in the parentheses. . . (n.d.). ResearchGate. https://www.researchgate.net/figure/tem-content-of-the-NEO-FFI-Item-numbering-in-the-parentheses-corresponds-to-that-in-the_tbl1_258102996

Thurston, T. (2009). Unity and diversity in the European iron age: Out of the mists, some clarity? *Journal of Archaeological Research*, *17*(4), 347–423. https://doi.org/10.1007/s10814-009-9032-z

Trait: Risk taking - IEU OpenGWAS project. (n.d.). https://gwas.mrcieu.ac.uk/datasets/ukb-b-14147/

Tryon, C., Pobiner, B., & Kauffman, R. (2010, July 24). *Archaeology and Human Evolution*. Evolution. https://doi.org/10.1007/s12052-010-0246-9

Uffelmann, E., Huang, Q. Q., Munung, N. S., De Vries, J., Okada, Y., Martin, A. R., Martin, H. C., Lappalainen, T., & Posthuma, D. (2021, August 26). *Genome-wide association studies*. Nature Reviews Methods Primers. https://doi.org/10.1038/s43586-021-00056-9

Vásárhelyi, Z., & Scheuring, I. (2018). Behavioral Specialization During the Neolithic—An Evolutionary Model. *Frontiers in Sociology*, *3*. https://doi.org/10.3389/fsoc.2018.00035

Venkataraman, V. V., Kraft, T. S., Dominy, N. J., & Endicott, K. M. (2017, March 6). Hunter-gatherer residential mobility and the marginal value of rainforest patches. *Proceedings of the National Academy of Sciences*, *114*(12), 3097–3102. https://doi.org/10.1073/pnas.1617542114

Vernon, P. A., Jang, K. L., Harris, J. A., & McCarthy, J. M. (1997). Environmental predictors of personality differences: A twin and sibling study. *Journal of Personality and Social Psychology*, *72*(1), 177–183. https://doi.org/10.1037//0022-3514.72.1.177

Weiss, A. (2018a). Personality Traits: A View From the Animal Kingdom. *Journal of Personality*, *86*(1), 12–22. https://doi.org/10.1111/jopy.12310

Weiss, A. (2018b). Personality Traits: A View From the Animal Kingdom. *Journal of Personality*, *86*(1), 12–22. https://doi.org/10.1111/jopy.12310

Weissenkampen, J. D., Jiang, Y., Eckert, S., Jiang, B., Li, B., & Liu, D. J. (2019). Methods for the Analysis and Interpretation for Rare Variants Associated with Complex Traits. *Current Protocols in Human Genetics*, *101*(1). https://doi.org/10.1002/cphg.83

Appendix

Bootstrapping results

Agreeableness: 21 populations having more than 10 individuals for each peak variant.

Original PRS	**Mean bootstrap PRS (from 1000 iterations)**	**Populations**
-0.0667349200000001	-0.0653345448415639	central_1_BA
-0.128808720000000	-0.131502065025364	central_1_IA

-0.214612978000000	-0.220070659735143	central_1_N
0.197654690000000	0.188545576498448	central_2_BA
0.202672260000000	0.203348399163998	central_2_IA
-0.132658979400000	-0.140635458339852	central_2_N
-0.107275062000000	-0.110776772802785	central_C
-0.613320462000000	-0.621946949226122	central_HG
0.0272786439999996	0.0324199036064223	central_Mod
0.163147358000000	0.155963504984562	east_BA
-0.281662172000000	-0.282619690581343	east_IA
-0.291415566000000	-0.296092001994564	east_Mod
-0.00663162599999995	-0.0112449899697069	east_north_BA
-0.363354807999999	-0.359801206330561	east_south_BA
0.519815880000000	0.521749274692195	italy_Mod
-0.917041830000000	-0.932682061021701	north_HG
-0.816775786000000	-0.800156476875798	north_N
-0.714819250000000	-0.716252229545490	ru_south_Mod
0.246474240000000	0.248758171366833	south_C
0.122030364000000	0.148693435113829	south_IA
0.232153114000000	0.233412933775642	south_Mod

Conscientiousness: 22 populations having more than 10 individuals for each peak variant.

Original PRS	**Mean bootstrap PRS (from 1000 iterations)**	**Populations**
2.17742637800000	2.17769013831372	central_1_BA
1.68826186200000	1.69087181331418	central_1_IA
1.66526798400000	1.66816117091323	central_1_N
1.82225778400000	1.80927697817131	central_2_BA
2.03123991800000	2.02593294556364	central_2_IA
1.69163166400000	1.70053312616824	central_2_N

1.45016796600000	1.43956565897994	central_C
2.41410141200000	2.40754255705044	central_HG
1.70610746000000	1.70486433710131	central_Mod
1.57527276200000	1.54828990924486	east_1_C
2.23807668800000	2.22975241386181	east_BA
1.60255054200000	1.61921363325763	east_IA
1.59114876800000	1.60043962293099	east_Mod
2.73702534000000	2.69530766979830	east_north_BA
1.86293331000000	1.86854882444291	east_south_BA
2.44102873600000	2.44950901592634	east_south_HG
2.29347800000000	2.27854846046835	italy_Mod
2.73798801800000	2.69496426232796	north_HG
2.72692781400000	2.73136101585227	north_N
1.47297789600000	1.48474085485819	ru_south_Mod
1.80734001440000	1.80004538172649	south_C
2.23876668600000	2.24093373696655	south_Mod

Extraversion: 21 populations having more than 10 individuals for each peak variant.

Original PRS	**Mean bootstrap PRS (from 1000 iterations)**	**Populations**
1.44546819000000	1.44595307928092	central_1_BA
1.62589236400000	1.62476857182363	central_1_IA
0.875415222000000	0.878358177836069	central_1_N
1.73403891800000	1.73038000514585	central_2_BA
1.04049170200000	1.03514550467099	central_2_IA
1.29517001800000	1.28721654037678	central_2_N
2.26128751600000	2.26533503086694	central_C
2.86940005400000	2.86107415755182	central_HG
1.28076913400000	1.29524951996996	central_Mod
1.20469709200000	1.19685235290135	east_BA

1.59634014800000	1.58660463618921	east_IA
0.828636730000000	0.835434667993092	east_Mod
1.08743041800000	1.09055915079646	east_north_BA
1.48420937000000	1.50326969671469	east_south_BA
2.47950708200000	2.50667688253649	east_south_HG
0.929692260000000	0.937538207059445	italy_Mod
1.97384632000000	1.97693972189916	north_HG
1.97097914600000	1.93674985939190	north_N
1.76004683000000	1.75558463732838	ru_south_Mod
1.46013758600000	1.44811424995182	south_C
1.55312880000000	1.55181873840451	south_Mod

Neuroticism: 21 populations having more than 10 individuals for each peak variant.

Original PRS	**Mean bootstrap PRS (from 1000 iterations)**	**Populations**
2.48569588000000	2.47954281921347	central_1_BA
2.71094581600000	2.70258244873733	central_1_IA
3.16076603400000	3.13788559370961	central_1_N
3.07939222800000	3.09029793966824	central_2_BA
3.09835598000000	3.08728175977028	central_2_IA
3.38266116600000	3.36773353888783	central_2_N
3.69332159400000	3.71029322879641	central_C
0.739180512400001	0.738121910972544	central_HG
2.55579584000000	2.56457520069056	central_Mod
3.78162219800000	3.78931001278822	east_BA
4.35218667600000	4.36340848610170	east_IA
2.99667120600000	3.01547804252103	east_Mod
1.75563220200000	1.76416751730657	east_north_BA
4.00022138800000	4.00636356375910	east_south_BA

4.00437050400000	3.98805099759687	east_south_HG
3.52284118200000	3.50403802150075	italy_Mod
1.64787188000000	1.64780666807616	north_HG
1.53583394000000	1.53980935445733	north_N
3.29055509000000	3.30034386337357	ru_south_Mod
3.47943714200000	3.47013085981787	south_C
3.57913087600000	3.57845236710186	south_Mod

Openness to experience: 20 populations having more than 10 individuals for each peak variant. The third column shows the cluster, with ending indicating the corresponding time period. The countries belonging to each cluster are listed in the results section 1.

Original PRS	**Mean bootstrap PRS (from 1000 iterations)**	**Populations**
-2.87126261000000	-2.86892442874649	central_1_BA
-2.95080774600000	-2.95313493582614	central_1_IA
-2.39487496200000	-2.38964727738099	central_1_N
-2.69439346800000	-2.69313608846307	central_2_BA
-2.08955312200000	-2.09058707054615	central_2_IA
-1.86954654400000	-1.86663317418919	central_2_N
-2.58045419400000	-2.56764176543785	central_C
-4.13555880200000	-4.15876270812675	central_HG
-2.48166169600000	-2.48092676486363	central_Mod
-2.83008572400000	-2.85289522116225	east_BA
-2.64382926200000	-2.62966435362942	east_IA
-2.43883392000000	-2.44301432823596	east_Mod
-2.87848530000000	-2.85764024645394	east_north_BA
-2.12078121200000	-2.14802188794074	east_south_BA
-1.90209364000000	-1.89768034381066	italy_Mod
-5.25938154400000	-5.21902035377061	north_HG
-3.69136657200000	-3.69124868536281	north_N
-2.62358254600000	-2.63353797772828	ru_south_Mod

-1.91072020800000	-1.89826135241917	south_C
-2.54953536500000	-2.55135971489411	south_Mod

Risk-taking: 21 populations having more than 10 individuals for each peak variant

Original PRS	**Mean bootstrap PRS (from 1000 iterations)**	**Populations**
0.0592014176000000	-0.0118562738269999	central_1_BA
0.0586690666000000	-0.0175720039224571	central_1_IA
0.0536466274000000	-0.0142473563779329	central_1_N
0.0531903466000000	-0.0235766293984798	central_2_BA
0.0533901254000000	-0.0134888019185733	central_2_IA
0.0549906944000000	-0.0142868986660716	central_2_N
0.0536986762000000	-0.0274491214049275	central_C
0.0507840568000000	-0.0248332191838016	central_HG
0.0512365438000000	-0.0302947717257809	central_Mod
0.0556490006000000	0.00442880613577349	east_BA
0.0500760668000000	-0.0332112285474644	east_IA
0.0511818628000000	-0.0155872900475569	east_Mod
0.0545854432000000	-0.0302065747030062	east_north_BA
0.0530479790000000	-0.0257162915211041	east_south_BA
0.0534600300000001	-0.0148668481113489	italy_Mod
0.0740700164000000	-0.0372202562349649	north_HG
0.0630012368000000	-0.0192284743415238	north_N
0.0535828788000000	-0.0174022878088775	ru_south_Mod
0.0633718874000000	-0.0136912093596709	south_C
0.0445944678000000	-0.0240636516350201	south_IA
0.0549441412000000	0.0548093342727010	south_Mod

T-test results for changes in the historical period transitions for two independent mean PRS of the bootstrapped scores. An arrow up '↑' indicates an increase in the mean PRS throughout the transition. An arrow down '↓' indicates a decrease in the mean PRS throughout the transition. A p-value in red reflects non-significant changes. A p-value that is lower than 0.00001 can be consider as a very significant change.

Transition		**p-value**					
Cluster	**Cluster**	**Agreeableness**	**Conscientiousness**	**Extraversion**	**Neuroticism**	**Openness to experience**	**Risk-taking**
Central_HG	Central_1N	< .00001 ↑	<.00001 ↓	< .00001 ↓	< .00001 ↑	< .00001 ↑	< .00001 ↑
Central_HG	Central_2N	< .00001 ↑	<.00001 ↓	< .00001 ↓	< .00001 ↑	< .00001 ↑	< .00001 ↑
North_HG	North_N	.000459 ↑	.039045 ↑	.276881 ↓	.000663 ↓	< .00001 ↑	
Central_1N	Central_C	< .00001 ↑	<.00001 ↓	< .00001 ↑	< .00001 ↑	< .00001 ↓	< .00001 ↓
Central_2N	Central_C	.031041 ↑	<.00001 ↓	< .00001 ↑	< .00001 ↑	< .00001 ↓	< .00001 ↓
Central_C	Central_1BA	.000553 ↑	<.00001 ↑	< .00001 ↓	< .00001 ↓	< .00001 ↓	< .00001 ↑
Central_C	Central_2BA	< .00001 ↑	<.00001 ↑	< .00001 ↓	< .00001 ↓	< .00001 ↓	< .00001 ↑
East_C	East_BA		<.00001 ↑				
Central_1BA	Central_1IA	< .00001 ↓	<.00001 ↓	< .00001 ↑	< .00001 ↑	< .00001 ↓	< .00001 ↓
Central_2BA	Central_2IA	.093775 ↑	<.00001 ↑	< .00001 ↓	.327083 ↓	< .00001 ↑	< .00001 ↑
East_BA	East_IA	< .00001 ↓	<.00001 ↓	< .00001 ↑	< .00001 ↑	< .00001 ↑	< .00001 ↓
Central_1IA	Central_Mod	< .00001 ↑	.08501 ↑	< .00001 ↓	< .00001 ↓	< .00001 ↑	< .00001 ↓
Central_2IA	Central_Mod	< .00001 ↓	<.00001 ↓	< .00001 ↑	< .00001 ↓	< .00001 ↓	< .00001 ↓
East_IA	East_Mod	.22223 ↓	.271101 ↓	< .00001 ↓	< .00001 ↓	< .00001 ↑	< .00001 ↑
South_IA	South_Mod	.000016 ↓					

CODE AND COMMAND LINE PROMPT REPOSITORY:

https://github.com/kducena/THESIS_2024_Katrina_Ducena.git

NON-EXCLUSIVE LICENCE TO REPRODUCE THESIS AND MAKE THESIS PUBLIC

I, Katrīna Ducena,

(*author's name*)

1. herewith grant the University of Tartu a free permit (non-exclusive licence) to

reproduce, for the purpose of preservation, including for adding to the DSpace digital archives until the expiry of the term of copyright,

Evolution of genetic variation underpinning human personality reflects changing lifestyle and environments in the European Holocene,

(*title of thesis*)

supervised by Jon Anders Eriksson.

(*supervisor's name*)

2. I grant the University of Tartu a permit to make the work specified in p. 1 available to the public via the web environment of the University of Tartu, including via the DSpace digital archives, under the Creative Commons licence CC BY NC ND 3.0, which allows, by giving appropriate credit to the author, to reproduce, distribute the work and communicate it to the public, and prohibits the creation of derivative works and any commercial use of the work until the expiry of the term of copyright.

3. I am aware of the fact that the author retains the rights specified in p. 1 and 2.

4. I certify that granting the non-exclusive licence does not infringe other persons' intellectual property rights or rights arising from the personal data protection legislation.

Katrīna Ducena

22/05/2024