Environmental Change and the Emergence of Human Cognitive Variation

Callum Scott

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University of York

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Abstract

This thesis investigates whether the emergence of cognitive and psychological variability had a significant impact upon our species' evolution. It explores the extent of this diversity, and its effect upon our ability to adapt to new, changing or fluctuating environments. An agent based model (ABM) is used to investigate whether an example of psychological difference, variance in extraversion, may have had an effect upon a key event of our evolutionary history: our dispersal out of Africa. The results of this study suggest that our psychological differences likely had a large impact upon both our ability to adapt to new environments, inventiveness, and our dispersal ability. In particular, reproductive advantages associated with extraversion may have provided individuals with an advantage when dispersing, albeit offset by the disadvantages of an increased mortality rate. More broadly, recognition that populations are evolving, diverse, and subject to different selective pressures while dispersing may significantly change how we view our dispersal out of Africa. This thesis suggests that our psychological diversity is an important, underappreciated feature of our species, which may have had a large impact upon key events during our evolution.

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Author's Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

Thesis Format

Several of the chapters in this thesis (chapters 3-6) were written for publication. In order to aid the reader they have been edited so that they refer to one another. For consistency references and any supplementary materials are presented at the end of each chapter, and tables and figures are numbered for each chapter individually. My supervisor, Penny Spikins, is listed as a co-author on chapter 3, as she will be a co-author on the paper once submitted for publication. This is due to her involvement in the previous studies of autism referred to in this paper. She also provided helpful guidance on how to structure this chapter, but did not contribute to any of the text.

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Introduction

This thesis explores the importance of recognising our species' cognitive and psychological diversity when discussing our evolutionary history. This section introduces the significance of this research and how it may fill a large gap in archaeological and evolutionary literature. The aims and objectives of the project are then outlined. Following this, the definition of 'cognitive variability' to be used in this thesis is clarified, and a broader term 'psychological variability' is explained. Finally, why our psychological differences may be an important aspect of our evolutionary history, how they represent an important aspect of our evolvability, and how they may be partially responsible for our ability to inhabit novel and changing environments, will be introduced.

Context and Significance

The cognitive complexity of our species is regarded as one of the key features that makes humans distinctive from other animals. Although, there are other traits that add to our uniqueness (e.g. anatomical differences (Howale et al. 2014)). The development of social-cognitive skills (e.g. theory of mind and collective intelligence) (Boyd, Richerson and Henrich 2011; Herrmann et al. 2007; MacLean 2016; Tomasello and Rakoczy 2003), enhanced executive abilities (Ardila 2008), and the relational reinterpretation of perceived stimuli (Penn, Holyoak and Povinelli 2008), are just some of the uniquely evolved cognitive features ascribed to humans.

However, there are many heritable cognitive and psychological differences that lead to variable performance in these and other skills, and change our perception of and reactions to the world around us. By viewing human cognitive evolution as a single, rather than branching, progression, we ignore a wide range of human behaviour which may have significantly impacted our evolution. Further, we ignore the evolutionary history of large portions of the population who are neurodivergent. This may lead to some people feeling like they don't fit into the story of human evolution. Therefore, in order to create a complete picture of our evolution, we must account for our cognitive variability.

There are many different types of cognitive and psychological variation within our species that are currently not accounted for within our narrative of evolution. Not only is this an issue of inclusivity, but it ignores an important characteristic of our species, which may have had a significant impact on our ability to adapt to newly encountered and changing environments. Archaeologists and evolutionary anthropologists have largely explored the impacts of environmental change and variability upon ‘averaged’, identical individuals. This thesis offers a novel perspective, by exploring how our differences might have been important when adapting to new, changing, or variable environments. Our differences may have provided alternate ways of perceiving and reacting to the world. Particular phenotypes may have had advantages within different ecological settings, or when completing particular tasks. Consequently, our species’ ability to adapt to rapidly changing or fluctuating environments and accomplish global dispersal, may in part be due to our diversity and our ability to use that diversity to our advantage. Hence, our psychological diversity may have had a significant impact upon key events during our evolutionary past, which has thus far been unappreciated.

Aims

The aim of this thesis is to explore the impact the emergence of cognitive and psychological variability may have had upon our species’ ability to adapt to changing and new environments. The impact of personality variation will be a particular focus of this thesis, however the consequences of other forms of diversity will also be discussed. The effect of personality variation on human dispersal out of Africa will also be explored using an agent based model. This aims to explore whether particular variations in life history traits associated with personality types may be associated with the differential distribution of genes associated with these personalities.

Objectives

To achieve the aims of this study, the following objectives will be completed:

1. Literature regarding the methods used to classify personality traits will be reviewed. This will assess the validity of the personality factors identified by these studies and a personality trait (extraversion) will be selected to be used as a case study through the thesis (chapter 1).
2. A literature review of the genetic, neurological, and life history traits associated with extraversion will be conducted, with a discussion of the evolutionary implications (chapter 2).
3. An analysis will be conducted, exploring more broadly how cognitive variability may have been adaptive for our species, and the evolutionary mechanisms acting upon this (chapter 3).
4. The method agent based modelling (ABM) will be introduced and its history within archaeology will be reviewed. This will also explore previous studies that have used

ABM to investigate hominin dispersal and land use. A limitation of these studies will be identified and will be addressed when constructing the ABM for this thesis (chapter 4).

5. An ABM of human dispersal will be created. This will explore the effects resource variability and accessibility in different biomes may have had upon our ability to disperse (chapter 5).
6. Using the ABM of human dispersal as its basis, an ABM of extraversion and human dispersal will be developed, to explore the impact individuals' extraversion may have upon their ability to disperse (chapter 6).

Relating to these objectives, the project will be completed in several stages. Firstly, personality must be defined, and the methods used to taxonomise personality must be explored. Several popular taxonomies of personality have been produced: Cattell's 16 personality factors (Cattell 1943, 1973, 35–37, 1977, 30–48), Eysenck's PEN (Eysenck 1947; Eysenck et al. 1992), and The Big 5 (Fiske 1949; McCrae and Costa 1987; Tupes and Christal 1961). By exploring the history of these taxonomies it will allow us to identify whether the aims of different researchers have impacted their results, when identifying personality factors. It also gives us a broader view of how diverse personality is, how personality affects the life history of individuals, and also how evolution may act upon these traits. The life history traits and evolutionary implications of the primary personality traits identified by these taxonomies will be briefly reviewed. Further, it allows us to determine the reliability of different personality factors in order to select an example trait for use as a case study.

Secondly, the chosen example personality trait (extraversion) will be explored in more depth. By exploring the genetic and neurological causes of extraversion, as well as its associated life history traits, this will provide the information needed to be input into the ABM. Further, it will introduce existing evolutionary theories related to extraversion, which may be evaluated later in the thesis.

Thirdly, the effects of cognitive and psychological variability upon our species will be discussed more broadly. This will define several established evolutionary mechanisms (balancing selection, green beard effect, multilevel selection) and discuss their impact upon our species' cognitive variability (see chapter 3 section 2). A mechanism for how psychological variability may have increased through our evolution will be produced. This will be discussed in relation to two case studies: extraversion and local processing bias. By discussing the effects of a personality trait, and a broader cognitive trait, this will highlight how different types of psychological diversity may have had a significant effect upon our evolution and the conditions under which this diversity may have thrived and increased.

Fourth, in order to introduce ABM, the history of its use in archaeology will be reviewed. This will critique the methodology, address misconceptions about the methodology held by archaeologists, and explore the benefits of using ABM. The reasons for its relatively limited use in archaeology and its negative reputation will be explained, and persisting difficulties in using ABM in archaeology will be addressed. The ways ABM has been used to investigate two archaeological topics relevant to this study (dispersal and land use) will be also reviewed. This will explore whether models researching the same topics using different methods produce congruent results. The versatility of the method and its ability to highlight different aspects of a problem are also shown, thus justifying its use in this study. This review will also help identify methods that may be applied to the current model, and improvements that may be made to further research in the two topics above.

Fifth, an out of Africa model of dispersal will be made. This will utilize the information gathered from the previous objective, as well as ethnographic and archaeological data. To further the work of previous ABMs, the amount of resources hunter gatherers can gather from different biomes will be estimated. This, as well as estimations of resource variability, will then be incorporated into the ABM to explore the effect resource accessibility has upon agents' ability to disperse.

Sixth, utilizing the information gathered in objectives one and two, a simplified representation of extraversion will be applied to the dispersal ABM. This will incorporate the primary life history effects of extraversion, as well as a genetic method of transmission. This will explore: 1) whether the life history traits associated with extraversion affect their ability to disperse, 2) whether geographic features producing population bottlenecks significantly affect the distribution of extraversion, 3) whether selection for extraversion is density dependent.

Lastly, the findings of this thesis will be discussed more broadly. The implications for our understanding of the impact of personality on dispersal, the evolution of psychological diversity, and our general understanding of human dispersal out of Africa will be discussed. The possible implications of other psychological differences than extraversion and local processing bias will be discussed, both in relation to our dispersal and our ability to adapt to different ecological settings.

The following sections will discuss some definitions to be used through the thesis, and will introduce why our psychological variability may have been an important aspect of our evolutionary history.

What are Cognitive and Psychological Variability?

Precise definitions of what is meant by cognitive variability may differ, but here it refers to differences in the way knowledge is acquired, processed and stored (Griffin, Guillette and Healy 2015). In this sense, cognition largely refers to intelligence and executive functions. This thesis discussed cognitive differences, such as differences in the way individuals with traits of autism process information. However, personality is also a particular focus of this thesis. Personality variation is in part caused by cognitive differences (see chapter 1); however it is also associated with dispositional and physiological differences which affect behaviour (Endler 2000; Stemmler and Wacker 2010). Therefore, where necessary these broader differences are described as ‘psychological’ or ‘behavioural’.

Why Might Cognitive and Psychological Variability be Important?

As noted above, humans exhibit high psychological variability. This variability likely increases our ability, at a population level, to adapt to different environments. This may be related to the concept of ‘evolvability’, taken from evolutionary biology. The evolvability of a species is its ability to produce adaptive, heritable phenotypic variation in response to selective pressures (Payne and Wagner 2019; Pigliucci 2008). Under conditions of environmental fluctuation or change, selection favours evolvability, and the ability of a species to produce phenotypic variation increases (Earl and Deem 2004). Our psychological differences may be the result of our high neurological evolvability (Eichler 2017). Our diversity may therefore have evolved in response to environmental and ecological changes taking place in the past, both anthropogenic and natural. The increasing complexity of social life, the material world and the exposure of our species to novel, changing and fluctuating environments may have led to conditions where no single psychological strategy was optimal. As a result, multiple psychological strategies, which are differently adapted to this complex, broad ecological niche, may have developed. Additionally, due to the structured, modular nature of these psychological differences, which are composed of a series of traits with high covariance, our ability to adapt to different environments may have increased, through evolution acting on a collection of traits simultaneously rather than a series of traits individually (Wolf and Weissing 2012). Therefore, our psychological diversity may have allowed us to adapt to a wide range of ecological contexts, but may also have provided a structure that evolution may efficiently act upon.

While there is still little recognition of the importance of our psychological differences to our evolutionary history, some studies have suggested ways in which particular cognitive and behavioural differences may have provided individuals with advantages within particular contexts or roles in the past (Armstrong 2015). For example, studies have explored the selective advantages associated with autism (Spikins 2013; Spikins and Wright 2016; Spikins, Wright and Hodgson 2016; Spikins, Scott and Wright 2017, 2018), dyslexia (Ehardt 2009; Kershner 2020b, 2020a), ADHD (Jensen et al. 1997; Williams and Taylor 2006) schizophrenia (Horrobin 1998; Kuttner, Lorincz and Swan 1967; Polimeni and Reiss 2002; Stevens and Price 2015) as well as personality differences (Buss 1991; Nettle 2005, 2006; Stone, Shackelford and Buss 2012). If people’s psychological traits provide them with advantages in different conditions, it suggests that our psychological diversity may be partially responsible for our ability to inhabit such a wide range of environments, and may have helped groups adapt to changing or fluctuating conditions. Further, if skills associated with particular traits make individuals more proficient at certain tasks, groups may have benefited from their skill, and groups composed of individuals with different ways of interacting with the world may have been more likely to develop novel solutions to problems.

Summary

In sum, despite a lack of recognition of its importance in current evolutionary narratives, cognitive and psychological variability may have been vital for our species’ ability to adapt to new, changing and fluctuating environments and ecological conditions. Therefore, this thesis will explore the nature of this diversity, by reviewing how individuals differ in personality (chapter 1 and 2). It will then explore the evolutionary mechanisms which act on and cause this diversity, as well as some of the advantages this diversity may have provided groups (chapter 3). An agent based model will then be produced to explore how an example of personality variation (extraversion) may have impacted a key event in our evolutionary history - our dispersal out of Africa (chapter 6). The findings of this thesis will then be discussed with a particular focus on (1) how psychological diversity may have affected our dispersal, (2) how our diversity evolved and how this may have helped us adapt to different ecological conditions, and (3) how this thesis affects the way we understand human dispersal more generally.

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Chapter 1: Personality and Cognitive Difference

Abstract

There are profound differences in the ways people think, feel and behave, the study of which is often subsumed under the topic of personality. Our species is composed of individuals with broad personality differences, however when discussing cognitive evolution, these differences are largely disregarded. Not only does this lead to a reductionist view of our psychological evolution, but it leads to many people who may think, feel or behave differently not being represented in our evolutionary narratives. As an example, this chapter reviews the concept of personality and explores how our personality traits may alter our life histories, and consequently our relationship with the selective pressures of our world. Firstly, a definition of personality is established. Secondly, how personality has been taxonomised is investigated. This shows that the number of personality traits identified varies according to researchers' aims or perspectives on personality, from as many as 4500 personality traits in early studies when the aim was to display our variety in personality, to as few as 3 when researchers were trying to condense the number of traits to their minimum number of factors. This reductionism may mask some of the complexities of personality differences, but aids research. Thirdly, the life history traits associated with several examples of personality traits are explored, with reference to their evolutionary implications. This shows the breadth of behavioural strategies used by humans to adapt to their environment and shows that selective pressures may act differently on individuals depending on their personality. However, it also highlights that personality research largely focuses on how individuals differ in their responses to the social world, rather than the natural world. The reliability of these personality traits is also critiqued. Some personality traits are shown to have been researched more extensively, while others are shown to be of low reliability and therefore may not currently be suitable examples for further use in this study. Extraversion is identified as a highly reliable, extensively studied trait which may be a suitable example of difference, useful for developing an evolutionary understanding of our diversity.

Introduction

The evolutionary trajectory of humans is often only regarded in a simplified way as a linear progression from our ancestors to anatomically modern humans (our own species). However, when conceptualizing ‘us' we often disregard the diversity within our species and create a uniform, simplified image of what being human is. Whilst understandable in simple terms, this generalisation masks considerable psychological diversity. For example, some people are more friendly and approachable than others, some are more hardworking, and some are more impulsive or less trustworthy. Due to the universality of these differences, they have likely had a large impact on our evolution.

This chapter considers personality and personality variation, with the aim of identifying personality traits that may be useful to develop an evolutionary understanding of difference. This will define what personality is, explore how personality has been taxonomised, and explore the life history and evolutionary implications of a series of personality traits. This will also critique the reliability of different taxonomies and personality traits. By assessing the life history traits of these personality traits, this chapter will highlight how our diversity may have led to selective pressures acting differently upon individuals depending upon their personality. It is however, important to highlight that personality is only an example of psychological difference and does not account for the full extent of our diversity.

There has been some research on the evolutionary importance of cognitive differences, such as those related to the autism spectrum (Spikins 2013; Spikins and Wright 2016; Spikins, Wright and Hodgson 2016; Spikins, Scott and Wright 2017, 2018), dyslexia (Ehardt 2009; Kershner 2020b, 2020a), ADHD (Jensen et al. 1997; Williams and Taylor 2006) or schizophrenia (Horrobin 1998; Kuttner, Lorincz and Swan 1967; Polimeni and Reiss 2002; Stevens and Price 2015), though it remains far from mainstream. Assessing the impact of cognitive difference is important. Nevertheless, broader forms of difference, which cause consistent variation in behaviour, should also be explored. Personality covers a broader set of differences directly related to behaviour. As noted by Endler (2000), personality usually broadly refers to motives, emotions, and how individuals react to their environment. As such these are influenced by a broad set of factors, including learnt behaviours. Cognition refers to intelligence, attention, memory, reasoning, behavioural inhibition, reaction time, and many more processes, with a more clear-cut hereditary component. It is how knowledge is acquired, processed and stored (Griffin, Guillette and Healy 2015). Personality differences may relate to these cognitive processes, such as cognitive biases and self-efficacy when processing external information, but also to broader long term affective dispositional and physiological differences which affect behaviour and may also be profoundly affected by the environment (Endler 2000; Stemmler and Wacker 2010). Historically, personality and cognitive research have been independent and difficult to integrate, because cognitive research largely refers to short term actions, while personality refers to long term states (Endler 2000). Nevertheless, information processing may be related to personality, for example it may increase the stimuli extraverts judge as attentionally relevant and increase their neural reaction to positive stimuli (Canli et al. 2001; Depue and Collins 1999). By exploring the broader psychological differences associated with personality, differences which are characteristic of our species, rather than just focusing on cognitive differences, a more complete view of how our psychological complexity has affected our evolution may be developed.

1.1 What is Personality Variation?

The first concept of personality and trait theory is credited to Hippocrates (~400 B.C.). Hippocrates suggested that there were four temperaments (Sanguine, Melancholic, Choleric, Phlegmatic) related to the humours of the body. This theory was further noted by Galen (200 A.D.) and then translated by Kant (1700 A.D.) (Merenda 1987). During the 1930s personality psychology became an established discipline, and work at this time provided the beginnings of modern personality research (McAdams 1997). While less trait oriented, more fluid, situation directed theories were developed during this time (Murray 1938), early research by Jung (1923) and Allport and Odbert (1936) progressed the trait theory of personality and provided the basis upon which the factor research discussed below could be conducted (for more extensive discussions of the history of personality psychology see Merenda (1987), McAdams (1997) and Endler (2000)).

Despite this extended history of ~2500 years, there is still an ongoing debate over how we define personality. Réale et al. (2010) have suggested that there are two definitions, designed to capture different aspects of the subject. Firstly, the broad sense definition describes it as consistent differences between two individuals involving any behavioural trait. Secondly, the narrow sense definition characterizes personality as consistent differences in specific behaviours in new or challenging circumstances. The former definition is used theoretically when assessing behaviour within an evolutionary framework. Whereas, the latter is used when determining the causes of personality differences. As this thesis will be assessing the evolutionary history and referring to the biological causes of personality difference, a more general purpose definition may be necessary.

Larsen and Buss (2010, 4) have defined personality as:

“the set of psychological traits and mechanisms within the individual that are organized and relatively enduring and that influence his or her interactions with, and adaptations to, the intrapsychic, physical, and social environments.”

This definition offers a broader perspective of what personality is. Further, it does not presume whether the causes are genetic or environmental (see chapter 2), and does not constrict what traits may be considered a part of personality. Additionally, it does not presume how these traits influence individuals' behaviour, or assume the relative importance of the personality of the person and the situation they are in, in determining behaviour.

This final point has an important relevance to defining personality. It has long been argued that the situation determines behaviour more than the person, and thus their underlying personality (Hunt 1965; Mischel 1973, 1979). If behaviour is strictly inconsistent across situations, personality is merely an artifact of observers. Alternatively, if personality is wholly responsible for behaviour individuals would be unable to efficiently adapt to their situation (Kenrick and Funder 1988). Kenrick and Funder (1988) have argued that evidence doesn't support personality being an observational artifact. Likewise, as stated above, the importance of the situation has also been emphasized. Thus, over time a compromise has developed which incorporates the importance of both determinants. The situation is regarded as a short term influence on behaviour. Individuals are aware of their situation and make a conscious choice of how to deal with it, and two individuals with the same personality may react differently. Meanwhile, personality accounts for long term trends and the average behaviour of individuals across an extended period of time (Fleeson 2004; Fleeson and Noftle 2008). Further, there is an interaction between a person's personality and their situation in the short term. Individuals may alter their behaviour depending on the situation, but ultimately the extent and nature of this change is determined by their personality which modifies the average levels of behaviour and the reactive thresholds for alternate behaviours (Funder 2006).

When defining personality, it is important to reference this interaction between personality and situation as it accounts for important aspects of plasticity in human behaviour. Nevertheless, as noted above, while two individuals with the same personality may have different reactions to a situation, the average behaviour of those individuals will be closer than two individuals of different personality types. This thesis focuses upon long term life history, thus these averaged impacts of personality are our primary concern. For example, extraverted individuals are more likely to put themselves in high risk situations, which may create resource opportunities or status rewards (Nettle 2005). This doesn't mean that introverts will never put themselves at high risk, it merely means that they are less likely to, compared to an extravert. If an introvert is in a high reward, high risk situation and an extravert is in a low reward, high risk situation it is likely that the introvert will be the more risky individual. Nevertheless, on average the extravert is more risk taking, which may lead to a lower life expectancy.

Personality is defined here as, “the collective persisting psychological traits which influence our behavioural thresholds, and thus our relationship with the environment, both in the short term and the long term.” This definition is similar to Larsen and Buss’s, however, following the discussion above, it is necessary to express that even though two individuals may have distinct personalities, this does not provide them with exclusive behavioural repertoires. Rather, it affects the relative likelihood that they will use/have specific behavioural responses. Hence, by phrasing our definition in this way we can already see that when modelling the tradeoffs of different personalities they will be determined by probabilities rather than strict rules. Further, this definition allows for the fact that these short term deviations from average behaviour are encompassed by the long term trends rather than contradictory to them. Thus, this definition provides the generality of Larsen and Buss’s explanation while incorporating a mechanism for how personality affects behaviour.

1.2 Taxonomies of Personality

While there had been previous attempts to taxonomise personality, Allport and Odbert’s (1936) attempt to create an exhaustive list of trait names can be seen as the beginning of modern research in this area. Following this there have been several key attempts to shorten this list further into cogent taxonomies of personality. Cattell developed his 16 Personality Factors, Eysenck developed his three factor PEN, and multiple convergent psychologists developed the 5 factor model (The Big 5), the modern structure of which is commonly credited to Norman.

This section will explore these different taxonomies and their strengths and weaknesses. Several case studies of personality traits will then be presented. This aims to highlight the psychological diversity of our species, the life history differences and selective implications of these traits, as well as to critique their validity.

Allport and Odbert

Allport and Odbert (1936) believed that an important human evolutionary adaptation was understanding other individuals’ behaviour and mannerisms, in order to predict and converse upon their future actions. They argued that this produced a Machiavellian advantage and thus was of high demand. Consequently, terms representing others’ traits and personalities were accurately developed. By exploring all the trait names in Webster’s Dictionary, they composed a list of 17,953 words descriptive of personality. Of these words 4,504 were identified as probable trait names. These trait names later become known as the Personality Sphere.

Importantly, this paper recognized several key characteristics of trait names. Firstly, they are merely reflective of what their native culture deems significant and of practical importance. For example, Cattell (1943) mentioned that some cultures only have 2 classifications for birds based upon utility, are they edible or not. Similarly, some personality traits of little practical significance would not be classified in this trait list and would be difficult, if not impossible, to identify. Secondly, they compare the delineation of personality traits to the delineation of the colour spectrum. Red may be red and orange may be orange, but there are many shades which are equally distinguishable between. Extraversion and introversion are different categories of personality, but between these classifications there is a continuous distribution of extremity towards one classification or the other. Thirdly, they state that many words are stylistically devised in response to the epoch they are produced. For example, they note that describing someone as mercurial was first developed during a period when Astrological superstition was popular. Thus, many synonyms may have been produced through time.

Allport and Odbert did not attempt to reduce their list of trait names by erasing synonyms as later personality taxonomists would do. On the contrary, they believed that synonyms should be increased to fully display the overlapping complexity of personality traits. Further, they argued that ‘synonyms’ actually have subtle differences which give them distinct meanings from one another. To them, it was merely contextual meaning which created the illusion of equivalence.

Cattell’s 16 Personality Factors

Raymond Cattell produced the first major method of taxonomy to be reviewed in this section - the 16 Personality Factors. In contrast to Allport and Odbert’s assertions, Cattell’s (1943) first objective was to reduce the number of trait names in Allport and Odbert’s list by grouping synonyms. This produced 160 categories with broad meanings. However, Cattell recognises that these categories coalesced and admits that their divisions were in some cases relatively arbitrary. He then added several psychological and clinical terms bringing the list to 171 items. Interestingly, Cattell also added interests and abilities believing that they were influencing or influenced by personality, thus showing he had an appreciation for the non-social influences of personality. These 171 items were then further condensed. Adult individuals (n=100) were rated according to the 171 traits by a companion. Tetrachoric correlations were calculated and any traits correlating above 0.8 were considered identical. Using this method 60 variables were identified.

Cattell continued to condense his categories by using factor analysis to identify underlying higher order traits accounting for the 60 variables. By using *L-data* (an observer rates a participant's behaviour based upon everyday life), Cattell narrowed down his 60 variables to 12 factors. By incorporating multiple methods using *Q-data* (participants describe and rate their own behaviour) and *T-data* (an observer measures participants' behaviour in a lab-based setting), Cattell expanded his findings to 16 Factors (Cattell 1973, 35–37, 1977, 30–48; Schuerger 1992). He then created the 16 Personality Factor Questionnaire (Cattell, Eber and Tatsuoka 1970).

Cattell's 16 personality factors (16PF) is the largest set of factorial personality traits and has been criticized for this. It has been suggested that he has over-factored his data, and that in reality his findings only represent 3 factors (extraversion, neuroticism, and socialization-superego) (Eysenck 1991). However, this criticism is unwarranted. Cattell has consistently argued for a hierarchical structure of personality, with primary and second order factors. The second-order factors were broader and were formed by factor analysing the more specific primary traits. This identified 4 second order factors: Anxiety-vs-Dynamic Integration; Extraversion-vs-Introversion; Cyclothyme-vs-Schizothyme Constitution; Unbroken Success-vs-Frustration (Cattell 1956). However, these factors have been known under different terms and have differed in number ranging up to 8 factors (Allen and Schuerger 1983; Cattell 1977, 120–123, 1973, 111–119; Gorsuch and Cattell 1967; Karson and Pool 1958). Consequently, their stability and replicability is questionable, and this may be a result of difficulty replicating Cattell's primary factors (Eysenck 1991; McKenzie 1988; Norman 1963; Tupes and Christal 1961).

Despite this replicability issue Mershon and Gorsuch (1988) found that by using a 16 factor method, as opposed to 6 or less, the real life predictive ability of personality classifications is doubled. Thus, although there are reliability issues, there is validity in the 16PF. However, the validity does not lie in the factors themselves, but in the use of a higher number of factors. As Mershon and Gorsuch (ibid) note, if there were only 5 or 6 factors, the predictive ability would not increase by using more. Perhaps this is a practical display of Allport and Odbert's (1936) view that synonyms are each subtly different and context creates an illusion of equivalence. In other words, as classifications encompass more terms, predictive ability is lost through reductionism. However, this reductionism provides a mechanism for quantifying personality in a manageable way. Thus, for our purposes, broader consistent categories are useful.

Eysenck’s PEN

Hans Eysenck has developed the smallest of the major personality taxonomies, which consequently has the broadest factors. Similar to Cattell, Eysenck supported a hierarchical model of personality consisting of primary traits and secondary higher order ‘superfactors’ (Eysenck 1947). Unlike Cattell’s analysis, Eysenck has focused on reducing personality to a minimum number of factors with greater emphasis on identifying superfactors. The superfactors identified by Eysenck were: Psychoticism, Extraversion and Neuroticism (PEN) (Eysenck et al. 1992; Larsen and Buss 2010, 68–71). It has also been debated whether a lie scale incorporated in Eysenck’s personality questionnaire represents another personality factor (McCrae and Costa 1983). However, difficulty interpreting these scores (Goffin and Christiansen 2003; Pearson and Francis 1989), and correlations with other personality factors, which indicate faking for appearances (Jackson and Francis 1998), suggest that it is unlikely to represent a personality factor on its own.

The Big 5

Of all the personality taxonomies, it is the “Big 5” which is perhaps the most widely known. Tupes and Christal (1961) were the first to identify 5 personality factors. They assessed Cattell’s 35 narrow factors for intercorrelations to identify whether there was a simpler structure of personality. Using multiple studies with samples of different education levels and raters with different amounts of experience, they showed that there were 5 factors of personality which were identified in each study: 1) Surgency, 2) Agreeableness, 3) Dependability, 4) Emotional Stability, 5) Culture. Norman (1963) further assessed these factors and found them to be independent of one another. As has been noted by Digman (1990), this five factor model of personality was replicated independently by several other researchers, bolstering its reliability (Borgatta 1964; McCrae and Costa 1987; Smith 1967). Further, earlier less recognised work also identified 5 factors which are relatively similar to those of the Big 5 (Fiske 1949). Although the labels of the five factors have differed considerably through time and between research groups (Digman 1990), there is more consensus on the terminology today. Following Costa and McCrae’s (2008, 223–257) NEO personality inventory their terminology became adopted by other researchers. The five factors are now called Extraversion, Neuroticism, Conscientiousness, Agreeableness, and Openness to experience.

It can be seen from this that there are reliable personality traits identified within these studies. However, each personality taxonomy has different aims. Allport and Odbert aimed to show the complexity and variety of human personality traits, and did not want to reduce these traits into more generalized categories, which may lose some of the specific nuances of an individual's personality. Alternatively, Cattell did reduce these traits for future research, but attempted to retain the detail of personality complexity by creating a hierarchical structure of personality, where the upper levels are more generalized factors. Finally, Eysenck and the researchers who created the Big 5 focused upon identifying reliable, generalized factors. While this does lose some of the complexity of personality, it makes it more manageable for future research, and aids in ensuring the compatibility of results from different research groups.

1.3 Personality Traits

The term "personality trait" has been used by some authors to specifically describe the lower order, primary traits described above, which are subsumed by personality factors (McCrae and Costa 1997). The term has also been used to describe personality factors, such as extraversion and neuroticism, with the terms factor and trait being used interchangeably. In this section the term 'trait' will be used in the broad sense. This section will explore the reliability and evolutionary implications of the broad personality traits identified by the taxonomies above. Personality traits are associated with distinct behaviours. Consequently, these behaviours may provide benefits or disadvantages, and are thus particularly relevant for an evolutionary understanding of personality difference. Whether a behaviour is advantageous may also be context dependent. For example, being a highly sociable extravert may be advantageous and increase reproductive rates (Nettle 2005). However, within a context of high disease prevalence, this may lead to higher mortality rates. Further, extraverts are more likely to struggle within an environment of social restrictions, such as those during the covid-19 pandemic, and experience more depressive symptoms (Wijngaards, Sisouw de Zilwa and Burger 2020). Consequently, personality variance may provide humans with the ability to inhabit a wider range of niches (MacDonald 1995), a topic we will return to in the discussion. This section will explore the life history traits associated with several personality traits. By doing so, the limitations of a monolithic approach to cognitive evolution will be apparent. However, some personality traits have been researched more, have a greater reliability than others, or have a greater interaction with other personality traits. Each trait in this section will be critiqued. The cross cultural validity of personality traits will also be discussed, with a particular focus on small scale societies. In the discussion following this section, a personality trait will be selected to be used as a case study for this thesis.

Psychoticism

High Psychoticism (P) scores are largely associated with antisocial behaviour, aggression and lack of empathy or remorse. This factor is viewed in a similar way to other personality factors, with multiple primary traits coalescing to form the overall score of the broad personality factor. This determines an individual’s place on a continual distribution from socially adept to social atypicality, disorder and diagnosable psychoses (Eysenck 1992). In this way Eysenck opposed the view that psychoses were distinct from neurotypical psychology (Rawlings and Dawe 2008). Rather, Eysenck (1992) believed that a reduced behavioural inhibition system (BIS) causes increased cognitive rigidity and inattentiveness, which promotes the associated behaviour of high P scorers, including those associated with psychological conditions.

This position has been furthered by Corr (2010), who argued that differences within the behavioural approach system (BAS) and flight-flight-freeze system (FFFS) may also contribute to variation in P scores. However, this biological support raises issues with the continuity of Eysenck’s P construct. The construct is shown to be divided, with differences in the biological causes of primary and secondary psychopathy and psychoticism. Primary psychopathy was seen as a cause of lower activity in the FFFS and decreased fearfulness, whereas secondary psychopathy was associated with increased activity in the BAS and greater impulsivity. This contradicts Eysenck’s theory of strict continuity.

Nevertheless, having a high P score has been shown to have a significant impact on life history. Individuals are more likely to engage in physical aggression and vandalism (Carrasco et al. 2006; Slee and Rigby 1993). They are more creative (Booker, Fearn and Francis 2012; Eysenck 1993; Merten and Fischer 1999). They are more sexually promiscuous, with sexually deviant behaviour associated with high psychoticism scores (Figueredo et al. 2005a). Further, they are more likely to engage in cheating behaviour (Jackson et al. 2002) and are less distressed when imagining engaging in deceitful behaviour (McBain and Devilly 2019). Most relevant for this study, Figueredo et al. (2005b, 2005a) have identified a *K*-factor in humans which is negatively associated with broadly defined P. This suggests that psychoticism is highly significant in determining an individual’s reproductive strategy, with those high in P being *r* strategists (reproducing rapidly). This is argued to allow individuals to fill different environmental and social niches. Yet, the difference between the Broad P defined in Figueredo et al.’s study and the psychoticism defined by Eysenck must be noted. Multiple factors from several different personality inventories were used to construct Broad P (Conscientiousness, Agreeableness, Psychoticism, Impulsivity/Sensation Seeking and Aggression/Hostility). Significantly, while the association between Eysenck’s P and Broad P was significant, it was not as firm as associations between Eysenck’s other personality factors and their respective broad factors defined in the study. The classification of Conscientiousness and Agreeableness into Broad P supports Eysenck’s assertion that they are facets of P (Eysenck 1991). However, it would be interesting to assess their impact on the *K*-factor individually, due to significant differences in how these facets interact to form different behaviour, a fact that has been shown to impact Eysenck’s narrow P (discussed below), let alone Broad P. Further, impulsivity is widely regarded as a facet of extraversion, which is also associated with increased promiscuity (see below). Therefore, this *K*-factor may be more associated with extraversion than with P. While this has shown that a collection of personality traits may impact the *K*-factor, it is presumptuous to assume that it is significantly affected by Eysenck’s psychoticism alone. Based upon the findings presented above, we may suggest that in the evolutionary past, individuals high in P may be more successful within a context of high competition, due to its association with aggression, promiscuity and deviant behaviour, which may give them an advantage. However, within a more collaborative context these behaviours may lead to ostracism or punishment.

Difficulties have been experienced when measuring this trait, with Eysenck’s own correlation clustering of P being less definitive than for E and N (Eysenck et al. 1992). Further, a longitudinal study assessing the ability of the P-scale to predict the development of psychotic conditions failed to support the scale (Chapman, Chapman and Kwapil 1994). Nevertheless, in this study those with high P-scores reported more experiences similar to those experienced by individuals with psychoses. The reporters argue that this scale may therefore only measure similar behavioural characteristics to psychosis, without actually identifying psychosis itself. Similarly, Block (1977) reported that the P scale was unable to discriminate between individuals with psychoses and neurotypical individuals. Block also argued that the internal consistency and reliability of the P scale may be greatly exaggerated. Hare (1982) had difficulty differentiating individuals with high assessments of psychoticism using the P scale. He suggested that the scale may identify certain factors linked to criminality and psychoticism (e.g. impulsiveness and antisocial behaviour), however there was no link to lack of empathy or guilt. Thus, while predicting criminality, it does not predict those factors explicitly associated with psychoticism. Similarly, Heym et al. (2013) found that inconsistencies in the predictive power of global P measurements may be due to the better ability of individual facets of the P test to differentiate more nuanced personality differences. They suggest that P likely encompasses 3 factors (affective, interpersonal and impulsive) thus confounding measurements and the applicability of global P scores for predicting psychosis-like traits. Further, Van Kampen (1996) disputed the actual construct of psychoticism. He argued that Eysenck's belief that different psychoses were determined by common genetic predispositions was false and that the P-scale only assessed schizoid personality differences. Due to this, he argued the broad continuum developed by Eysenck could not be upheld.

The reliability of Eysenck's P is questionable. As mentioned above, Eysenck has argued that the Five Factor traits Conscientiousness and Agreeableness are facets of P (Eysenck 1991). However, in a subsequent study when asked to classify 100 clusters of trait synonyms into his PEN factors it was found that while traits associated with agreeableness in the Five Factor Model (FFM) correlated with psychoticism in the expected way, those associated with conscientiousness were classified as belonging to E by Eysenck (Goldberg and Rosolack 1994). Further, confusions and contradictions in how P is assessed may be caused if it is regarded as a combination of Agreeableness and Conscientiousness, as they have been shown to measure separate behavioural traits, some of which are contradictory (Costa and McCrae 1995b). Due to this, combining the two may lead to important behavioural differences being lost, which will affect overall scores for P.

Applying this to an evolutionary context is problematic. At present findings may not be consistent enough for it to be considered a singular personality factor. This is particularly evident when contrasted against findings from research on other personality factors, such as extraversion and neuroticism, which show high replicability. Extraversion and Neuroticism have both been identified as primary personality traits by each of the major theories assessed in the previous section. Further, extraversion has been identified in every personality measure, taxonomy and even surveys which were not specifically assessing personality (Watson and Clark 1997). Thus, they are likely to be the most stable traits identified in the psychological literature.

Extraversion

A more promising trait for potential application in the context of human evolution is extraversion. The concept of extraversion developed gradually through the 20th century. Extraversion was first popularized in psychology by Jung (1923, 510–523). He described three categories of person. Firstly, the extravert, who was described as being primarily motivated by external forces and the feelings of others. Secondly, the introvert, whose motivations are primarily internally derived and are in no way determined by external social pressures. Thirdly, ‘normal man’, described here as being the prevalent generalist who incorporates both internal and external influences. This same view was championed by Conklin (1927). Importantly, a common misconception is that Jung and other like-minded researchers did not regard extraversion as a continuum, rather they described it as categorical types. The origin of the spectral view of extraversion is often credited to Gerard Heymanns on which Eysenck is suggested to have expanded (Wilt and Revelle 2009). Eysenck (1960, 9–14, 1973, 19) has given evidence against this view and shown that both Jung (1923, 510–523) and Kretschmer (1922) (the primary personality theorists during his early career) believed in a continuous ‘fluidity’ from one dichotomous personality type to another. Eysenck then expanded on this view and supported it statistically (Eysenck 1973, 19). However, firm definitions of extraversion and Introversion were unavailable at this time. Thus, Eysenck collated the available definitions and noted several key factors: introverts were more subjective, showed more self control, and showed more cerebral activity (with extraverts showing more behavioural activity). From this it can be seen that Eysenck emphasised the importance of impulsivity in extraversion. This contrasts starkly with Cattell’s more socially oriented definition of extraversion, which argues extraversion is associated with dominance and surgency, and extraverts are characterised by being sociable rather than reclusive (Cattell 1956). However, despite controversy regarding the unitary nature of extraversion (Carrigan 1960; Eysenck and Eysenck 1963; Plomin 1976; Sparrow and Ross 1964), Eysenck deemed the correlations between impulsivity and sociability sufficiently high enough to constitute a single extraversion trait.

The definition of extraversion has evolved over time and holds different meanings in different research groups (Watson and Clark 1997). As Watson and Clark (1997) have argued, Costa and McCrae hold a more positive view of extravert sociality, while Eysenck’s view, that extraverts are risk takers and impulsive, is a more negative view suggesting unreliability. Due to conflicts such as this, they decided to construct an inclusive definition of extraversion accounting for all of these differences. While there are disagreements in how to define extraversion, there are several points of agreement highlighted by Watson and Clark. Socially, extraverts are more friendly, confident, dominant and comfortable in social situations. Beyond this, they are more adventurous, active and seek excitement. Finally, they are associated with a more optimistic outlook on life and are argued to be happier individuals in general.

The importance of these characteristics when defining extraversion is supported by experimental and observational research. Extraversion scores have been found to correlate with popularity and social status (Anderson et al. 2001; Ilmarinen et al. 2015), while introverts are more likely to be bullied (Slee and Rigby 1993). Extraverts show a greater activation in areas of the brain associated with positive emotion when they see happy faces (Canli et al. 2002), and show a greater monopolization of neural processing power by social stimuli (Fishman, Ng and Bellugi 2011). They are more likely to use self presentation features on social media (Ong et al. 2011), and there is a slight relation with the ability to manage self-image on social media (Krämer and Winter 2008). Further, every layer of their social network is likely to be larger, but the relationships are not more emotionally meaningful (Pollet, Roberts and Dunbar 2011). Extraverts also experience more positive affect than introverts and are generally happier (Costa and McCrae 1980; Rusting and Larsen 1997; Wang, Shi and Li 2009; Watson and Clark 1997; Wilt and Revelle 2009). Additionally, while extraverts show more prosocial behaviour, they are also more likely to engage in antisocial and criminal behaviour (Carrasco et al. 2006).

While much argument has surrounded classifying impulsivity as a facet of extraversion, it must be recognised that impulsivity is also a broad term encompassing many facets. Whiteside and Lynam (2001) have shown that different aspects of impulsivity are associated with different personality factors. Importantly, the form of impulsivity associated with extraversion is sensation seeking. Zuckerman (1979, 10–11) has defined sensation seeking as a need for new and varied experiences regardless of risk. This personality factor is associated with a myriad of maladaptive behaviours, such as an increased susceptibility to addiction (Coventry and Brown 1993; Kosten, Ball and Rounsaville 1994; Mehroof and Griffiths 2010; Sarramon et al. 1999), decreased job performance (Reio and Sanders-Reio 2006), increased risky sexual behaviour such as unprotected sex and infidelity (Donohew et al. 2000; Henderson et al. 2005; Lalasz and Weigel 2011), and increased behaviour that may lead to injury or death (Horvath and Zuckerman 1993; Jonah 1997). In a prehistoric or hunter gatherer context, sensation seekers may have been more likely to gain access to resources and mates. Collecting resources and competing for mates has large risks, such as predation, injury and conflict. While many individuals would be deterred by these risks, sensation seekers find them enjoyable and thus are more likely to compete for them (Zuckerman and Kuhlman 2000). Buss (1991) has also suggested that the retention of individuals with different thresholds for risk taking was due to the relative importance of the benefits and costs being determined by the environment. While an environment has a high amount of resources, risk taking is unnecessary and disadvantageous. However, if resources are scarce, taking risks to acquire them before others may be beneficial.

As can be seen above, there are many advantages to being an extravert. Extraverts generally have a higher status, a broader social network, understand how to present themselves to others and are more interested in doing so, and are more likely to take risks to acquire desired resources. These characteristics may lead to an increased chance of reproduction and, in a non-egalitarian group, more resources. Conversely, through taking risks, injury is more common. Further, through increased social and sexual interaction they are more likely to contract diseases and parasites (Henderson et al. 2005). Thus, life expectancy is lower in extraverts than introverts. Due to the explicit effects of extraversion on life history, and its high replicability, it is highly suitable to be used as a case study within this project.

Neuroticism

While extraversion is associated with more frequent experiences of positive emotion, neuroticism is associated with negative affect (Costa and McCrae 1980; Rusting and Larsen 1997; Wang, Shi and Li 2009; Watson and Clark 1997; Wilt and Revelle 2009). People with high neuroticism have more intense emotional reactions, worry often, experience negative moods commonly, are prone to addiction and overall show an increased risk of both somatic and psychological morbidity (Claridge and Davis 2001; De Moor et al. 2015; Lahey 2009). Although, it must be noted that while Neuroticism raises individuals’ risk for illness, both psychological and physical, morbidity increases the risk of developing a more neurotic personality (Neeleman, Bijl and Ormel 2004). Further, individuals in relationships with people with high neuroticism have lower levels of marriage satisfaction, although it did not affect changes in this satisfaction (Karney and Bradbury 1997), or the likelihood of terminating relationships in adolescents (Lehnart and Neyer 2006). However, an early long term (45 years) study found that neuroticism was related to the likelihood of divorce (Kelly and Conley 1987). This may suggest either that: 1) over time the initial lower satisfaction leads to divorce, or 2) it takes a longer time for marital satisfaction to decrease, due to factors associated with neuroticism. Thus, high neuroticism has the effect of increasing the chance of relationship termination in the long term.

Due to the difficulties associated with high neuroticism, Nettle (2006) has questioned what positive function it may have to facilitate its retention in our species. He argues that there are two advantages. Firstly, neuroticism is associated with risk avoidance. Secondly, people with high neuroticism are more competitive. Thus, these factors may mitigate some of the costs. I would further argue that due to the effects on relationships being very long term, they do not necessarily affect reproductive success.

Similar to extraversion, neuroticism is a reliable trait with significant life history implications. Further, it has been shown to be highly genetically determined (40-60%) (De Moor et al. 2015). However, there has been difficulty identifying a biological cause of the differences associated with high neuroticism. Several biological correlates have been highlighted as causes of high Neuroticism, as has been reviewed by DeYoung (2010) and Ormel et al. (2013). Increased activity in the amygdala, insula and anterior cingulate; preferential activation of the medial prefrontal cortex in response to emotionally negative stimuli (Haas, Constable and Canli 2008); greater baseline and reactive levels of stress related hormones such as cortisol in aggressive situations (Netter 2004); greater hippocampal activation during fear learning (Servaas et al. 2013); and more persistent reactions to stress related stimuli due to a reduced connectivity between the amygdala and anterior cingulate cortex are several of the noted causes (Ormel et al. 2013). Further it has been argued that the overall architecture of the connections in the brain of individuals with high neuroticism is more oriented towards stronger connections for emotional and salience functions rather than sensory and cognitive control functions (Servaas et al. 2015). Claridge and Davis (2001) have argued that neuroticism moderates the intensity of different, already established personality traits.This may be due to more sustained emotional reactions being caused by neuroticism, while the initial emotions themselves are a product of other personality traits. They argue that this is why neuroticism is associated with such a wide range of psychological conditions. It must be noted however, that there has been a lot of contradiction in this subject. Consequently, most researchers view their results as preliminary.

Conscientiousness

High Conscientiousness is associated with a strict adherence to social norms, high impulse control and the ability to delay gratification. Further, it is associated with more goal directed, planned behaviour and greater industriousness (Bogg and Roberts 2013; Larsen and Buss 2010, 68–88). Conscientiousness is often associated with a greater job performance, although this may vary depending on the other personality characteristics the individual has and their type of job (Witt et al. 2002; Judge and Zapata 2015). Further, it is associated with a number of consequences to health as reviewed by Bogg and Roberts (2013). Individuals with high conscientiousness often live longer (Kern and Friedman 2008; Martin, Friedman and Schwartz 2007), are less likely to be affected by a series of medical conditions, ranging from high blood pressure and diabetes to strokes and tuberculosis (Goodwin and Friedman

2006). Individuals with high conscientiousness are less likely to be affected by stress, and are more likely to use practical coping mechanisms. When there is a problem they tend to solve that problem to cope with it. This leads to greater positive affect, and thus may account for the lower levels of depression seen in conscientious people (Bartley and Roesch 2011; Besser and Shackelford 2007). From an evolutionary perspective, high conscientiousness has several effects on life history. Firstly, they are more likely to live longer. Secondly, they are likely to produce more resources. This suggests that there are no evolutionary disadvantages to high conscientiousness. However, Nettle (2006) has addressed this and presented several disadvantages from an evolutionary point of view. He has argued that highly conscientious individuals are less likely to gain resources and opportunities for reproduction at the expense of another. Further, they are more likely to forgo immediate gratification in order to follow a plan. Both of these features lead to less opportunistic behaviour. Nettle argues that this may have been highly disadvantageous in certain conditions. For example, in a highly unpredictable environment where resources are sparse, opportunistic behaviour may be favoured. Thus, like extraversion and neuroticism, conscientiousness is also associated with a tradeoff which is likely context dependent.

However, the lower facets associated with conscientiousness have not been studied extensively. This has led to studies defining this factor differently. Roberts et al. (2005) have noted that 9 facets of conscientiousness have been identified: order, achievement, responsibility, impulse control, moralism, persistence, traditionalism, formalness, and decisiveness. However, no method of analysing conscientiousness covered all of these facets, and no personality inventory was in agreement as to which of these facets should be incorporated into the factor. Roberts et al.’s (2005) study attempted to bring some clarity to this topic. By assessing 36 personality scales related to conscientiousness they found that 6 factors showed high validity (industriousness, order, self-control, responsibility, traditionalism, and virtue). However, a later study conducted by the same group found 8 lower facets (MacCann, Duckworth and Roberts 2009). Further, they have also more recently stated that more work must be done to identify the structure of the factor (Roberts, Lejuez and Krueger 2014). Thus, although the factor may be associated with these life history differences, the actual construct of the factor requires more work to increase the validity and comparability of research. The use of different measures in the studies cited above may have greatly impacted the results found.

Agreeableness

Agreeableness is a continuous quality describing individuals' differences in inclination towards cooperation and the importance they place on conserving relationships (Crowe, Lynam and Miller 2018). Conducting similar analysis to Roberts et al.'s (2005; 2014) work on Conscientiousness, Crowe et al. (2018) identified 5 facets of agreeableness (compassion, morality, trust, affability, and modesty). These findings are similar to Costa and McCrae's (1995a) facets. However, several (straightforwardness, compliance, and tender-mindedness) are either superseded or abandoned in this study. Similar to conscientiousness, the structure of lower facets is still under consideration which complicates the comparability and assimilation of results from different research groups. Nevertheless, there are several behavioural differences which are consistently found in individuals with an agreeable personality. As expected, individuals who are highly agreeable have relationships of a greater quality. This was found on an individual level, within a group, and with people from outside of their group, with agreeable individuals showing fewer xenophobic characteristics and a greater motivation to help others no matter the situation (Graziano et al. 2007; Jensen-Campbell et al. 2002; Jensen-Campbell, Knack and Gomez 2010). Further, those with high agreeableness are likely to have greater academic achievements, and a greater job performance in a cooperative setting (Hair and Graziano 2003; Kern et al. 2013; Laursen, Pulkkinen and Adams 2002). Agreeableness has been seen to moderate the effects of conscientiousness on job performance in social settings (Witt et al. 2002), and in a longitudinal study has been shown to interact with other personality factors to enhance positive aspects of those traits if agreeableness is high, and increase undesirable features of those traits if it is low (Laursen, Pulkkinen and Adams 2002). Thus, with effects determined in tandem with other personality factors, being highly agreeable can have considerable positive outcomes. However, agreeableness has been found to be inversely related to income and wealth (Duckworth et al. 2012), suggesting that the increased productivity at work outlined above does not translate to greater personal resource acquisition.

From an evolutionary point of view, agreeableness has several positive and negative qualities. Positively, individuals with high agreeableness perform more effectively at work, suggesting they produce more resources for their group, even if they do not get these resources themselves. They are more likely to be selected as long term mates, and the trait is positively related to partner satisfaction (Botwin, Buss and Shackelford 1997). Further, a U-shaped curvilinear relationship has been found between agreeableness and sexual promiscuity (Markey and Markey 2007). However, Jensen-Campbell et al. (2010) have suggested that there are different motives behind this promiscuity for high and low agreeable individuals. People high in agreeableness perceive it as an intimate event to pleasure others, while low agreeables exploit others for their own pleasure. Jensen-Campbell et al. (2010) have also argued that a group with a high proportion of agreeable individuals provides a ‘safe context’ for innovation. This provides the benefit of being able to adapt better to changing contexts and novel problems; however, Jensen-Campbell et al. (2010) have also noted that highly agreeable individuals may be more likely to accept maladaptive innovations rather than risk upsetting the inventor. Thus, the adaptive advantages of this feature will be highly variable and may only be worth the risk in adapt or die situations. Finally, agreeableness has been related to longevity and health (Brummett et al. 2006; Friedman, Kern and Reynolds 2010; Ironson et al. 2008; Jackson et al. 2015; Weiss and Costa 2005). As well as less of a proclivity towards interpersonal violence, agreeable people are more likely to follow doctor’s instructions, thus increasing the likelihood of recovery from illness (Jensen-Campbell, Knack and Gomez 2010). However, many studies have failed to show a relationship between longevity and agreeableness leaving these findings questionable (Iwasa et al. 2008; Masui et al. 2006; Wilson et al. 2004). During a longitudinal study spanning 70 years, agreeableness had a significant impact on mortality from 1940 to 1991. However, using an alternative sample of data from 1950-2000 this association was weaker and found to be non-significant (Martin, Friedman and Schwartz 2007). The other studies referenced above which failed to find a relationship between agreeableness and mortality sampled centurions and older individuals, thus it may be the case that the protective benefits of being highly agreeable, weaker initially when compared to conscientious, may decrease with age. This may in part be due to the number of interpersonal conflicts an individual experiences reducing, and reactions becoming milder with age (Birditt and Fingerman 2005; Birditt, Fingerman and Almeida 2005), causing the protective benefits of being agreeable to become less relevant.

The primary trade-off associated with being highly agreeable is summed up by the phrase, ‘nice guys finish last’. While being trusting, and trustworthy may be beneficial in certain contexts, and is highly sought for in a mate, being deceptive, aggressive and being suspicious of others may be highly beneficial (Nettle 2006). As has been noted by Buss (2003, 19–48), the ability of a person to provide resources is highly important when selecting a partner (particularly for females). Generally, deceptive and dishonest individuals can gain more resources while using less energy by cheating (McNally and Jackson 2013). A clear demonstration of how selectively beneficial deceptive tactics can be is seen in Byrne’s, Whiten’s and their colleagues’ work (Byrne 1995, 203–205; Byrne and Corp 2004; Byrne and Whiten 1992). This posits that the need to use social information to deceive and manipulate others was a major selective pressure on our evolution, to solve problems and gain access to otherwise inaccessible resources. They demonstrated this relationship by showing that there is a linear relationship between neocortex size and deception rates in primates (Byrne and Corp 2004). Highly agreeable individuals are less likely to involve themselves in such self serving manipulations at the expense of others. Therefore, they are forfeiting resources which could be gained with little energy use. In a modern context, as has been noted by Nettle (2006), agreeableness is negatively associated with executive's wage, job level, and employability (Boudreau, Boswell and Judge 2001). Agreeable executives have been described by Boudreau et al. (2001) as naive followers, and in both a historical and modern setting are less likely to gain access to resources and status. Thus, despite agreeableness being a highly sought after trait in mates, this may only be up to a certain level, as highly agreeable people put themselves at a relative disadvantage compared to the more assertive and disagreeable members of their group, particularly if resources are scarce.

Openness to Experience

The final trait of the five factor model of personality is still termed differently depending on the researcher. The two most common terms used are 'Openness to Experience' and 'Intelligence'. Although, other names such as intellectance (Hogan and Hogan 2007), Culture (Tupes and Christal 1961), and, in its early discovery, Inquiring Intellect have been used (Fiske 1949). Digman (1990) has argued that this factor probably incorporates all of the facets ascribed to these terms, thus making it a broad term where different researchers emphasise different aspects of the factor. Costa and McCrae's Openness to Experience (Openness) is characterized by intellectual curiosity, imagination, predilection to art, a life with emotional depth, and a more accepting attitude towards novel ideas and experiences (Costa and McCrae 1992; McCrae and Costa 1999, 164). In contrast, Hogan and Hogan's (2007) intellectance places a greater emphasis on educational attainment. When directly tested against the Openness factor, intellectance showed correlations with the lower level facets Openness to Ideas and Openness to Aesthetics, however other facets show no correlation (Costa and McCrae 1995a). This suggests that despite Digman's (1990) argument researchers are assessing fundamentally different things. Connelly et al. (2014) have conducted a meta analysis to integrate separate results and help identify the primary facets of Openness. They argued that there are six facets of Openness: intellectual efficiency (the ability to understand complex information), non-traditionalism (tendencies to adopt unconventional political and moral attitudes), curiosity (a drive to learn new things), introspection (philosophical reflection in general and of one's own actions), aesthetics (interest in art and beauty) and openness to sensations (enjoyment of sensory experience).

They argue that researchers using different terms are merely placing greater emphasis on different aspects of the factor. They refer to the fact that there are two subfactors which are factorially separate, an Intellect subfactor and an Openness subfactor. DeYoung et al. (2007) have argued that this is the cause of results such as Costa and McCrae’s (1995a), referred to above.

The outcomes of having high Openness/Intellect are split in the same way as the factor. Firstly, Intellect is associated with cognitive ability, academic achievement, scientific achievement, intellectual curiosity and being focused on academic goals (Connelly and Ones 2014; Kaufman et al. 2016). As expected of a closely correlated subfacet, Openness is also associated with many of these qualities, however it is more correlated with creative and artistic achievement (Kaufman et al. 2016). In evolutionary terms this seems a very advantageous quality. Groups who are more creative and inventive both technologically and socially are more likely to survive as problems arise (Pereda et al. 2017). Further, being creative and artistic can be considered highly attractive (Nettle 2006). However, the tradeoff of this personality trait is that it can increase unusual thinking (e.g. of paranormal beliefs), and even depression and psychosis (Nettle 2006). Further, it has been shown that while Openness may increase job performance in investigative and artistic jobs, in other professions it has no effect. Thus, depending on the context, Openness may not be advantageous.

Personality Traits in Small Scale Societies

The Big Five personality traits have been found to have high cross cultural validity when assessing multiple industrialised countries (McCrae and Costa 1997). However, there are some culture specific differences that affect the consistency of personality traits over time and situation. For example, more collectivist cultures have been found to have less of a predictive relationship between personality and behaviour (Church 2010). Nevertheless, within industrial societies, the cross cultural replicability of the Big Five is high.

Within small scale societies this becomes more complex. Gurven et al. (2013) assessed the personality of Tsimane forager-horticulturalists in Bolivia and found lower than usual internal consistency for the Big Five traits. While evidence was found for extraversion, agreeableness and conscientiousness, it was argued that the Tsimane have 2 factors of personality. The first factor is largely a mixture of extraversion and agreeableness, characterised as prosociality. The second factor is largely related to conscientiousness and has been interpreted as reflecting industriousness. In a later study, van der Linden et al. (2018) identified a general factor of personality (GFP) superseding the Big Five traits in the Tsimane, which is associated with social effectiveness. This has also been identified in industrial societies (van der Linden, te Nijenhuis and Bakker 2010; Van der Linden, Dunkel and Wu 2021). However, in comparison to Western samples intercorrelations between the Big Five, leading to the GFP, were much higher in the Tsimane. They argued that this may have made it harder to distinguish the Big Five in the Tsimane.

Following Nettle's (2011) suggestion that personality factors covary due to synergistic effects, for example individuals with higher status (or ambition) would have a greater payoff from high mating motivation, Gurven et al. (2013) have argued that synergisms may have different consequences in different settings. If this is the case, the structure of personality should vary. They have further argued that the genetic architecture for personality may be the same, but that this architecture may have different effects in different environments. This may account for the finding of a smaller number of personality factors in small scale societies, where there are a limited number of niches individuals may specialize into. Covariance in personality traits may therefore be higher in small scale societies, in comparison to industrial societies, which have a wider diversity of niches where traits may vary more independently (Durkee et al. 2020; Lukaszewski et al. 2017). This is supported by an agent based model, which found that increasing niche diversity increased trait diversity and reduced covariance (Smaldino et al. 2019). Consequently, it has been suggested that personality structure differs depending upon the socioeconomic environment of the society. This is a reasonable suggestion, however it does not preclude the existence of wider personality variation within small scale societies. It merely suggests that within this setting selection has led to strong covariance between particular traits reaching fixation. Wider research examining different small scale groups is needed to confirm the suggestions above.

Life history effects caused by the Big Five have been found in small scale societies. In particular, facets of the prosocial trait identified by Gurven (2013) were found to be associated with increased fertility and number of sexual partners in men, with extraversion having the highest effect (Gurven et al. 2014). This association with extraversion was also found when assessing the Ache (Bailey et al. 2013). Further, extraversion and openness were associated with a greater number of conflicts in the Tsimane (Gurven et al. 2014). Therefore, despite research in this area still being rare, the Big Five personality traits, and in particular extraversion, have been associated with fitness and life history differences in traditional societies, which are comparable to those observed in industrial societies. This suggests that these personality traits and their associated life history effects may be explored on an evolutionary timescale.

Table 1. Showing some of the possible tradeoffs of behaviour associated with personality traits. Dotted lines show where a single or multiple behaviours may have multiple adaptive effects.

Personality Trait	***Behaviour***	***Advantages***	***Disadvantages***
Psychoticism	Creative	More innovative	
	Impulsive	Rapid reproducers Increased chance of getting resources	Lower life expectancy
	Sexual deviance Aggressive Criminality		Lower social reputation
	Antisocial		
Extraversion	Social Dominant/confident	High social status Larger social network	Infidelity Lower life expectancy (due to injury or disease)
	Sensation seeking Impulsive	Greater access to resources or mates	Addiction Criminal behaviour Lower production of resources
	Generally happier	Positive affect	
Neuroticism	Risk avoidant	Lower injury rate	Loss of potential resources
	Competitive	Greater production of resources	Can lead to lower social reputation
	Negative affect		Addiction Somatic and psychological illness Low partner satisfaction
Conscientiousness	Adhere to social norms	Increased social success	Less likely to cheat to get resources Less opportunistic
	Low impulsivity Goal directed	Higher life expectancy	
	Less affected by medical conditions Less affected by stress Positive affect		
	Industrious	Greater job performance	
Agreeableness	Low xenophobia	Greater quality relationships Better job performance Facilitate innovation Better long term mates	Low wealth Less successful in competitive setting
	Unconditionally help others		
	Low interpersonal violence		
	Follow advice of doctors	Higher life expectancy	
Openness to Experience	Understand complex information Learn and use new ways of thinking Greater academic achievement More creative	Innovative Greater job performance	Depression/psychosis

Discussion and Conclusion

This chapter has given a definition for the term personality, provided some contextual history of how the field of personality has developed over time, and given a review of the primary personality traits that have been identified through this research, with a brief review of the evolutionary tradeoffs associated with each trait. Table 1 provides a summary of these possible tradeoffs, highlighting where a single behaviour associated with a trait may have multiple selective effects, or where multiple behaviours contribute to the same selective effect. This chapter has shown the variety of personalities within our species, particularly as personality traits are not mutually exclusive, or categorical, but are continuous. These traits, while influenced by life experience and other environmental effects, have a strong genetic influence, and have a significant impact upon individuals' life histories. This may lead to differences in fitness depending upon the environment individuals are in. Thus far, this discussion has focused upon the benefit psychological variability may have had for the individual. However, on a population-level scale this variability may be a factor which aided our evolutionary success. The impact of population-level diversity and the effect of evolutionary selective mechanisms (e.g. frequency dependence) will be discussed further later (see chapter 3). However, the reliability and validity of some personality traits is uncertain (e.g. psychoticism). Further, some personality traits have received less research (e.g. openness to experience), and others have shown significant interactions with and may moderate the effects of other traits (e.g. neuroticism), which complicates their life history implications.

Some people may be uncomfortable with the concept of personality and there is sometimes resistance to its application to the present or past, or to the development of an evolutionary perspective. As a result of these concerns, evolutionary explanations for personality and individual differences have been neglected in comparison to other areas of evolutionary psychology. Buss (2009) has argued this neglect is due to a lack of cogent powerful theories for the existence of personality variation and also due to dismissal of the issue. For example, Tooby and Cosmides (1990) suggested that personality differences may just be noise and therefore not warrant an explanation based upon adaptation. Further, Lukaszewski (2021), has suggested that the personality traits outlined above are less useful for evolutionary research than studying lower order traits, such as jealousy. This is due to difficulty identifying the mechanisms which have led to broad trait behaviours, which has often led to a "black-box" approach. Rather than focusing on the broader traits themselves, they suggest a bottom up approach is useful, identifying evolutionary problems, exploring what lower order traits may have developed to solve this problem, what causes there are for variation in this trait, and then assess whether it is associated with a broader factorial trait. This essentially shifts the focus from the broader constructs, which may be harder to explain initially, to easier to explain lower level traits. This may be an effective method for moving forward. However, it may lead to the neglect of pleiotropic or synergistic effects, which may be responsible for the covariance of traits (Nettle 2011), and may alter the cost-benefit outcomes of lower level traits. Therefore, this approach may mask some of the complexities of personality evolution. Finally, some may be uncomfortable with applying personality constructs that have primarily been developed in western, educated, industrialized, rich and democratic (WEIRD) societies. However, as discussed above, while research on small scale societies is uncommon, this research has shown that the Big Five, and in particular extraversion, do have significant life history effects. However, due to the small number of niches available to specialize into, there may be less diversity in personality types in small scale societies. Personality, and the broad traits discussed in this chapter, remain an important and under researched means of developing an understanding of our psychological differences in an evolutionary context. Nonetheless, these concerns imply that research should be carried out with care and attention to the use of appropriate evidence and careful methodology.

This chapter has also shown that current classifications of personality are very socially oriented and do not significantly acknowledge possible non-social traits. While some researchers such as Cattell recognised the importance of non-social traits, others focused explicitly on social traits, such as Eysenck’s PEN. Further, while the Five factor theory recognises Openness/Intelligence as a personality trait, it is the least explored and most contentious of the five. Buss (1991, 2009) has suggested that the five factors are so notable because they are the traits we assess before deciding to cooperate or reproduce with someone. He argues that they represent alternative strategies used to survive the ‘social landscape’ humans inhabit. It is widely acknowledged that humans are highly social and have experienced tremendous social evolutionary pressures. Nevertheless, there are non-social cognitive differences within our population that should be considered alongside personality traits. The effect of an example non-social trait (local processing bias) upon our species’ success will also be explored in this thesis (chapter 3).

Whilst appreciating the need for a better understanding of the evolution of human psychological and behavioural differences, through further research into personality differences, this review has identified extraversion as possibly the most widely studied and replicated personality trait. Further, it has defined implications for life history. This makes it ideal to study from an evolutionary perspective. The following chapter (chapter 2) will explore the genetic and neurological causes of extraversion, as well as it’s life history traits in more detail. Following this, the evolutionary implications of extraversion will be explored using an agent based model.

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Chapter 2: Extraversion

Abstract

Human individuality is characterized by wide variability in personality and cognition. Where we lie on the scale of introversion-extraversion, which is primarily associated with sociability and impulsivity, is an important aspect of our personality. Despite the personal importance many place upon personality, its evolutionary impact has not been extensively studied. This chapter explores the genetic, neurological and life history traits associated with extraversion. It is shown to be a highly heritable trait, although significantly affected by environmental factors. Further, the neurological correlates of extraversion variation are largely associated with the dopaminergic system. However, other areas such as the Broca's area and prefrontal cortex are also associated. Importantly, the areas of the brain affecting extraversion are areas of the brain which have undergone significant change throughout our evolution. This suggests that variation in extraversion may have been either under active selection, or a by-product of other evolved characteristics. Differences in extraversion are found to be associated with significant life history implications of evolutionary importance. Introverts are associated with more *K* specialist behaviour, while extraverts are associated with *r* specialist behaviour. These behavioural strategies may have been beneficial within different circumstances. Therefore, selection likely favoured population variability for this trait.

Introduction

It is commonly acknowledged that our species exhibits large variations in personality. The previous chapter explored how psychologists have taxonomised these differences, and provided a review of the life history traits associated with several personality traits. Extraversion was identified as one of the most persistently identified traits in personality psychology and has appeared in each of the major theories of personality. It also has distinct behavioural traits, with high replicability, and evolutionary implications. Therefore, differences in extraversion have been selected as a case study of cognitive diversity. Although different taxonomies place emphasis on different facets of the trait, high extraversion is associated with two primary traits: prosociality and impulsivity/sensation seeking (Watson and Clark 1997).

This section will explore the genetic causes, neurological correlates, and life history differences caused by extraversion in greater detail. This will introduce several different evolutionary theories for the causes of this variation in extraversion within our species. These sections will be compiled to suggest some defining features of extraversion in evolution, which will be used to inform the construction of an agent based model (chapter 6).

2.1 Genetics

It has been suggested that behaviour and personality is primarily genetically determined, although they are also complexly associated with environmental influences (Turkheimer 2000). Studies of extraversion support this, with it being approximately 50% heritable, with the other 50% being primarily attributed to unshared environments (Eaves and Eysenck 1975; Rettew et al. 2008; Van Den Berg, De Moor and McGue 2014; van den Berg et al. 2016). This is similar to other personality traits (Sanchez-Roige et al. 2018; Vukasović and Bratko 2015). Extraversion's heritability is due in equal part to additive and non-additive genes (Rettew et al. 2008; Van Den Berg, De Moor and McGue 2014; van den Berg et al. 2016). However, contrary to other personality traits, the effect of single nucleotide polymorphisms (SNPs) is suggested to be low. Vinkhuyzen et al. (2012) found that 12% of variance was explained by SNPs, whereas Van Den Berg et al. (2016) found that SNPs explained only 5% of variance (a result which did not show significance). Van Den Berg et al (2016) note that this estimate may be decreased due to different procedures being used in the studies which make up this meta analysis. Despite this, these studies found that extraversion is highly polygenic, with individual genes having a small effect size, the largest of which accounts for less than 1% of variance (Turkheimer, Pettersson and Horn 2014; van den Berg et al. 2016). The discrepancy between heritability estimates and estimates of the effect of SNPs is likely caused by the additional effect of rare variants and non-additive effects, such as interactions between genes (van den Berg et al. 2016; Vinkhuyzen et al. 2012).

The manifestation of a genetic predisposition towards extraversion is significantly affected by the environment. So much so that it has been suggested that, rather than differences in extraversion being maintained by balancing selection through our history, facultative calibration maintains this variation (Lukaszewski and Roney 2011; Lukaszewski and von Rueden 2015). Facultative calibration is where the behaviour of an individual is not solely determined by the genetics related to the trait of interest, but rather are responsive to the environment and other phenotypic traits of the individual, only allowing behavioural phenotypes to manifest in certain conditions. Lukaszewski and von Rueden (2015) suggest that this theory is supported because mutational loads from inbreeding are negatively correlated with both physical and personality attributes (Verweij et al. 2012, 2014). However, Zeitsch (2016) has argued that this ignores two key findings. Firstly, people who are physically attractive receive more positive reactions to their social efforts. This would provide more reinforcement to be social, producing a similar result to reactive heritability (where the heritability of extraversion is dependent on inheriting other physical and psychological attributes). Secondly, twin studies show no correlation between height and BMI and extraversion (Haysom et al. 2015). Lukaszewski and Roney (2015) have argued that this does not completely negate the theory. However, it can be seen that the mechanisms of selection for extraversion are not fully understood. Due to this uncertainty surrounding the reactive heritability hypothesis, and the clear interaction extraverted behaviour must have with the environment, which leads to differences in individual life history (see below), it seems reasonable to suggest balancing selection is a mechanism which affects extraversion (Penke, Denissen and Miller 2007). However, as is evident by the fact that extraversion is only 50% heritable, it is also likely that the expression of an individual’s genetically predisposed personality is altered by environmental factors.

Despite the difficulties experienced by researchers exploring the genetic mechanisms behind extraversion, several alleles have been identified which are associated with the personality trait. For example, variants in catechol-O-methyltransferase (COMT) and dopamine receptor genes are associated with more extraverted behaviour and novelty seeking (Benjamin et al. 1996; Ebstein et al. 1996; Faurie et al. 2017; Golimbet et al. 2007; Smillie et al. 2010), including increased promiscuity (Garcia et al. 2010). These genes are associated with the dopaminergic system. Importantly, allelic differences in these genes are associated with either highly functional or less functional dopaminergic systems. As will be discussed below, a highly functional dopaminergic system is associated with more extraverted behaviour. The expression of these dopamine related genes may also be affected by environmental conditions. Fischer et al. (2018) found that population-level genetic differences in the dopamine system were related to extraversion levels, but only in demanding and dangerous climates. Genotypes associated with increased dopaminergic brain function were likely to be more extraverted, but only in demanding climates. This may allow the disadvantages of extraversion within a stable population to be mitigated, allowing the genes to persist for future times when conditions become unstable and an extraverted phenotype is advantageous. It would be interesting if other extraversion associated genes are similarly moderated by environmental conditions. We may speculate that this could account for some of the difficulty identifying common genetic variants associated with extraversion.

Extraversion has also been associated with other genes not associated with the dopaminergic system. For example, it has been associated with ADH4 variations, which increase the likelihood of developing substance dependence (Luo et al. 2007). In contrast, introversion has been correlated with the Gly49 allele in the ADRB1 gene. This gene is associated with a decreased heart rate, which is also present in some forms of social phobia (Stein, Schork and Gelernter 2004). Therefore, while extraversion may be significantly associated with the dopaminergic system, other genes may also be associated with specific characteristics of introversion-extraversion.

We may conclude from this section that extraversion is a highly heritable, polygenic phenotype, which is caused by a series of genes and genetic interactions of low effect size that are subject to environmental interaction. Consequently, it has been difficult for behavioural geneticists to determine its specific genetic architecture and evolutionary history. Despite this, extraverted behaviour has been associated with a number of specific polymorphisms. Most interestingly, it has been associated with dopamine receptor genes and the dopaminergic system.

2.2 Neurology

Several neurological correlates have been found that may cause extraversion. It is argued that extraversion is largely determined by the activity levels of dopamine in the brain’s reward system. Depue and Collins (1999) have suggested that for any incentive stimulus individuals with a higher extraversion will have a larger dopamine response than more introverted individuals. They argue that this would then lead to a difference in how extraverts/introverts would judge the importance of incentive stimuli, with extraverts judging a wider range of stimuli as important. Further, they suggest that this may increase cognitive and stimuli response flexibility in extraverts. This would increase their adaptability to changing environments, as they are more likely to adopt new ways of thinking and new strategies to survive in different environments. Depue and Collins’ theory is supported by the correlations seen above between extraversion/introversion and genes which affect the dopaminergic system. Further, Canli et al. (2001, 2002) have found significant correlations between brain activation in response to positive stimuli and extraversion. This supports Depue and Collins’ theory that extraversion is associated with larger reward responses.

Correlations with extraversion have also been found for the thickness of the prefrontal cortex (Wright et al. 2006). Reduced blood flow has been found in areas of the brain associated with the behavioural inhibition system (e.g. lateral frontal cortex and insular cortex) and in areas of the brain associated with introspective cognition (e.g. Broca’s area and anterior insula), such as internal monologue and memory recall (Johnson et al. 1999; Kumari et al.

2004). Conversely, increased blood flow has been found in areas associated with processing external stimuli (posterior insula; ibid).

Evolutionary theories have suggested that encephalization is the product of an expanded dopaminergic system (DeLouize, Coolidge and Wynn 2017; Previc 1999, 2011). These theories have argued that increased meat eating led to an increase in tyrosine, which then led to an increase in dopamine within the brain. This increase in dopamine and, in particular, its precursor levodopa may have led to an increase in the size of the dopaminergic system by preventing cell death during brain development, increasing the recovery of damaged areas in the dopaminergic system, and increasing tissue reorganisation and plasticity (DeLouize, Coolidge and Wynn 2017). Previc argues that an increase in dopamine would increase endurance running capacities, as dopamine is associated with a reduced core temperature. Further, the dopaminergic system has been associated with executive functions, novelty seeking, increased REM sleep, which decreases the time humans need to sleep (Samson and Nunn 2015), and increased sociality.

Interestingly, when comparing the theory that encephalisation may largely be due to the expansion of the dopaminergic system, which would increase extraversion, to the findings above and to the areas of the brain which have most expanded, we see that not all of these expansions are associated strictly with high extraversion. For example, increased activity in the Broca's area has been associated with introversion and more introspective thinking. This is an area of the brain which has shown continuous increases in size throughout our lineage (Balzeau et al. 2014). However, these measurements were found when participants were in a resting state. Therefore, more work exploring differences in the activation of the Broca's area during social situations would be highly beneficial, as this finding may support the theory that extraversion is related to reduced arousal during a resting state (Kumari et al. 2004), but then increases more rapidly in response to reward. Hypothetically, we may suggest that individual differences in the activation of the Broca's area, and the corresponding behaviour, may have become more extreme or complex as the size of this area increased. This is a suggestion which may equally apply to other areas of the brain that have expanded and show high individual variation in activation.

Increases in the thickness of the prefrontal cortex in extraverts indirectly supports the theory that the dopaminergic system is at least partially responsible for the evolved characteristics of the human brain. This is an area of the brain which is highly reorganized in comparison to other species, with the frontal cortex being three times larger than that of chimpanzees (Teffer and Semendeferi 2012). Importantly, this area is associated with executive functions, which are considered an important feature of modern human cognition. The executive strengths of introverts and extraverts have been shown to differ, with extraverts being better at updating tasks (integrating new information while completing a task) and introverts better at shifting tasks (being able to change from one task to another) (Campbell et al. 2011). Complex personality phenotypes, with different cognitive abilities such as this, may have been another feature developing during encephalization which was responsible for the brain’s rapid evolution. This extends Previc’s (1999, 2011) and DeLouize et al.’s (2017) theories, adding the suggestion that the development of the dopaminergic system increased intra species cognitive variation. This may have been positively selected for two reasons (as will be explored more fully in chapter 3). Firstly, it may have enabled populations to survive a wider range of social and environmental conditions (Nettle 2006). Secondly, it may have reduced intra-group competition by predisposing individuals towards different lifestyles, which may reduce competition for particular resources (Penke, Denissen and Miller 2007).

2.3 Life History Traits and Evolutionary Traits

Introversion and extraversion are associated with distinct behaviours. These behaviours are evident at a population level, although extraverted and introverted individuals may not necessarily exhibit all of these behaviours equally. Generally, extraversion is characterised by increased sociality and impulsivity, whereas introversion is associated with more introspective cognition and greater behavioural inhibitions. This leads to very different life histories for individuals at the extreme ends of the continuum.

As has been briefly discussed in chapter 1 but will be more extensively reviewed here, extraverts are more likely to engage in social activity, and be more friendly, confident and dominant. They are also more adventurous, more active, and excitement seeking, with a more positive outlook on life (Magnus et al. 1993; Watson and Clark 1997). As a result of these characteristics, extraverts are more likely to be popular and have a larger social network, due to their increased willingness to engage in social activity (Anderson et al. 2001; Ilmarinen et al. 2015; Krämer and Winter 2008; Ong et al. 2011; Pollet, Roberts and Dunbar 2011; Slee and Rigby 1993) - which is further evidenced by their increased engagement with social media (Bowden-Green, Hinds and Joinson 2020) - and may engage in more creative divergent thinking (Gocłowska et al. 2019). However, they are also more susceptible to addiction (Coventry and Brown 1993; Kosten, Ball and Rounsaville 1994; Mehroof and Griffiths 2010; Sarramon et al. 1999), antisocial and criminal behaviour (Carrasco et al. 2006), gambling (Palomäki et al. 2021), have a decreased job performance (Reio and Sanders-Reio 2006), are more likely to engage in risky sexual behaviour (Donohew et al.

2000; Henderson et al. 2005; Lalasz and Weigel 2011), and have a higher injury and mortality rate (Horvath and Zuckerman 1993; Jonah 1997).

Studies of mate selection have shown that the majority of selection for personality, that is not accounted for by assortative mating, is in preference for greater agreeableness and intellect. However, the dominance facet of extraversion has been found to be desirable in men (Botwin, Buss and Shackelford 1997). This confers advantages for extraverts for long term mating. Extraverts are also more successful at short term mating and stealing mates (Buss 2009). In general, visual cues for extraversion are preferred when selecting a partner for a short term relationship, and when selecting a female for a long term relationship. Introversion was only preferred when selecting a male for a long term relationship (Brown and Sacco 2017). As a consequence, higher extraversion has been associated with having more children and grandchildren both in western societies (Berg et al. 2014), and in polygynous populations in Senegal (Alvergne, Jokela and Lummaa 2010). Therefore, it is clear that the reproductive success of extraverts is greater than introverts.

Extraversion is associated with more risky behaviour. Consequently, it has been suggested that extraverts (due to risk taking) have a higher injury and mortality rate (Buss 2003, 199–201). This is supported by findings that people with a higher extraversion are more likely to have been hospitalized recently (Hajek, Bock and König 2017; Lajunen 2001; Nettle 2005). Further, trauma patients were also more likely to be risk takers and were less likely to say that engaging in risky behaviour will lead to injury (Field and O’Keefe 2004). In contrast, it has been suggested by some that extraverts have a lower mortality rate (Graham et al. 2017; Iwasa et al. 2008; Masui et al. 2006; Turiano et al. 2015; Wilson et al. 2005; O’Súilleabháin and Hughes 2018). Five of these studies focused on an older age range, one of which only found this trend in the U.S. and not in non-U.S. studies (Graham et al. 2017; Iwasa et al. 2008; Masui et al. 2006; O’Súilleabháin and Hughes 2018; Wilson et al. 2005). Therefore, it may be that extraversion reduces mortality during old age, due to the wider social bonds and social support that extraverts have. These mixed findings have been argued to be due to differences in the way extraversion is measured (Ploubidis and Grundy 2009). As stated above, the increased injury and mortality rate is suggested to be due to sensation seeking and impulsivity leading to risk taking. Therefore, if the personality test being used places more emphasis on sociality, extraversion is less likely to correlate with mortality. Additionally, the increased likelihood of extraverts being hospitalized suggests that they are more likely to be injured. In a modern setting these injured individuals have a much higher likelihood to recover from extreme trauma than they would in the past. Therefore, the number of extraverts dying from trauma has probably decreased. Meanwhile, due to the high sociality of extraverts, more people are around them to alert them of potential health issues and to advise them to seek medical help. Consequently, in the modern day the combination of better healthcare and increased social support reduces extravert mortality (particularly in old age). However, in times when healthcare was less effective, increased support would have had less of an advantage than simply avoiding injury and illness. More work assessing traditional hunter gatherer personality traits and mortality would greatly benefit this research, as modern healthcare systems may have significantly changed the selective pressures acting on personality. Meanwhile, the view that extraversion would be associated with higher ancestral mortality is supported by recent work in Java, where genetic data shows selection for more introverted (risk averse) genotypes in more dangerous areas around Mount Merapi volcano (Faurie et al. 2017).

There appears to be a distinct evolutionary tradeoff associated with the introversion-extraversion continuum. More extraverted individuals are likely to be socially dominant, have more social bonds, and therefore are more likely to reproduce than introverts. Conversely, they are also more likely to engage in risky and sensation seeking behaviour. While this further increases their reproductive success, it also increases their chance of injury and mortality. These phenotypes may represent *K* (introvert) and *r* (extravert) specialist phenotypes (Rushton 1985). *K* specialists are individuals who may live longer, reproduce less, but provide more support to each offspring. In contrast *r* specialists generally have a lower life expectancy, reproduce more, and provide less support to offspring. These strategies may be advantageous in different conditions. Therefore, population variability within this trait may lead to a species being more resilient to different ecological and social conditions or changes.

As noted by above, Fischer et al. (2018) have argued that the dopamine receptor genes associated with extraversion may only be expressed in demanding climates. We may suggest this is similar to Draper and Harpending’s (1982) reproductive strategy hypothesis. They suggested that in response to the absence of a father, females develop a faster reproductive strategy, being more sexually promiscuous. This theory became more generalized and incorporated other forms of childhood stress, such as insufficient resources and environmental harshness (Belsky 2012; Mell et al. 2018). The expression of extraversion genes under harsh, but not stable conditions may be an example of this mechanism. However, the adaptive benefits of reproductive acceleration have recently been disputed using a baboon primate model (Weibel et al. 2020). This study found no relationship between early life adversity and reproductive acceleration. Further, a connection between reproductive acceleration and fitness was only found in individuals who also lived a long life, while early life adversity was associated with decreased life expectancy. This study found no fitness advantages for individuals who had shorter lifespans. Although, as the authors note, in order to have additional offspring the baboon would have to mature a significant proportion of its life sooner. Therefore, in longer lived animals where this proportion may not be as large, such as humans, this may have a greater effect on fitness. Therefore, extraversion may represent an alternate life history specifically adapted for when conditions are uncertain, with the expression of some associated genes being moderated by environmental conditions.

This section has presented a series of characteristics associated with extraversion. These characteristics strongly support that extraversion is associated with faster and increased reproduction, but also increased mortality in an ancestral setting. Further, while it has been suggested that personality differences associated with dopamine receptor genes only manifest in uncertain conditions, more evidence is needed to explore the validity of this suggestion, and whether this mechanism would provide adaptive benefits.

Conclusions

This chapter has explored the genetic causes, neurological correlates, and life history associated with extraversion/introversion. Three primary conclusions can be drawn from this section. Firstly, extraversion is highly heritable and, while specific genes have been associated with the trait, its heritability is the result of many genes and genetic interactions of small effect size, most likely under balancing selection. Similar to other complex heritable phenotypes, there is significant gene-environment interaction. Secondly, the neuroanatomical causes of variation in extraversion are largely associated with the dopaminergic system, and areas of the brain which have drastically changed since the last common ancestor with chimpanzees. It has previously been suggested that the dopaminergic system has been under a large amount of selective pressure, due to its associations with endurance running, complex sociality and other important functions. This section adds to this and suggests that, as the dopaminergic system evolved, it was partially selected for because it increased intra species cognitive variation in extraversion. Thirdly, this section has shown that the life history of introverts and extraverts differs widely. This evidence suggests that, in a Palaeolithic setting, introversion and extraversion would likely represent K and r specialised phenotypes. By incorporating and increasing this variation within our species, past populations may have been able to survive in a wider variety of environments.

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Chapter 3: The Evolution Of Human Neurodiversity

Callum Scott
Penny Spikins

Abstract

This chapter will review how cognitive variability may have been an adaptive feature of our species. The evolutionary mechanisms acting upon humans that may have encouraged cognitive differences will be investigated. This will explore the effects of established selective mechanisms and suggest a human specific mechanism which may have increased cognitive diversity, with a chronology of how this developed being suggested. Following this, the impacts of two examples of neurodiversity will be explored with reference to the archaeological record. Firstly, the evolutionary implications of several recent studies on autistic traits, conducted by this research group, will be reviewed (Schofield et al. 2020; Spikins, Scott and Wright 2017; Spikins, Wright and Scott 2017). Secondly, the effects of variation on the extraversion-introversion continuum on human dispersal out of Africa will be investigated. The role that neurodiversity may have had upon our species' success, as well as our ability to tolerate periods of climatic instability, will be explored.

Introduction

Whilst we intuitively feel that human cognitive differences bring something important to human societies, and may have played a significant evolutionary role, the mechanisms behind this remain poorly understood. Differences such as those along spectrums of diagnosable conditions such as the autism spectrum (Spikins 2013; Spikins and Wright 2016; Spikins, Wright and Hodgson 2016; Spikins, Scott and Wright 2017, 2018), dyslexia (Ehardt 2009; Kershner 2020b, 2020a), ADHD (Jensen et al. 1997; Williams and Taylor 2006) or schizophrenia (Horrobin 1998; Kuttner, Lorincz and Swan 1967; Polimeni and Reiss 2002; Stevens and Price 2015) as well as personality differences with a significant cognitive basis (Buss 1991; Nettle 2005, 2006; Stone, Shackelford and Buss 2012) have been argued to have played a significant evolutionary role in human success (Armstrong 2015).

Here we discuss how cognitive differences in human populations may have arisen, the evolutionary pressures affecting them, and the archaeological evidence for them in the past. In particular, two examples are discussed: local processing bias and extraversion.

3.1 Human Genetic Predisposition Towards Cognitive Diversity

The focus in human cognitive evolutionary research has been upon explaining how a generalised, ‘normal’ human cognition has developed within our ancestors. In reality, human cognition is highly diverse. Within this diversity is a wide range of personality traits and psychological conditions, which are a large part of what makes our species unique.

Recent research has revealed that the human species may have a genetic propensity towards cognitive diversity. This is the result of two genetic causes: segmental duplications, and tandem repeats (Eichler 2017).

There are a high number of interspersed segmental duplications in the human genome (Bailey et al. 2002; Bailey and Eichler 2006). These duplications account for the majority of our genetic divergence from chimpanzees (Gangestad 2010), and increase the instability of regions between segmental duplications. Consequently, this increases the likelihood of these regions having copy number variations or deletions, which are associated with genetic conditions (Cantsilieris et al. 2020). Nevertheless, they have also been associated with the expansion of the prefrontal cortex and increased neuronal connectivity (ibid). This has led to the suggestion that this increased genetic instability, as well as accounting for a range of psychological conditions, may also account for personality differences (Gangestad 2010).

Similar to segmental duplications, tandem repeats (where nucleotides are repeated in an adjacent section of the DNA) also affect gene expression, have a high mutation rate, and are a cause of within and between species variation in genetically determined functions. Interestingly, human specific tandem repeats are enriched in or near genes associated with brain functions and are more expressive in humans than in other primates (Kim et al. 2019).

It is clear from this that our evolutionary trajectory has led to genes associated with the brain being highly mutational, and highly variable between individuals. In fact, mutation rates are highest in essential genes, leading to the suggestion that when a gene becomes functionally important, selection favours increased mutability to promote diversity and increase adaptive fitness (Michaelson et al. 2012). Without this high mutation rate it is unlikely that the human brain would have expanded so rapidly and that it would be characterized by so much functional diversity. This genetic route towards cognitive diversity has formed the base upon which various mechanisms of selection have acted to produce human personality and cognitive variation.

3.2 Mechanisms Of The Evolution Of Human Personality And Cognitive Diversity

This section will consider three evolutionary mechanisms (balancing selection, green beard effect, multilevel selection) and explore the effects they may have had on the evolution of cognitive diversity. The effects of these mechanisms will be explored broadly, addressing any critiques, before focusing upon their effect on cognitive diversity. In particular, the effects of the green beard effect on personality and the effect of multilevel selection on the development of cooperation, which may be one mechanism that facilitates cognitive specialization, will be discussed.

Balancing selection

Balancing selection is a collective term for a number of mechanisms that maintain allelic diversity within a population. It has been shown to have a significant effect on the human genome, affecting ~8% of protein coding genes (Keller and Miller 2006). This mechanism retains genetic diversity within a population when a polymorphism may both increase and decrease an individual's fitness. This inconsistency in fitness payoff may occur in five ways: 1) payoff varies spatially and temporally; 2) the allele may only give an advantage when it is heterozygous (overdominance); 3) it may have a pleiotropic effect, increasing the fitness of one trait while decreasing another; 4) the degree to which the polymorphism is advantageous may vary with its frequency within the population (Keller and Miller 2006); 5) a series of genetic variants may collectively lead to a phenotypic outcome, but individually have a small effect size, this leads to quantitatively distinguishable continuums of traits (e.g. height) (Plomin, Haworth and Davis 2009). Therefore, balancing selection retains diversity due to the evolutionary advantages or disadvantages of the gene being context dependent, both referring to the environmental context of the individual and the genetic context of the gene.

Spatiotemporal variability in selection has been argued to explain the existence of personality variability. MacDonald (1998) suggested that personality differences are continuously distributed. However, in different ecological and socio-cultural conditions the mean value of characteristics changes in response to the distinct selection pressures of that environment (Nettle 2006). For example, within a dangerous environment selection may favour less risk taking phenotypes, or even more neurotic personality types, which are more conscious of dangers.

Similarly, frequency-dependent selection may account for some of the variations in personality and cognition seen in our species (Figueredo et al. 2005). This has been applied to differences in promiscuity (Berrio et al. 2018; Gangestad and Simpson 1990; Wlodarski, Manning and Dunbar 2015), Machiavellian intelligence (Bereczkei 2018), and psychopathy (Mealey 1995). Individuals having differentiated life-history traits in this way is thought to have the added advantage of reducing intragroup competition by predisposing individuals to different roles (Penke, Denissen and Miller 2007). For example, psychopathy or cheating may be advantageous within populations of honest individuals, however if everyone is a cheater the rewards of cheating may not be as great. Further, selection for different perceptual mechanisms, such as a local versus global processing bias, may be maintained because they predispose individuals towards particular jobs or lifestyles and reduce competition.

Heterozygous advantages primarily are seen to influence immunological functions (e.g. sickle cell) (Allison 1954). Despite this, examples affecting cognition do exist (e.g. handedness (Annett 1998; McManus, Shergill and Bryden 1993), cognitive control (Sadaghiani et al. 2017), protection against depression (Uddin et al. 2010)). However, examples of this mechanism affecting cognition are rare and we can perhaps consider them unlikely to have contributed significantly to human cognitive diversity.

Quantitative liability affects all complex traits (Manolio et al. 2009; Plomin and Deary 2015). For example, no single genetic variant determines more than 1% of difference in height and weight (Plomin and Deary 2015). This additive mechanism is thought to underlie the difficulties in studies of Autism Spectrum Conditions (ASC) for finding consistently replicable genetic associations using linkage analysis. However, the cumulative liability attributable to common variants is currently difficult to determine (Anney et al. 2010, 2012). As will be discussed below, these additive mechanisms are significant in determining personality and visual processing biases. They are likely to be responsible for a high proportion of the cognitive diversity observable in humans, particularly when they are not associated with maladaptive behaviour.

Green beard effects

The green beard effect is a mechanism by which support is preferentially given to others with a visible phenotypic trait (e.g. green beard) indicating genetic similarity, in order to increase the frequency of shared genes in future generations. This was suggested by Hamilton (1964b) and extended by Dawkins (1976). Hamilton (1964a) suggested that despite the costs of altruism, it may be evolutionarily beneficial if the recipient of the altruistic behaviour is genetically similar to the giver. The largest indicator of genetic similarity is relatedness, and therefore it operates through kin-based selection. However, if a phenotypic trait highlights genetic similarity, then this may also promote altruism (Hamilton 1964b). Dawkins (1976) highlighted this theory by presenting an example where the phenotypic trait was a ‘green beard’. This subsequently became the common example from which the theory gets its name. He also suggested that acts of altruism themselves may be classed as ‘green beard’ signals, advertising to others that they have an ‘altruism gene’. Individuals with these common phenotypic signals are aware that others share genetic similarities. Therefore, rather than only focusing on individual fitness to increase the presence of this gene within their species, they may also increase it by altruistically taking costs upon themselves to ensure that others pass on this gene. This increases their ‘inclusive fitness’, which is their ability to pass on their genes both through classical fitness, but also through their neighbors and relatives who share similar genes (Hamilton 1964a). This mechanism may develop if the collective benefits of altruism and cooperation are greater than or equal to the costs (Changcao and Xin 2018).

Several arguments have been made to suggest green beards would be rare or non-existent in nature. Firstly, the pleiotropy necessary to produce a green beard effect is argued to be highly unlikely (Blaustein 1983; Dawkins 1976; Hamilton 1964a; Madgwick, Belcher and Wolf 2019; West and Gardner 2013). Secondly, if green beards were so advantageous false beards would be selected for, which would enjoy the benefits of the beard without incurring the costs of helping others (Gardner 2019; West and Gardner 2010). Thirdly, green beards would be ‘outlaw genes’ competing with the rest of the genome, which would act to suppress it (Biernaskie, West and Gardner 2011; Bourke 2011).

Madgwick et al. (2019) reviewed these criticisms and suggested that researchers have misunderstood that Dawkins’ (1976) green beard example was a simplified illustration. They suggest that the green beard should be viewed more generally. In this more general view, an assortment factor is associated with a gene (not determinative), which promotes altruism or selfishness in response to the presence or absence of that gene. Importantly, this gene may not create the assortment factor but may promote responses to environmental cues that lead to assortment (Madgwick, Belcher and Wolf 2019). Further, by operating through multiple associated genes rather than a single gene, with the presence of multiple beard phenotypes, the green beard effect is less unstable and less likely to reach fixation (Jansen and van Baalen 2006). Consequently, rather than the classical single gene green beard effect, researchers should also be looking for polygenic phenotypes that are associated with differences in individuals’ relationships with the environment. These differences in relationship should be distinguishable and such features (either behavioural or physical), if not directly prosocial themselves, should be associated with prosociality towards others exhibiting similar features.

While examples of the green beard effect have been found in nature (Keller and Ross 1998), few examples of green beard effects have been suggested for humans. The evolution of language has been suggested to be subject to a green beard effect (Lindenfors 2013; Sigmund and Nowak 2001). Individuals take the metabolic costs of a larger brain, which is needed for language use, in order to increase social cooperation between individuals. This cooperation is only available to others who are able to understand or use language, and the use of language is the signal for genetic similarity. This is argued to make false beards impossible in this case. Smiling has also been regarded as a signalling trait to promote cooperation between individuals (Owren and Bachorowski 2001), although it has been argued that there is no genetic link between smiling and altruism/cooperation, therefore it is not a green beard effect (West, El Mouden and Gardner 2011). While this argument is suitable for the strict caricature of the green beard effect described by Dawkins, the broader definition specified by Madgwick et al. (2019) would suggest this association is a green beard effect.

While these theoretical examples are interesting, practical attempts to identify the green beard effect in humans have been unsuccessful. For example, while it has been shown that altruism can be reliably identified in others, altruists are not better at identifying other altruists (Oda et al. 2009; Naganawa et al. 2010). This may be an oversimplified example. Humans have likely developed to identify altruism in others for both genuine beard dynamics and to know when to use a false beard, therefore there would be no difference in detection. Further, as shown above, beard dynamics are more likely to be stable when multiple beards are available. Therefore, it may be more beneficial to assess the genetic similarity between cooperators more broadly.

Friends are unrelated individuals who engage in extended cooperation, and therefore may be a suitable test group for identifying green beard effects. Friends tend to be more genetically and phenotypically similar to one another in general (Christakis and Fowler 2014; McPherson, Smith-Lovin and Cook 2003). This suggests that non-kin-based similarity is an important determinant in assortment and cooperation more generally in humans. In particular, personality dimensions are used in friendship selection (Selfhout et al. 2010). This was also found in chimpanzees, suggesting that this personality-based discrimination was also present in the last common ancestor (Massen and Koski 2014). In humans, judgments of similarity based upon clothing and subculture are used to develop impressions upon first meeting (Back, Schmukle and Egloff 2011). Humans use a range of signals to judge how similar other individuals are to themselves, including static facial shape which has been shown to accurately display personality type (Holtzman 2011; Kachur et al. 2020; Walker and Vetter 2016). This may be to ensure cooperators/friends have shared knowledge (making communication easier), and shared needs (meaning those needs are at least partially accounted for when the friend is just taking care of themself) (Christakis and Fowler 2014; McPherson, Smith-Lovin and Cook 2003; Tooby and Cosmides 1996). Friendships largely involve reciprocity in aid and therefore this may not represent a strict green beard effect. It may in fact lead to no reduced fitness in the altruist at all and the long term effects may lead to individual fitness increases for both (Hallpike 1989). Nevertheless, the bias towards individuals who are phenotypically similar was even found in strangers (Rushton, Russel and Wells 1985), where individuals are willing to apply a cost to themselves for the benefit of a similar stranger (Krebs 1975).

Humans are more likely to behave altruistically to others based on similarity, and in particular similarity in personality. Personality may be broadcast through cultural visual cues such as clothing, or biological visual cues such as face shape. This information is used to determine the probability of behaving altruistically to strangers and the formation of friendships. To put it another way, external information is being used to judge similarity in a trait which has large genetic determination, in order to inform an individual’s decision whether to behave altruistically or cooperatively with that individual. Regardless of whether the visual cues prompt the development of a specific personality type or not (Holtzman 2011), this assortment is indicative of a green beard effect. This is further supported by the genetic similarity between friends. The stability of this green beard may be caused by similar mechanisms to Jansen and van Baalen’s (2006) model, operating through multiple genes with multiple beards.

Multilevel selection

Multilevel (group) selection may occur when a decrease in an individual’s fitness is favoured because it provides an advantage to a group that is in competition with other groups (Gardner and Grafen 2009). This may require the pressures for group survival, or group adaptation, to be large relative to pressures for individual selection (Wilson 1997). However, it has been regarded as an alternate perspective for fitness accounting, rather than a separate process (Henrich 2004a). By applying a multilevel perspective to change, we can explore selective pressures that operate at different scales, which otherwise may not be clear. For example, increasing the reproductive ability of your kin or others who share similar phenotypic characteristics as yourself doesn't make sense from an 'individual selection' perspective. However, as has been reviewed above, this increases the inclusive fitness of the individual and ensures their genes are copied to the next generation through another individual. Similarly, multilevel selection may take this function and apply it to higher levels (e.g. groups and societies). If between group genetic variance is high, in comparison to within group variance, cooperation within the group is beneficial to the inclusive fitness of the individual (Gardner 2015; Henrich 2004a; West, Griffin and Gardner 2007). As West et al. (2007) have said, this is the same as increasing the level of relatedness in Hamilton's (1964a) kin selection equations. Importantly, rather than this definition arguing adaptations develop for the benefit of the group explicitly, as has been argued and refuted in the past (Rushton 1989), they adapt for the benefit of the individual's inclusive fitness (West, Griffin and Gardner 2007). Hence, in a similar way to what is seen above, individuals may behave cooperatively and altruistically if it increases their inclusive fitness.

Cooperation and selfless punishment (which may involve a cost for the punisher) have both been shown to have positive effects for individual agents when these processes have been modelled (Krasnow and Delton 2016a). The cost-benefit conditions for cooperation are asymmetrical. The cost of not cooperating and missing the opportunity for long term reciprocity is much larger than the cost of helping someone who may not reciprocate in the future (Delton et al. 2011). Punishment has also been shown to be effective at increasing individual fitness if punishment encourages future cooperation in defectors (Krasnow et al. 2015). The advantages of cooperation for group survival are highlighted by Shaffer et al.'s (2016) study of harvester ants. Further, they showed selection for cooperation increases with population density.

Krasnow and Delton (2016b) and Pinker (2015) have argued that such findings do not imply group selection. However, it could be argued that their misgivings are largely directed at the older definition of group selection. For example, Pinker (2015, 4) has stated, "Some mathematical models of 'group selection' are really just individual selection in the context of groups". He has argued that this is no different to gene-level selection operating in groups. Similarly, Krasnow and Delton (2016b) have argued that group selection is a byproduct of individual selection. These arguments actually highlight the aim of multilevel selection theory: to allow us to explore how gene-level selection operates within groups. It is a term used to identify for the reader that we are discussing the impact of group level cooperation/mechanisms, which may operate on multiple levels at once, on gene-level selection (similar to how kin level selective mechanisms are explored). For example, Shaffer et al. (2016) have stated that their findings from harvest ants may be entirely explained from the perspective of the individual. However, they argue that doing so would make it difficult to highlight the effect of between group competition. Consequently, we may argue that multilevel selection is individual selection reconceptualised to highlight the impacts of interactions with conspecifics.

In humans, multilevel selection operates at an exaggerated level. Not only do we belong to multiple different groups simultaneously, but we perform acts of altruism and cooperation without evidence that these efforts will be reciprocated. This form of cooperation has been argued to be the result of a generalisation of methods adapted for smaller, close groups applied to the larger groups of the modern day (Richerson et al. 2016). Consequently, cooperation and altruism are examples of cognitive mechanisms evolved for specific purposes in the past that are now having novel effects in our drastically different modern environment (Tooby and Cosmides 1989). This is similar to the social heuristic hypothesis, which argues that people develop automatic adaptive reactions for cooperation in response to their daily environment. However, these reactions, when taken into novel environments such as a laboratory, may lead to cooperation even when reciprocity is unlikely (Amir, Jordan and Rand 2016). Adaptive behaviours have been taken out of their niche and as a result cooperation operates in seemingly maladaptive and evolutionarily unusual ways. Alternatively, this may be the result of cultural norms developed to reduce the loss of possible future returns from cooperative action. Additionally, it may be suggested that selection for tolerance and cooperation between groups may be the cause of this (Pisor and Surbeck 2019). However, if these groups are in frequent contact and are part of the same social network, we may suggest that this doesn’t represent cooperation without the prospect of reciprocity, and that this supports the concept of multilevel selection.

It is clear that group cohesion and cooperation increases group survival and may also increase the inclusive fitness of group members. Within groups, balancing selection (where selection for a gene is context dependent) may lead to increased phenotypic and genetic variability in order to decrease intra-group competition. Further, the green beard effect may encourage cooperation between phenotypically similar individuals. Associated with and extending this, multilevel selection quantifies the effects of group cooperation, where individuals may take a reduction in their own fitness for the benefit of the group. By aiding others who may not be similar to you in many ways, but may share some genetic similarity as a consequence of being part of the same group, this may increase intra group diversity. While these are not the only mechanisms which may be responsible for our cognitive diversity (e.g. mutation-selection balance, selective neutrality) (Penke and Jokela 2016; Stone, Shackelford and Buss 2012), the social focus of these mechanisms makes them uniquely interesting for the study of human evolution. In particular, the effect of group dynamics and the extension of social network sizes (Dunbar 2016), suggests that multilevel selection possibly had a significant effect on human evolution and may have impacted the evolution of human cognitive diversity. The following section will explore how multilevel selection may have led to the development of cultural identity. Following this, the effect of increasing cultural complexity on cognitive diversity will be assessed.

3.3 Within Group Niche Specialization and Cognitive Diversity

Drawing upon the selective mechanisms above, this section will describe a potential mechanism for the development of specialization and cognitive diversity in humans, explore the archaeological evidence supporting this mechanism, and the limitations of this theory. This will then be applied to two examples of diversity in the following section.

A possible mechanism for the increase of task specialization and cognitive diversity is outlined in figure 1. This mechanism suggests that as the social network sizes of hominins increased due to favourable conditions, more individuals were contributing to material culture (figure 1, box 1-2). Due to this, tags related to group membership became more accurate, which facilitated further social network expansion (figure 1, box 2-3). This operated in a feedback loop, increasing social network sizes and material complexity, until they were able to function anonymously. Shared group norms were then developed to display trustworthiness to strangers (figure 1, box 4). These norms were likely used to enforce altruistic behaviour (figure 1, box 5). Through this enforced helping, individuals who found it difficult to do particular tasks were aided, provided they contributed to the group in another way. Over time this allowed individuals to specialize into particular roles (figure 1, box 6). As a consequence, more extreme cognitive traits predisposing individuals towards particular group tasks became selectively advantageous, increasing cognitive variation within groups (figure 1, box 7). Effectively, the diversity of niches available to individuals likely increased, which has been shown to increase personality diversity (Smaldino et al. 2019). This likely increased cognitive diversity generally. By increasing the cognitive diversity of our species and allowing individuals to specialize, it may increase the conditions humans are able to thrive in (figure 1, box 8). The mechanism described here does not need to be explained by a cognitive change towards collaborative morality within our species. Rather, it represents a change in demography, materiality, and consequently sociality. This section describes this theory more fully.

Spikins et al. (2016) have argued that cognitive diversity has its roots in collaborative morality. Whilst collaborative morality may provide an environment for neurodivergent individuals to flourish, I argue here that the development of collaborative morality is part of a larger set of social changes that increased cognitive diversity. These developments include: increases in population/network sizes, which may reduce selective pressures; the use of cultural tags, which may enable social network sizes to further increase and may specifically be a product of neurodivergent individuals; specialization, which may be facilitated by the use of group norms and a collaborative morality, and may provide niches where neurodivergent individual may contribute greatly to the group.

Supporting box 1 of the mechanism, it has been argued that during the Palaeolithic an increase in population density in combination with a decrease in habitat suitability and resource clustering in refugia zones (Ziegler et al. 2013), led to selection for cooperative group dynamics (Spikins et al. 2021). We have increasingly appreciated the significance of extended social networks in our evolutionary past (Dunbar 1998, 2009, 2016). The network sizes we have developed are larger than those of our relatives and require the development of specific cognitive mechanisms, such as theory of mind and language, which allow more efficient management of social relationships (Aiello and Dunbar 1993; Dunbar 2004, 2017).

In support of box 2, there is general agreement that the material and cultural complexity of early modern humans was facilitated by larger populations and social network sizes (Powell et al. 2009; Powell et al. 2010; Shennan 2001), which allowed the accumulation and recombination of a large diversity of material culture at a higher skill level (Henrich 2004b; Muthukrishna and Henrich 2016). For example, in Tasmania there was a loss of complex technology when the island was isolated from the mainland due to rising sea levels (Henrich 2004b). This example of the loss of material culture in Tasmania when the population was isolated, highlights that small fragmented populations may be less able to maintain complex specialized material culture, let alone develop it. Henrich (2004b) suggests this idea may also be applied to the technological differences between highly fragmented Neanderthal populations and more cohesive early modern human populations. Hence, our ability to encourage cooperation between a broad range of individual groups and create social networks may be another example of multilevel selection operating in humans according to the definition outlined above. This is particularly apparent when framed in the context of competition with Neanderthals. Nevertheless, the dependence of material complexity on population size may have a long history, and has been suggested to be the reason why Mode 1 technologies were used by some populations during the Acheulean (Lycett and von

Cramon-Taubadel 2008). Therefore, we may suggest that at particular points in our evolutionary history groups became more or less culturally and materially complex, in response to fluctuations in population size (figure 2, box 1-2).

This idea has been critiqued and it has been argued that: the degree of specialization within a population, Malthus-Boserup population pressures (where a population reaches a carrying capacity and then invents new technology to increase that carrying capacity), and other environmental pressures may be more determinant of cultural complexity (Collard and O'Brien 2013; Collard et al. 2016; Vaesen et al. 2016). Henrich et al. (2016) have replied to this argument stating that they would not expect population density to be the only determinant of cultural complexity. However, they have shown that it has a significant effect. Further, they have argued that ethnographic findings that do not support their theory do not account for the communicative network sizes of populations, but focus on the census sizes of populations, which may not relate to cultural complexity. In addition, it should be argued that the alternative causes noted above are likely impacted by population size. For example, Malthus-Boserup pressures are unlikely to be an issue in a sparsely populated area, and specialization is less likely to occur in a small population due to the associated costs (Sinclair 2015).

As will be discussed below, the establishment of defined recognisable cultures, facilitated by symbolic and stylistic objects (Wobst 1974; Wobst 1977), may increase the size of a social network further, meaning that more individuals may contribute to material culture. This is similar to a Malthus-Boserup effect, but relating to the carrying capacity of the social landscape. Consequently, once material culture is used to extend social network sizes, it may create a feedback loop with material culture complexity and effective population size increasing together (figure 2, box 3). This is likely balanced with the disadvantages of a complex material culture. For example, the time it takes to learn and produce objects may be a limiting factor. Nevertheless, the development of new mechanisms, such as specialization, may have increased the maximum complexity groups' technology could reach.

Cultural complexity may have functioned in one of two ways during our evolution. Firstly, developing a cultural identity and mediating migration based upon culture has been shown to decrease within-group genetic diversity, and genetic diversity more broadly, while also increasing genetic difference between groups (Premo and Hublin 2009; Premo 2012). As a consequence, constraining migration based upon cultural similarity increases how related individuals within a group are to one another. However, recent research does not support this theory and suggests that, while foraging groups may be small, hunter gatherers are members of wider, interconnected, fluid groups and this was likely the case with our ancestors (Bird et al. 2019). Alternatively, we may suggest that material and behavioural broadcasts of cultural identity signalled similarity, which promoted cooperation within and between groups, helping to establish extended networks. Spikins et al. (2021) have highlighted the importance of inter group tolerance in harsh environments. The ability to share resources at the boundaries between groups increases group survival in harsh environments (up to a threshold at which tolerance no longer provides an advantage). Active cooperation, gift giving and the ability to maintain a broader shared material culture would likely accentuate the effects seen in Spikins et al.'s model. Therefore, as per box 3, material culture may have been used to extend social networks and broadcast or even created shared needs, which encouraged cooperation.

Moffett (2013) has produced a theory of how cultural identity and society labels may have developed to facilitate population expansion, which may inform our understanding of how materiality and divergent cognitive specialization evolved. This argues that vocalisation was the first social label, developed as a form of “password” and later evolved into explicit language (which further enabled speech to be used as social labels both in content and accent (Cohen 2012)). Following this, the development of group activities and material identifiers was important for instant recognition (Moffett 2013). As was mentioned above, the use of material objects and the creation of ‘traditional’ tasks can simplify social problems, allowing social networks to be extended (Gamble 1998).

While most forms of cultural activity do not leave traces in the archaeological record, the Acheulean material record may provide an early example supporting box 4. Handaxes may be suggested to be an example of material symbolism denoting trustworthiness (Spikins 2012). However, despite their non-functional shape and weight variation (Key and Lycett 2017), it is unlikely that handaxes are evidence of emblemic symbols denoting cultural group affiliation. As Key and Lycett (2017) have suggested, it is more likely that these variations are due to cultural drift and copying error. However, handaxes are so prone to copying error that other mechanisms would have been needed to maintain their form across time and space (Kempe, Lycett and Mesoudi 2012; Lycett et al. 2016; Schillinger, Mesoudi and Lycett 2014). While retention of shape may be due to ergonomics or functional constraints (Kempe, Lycett and Mesoudi 2012; Lycett et al. 2016), cultural norms may also have played a role. It may be argued that explicit deviations in size, such as the Furze Platt handaxe may be a product of strictly cultural practices. While it is unlikely that handaxes provided information about group membership or status, the practice of adhering to more isochrestic cultural norms in tool form may have been a signal of altruism and trustworthiness (Spikins 2012), at a time when altruism would have been prized more than at any previous time, due to the high energy budgets of *Homo erectus* (Aiello and Key 2002). More cohesion between the extended family and other groups as a result of these energetics would have been required, particularly in areas with patchy resources (Finlayson 2014, 69–83). Hence, an evolved signal of altruism displaying a willingness to invest time to help others, as well as the probability that flint knapping was a ‘musical’ community activity beyond the product itself (Montagu 2004, 2017), may have reaffirmed bonds within groups. It may also have been a way of detecting free-riders not willing to invest resources in group activities (and consequently for the good of the group). Within the Acheulean the material world may have been utilized to produce signals similar to a green beard effect to broadcast altruism, increase group cohesion and increase the likelihood of inter group cooperation – if individuals from different social groups were able to recognise shared altruistic signals that were widespread within the local area.

While material objects may have been recruited to reaffirm the bonds within groups during the Lower Palaeolithic, the proliferation of material culture often called the “Upper Palaeolithic Revolution”, may be evidence of an increased use of symbolism to denote cultural affiliation. As I have stated above, social network size is an important determinant of material complexity, and consequently label accuracy. It is the size of the population contributing to material culture which is important, as well as the potential for competition. Both of which likely increased during the Upper Palaeolithic.

The specialization of material culture for identifying social information may imply increasing stratification of the social world. For example, Guy (2020) has suggested that the specialization required to produce naturalised artwork implies hierarchy. He suggested that Upper Palaeolithic artwork shows hierarchy in three ways. Firstly, training and resources would need to be supplied to those engaging in and learning art, therefore suggesting controlled wealth distribution and possibly patronism by wealthier members of a group. Secondly, he argues that realistic depiction is always the product of hierarchical society, and therefore this should be expected for the Palaeolithic. Thirdly, the standardization of style, lack of humans, and placement of artwork in public and private spaces may suggest these are family prestige emblems. Hayden (2020) has long argued that hunter gatherer groups in locations with plenty of resources are transegalitarian, with hierarchical but not necessarily centralized leadership. Thus, they are midway between egalitarian and chief-based (Owens and Hayden 1997). He argues that as groups gained and were able to store a surplus of resources, particular families or individuals were able to take ownership of resources and used them to trade for a range of prestige items or used them for other displays of wealth.

Similar to the above interpretation of Palaeolithic art, many of these objects require the recruitment of specialists, and large investments of time to produce these displays. For example, the burial at Saint-Germain-la-Rivière was associated with an assemblage of 69 red deer canines, collected over several years. These teeth were exotic to the region and each had a standardized perforation. This was interpreted as a significant investment made by a group for an individual of high status (Vanhaeren and d'Errico 2005). More broadly, Hayden (2020) has suggested that the rarity of burial suggests that it is a prestige activity more generally. Consequently, in areas with a high amount of resources, social groups may have been formally structured in a hierarchy during the Upper Palaeolithic. This argument does not suggest that social inequality originated at this time, as this may have a much more extended history (Grove 2020). Rather, that inequality became more structured at this time.

As a consequence, material culture has been recruited to portray not only between group information, but within group status information. Social stratification may increase the benefits of having specialists within a group. Having more broad viewed individuals higher up the hierarchy coordinating the actions of specialists has been shown to be beneficial (Hart and Moore 2005). Therefore, while not necessarily leading to a single leader within a rigid hierarchy (Wengrow and Graeber 2015), stratification may produce leadership roles for orchestrating particular group tasks (e.g. hunting or movement) (Garfield, von Rueden and Hagen 2019). Further, stratification may lead to attached specialization, where the actions of specialists are controlled by those of high prestige (Arnold 1996). This may be used to increase the reputation of powerful individuals, through material culture (Arnold and Munns 1994), or more generally assigning the most proficient individual to complete a task may increase whole group fitness (Smith 2007). The advantages of specialization and trade have been argued to be partially responsible for the success of humans relative to Neanderthals (Horan, Bulte and Shogren 2005; Smith 2007). Therefore, the development of group organisations which enabled task division may have been significantly advantageous to groups' fitness.

The conditions under which specialists were able to develop was likely one where group norms and the cultural identity of the group were paramount (figure 1, box 4). There are significant costs when specializing in a particular task, for the individual, their family, and their group (Sinclair 2015). Therefore, the social mechanisms for specialization likely initially developed in more stable suitable environments with less resource stress, before being applied to more dangerous unpredictable environments where people were more reliant on complex technology to reduce the risk of shortfalls in resources (Torrence 1989, 57-66; Torrence 2000, 74-78).

The social mechanisms leading to the establishment of specialization may stem from a shared identity and morality. The establishment of norms reinforced by a shared identity, which promotes altruism between unrelated or even unfamiliar individuals, is a departure from the individual alliances formed by other primates (Spikins, Wright and Hodgson 2016). As the importance of group membership (broadcast through material objects), rather than personal familiarity, and group norms became more generalised, this may have led to an extended collaborative morality (Spikins, Wright and Hodgson 2016) (figure 1, box 5). This collaborative morality may have been rooted in shared spiritual beliefs, which often include explicit rules encouraging prosocial behaviour within the group, and provide behavioural checks to aid cheat detection (e.g. costly rituals) (Atran and Henrich 2010). Spikins et al. (2016) have argued that this provided a buffer for shortfalls in both resources and skills (figure 1, box 6). Therefore, specialization for different roles is more likely to take place. Spikins et al. (2016) focus primarily upon how this may function within egalitarian groups. In these groups skills may be recognised and enable the individual to gain reputation, while shortfalls are managed due to the broader sharing of resources. However, within transegalitarian groups the recognition of others' skills and buffering of their difficulties may have operated in a similar way to Guy's (2020) interpretation of Palaeolithic artists, with more powerful patrons taking the costs (or distributing the costs throughout the group) to allow them to focus upon tasks which they excel at. This may be for the personal gain of the elite or be generally for the good of the group, and may allow specialization to a greater extent. Spikins et al. (2016) have argued that specialization would broaden the cognitive niches available to be occupied (figure 1, box 7). Consequently, this would lead to selection for a broader range of cognitive and psychological differences, which may allow humans to inhabit a wider range of environmental niches (figure 1, box 8).

It must be recognised that there are alternative explanations for the development of specialization and cognitive diversity and several limitations to this theory. Klein (2008) has argued that an unidentified neurological change may have occurred during the mid-upper palaeolithic which led to the development of complex specialization. However, evidence for this theory is lacking. Further, it has been argued that during periods of climatic instability groups may invent new technologies to aid survival. These technologies may then be used to survive in new environments once the climate stabilizes (Grove 2014; Grove et al. 2015; Potts 1998, 2013). Whilst this explanation may account for changes in functional tool use, it may not account for the proliferation of non-functional objects during the upper palaeolithic. Additionally, as has been discussed above, there are other explanations that may account for the large amounts of psychological diversity in our species (e.g. selective neutrality and mutation-selection balance). However, these explanations have their limitations, particularly when accounting for the large differences in life history associated with some psychological differences. Likewise, the theory presented in this paper has several limitations. Firstly, it is difficult to test archaeologically, although simulation methods may be useful to help overcome this issue. Further, increased technological complexity does not rely upon cognitive diversity, and vice versa. However, the discussion above and the subsequent sections show how they likely affected one another. Nevertheless, it is unlikely that every technological change occurred in this way.

The following sections will explore two case studies of neurodivergence in our species, local processing bias and introversion/extraversion. How these variations may have impacted palaeolithic populations will be explored using archaeological evidence.

3.4 The Archaeology of Neurodiversity

Archaeology may have a significant role to play in understanding the role of neurodiversity on our evolution. It brings a material record with a chronological and geographic control over changes taking place in human behaviours. It also allows us to identify changes in material culture which may be associated with psychological and cognitive differences.

The present section will define two examples of psychological difference, Local Processing Bias (LPB) and extraversion. The genetic causes of LPB, differences in relationships with the material world, and the evolutionary implications of variations in processing will be discussed. The genetic causes of extraversion will then be reviewed. In particular, the effect of dopamine receptor genes and their association with population dispersal will be investigated. The wider implications of increased diversity in extraversion for group dynamics will also be explored.

Example One: Local processing bias

Local Processing Bias

Individuals with a Local Processing Bias (LPB) process the detailed components of information before processing the global, whole overview of that information. LPB is often associated with Autism Spectrum Condition (ASC), although it is a trait identified in relatives of individuals with ASC (Briskman, Happé and Frith 2001; Happé 1999; Happé, Frith and Briskman 2001), and is also more widely distributed and phenotypically expressed throughout the population (Grinter et al. 2009; Hoekstra et al. 2007; Robertson and Simmons

2013). LPB is a trait of ASC, a condition which causes the brain to function differently and causes social and perceptual differences. Consequently, the majority of research has focused upon LPB in individuals with ASC. Therefore, this section will explore the genetic causes of ASC, which has significance for the genetics of LPB, before investigating the possible evolutionary effects of LPB and ASC.

LPB is associated with a range of advantages and disadvantages (table 1). The advantages predispose individuals with LPB to be particularly successful in professions such as engineering, mathematics, science, art and music (Baron-Cohen et al. 2001, 2009; Craig, Baron-Cohen and Scott 2001; Happé and Vital 2009; Heaton, Hermelin and Pring 1998; Meilleur, Jelenic and Mottron 2015; Spikins, Scott and Wright 2018). Meanwhile, the disadvantages of LPB may contribute to the social difficulties associated with ASC. This impact on sociality is separate from the effects of delayed theory of mind (Happé 1999), and is present in the wider population (Grinter et al. 2009).

Table 1. The advantages and disadvantages associated with local processing bias.

Advantages	**Disadvantages**
Better able to identify embedded figures (Jolliffe and Baron-Cohen 1997; Shah and Frith 1983).	Conversational difficulties: contextualizing words for meaning or metaphor, altering conversation to match social context, ensuring replies are related to the current topic, relating previous points of the conversation to the whole (Frith and Snowling 1983; Happé 1997).
Better at assembling a whole image from its parts (e.g. in a block design test) (Shah and Frith 1993).	Difficulty contextualising social information to understand others' mental states (Baron-Cohen and Hammer 1997; Frith and Happé 1994/4; Jarrold et al. 2000; Skorich et al. 2016). This is a separate contributing factor not a determinant of difficulty in ToM (Happé 1999).
Enhanced musical ability, due to an enhanced ability to acquire perfect pitch (Heaton, Hermelin and Pring 1998).	Inform decisions using recent (local) information, rather than past (global) observations, which may make behaviour

	more flexible but less adaptive to “noise” (minor temporary deviations from expectation) (Nassar and Troiani 2020)
Enhanced artistic ability, due to constructing images from their details rather than from stereotyped images (Selfe 1977; Humphrey 1998; Kellman 1998).	Difficulty understanding uncertain systems, such as social systems (Baron-Cohen 2006).
Better understanding of complex systems (Baron-Cohen 2002, 2006).	Higher levels of depression (Beatteay and Wilbiks 2020; de Fockert and Cooper 2014).

Genetics of Autism Spectrum Condition and LPB

ASC is a collective term used to describe a series of related and highly heritable psychological conditions. ASC is generally regarded as primarily affecting three cognitive functions: theory of mind, central coherence (processing bias), and executive functions. Twin studies estimate concordance between monozygotic twins to be between 39-96% and 15-31% for dizygotic twins (Castelbaum et al. 2020; Huguet, Benabou and Bourgeron 2016; Lichtenstein et al. 2010; Ronald and Hoekstra 2011; Rosenberg et al. 2009; Taniai et al. 2008), with heritability estimates between 38-83% (Hallmayer et al. 2011; Huguet, Benabou and Bourgeron 2016; Lichtenstein et al. 2010; Sandin et al. 2014, 2017). However, trait severity may be discordant depending on non-shared environmental conditions, which accounts for some of the variation in heritability estimates (Castelbaum et al. 2020; Hallmayer et al. 2011), particularly in studies with small sample size. A large-scale study of 2,049,973 children estimated heritability to be approximately 50% (Sandin et al. 2014). This study attempted to account for the effect of follow up time on estimates of familial aggregation of the condition. However, a recent re-evaluation of this data suggests this may have dampened the estimates of heritability. The updated results suggest that ASC is 83% heritable, with additive genetics accounting for 69% of concordance and non additive genetics accounting for 10% (Sandin et al. 2017). Further, estimates of the heritability of ASC with and without intellectual disability differ (64.6% and 33.4%), which may suggest that they are caused by different genetic mechanisms (Xie et al. 2020).

As stated above, the majority (90-95%) of the heritability of ASC is caused by a range of additive genes (Klei et al. 2012; Sandin et al. 2017), individually of small effect (El-Fishawy and State 2010). However, ASC has several distinct causes which lead to similar phenotypes of varying severity (de la Torre-Ubieta et al. 2016). In particular, the genetic mechanisms leading to ASC comorbid with intellectual disability or low IQ may be distinct from less severe phenotypes (Ronald and Hoekstra 2011). Genetic research suggests that this comorbidity may be caused by rare de novo loss of function mutations, CNVs and truncated genes of high penetrance (Iossifov et al. 2014; Leppa et al. 2016; Robinson et al. 2016; Ronemus et al. 2014; Toma 2020). In contrast, more high functioning phenotypes are caused by additive single nucleotide polymorphisms and copy number polymorphisms of low penetrance, which account for the majority of heritability (Toma 2020).

As we have argued elsewhere (Scott 2017; Spikins, Scott and Wright 2017), the genetic mechanisms leading to autism with and without intellectual disability may have been under different selective processes.

The SNPs associated with ASC without intellectual disability are not necessarily deleterious and some have been under positive selection due to their association with educational attainment, years of study, neurogenesis and cognitive ability more broadly (Warrier et al. 2016; Polimanti and Gelernter 2017). Following the Common Disease-Common Variant hypothesis, it is likely that these common variants were likely present in the early modern human ancestral population (Scott 2017). Mild phenotypes or traits of ASC may even have been under positive selection in these populations. There is considerable overlap between the genes associated with ASC and genes associated with traits of autism in the wider population, regardless of trait severity (Bralten et al. 2017; Lundström et al. 2012; Robinson 2011). This supports theories that ASC is an extreme variant of a spectral collection of traits distributed throughout the population (Baron-Cohen 2006; Ronald and Hoekstra 2011). The history of these common variants is unclear, however it is likely that their history extends far back in our evolution. It is possible that the increased variance of traits (the extreme of which collectively cause autism) may have occurred at different times through our evolution. For example, as will be discussed further below, variations in individuals’ attention to objects and details may extend as far back as the first time an object adhered to a strict form, in the Acheulean. Meanwhile, extreme variations in sociality may have developed later when pressures for explicit sociality were relaxed.

In contrast, humans have relatively recently become more susceptible to the rare variants that may cause ASC with intellectual disability, following our divergence from Neanderthals (Scott 2017). For example, a duplication in BOLA2, which aids in iron regulation (Giannuzzi et al. 2019; Philpott et al. 2021), occurred 282 ka and was strongly selected for. This duplication led to instability in the 16p11.2 chromosome, leading to an increase in CNVs associated with ASC and/or intellectual disability (Duyzend et al. 2016; Nuttle et al. 2016). Other examples of human specific genetic susceptibility to de novo or CNV related ASC are AUTs2 CNVs and duplications (Oksenberg and Ahituv 2013; Oksenberg et al. 2013), DUF1220 (also called the Olduvai domain due to its connection with human encephalization) instability and dosage effects (Davis et al. 2014; Dumas and Sikela 2009; Sikela and van Roy 2017), and 15q13.3 instability (Antonacci et al. 2014). While these types of mutations are not human specific causes of ASC (Yoshida et al. 2016), rapid changes in our genomes have increased our susceptibility to them (see above).

To summarize, ASC without intellectual disability and autistic traits in the general population, such as LPB, are caused by common variants, which lead to distinct phenotypes with advantages as well as disadvantages. This suggests that autistic traits are the extreme tail end of a normal distribution within our species. In contrast, ASC with intellectual disability is caused by rare variants that modern humans are particularly vulnerable to, but which contribute to a much smaller proportion of heritability.

Autism and Material Culture

This section draws on evidence collated from a series of separate projects, to which the current author contributed (see below). The evidence has been separately published (Schofield et al. 2020; Scott 2017; Spikins, Scott and Wright 2017; Spikins, Wright and Scott 2017), but here is discussed in a novel way in relation to the evolutionary implications (not discussed elsewhere). These studies explored the effects of ASC on engagement with material culture, using surveys:

- Visual Perception and Cognition Survey (VPCS; the author contributed to the construction and distribution of this survey, completed the data analysis and discussed the implications of this survey as part of his master’s thesis)
- Material Objects Beliefs and Engagement Survey (MOBE; the author completed the data analysis for this survey)
- Buildings and Relationships Survey (BRS; the author helped construct and distribute this survey, and completed the data analysis)

The psychological implications of these studies have been explored elsewhere (Wright et al. 2021); this section will focus on some of the evolutionary implications of the findings.

Within each study reviewed in this section the AQ test was used to determine the presence and severity of traits of autism (Baron-Cohen et al. 2001). This test displays high validity for identifying ASC, however it is not diagnostic (Wheelwright et al. 2010; Woodbury-Smith et al.

2005). If participants scored above 32 (the cut-off suggestive of ASC) participants were classified as having an above average amount of traits associated with autism (AU). Participants below this were considered neuro-typical (NT).

The VPCS survey (n=1062) explored the hypothesis that traits of autism would influence the ways individuals engage with art (Scott 2017). In particular it explored whether participants with autistic traits were better able to perceive hidden figures in Palaeolithic art. The survey asked background questions regarding participants' experience of art and asked participants to identify several embedded (hidden) figures in Palaeolithic artwork. Two blank control images were also included. This survey revealed that AU participants were more likely to have a high experience of art and that a higher AQ was related to having more experience of art more generally. Participants with an LPB (high attention to detail) were also more likely to engage in art (Spikins, Scott and Wright 2017). Interestingly, while participants in this survey showed no difference in their ability to identify embedded figures in Palaeolithic art, participants with above average attention to detail were more likely to see imagined images in the controls (Scott 2017). The implications of this suggest that individuals with autistic traits, and more specifically an LPB, are more likely to have engaged in art during the past. They are also more likely to perceive pareidolic cues, which may have been an inspiration for the earliest art, similar to Hodgson’s (2008) hyperimages.

The MOBE survey explored how autistic traits affect participants’ (n=550) attitudes toward valued personal possessions (Spikins, Wright and Scott 2017). When asked what they would take with them in a series of disaster scenarios, AU participants were more likely to take functionally useful objects (such as a coat or a computer with work on it) rather than sentimentally significant objects (such as photographs). Further, if participants still owned their favourite childhood objects, AU participants were more likely to still use that object. Sensory aspects were often an important part of what made these objects special to the participants. We previously argued that a preference for taking functional objects may be significant for survival in the Palaeolithic, as individuals could only transport a finite amount of items. Therefore, while taking items of emotional significance may help to reinforce social alliances, the direct costs of leaving something functional may lead to group extinction. If a group diversifies their approach and some individuals take functional and some sentimental objects, it may increase group survival by allowing them to cope with both social and natural crises (see Evolutionary Implications).

The BRS survey explored how traits of autism may affect peoples’ perception of the built environment (Schofield et al. 2020). Participants (n=760) were asked questions about their relationships with buildings, what their favourite buildings within their local environment were, both now and as a child, and what features made them significant. They were also shown photographs of different types of buildings and aerial photographs of different types of city and asked where it might be most comfortable to live. This study revealed that AU participants were less likely to enjoy visiting new places, ranked the importance of communal/social aspects of a building lower when discussing their favourite buildings, but ranked the function and aesthetics of the building as more important and also placed high value on the evidential features (historical significance) of buildings. AU participants disliked change in buildings, however in contrast to NT participants, this dislike for change was more general rather than related to a loss of historical significance, even if the change was positive.

Evolutionary Implications

Differences in the ways individuals with traits of autism engage with the material world may have evolutionary implications, not only for the individual, but for the groups those individuals are in. This section will explore the impact the evolutionary mechanisms discussed above may have had on traits of ASC and in particular LPB, both looking at general selective mechanisms, which affect all species, and looking at the more human specific mechanism outlined above.

From a general perspective, balancing selection may have had a large effect on the evolution of autistic traits. Genetically, traits of autism are highly polygenic (Anney et al. 2010, 2012). Phenotypically, they are likely subject to spatiotemporal and frequency dependent selection. Traits of autism may be associated with a tradeoff. For example, the increased flexibility of preferentially using recent information (local) to inform decisions, rather than past experiences (global), may make individuals more flexible when faced with environment change. However, this may be disadvantageous in a stable setting (Nassar and Troiani 2020), and may also lead to increased dispersal rates if individuals do not use past experience and foresight to help them select preferred environments when moving (Wren et al. 2014). However, in the case of ASC it is likely that other traits of the condition, such as a preference for the familiar, would counteract this. More broadly, there is a tradeoff between understanding complex systems (e.g. natural systems), which is easier for individuals with LPB, and understanding uncertain social systems (Baron-Cohen 2002, 2006), which likely applies to individuals without ASC who have LPB. Additionally, while this is associated with ASC more broadly, the studies outlined above show that individuals with a less socially oriented view of the world prioritize functional aspects of the material world. This was seen both in the MOBE survey and the BRS survey. Selection for this functional orientation will likely vary according to the severity of social and ecological pressures, as well as according to the frequency at which this trait is represented within a group.

Spikins et al. (2016) have argued that extraordinary skills associated with autism (e.g. enhanced memory) and LPB, would have been extremely advantageous within certain contexts in the past. For example, they suggest that these enhanced perceptive abilities may improve hunting and foraging success, as well as tool making abilities. They have argued that mid to high latitude and variable environments may be settings where traits of ASC are/were particularly selected for. This is due to the need for attention to detail to make reliable tools, increased pressure on technological developments, and environmental pressures to collaborate and support one another (which may reduce the costs of cognitive specialization). Further, in highly variable environments, having individuals with different adaptive strategies may increase group survival (Spikins, Wright and Scott 2017).

Following the mechanism above (figure 1), multilevel selection may have had a large impact on the evolution of LPBs. As has been mentioned above, diversification in the amount of attention individuals showed objects may extend as far back as the Acheulean. However, this diversification was unlikely to reach modern levels as individuals were required to be generalists, contributing to or completing many different types of tasks. Following the development of collaborative morality (Spikins, Wright and Hodgson 2016), and/or the development of elite based patronism (Guy 2020), individuals were able to specialize into particular roles favouring different cognitive abilities. Consequently, as Spikins et al. (2016) have argued, this may lead to selection for detail based processing, at the expense of complex social understanding. This likely occurred during the Upper Palaeolithic. Previous studies have identified several aspects of Upper Palaeolithic material culture which may be associated with traits of autism: specialised tools, calendrical systems (e.g. the Abri Blanchard plaquette), and artwork (Scott 2017; Spikins 2009; Spikins, Wright and Hodgson 2016; Spikins, Scott and Wright 2018; Spikins and Wright 2016). Following this review, I would add explicitly that the creation of cultural tags in order to increase the predictability of the social landscape may be due to the influence of individuals with traits of autism, who would benefit most from this (figure 1, box C). The preservation of cultural norms may also have been encouraged to a greater extent by those with traits of ASC. As seen from the MOBE and BRS studies, they are more resistant to change, continuing to use childhood objects and being less pleased with changes to buildings. Therefore, individuals with traits of ASC may have been maintainers of material culture as well as inventors.

While the development of mechanisms to include individuals with traits of ASC (including LPB) may be due to environmental variability, following the discussion above I would argue that the population size of groups is also significant. As Spikins (2016) has noted, the first proliferation of technological innovations occurred ~100ka at a time of environmental fluctuation. This increase in technological complexity is also associated with an increase in population size (Sherry et al. 1994), which has been regarded as the effect of technological achievements increasing the landscape's carrying capacity (Mellars 2006). Alternatively, pulses of climatic humidity have been associated with cultural innovation throughout the Middle Stone Age (Ziegler et al. 2013). These pulses may have allowed the population size and density to increase within refugia regions and more networking to occur, leading to increased cultural complexity (Powell et al. 2009; Powell et al. 2010; Shennan 2001; see section 3.3). Further, D'Errico et al. (2017) have argued that the diversification in manufacturing methods, as well as tool forms, seen in the Howiesons Poorte industry, is the result of 'product copying' rather than 'process copying'. They argue that this occurred during a period of intense aridification and by facilitating a more flexible toolkit they were able to expand their niche and survive in these regions. Interestingly, 'product copying' may be enhanced in individuals with an LPB, as is seen in block design tests with individuals with ASC (Shah and Frith 1993). The ability to produce similar tools regardless of procedure, as D'Errico et al. (ibid) have argued, would likely be highly advantageous in particular environments where flexibility is needed. Consequently, we may hypothesise for future research that as humans increased in density within regions of refugia, the cognitive niche was able to expand due to the ability to produce larger extended networks. These networks may have reduced reproductive selective pressures, due to there being more potential mates, which may have allowed less socially oriented phenotypes to thrive (figure 2, box A). The creation of these extended networks was facilitated by social technological innovations, which led to an increase in both social and functional material culture. This proliferation of material culture likely occurred due to increased horizontal transmission, but also due to an increase in technology focused, innovative cognitive types.

Von Hippel and Suddendorf (2018) have argued that low rates of innovation suggest humans have evolved specifically to innovate to solve social problems, and only a few more technically oriented individuals are responsible for the technical innovations humans have succeeded in producing. They suggest that the increased level of autistic traits in engineers and scientists is evidence of this (Baron-Cohen et al. 1998). The evidence found in the MOBE and BRS surveys support the idea that individuals with traits of autism are more focused on the functional rather than the social world, particularly in terms of materiality. This may be interpreted in a different way however, as a method of optimising the retention of innovations, as more socially oriented individuals may be responsible for transmitting innovations. For future research it may be beneficial to model what proportion of innovators to socially oriented individuals, who may distribute knowledge of these innovations to the rest of the population, is optimal and compare this to the proportions of LPB observed in reality.

Example Two: Extraversion- Introversion

Similar to traits of autism, extraversion is a continuous spectral trait. This trait is characterised by two dichotomous extremes (introversion/extraversion), with individuals plotting between these extremes according to a normal distribution. Extraversion is associated with increased sociality and impulsivity, whereas introverts are less social, more introspective and less impulsive. This leads to a divergence in behaviour within the population, one suited to faster reproduction but also a greater likelihood of injury, which would likely translate to an increased mortality in ancestral conditions, and one slower reproduction but increased longevity.

Extraversion, to a large extent (~50%), is determined by highly polygenic and additive genes, each of small effect size (<1%) (Turkheimer, Pettersson and Horn 2014; van den Berg et al. 2016). Despite this, several genes associated with the functionality of the dopaminergic system have been associated with extraversion (Golimbet et al. 2007; Luo et al. 2007; Smillie et al. 2010; Stein, Schork and Gelernter 2004). In particular, novelty seeking and risk taking behaviours are increased in individuals who have the 7 and 2 repeat alleles of the dopamine receptor gene D4 (DRD4) (Benjamin et al. 1996; Ebstein et al. 1996; Faurie et al. 2017; Garcia et al. 2010). These variants of this gene are highly plastic and have also been associated with extremes of social behaviour, from aggression to prosociality, according to environmental conditions (Bachner-Melman et al. 2005; Buil et al. 2015; DiLalla, Elam and Smolen 2009; Jiang, Chew and Ebstein 2013; Knafo, Israel and Ebstein 2011).

7R and 2R DRD4 variants are thought to have originated in the Upper Palaeolithic (Ding et al. 2002; Wang et al. 2004). They are distributed with an increased prevalence further from Africa (Chen et al. 1999), due to positive selection in dispersing groups (Matthews and Butler 2011). Wang et al. (2004) hypothesised that this distribution was caused by either sexual-selective mechanisms, or an increased adaptability to the environment.

Increases in extraversion are also significantly associated with the number of long distance relationships an individual has, with a single point in extraversion increasing the likelihood of having an additional long distance relationship by 1.5 times in Bolivian horticulturalists (Pisor and Jones 2020). Therefore, we may suggest that extraverted individuals were responsible for extending the social networks of past groups and forging relationships between groups (figure 1, box B). As has been outlined above, this would increase the cognitive niche of humans and increase material complexity within groups. In contrast to Previc (1999, 2009), I would not suggest that the Upper Palaeolithic was explicitly the result of a drastic change in the dopaminergic system. I would suggest that it is due to population size and density increases at this time (Ziegler et al. 2013). During this period more socially oriented individuals, such as extraverts, may have developed exchange networks of both information and supplies. Group norms may lead to a collective group personality determined by the group's mean personality composition (Ogunfowora and Schmidt 2015). Therefore, a group with more extraverted individuals is likely to be more extrospective and social with other groups. By having individuals who are more socially focused within the group developing long range connections, they increase their network population sizes, allowing materiality to develop. As discussed above, when the selective pressures for reproduction are reduced due to increases in the population size of the mating network, this allows other cognitive niches to develop. Using the examples above, the mixture of more inventive high attent to detail individuals and social individuals who may transmit these inventions widely, may lead to a rapid increase in material culture complexity.

While this is a rather reductive example, which in reality should incorporate the collective actions of a much broader range of personality and cognitive types, it highlights the effect demographic and cultural changes may have had upon the psychological diversity of past populations. Further, unlike other theories of material culture change, it does not require the effect of an unidentified gene of high efficacy, or neurological change (Klein 2008). It merely recognises the importance of the vast cognitive diversity observable within our population today.

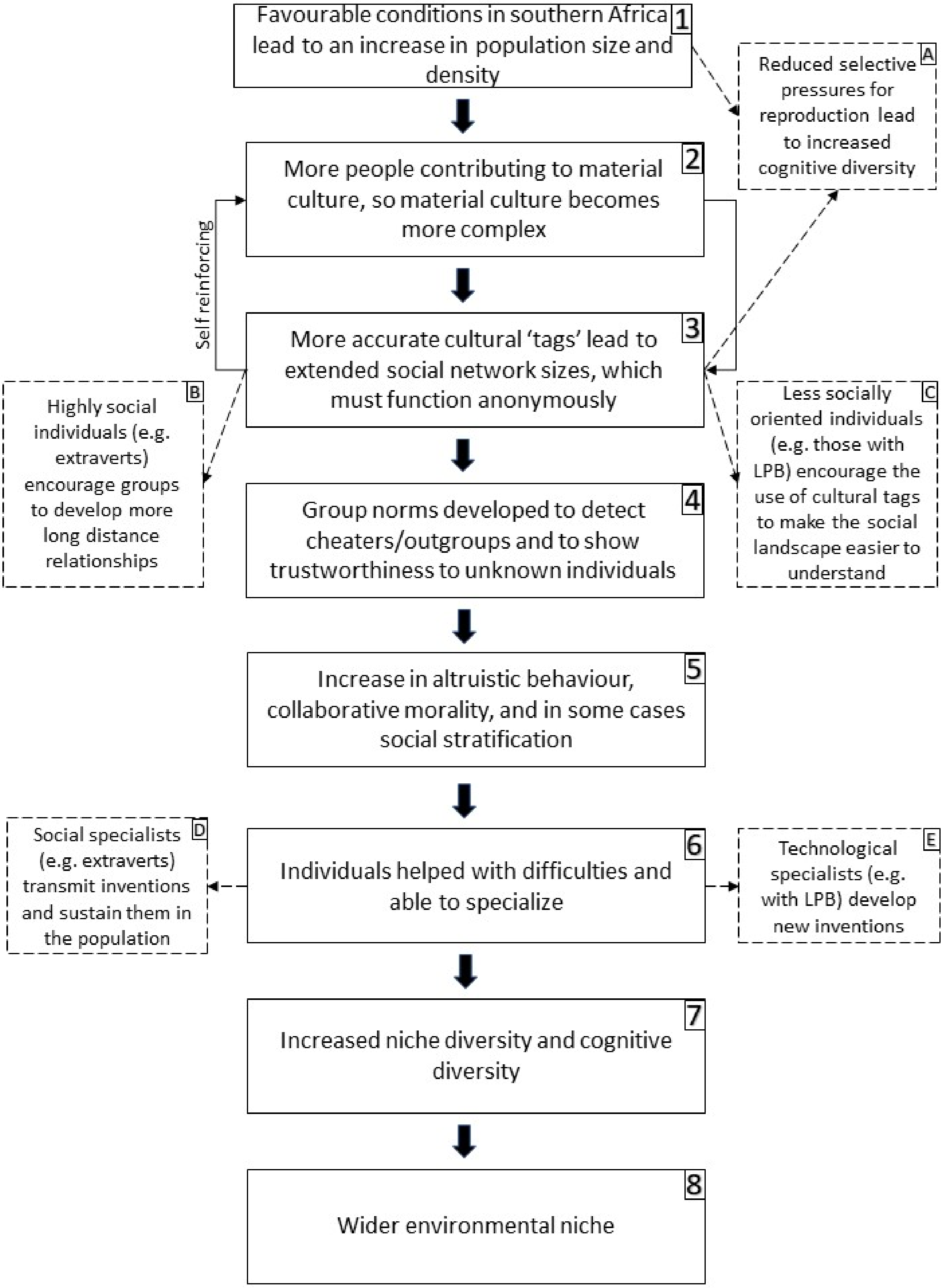
Favourable conditions in southern Africa lead to an increase in population size and density
1
More people contributing to material culture, so material culture becomes more complex
2
More accurate cultural 'tags' lead to extended social network sizes, which must function anonymously
3
Group norms developed to detect cheaters/outgroups and to show trustworthiness to unknown individuals
4
Increase in altruistic behaviour, collaborative morality, and in some cases social stratification
5
Individuals helped with difficulties and able to specialize
6
Increased niche diversity and cognitive diversity
7
Wider environmental niche
8
Self reinforcing
Reduced selective pressures for reproduction lead to increased cognitive diversity
A
Highly social individuals (e.g. extraverts) encourage groups to develop more long distance relationships
B
Less socially oriented individuals (e.g. those with LPB) encourage the use of cultural tags to make the social landscape easier to understand
C
Social specialists (e.g. extraverts) transmit inventions and sustain them in the population
D
Technological specialists (e.g. with LPB) develop new inventions
E

Figure 1. Flowchart explaining how material culture may have developed during the Middle-Upper Palaelithic. Dashed boxes highlight the probable impact of extraversion, LPB and cognitive diversity more broadly (numbers and letters used to refer to boxes in the text).

Whilst these interpretations are plausible, it remains to test them using computer modelling and against the archaeological record. This will be done for extraversion in chapter 6, where the importance of variation in extraversion for our dispersal ability will be explored.

Conclusions

This chapter has explored the origins and implications of human neurodiversity. Genetically humans seem predisposed towards mutations which cause cognitive differences. While some cognitive differences may be disabling, others may cause distinct advantages. These advantages may form alternate adaptive strategies to the ‘neurotypical’ strategy. The actions of several evolutionary mechanisms on human evolution were explored. This found considerable evidence for broad-sense multilevel selection in humans. Cooperation has been highly important to the success of humans. This may have been facilitated through broadcasts of relatedness and similarity, initially verbal but eventually material. The complexity of material cultural identifiers may have increased in a feedback loop with population size. Eventually, during the Upper Palaeolithic, these identifiers may have functioned anonymously for the identification of trustworthy allies and for the identification of status. Once anonymous, other measures were likely required to ensure trustworthy behaviour. This likely took the form of an enforced collaborative morality. This altruism would have enabled the difficulties of individuals to be buffered, specialization to develop, and the cognitive niche to widen. Consequently, the selective pressures that were previously reducing diversity may have relaxed. Due to the benefits of division of labour and specialization, cognitively diverse groups with individuals predisposed towards particular tasks may increase their survivability and fitness.

The origins and effects of two contrasting examples of neurodiversity (LPB and extraversion) were explored. Several surveys of traits of autism were reviewed. This review suggested that in general individuals with ASC, and in particular LPB, are more likely to have a more functional relationship with material culture rather than social. Individuals with LPB are more likely to be technological specialists, may benefit more from the use of easily identifiable cultural tags, and may be more likely to maintain aspects of material culture, due to an aversion to change. Of course, these are statistical studies about a population in general and do not imply that every individual with ASC conforms to each of these characteristics. In contrast, extraverted individuals are more likely to disperse, possibly due to a reproductive advantage, they have more long distance relationships and may consequently be responsible for the development of large ranging social networks. They may also have been transmitters of the inventions of other more materially focused individuals. Future research should aim to explore the potential origins and group benefits of other examples of neurodiversity.

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Chapter 4: Agent Based Modelling in Archaeology

Abstract

The use of agent based modelling (ABM) in archaeology is currently increasing. However, due to the post-processual movement during the 1980s, ABM experienced a period of stagnation in archaeology. This critical period has led to misconceptions about ABM, and a dearth of teaching supplies and protocols for researchers who are new to ABM. Critiques of ABM that developed in this time, which are still used today, focus upon the idea that ABMs are too reductionist or simplistic. However, simplification is necessary in all research and the limitations of this simplification are determined by the context of the model's purpose. This paper explores the advantages of ABM, as well as the critiques and the history of this methodology in archaeology. It then investigates and critiques how ABM has been used to explore two topics: dispersal and land use. The similarities and differences in methodology and results between models exploring the same topics are compared, which shows that models using different methods often lead to congruent results, or highlight different aspects of a topic. This also emphasises the versatility of this method, which can be used to explore the same topic in vastly different ways.

4.1 Introduction - What is ABM?

Agent based modelling (ABM) is a term used in archaeology, frequently without a full understanding of what ABMs entail or how they can be used. Within archaeology, the results of behavioural, ecological and taphonomic processes are observable within the archaeological record. However, the processes leading to the formation of this record are unclear. Consequently, a methodology which can test the effect of components of a system upon that system's output is ideal for hypothesis generation and testing in archaeology. ABM has been described as a suitable alternative to running Gould’s (1989) imaginary and manipulable tape of human history, where conditions may be changed (Premo 2006a). Despite its suitability, due to the history of theoretical thought in archaeology, ABM has been underused (Lake 2015). This paper will explore: some of the advantages of ABM and the reasons why the use of ABM has been limited in archaeology when compared to other subjects. It will then explore how ABM has been used to explore two subjects in archaeology (dispersal and land use). This will explore whether methodologies differ greatly between studies assessing similar topics, how the results of these models complement one another, and what critiques may be made of the models.

Agent based modelling (ABM) is a method used to explore how the result of a system may have arisen from the actions of its parts (agents). Agents may represent individuals or groups. Their behaviour must be autonomous, they must have their own goals, be situated within an environment, and reactive to that environment. Their reactions to the environment are determined by rules which create a system. This system is a simplified version of a feature in reality. Simplification is necessary for three reasons. Firstly, modelling every variable that affects a population would be very time consuming, difficult and arguably impossible. Secondly, by having fewer variables and a simpler model it is easier to understand how each part of the system affects the outcome (Costopoulos 2008; Lake 2015). Thirdly, when the complexity of the model is increased and additional lines of code are added, the likelihood of error increases (Romanowska 2015b).

Usually, ABMs assess the impact that different scenarios have on the outcome of the model, either changing the environment, how agents respond to that environment, or how agents respond to each other. Researchers may develop Hypothesis Testing Models which compare outcomes of the model to the archaeological record. This allows them to identify circumstances which lead to output similar to the archaeological record so they may suggest those conditions as a viable cause for what is seen in the record. Alternatively, ABMs may be used more heuristically. Heuristic modelling is used to support theory building and may not need to be compared to the archaeological record (Breitenecker, Bicher and Wurzer 2015; Lake 2014, 2015). This type of modelling is used to help researchers understand how the processes of a system are interconnected and how changes may affect the whole.

ABM has been used to explore a wide range of subjects in archaeology. This ranges from more traditional studies such as simulating the emergence of cooperation (Pereda et al. 2017; Santos et al. 2015), and population dynamics and genetics (Wren and Burke 2019), to more novel studies such as simulating battlefield archaeologists to assess what methods are most useful for understanding what took place in a battle (Rubio Campillo, Cela and Hernàndez Cardona 2012).

ABM can help develop an understanding of the formation of the archaeological record. Due to its fragmented and static nature, archaeologists are forced to infer the conditions which may have led to a feature in the archaeological record. This is regarded to be a form of modelling in itself (Lake 2015). However, computer simulations offer the opportunity to gain a deeper understanding of the processes leading to a feature, which may help in the rejection of unsuitable hypotheses. For example, archaeologists have used a ‘dot on the map’ method to infer the causes of Lower Palaeolithic site distribution, arguing that the lack of sites in central and eastern Europe may be caused by the dispersal route used by hominins (Grove 2012). Romanowska (2015a) developed a model to test this hypothesis. By incorporating data such as the fertility rates of modern hunter gatherers, the topography of the environment, a vegetation map and information on hominins’ difficulty traversing different environments, Romanowska tested whether differences in dispersal route would affect the prevalence of archaeological sites in central and eastern Europe. No difference was found and the hypothesis was rejected. This example has shown that ABM may be used to further our understanding of the processes which have led to the formation of a pattern in the archaeological record.

4.2 Advantages of Using Agent Based Modelling

ABM has generated a lot of attention as a potential archaeological tool. Several advantages have been noted in sociology for the use of ABM, which equally apply to archaeology (Chattoe-Brown 2013): ABMs can provide a method to aid in understanding non-linear causal relationships; they may combine both quantitative and qualitative data; and are a useful aid for producing new theories and hypotheses.

The behaviour leading to a pattern in the archaeological record can be extremely difficult to understand, as they are the result of a complex series of events. As has been noted by Breitenecker et al. (2015), even when the individual parts of a system are simple, it can lead to complex behaviour as these parts interact. By using ABMs the effect of these interactions can be seen as they take place in the model. Further, we may use the model to ask ‘what if’ questions to see if they have a significant impact on the outcomes of the model (An 2012). Therefore, we can gain a better understanding of the conditions within the system and judge whether they may be causally linked to what is artifactually observed. In this way we may better understand the complex systems which contribute to creating a feature of the archaeological record.

The ability to integrate both quantitative and qualitative data within a model has several advantages. It gives more of a broad view of the investigated subject, as quantitative data often provides evidence of what happened, while qualitative research provides information on why the observed feature has developed in a particular way (Kelle 2006). As Chattoe-Brown (2013) has stated: quantitative data provides data to produce simplified observations which may be generalized, while qualitative data provides details which ensure the data remains relevant to the case being studied and that the study does not become overly reductionist and disregard relevant associations. Due to this, ABM is a method which may be used to more fully understand the complexity of the processes which lead to an observed feature in the archaeological record.

In contrast to theoretical discussion, an ABM requires the variables used, the interactions between these variables, and the scope of the model to be clearly defined (Breitenecker, Bicher and Wurzer 2015). This makes the scope of the model more apparent (Barceló and Del Castillo 2016). Thus, promoting scientific method, encouraging reproducibility and reducing misunderstandings. This also has the added advantage of highlighting gaps in the data which may otherwise be missed when constructing a theoretical discussion, leading to new avenues of research and hypotheses (Kowarik et al. 2012; Rogers and Cegielski 2017). Therefore, not only does ABM provide an effective way to explore complexity, it also provides a very pragmatic way to document this complexity, and highlights where further work must be done.

4.3 Why Is The Use of ABM Limited In Archaeology?

Despite these advantages, attitudes towards and the use of computer simulations and ABMs in archaeology have fluctuated widely through time. As has been discussed by Lake (2014) the application of ABMs went through several phases in archaeology. Pioneered in the 1960s it reached a state of relative maturity during the mid 1970s (here termed the ‘pioneering period’). However, during the post-processual movement, and the abandonment by many of scientific quantitative methodologies in the 1980s, simulation appeared to no longer have a place in archaeology (McGlade 2006) (termed the ‘critical period’). Several of the reasons this occurred will be explored below as they are still relevant today.

Following this time there has been an increase in the use of ABMs in archaeology (termed the ‘second flourishing period’). This increase has continued into the 2000s, with a steady increase in the amount of publications using ABM (Cegielski and Rogers 2016). These differences in the amount of ABM publications are argued by Lake (2014) to be a product of how the papers were presented, rather than them not being published at all. ABMs were not the focus of papers published in the 1980s, like they are now, but were secondary to other methods and theoretical discussions in the papers. Further, many studies taking place during the 1980s were only published during the 1990s. Therefore, Lake argues that this leads to the illusion that less work was being done using ABMs in archaeology during this critical period in the 1980s, when actually work was either being presented in a different way, which presented them as part of a theoretical discussion in comparison to during the 1990s when they were presented much more explicitly as simulations, emphasising the importance of simulations for archaeological theory, or were only completed and published later.

However, if we look at the general perception of ABMs during the critical period we can see that it was very negative. For example, Bahn (1991) compared ABMs to the Stepford Wives, saying they are, “idealized, simplified robots without wrinkles or imperfections, built to flatter and agree with their owners”. As Gummerman and Kohler (1996) have stated, post-processualists believe that to understand behaviour we must begin by understanding the individual, the culture of that individual, and how that individual would have experienced the landscape (Lock 2009). ABMs (particularly top-down simulations) were seen as too simplistic and reductionist, unable to capture the complexity of human cognition, and consequently to post-processualists were not suitable for study (Doran 1999; Gummerman and Kohler 1996; Thomas 1991). Further, Hodder (1978) was and has remained (Hodder 2011), very complimentary towards simulation, saying that its ability to help identify assumptions and reduce conflict within the subject were its most valuable assets. McGlade (2006) regards these views as what helped make simulations more mainstream in archaeology, but that Hodder’s later post-processual publications implied that modelling methods were not suitable for archaeology and damaged perceptions of the methodology considerably. Meanwhile, the methodology was developing in other subjects and was increasingly being used at this time (Romanowska 2015b). Nevertheless, as has been noted above, its use is increasing in archaeology today (Cegielski and Rogers 2016).

There are several obstacles to overcome when first studying ABM in archaeology, some of which are derived from the critical period that caused stagnation during the 1980s. Firstly, there is a lack of textbooks to aid in learning how to produce ABMs for archaeologists (Romanowska 2015b), as the use of ABMs was still seen as a subject for debate (Lake 2014). Recently, a tutorial has been provided for learning how to produce an ABM using NetLogo, which will prove very valuable to archaeologists who want to engage with these methods (Crabtree et al. 2019; Davies et al. 2019; Romanowska et al. 2019). However, as has been noted in the past by Doran (1999), but is still relevant today, there is not a standardised methodology for producing ABMs. This has been suggested to be a negative aspect of the method. However, it may actually be a feature of its versatility. Depending on the way standardisation was applied, it may limit its innovative abilities and application in different subjects. Of greater importance is the issue of ensuring ABMs are documented in a uniform way to increase replicability. Development has been made in this area with the creation of the Overview, Design concepts and Details (ODD) protocol, which is a specific outline to use when publishing ABMs (Grimm et al. 2006, 2010, 2020). This method focuses on producing an overview of the model, explaining the concepts behind the model design and then explaining the details of how the model functions. Although, it must be noted that this method is still under development and has several limitations, in particular the length of the ODD descriptions and difficulty applying it to more complex models (Polhill 2010; Grimm et al. 2020). Therefore, due to debates as to whether ABM is a valid methodology for archaeology, the variety of ways and languages in which an ABM may be constructed, and the ongoing development of a uniform way to document ABMs, there is a lack of material aimed at helping archaeologists learn the method. This lack of protocols, standardisation and teaching are likely the primary reasons why the use of ABM is still limited in archaeology.

Several arguments against the use of ABM have been identified above and must be addressed: that ABMs are reductionist, don’t allow for the complexity of human cognition, and that they are idealized and created to support the researchers view.

The first two arguments may be discussed in tandem, as they are both a product of a necessity of research - simplifying the problem in order to enable interpretation. This has been briefly mentioned above when introducing what ABMs are, however due to this being one of the primary objections to the use of ABM in archaeology it warrants further discussion. Three explanations for this simplification have already been mentioned: 1) it is impossible to model every variable which would affect a population; 2) by reducing the amount of variables in the system it is easier to interpret causality in the model and gain useful results; 3) when increasing the complexity of a model it increases the chance of error. Further, simpler models with a specific purpose used to explore a particular aspect of a system are more useful, because often they are more generalisable. This allows the researcher to apply their findings to a broader range of real world cases (Lake 2015; Wobst 1974).

Due to simpler models being easier to interpret, agents are usually simplistic in ABMs (Kohler 2012). Therefore, agents do not account for the cognitive complexities of humans. As stated above this is one of the primary post-processual arguments against the use of ABM in archaeology. Consequently, it has been argued that researchers need to create agents with their own beliefs and goals which shape the actions of agents. These agents should be situated within and influenced by a social network (Costopoulos 2008; O’Sullivan and Haklay 2000). However, it must be recognized that adding too much cognitive complexity to the model for the question being asked would only increase the difficulty of interpretation, and contradicts the emphasised importance and advantages of simplification in ABM previously discussed. Developers of ABMs are not trying to create a representation of the past, but are attempting to test the interaction of particular variables within a system which may be responsible for creating an observed feature of the archaeological record, and where realism is the aim, models can often end up being uninformative (Premo 2006a, 2006b). Nevertheless, where an attempt has been made to incorporate sociality and cognitive complexities such as emotion (Mithen 1990), it was branded as, “an extension of a reductionist framework to a new set of phenomena… allowing nothing to escape the relentless grasp of adaptive logic” (Thomas 1991, 16 and 19). Therefore, I would suggest that some arguments against the use of ABM are less related to the actual method, but are more a result of partisan prejudices against the processual school of thought - even when models are attempting to meaningfully engage with more subjective topics. This argument that ABMs are too reductionist contrasts with arguments in ecology, which suggest ABMs are too complex to be sufficiently explored. Researchers are advised to either reduce the complexity of their models or use methods to explore in depth how these complex models function to overcome the difficulty of complexity (Grimm 1999).

The issue of ABMs being idealized and built to support the preconceptions of the developer stems from the fact that agents' autonomy is limited by the rules used to program them (Bahn 1991; O’Sullivan and Haklay 2000). Therefore, they may be constructed in a way to achieve a particular result deliberately. Of course we can’t eliminate bias in ABM any more than any other method where choices are made about what to research. However, this view misunderstands the purposes of ABM and is a view held not only by those critiquing the subject but also, in some cases, those engaging with it. There are two types of simulation: emulation and exploration (Premo 2008). Emulation attempts to reproduce features seen in the archaeological record. Premo (2008) argues that this is not a useful technique for archaeology, as so little is known about the system which has formed the feature and following the rules of equifinality the same result may be reached in multiple different ways (Richardson 2003). Therefore, it does not provide more information than what we already know and allows experimenters to create models which support their preconceived opinions. In contrast, when models are used heuristically as experimental landscapes rather than for realism, we may alter variables of the system and learn more about the processes which have led to a phenomenon and how those processes interact. In this way we do not search for a solution to problems, but rather generate new hypotheses and may perceive the problem in different ways (Premo 2006a, 2008). Therefore, ABMs should be built to test the interactions of parts of a system to determine what variables are important for the outcomes of that system in order to direct future research. Beyond this, although models may be tuned to provide a result synonymous with the beliefs of the researcher, models produce very complex interactions between variables and are also subject to path dependence, where previous interactions within the model influence later ones (McGlade 2014). Therefore, the emergent properties of models may be difficult to estimate. Further, where models are tuned towards a specific result, the transparency of writing a theory in code where all assumptions are made clear should allow reviewers to identify these models easier than biased theories, or theories which rely on many unclear assumptions. Therefore, when correctly done ABMs are a valuable tool to explore the relative impact of different conditions upon the emergent characteristics and outcomes of the model.

4.4 Examples of Applications

This section will explore how ABMs have been applied to two different areas of research: dispersal and land use. These subjects were selected because they have been explored extensively using ABM, in a variety of different ways. Through this we will see what similarities and differences there are between the methods used in the models, whether different approaches lead to similar results, how models exploring the same subject may have very different purposes. Their use will also be critiqued.

Example 1: Hominin and Modern Human Dispersal

Understanding the timing, route and causes of our species' dispersal out of Africa is a key area of debate. In particular, how these aspects of our dispersal have been impacted by ecological or social factors. The characteristics of our dispersal are important not only for archaeological research, but also medical and genetic research, and are important to people's national identity. Despite the importance of this topic, due to new and conflicting skeletal finds (Bae et al. 2014; Harvati et al. 2019; Liu et al. 2010, 2015; de Lumley 2019; Reyes-Centeno et al. 2017), and genetic evidence (Mondal et al. 2016; Rasmussen et al. 2011; Malaspinas et al. 2016), the dispersal of our species is still an area of contention.

ABM has been used extensively to test and generate hypotheses for hominin and anatomically modern human (AMH) dispersal. Several of these models will be explored in this section (Callegari et al. 2013; Hölzchen et al. 2016; Mithen and Reed 2002; Romanowska 2015b; Vahdati et al. 2019; Wren and Burke 2019; Wren et al. 2014).

While these models all explore dispersal, there are differences between their purposes. For example, most explore the impact of environmental pressures and social mechanisms upon dispersal and the arrival times of hominins and modern humans in different areas of Europe and Asia (Callegari et al. 2013; Hölzchen et al. 2016; Mithen and Reed 2002; Romanowska

2015b; Vahdati et al. 2019; Wren et al. 2014). Others, however, explore their effect on the genetic landscape of the Upper Palaeolithic and how this may have impacted material culture (Wren and Burke 2019). Nevertheless, even those explicitly exploring dispersal are interested in different aspects of the process. Romanowska (2015b) focused on the impact of different dispersal routes on site distribution. Scherjon (2013) focused upon the effect following water routes would have upon chosen dispersal paths. Callegari et al. (2013) and Mithen and Reed (2002) focused upon the speed and path size of dispersal under different conditions. Vahdati et al. (2019) focused on the effects of equifinality and historical contingency on arrival times in different conditions. Despite these differences in purpose, the models have several similarities in their methodology. The similarities, as well as the difference in their methodologies, will be explored now.

The models are similar in several characteristics. Firstly, the environment is similar within each of the models. It is divided into cells, which carry characteristics that either explicitly or implicitly represent its carrying capacity and/or permeability to dispersal. Secondly, this environment is interacted with and inhabited by agents according to specific rules. Thirdly, these models test different scenarios by changing the parameters of the model to see how this impacts results.

The models differ in the complexity of their agents. For example, agents within Wren and Burke’s (2019) model are uniform and do not differ from one another in the way they interact with the environment. Conversely, Callegari et al.’s (2013) agents hold information on their fertility and genetics, which affects their interactions with other agents and likelihood of reproduction. Further, emergent characteristics such as energy level are used by Callegari et al., which influences agents’ mobility. They used a stochastic Fisher– Kolmogoroff–Petrovsky–Piscounoff (FKPP) model, affected by the above parameters, to simulate population growth. Hölzchen et al. (2016) also used more complex agents. The body size of their individuals affected the amount of energy they required, their range size and range of interaction. Their brain size also affected their need for meat, technology level, communication level and their social organization. The latter three characteristics in turn affect their ability to gather resources, their maximum group size, and their ability to share resources.

Usually, changing the scenario of the model also includes a gradation from more simplistic scenarios to more complex ones to see how the added parameters affect the output of the model, rather than merely seeing the effect changing a parameter may have upon the results. For example, Callegari et al. (2013) developed the complexity of the environment in their model, from a simple homogeneous landscape to an environment inclusive of continents, topography, and depleting and variable resources. In a later paper by the same researchers, this methodology was used again (Vahdati et al. 2019). In the newer model estimates for net primary product (NPP) were used and the model included an invariable NPP scenario and a time-variable NPP scenario, where the distribution of NPP changed over time. However, models are not always constructed in this way. For example, Romanowska (2015b) used different scenarios to test the effect of different dispersal routes out of Africa.

While it is not possible to discuss all of these models in depth, it is useful to compare some which have similar goals but use different methods. Mithen and Reed (2002) and Callegari (2013) both explore how dispersal speed is affected by environmental and social factors. However, their methods differ vastly. Mithen and Reed explore the dispersal of hominins in the first exit from Africa approximately 2 million years ago. They utilize a cellular automata (CA) structure, where the population of interest are not explicitly modelled but are a variable of environmental cells defining whether a hominin population is present or not. In contrast, Callegari et al. (2013; Vahdati et al. 2019) model the dispersal of AMH. Populations are represented as agent objects. The agents represent individual hominins, or predators and prey, located within continuous space. These agents carry information about themselves (as stated above).

Using these different methods, these studies have revealed some similar results. Firstly, the importance of environmental conditions is apparent in both simulations. Mithen and Reed (ibid) found that changing the severity of the effect of glacials and interglacials impacted agent mobility. Further they found that dispersal was largely affected by desert barriers, followed by rapid colonisation upon reaching Europe. Likewise, Callegari et al (ibid) found that the outputs of their simulations were greatly influenced by the environmental parameters used. This was even more apparent in Vahdati et al.’s (2019) later study using the same model, which showed that the climatic variability over time in their model opened and closed pathways of dispersal. This increased the predictability of arrival times due to the closing of barriers controlling the rate of dispersal. Further, they showed that dispersal routes to the Horn of Africa and Patagonia were not significantly affected by climatic variables, suggesting the landscapes in these areas are uniform, similar to more simplistic runs of their model. Therefore, unsurprisingly these models all support the hypothesis that environmental conditions constrain and facilitate dispersal, and show the regional effects this may have had on our dispersal to different areas - some of which support longstanding archaeological theories (e.g. the desert barrier of the Sahara).

The results of these studies also show discrepancies with the archaeological data for arrival times in different regions. Callegari et al. (ibid) has shown that the wave of expansion within their model is much slower than that of a more traditional linear diffusion model (FKPP model: see (Fisher 1937)). Meanwhile, Mithen and Reed (ibid) showed a much faster rate of dispersal compared to archaeological data. These discrepancies are largely due to how the models are structured. Callegari et al.'s agents are limited in their movements by energetics. Further, agents have habitat preferences, therefore even if they are able to move they may choose to stay within their current habitat if those surrounding them are less desirable. Propagation speeds, and thus expansion speeds, are then further slowed by variations in the carrying capacities of different environment cells. These factors, which cause stochastic effects, may slow the rate of dispersal when compared to the traditional FKPP model. In contrast, Mithen and Reed's model is a more coarse approach. It does not have many of the complexities of the above model, with dispersal rate being defined by a parameter upon initialization. This colonization rate is not influenced by environmental factors, with environmental factors having an effect on extinction rate. Due to this reduced complexity, the simulation is susceptible to less of the stochasticity of the model above that reduced expansion speeds. Further, using a cellular space, rather than a continuous space, may bias the model towards faster dispersal, significantly affecting the results of Mithen and Reed's model (Chipperfield et al. 2011). It is almost certain that the actual expansion out of Africa involved much more complex factors (such as the impact of human agency). Using the results of these models, we can so far suggest two things. Firstly, based upon the models reviewed above, if our species had dispersed at a constant rate, as suggested by traditional models, this rate may have been slower than the traditional models suggest, as the increased complexity of Callegari et al.'s (2013) model largely reduced dispersal speeds, and the real world is infinitely more complex than these models (Callegari et al. 2013). However, other complexities not included in Callegari et al.'s (2013) model, including an inconstant rate of dispersal punctuated by episodes of long distance dispersal, may actually increase dispersal speeds. For example, in studies of plant migration, estimates of expansion speeds far exceed the expectations from diffusion models, this is called Reid's paradox (Clark et al. 1998). This is argued to be due to rare events of long distance dispersal, possibly due to birds, and due to spatial assortment of the best dispersers, which may lead to the evolution of increased dispersal speeds (Clark et al. 1998; Phillips et al. 2008). Similar processes may account for the faster than expected dispersal speeds of AMH (Spikins 2015). Therefore, the effect on the rate of dispersal depends on the types of complexity added to the model. Secondly, the impact of geographical barriers likely led to bursts of dispersal and multiple waves of dispersal into certain areas (e.g. the rapid colonization of Europe), while a constant rate of colonization occurred in others (e.g. the Horn of Africa). This addresses a complexity which previous wave dispersal studies were unable to address and may suggest that geographical barriers are responsible for arrival times not being directly related to distance from Africa (Young and Bettinger 1995). Genomic data and climatic reconstructions support that geographic barriers may have caused multiple waves of expansion, or inhibited expansion into particular areas in similar ways to what is seen in these models (deMenocal and Stringer 2016; Obreht et al. 2017; Tassi et al. 2015; Reyes-Centeno et al. 2015).

The results of these models also highlight the effects of equifinality, and historical contingency discussed above. Vahdati et al. (2019) found that the results of models with parameters as different as 92% of the maximum difference could yield similar results, while the results of highly similar models could be vastly different. Similarly, Mithen and Reed (2002) found that the stochasticity of their models could lead to very different arrival times being produced from the same model when run multiple times. Further, stochasticity could lead to a lack of colonization in America and dispersal from Africa in Vahdati et al. and Mithen and Reeds studies respectively. Mithen and Reed argue that this highlights the importance of chance upon our evolutionary history. This is a reasonable suggestion, and a feature which should be expected from any event influenced by many complex, interacting processes. However, these results may also show that other push and pull factors (whether social or environmental), which are not present in these models, influenced our species' dispersal.

This last point is not a critique of the models in question, as they are designed with specific purposes and have fulfilled them exceptionally, challenging our past perceptions of the topic and highlighting hypotheses for future study. This is true whether the models support hypotheses, such as Mithen and Reed's model supports the desert barrier hypothesis, or challenge hypotheses by highlighting how chance may have been a determining factor in hominin dispersal (Vahdati et al. 2019).

By exploring the results and methods of these models simultaneously it has been shown that similar emergent behaviour has been produced by these different models. This not only reinforces their results but also the validity of the method itself. Further, assessing the results of these methods in conjunction with one another highlights that the factors constraining and facilitating AMH dispersals were similar to those of early hominin dispersals.

Due to the transparency of the ABM methodology in comparison to more discursive or unquantified theoretical approaches, they are more open to critique than other methodologies. For example, we may critique that Mithen and Reed's (2002) model is too reductionist and does not account for the agency of individuals (although this is arguably an unwarranted critique as mentioned above). Further, we may critique that having environmental factors only relating to extinction rather than dispersal may lead to agents inhabiting areas where they otherwise would not have gone, as it is not their preferred habitat. Despite them stating that the primary relationship for dispersal is between colonization and extinction, I believe this may lead to a more rapid dispersal following routes that were unlikely to be used in the Palaeolithic. Further, rather than exploring the colonisation times of different areas in alternate scenarios, it would be advantageous to explore the effect different parameters explicitly have upon colonisation and movement in general, using statistical methods. This would help determine how much of the variance in results between simulations is caused by a particular parameter or interactions between particular parameters. This was explored and presented in a very useful way by Vahdati et al. (2019).

Finally, a critique which applies to many of the models explored above, is that often parameterizing and quantifying theories requires assumptions to be made, or imperfect data to be generalized. For example, assumptions made regarding habitat suitability and carrying capacity can often affect the results of models. This is unavoidable as we have no explicit way of knowing which habitats our ancestors were most suited to and how efficiently they used those landscapes. Therefore, habitat suitability is either assigned arbitrarily, or inferred from either ethnographic data, or from the locations of archaeological sites. For example, Romanowska (2015a) arbitrarily assigned habitat suitability values informed by the archaeological literature but with no direct relation to actual data, while Mithen and Reed (2002) and Nikitas and Nikita (2005) seemingly assign probabilities of colonization arbitrarily as a parameter to be varied in different scenarios. Wren and Burke (2019) used data from a previous study of theirs, which used Random Forest modelling to predict the most suitable habitats for archaeological sites during the last glacial maximum (Burke et al. 2017). This example suffers from the inevitable issue that not all archaeological sites are found. Further, as Romanowska (2015a) has noted, preservation issues and practical difficulties mean that finding archaeological sites is unlikely in particular environments (particularly in tropical forests), leading to a significant observational bias. This would influence the accuracy of Burke et al.'s (2017) results and thus influence Wren and Burke's (2019) model. Likewise, the ethnographic record also has limitations for predicting habitat suitability. As noted by Burke et al. (ibid), the predictive ability of ethnography depends on the groups being used.

Further, when ethnography is used, as it is for calculating the population growth rate in Wren and Burke’s (2019) study, it is important to remember that contemporary hunter gatherers exist in very specific conditions which are separate from those of our ancestors. Further, technological advancements which were unavailable to our ancestors may enable modern hunter gatherers to inhabit environments inaccessible to our ancestors and even increase the carrying capacity of landscapes to which past humans were specialized. Therefore, there is a danger of a circularity of reasoning, and caution must be used when applying ethnographic information to the archaeological record. If hunter gatherers behave in a particular way, or inhabit a particular environment, it does not necessarily mean that our ancestors also behaved in this way.

Alternatively, more abstract models may use other methods to explore habitat suitability, such as the relative resource abundance of the agent's cell when compared to the rest of the environment (Wren et al. 2014). Methods such as this are often exempted from critique as they are not attempting to explore these issues in a realistic way, but are rather exploring a specific mechanism of which habitat suitability is a part. This is an argument which should be made in defence of each of the models mentioned above. As has been argued through this paper, critiquing ABMs because they are reductionist or do not exactly reflect reality misunderstands their purpose. While the critique above centres around the issue of assumptions using habitat suitability and carrying capacity as an example, it is important to recognise that this is not just an issue with computer simulations, but is an issue with all research which ABM makes more explicit. Therefore, while this is a limitation of the ABMs, if these limitations are addressed, particularly by using parameter sweeps to assess whether the choice of parameter values significantly affects the results, and by transparently acknowledging where and how assumptions are made, such as these models have done, this need not be a negative point for critique.

This section has explored the similarities and differences between models used to explore dispersal from Africa. This briefly introduced the wide variety of purposes models have had even within this topic, before comparing two models in more detail (Callegari et al. 2013; Mithen and Reed 2002; Vahdati et al. 2019). These models were structured very differently and assessed different dispersal events. However, despite these differences they show some similarities in their results. Particularly, they showed the importance of environmental barriers in determining expansion times both on a local and global scale. While it is not suggested that wave diffusion models predict that our ancestors migrated at a constant rate out of Africa, it can be seen that ABMs are much better suited to exploring the non-linear, variable and highly stochastic mechanisms which impacted our species’ ability to disperse from Africa. However, it must be reiterated that ABMs are designed not to simulate reality, but to explore the relative importance parameters may have upon the outcomes of a system which is isolated from reality. The parameters within models, even when striving for realism, are unlikely to perfectly reflect what is seen in the real world. The example above, of how carrying capacity and habitat suitability has been derived in the models assessed within this paper have shown that. However, when this is acknowledged by the authors of models it need not be a damaging critique implying that nothing may be learned from the model. Rather, these models are abstractions and even exceedingly abstract models may be useful. This critique has shown that ABMs can be useful to explore the mechanisms of large scale population changes, particularly where environmental changes have important influences on behaviour.

Example 2: Land Use In Archaeology

This section will explore how ABMs have been used to explore land use and subsistence, with the use of several examples (Axtell et al. 2002; Balbo et al. 2014; Dean, Gumerman and Epstein 2000; Janssen and Hill 2016; Mithen 1990, 1991).

These models explore how a variety of spatiotemporally different groups, both hunter gatherer and agricultural, manage their subsistence within the land they inhabit. Axtell et al. (2002) and Dean et al. (2000) developed the Anasazi model to explore whether agricultural difficulties were the primary cause of the Anasazi's abandonment of Long House Valley and whether changes in environmental conditions affected the movement of farmers within the valley (between 1800 BC and AD 1300). The Anasazi are a typologically identified culture, however there is geographical variety leading to several subcultures also being identified (Axtell et al. 2002). While the validity of using typologically identified cultural labels has been questioned and may not represent the true social landscape of the past (Colwell-Chanthaphonh 2009; Speth 1988), labels such as this allow easier communication between scientists when discussing the social and economic dynamics of a region. Balbo et al. (2014) have also explored the effects of changes in the variability and total amount of precipitation on the survivability of hunter gatherers in Kutch Saurashtra, NW India, during the mid-late Holocene (12 ka - present). This assesses the impact of yearly variations in precipitation at different geographical scales (continental, regional and local). In contrast, Mithen (1990) explored the impact different hunting decisions and strategies may have had on the composition of Palaeolithic faunal assemblages using the Thoughtful Foragers model (discussed below). Further, Mithen (1988, 1990, 1991) used a model (Deer Model) to explore whether changes in faunal population sizes may be associated with the production and function of Palaeolithic artwork.

The environments in these models are represented by the productive capacity of the landscape. In the Anasazi model, this is determined by drought severity, which controls the crop yield of different parts of the model landscape (Dean, Gumerman and Epstein 2000). Similarly, Balbo et al.'s (2014) model utilizes a precipitation model which determines the amount of biomass available in each landscape cell at a given time. Precipitation causes an increase in resources up to a maximum during the wet season, which then decreases through the dry season. The maximum amount of resources in the landscape cells is determined by the estimated primary biomass for the biome of interest and then adjusted using Kelly's (1983) calculations (critiqued below). Finally, Mithen's (1990) Thoughtful Foragers model largely focuses on the encounter probabilities, pursuit times, probability of killing, processing time, and utility of animals within the landscape. These animals are not explicitly modelled but rather exist through the five values above, which are attributed to the landscape and vary depending on the species of the animal in question. The probability to encounter prey is reactive to the actions of agents. As hunters inhabit an area the probability of encounter decreases, firstly due to the direct reduction in prey due to successful hunts, and secondly due to prey fleeing the area due to the noise and smell of the hunters. However, while this appears to be a very different way of constructing the environment, it is actually similar to the previous two examples. Similar to how precipitation determines maximum resources in the previous models, this model has a maximum potential resource abundance determined by the number of prey within the environment. In the same way precipitation limits the proportion of that maximum available to agents in Balbo et al.'s (2014) and the Anasazi model, the five values above limit the amount of resources available to agents within Mithen's model. Therefore, while the details of the environments may differ, the actual structure of how they are represented is quite similar.

Excluding Mithen's (1988, 1990, 1991) Deer model, each of these models explicitly represent agents as an object. The Anasazi model and Balbo et al.'s model both use agents to represent family groups, while in the Thoughtful Foragers model agents are individuals. This foreshadows the agents having different levels of complexity. For example, while the agents in the Anasazi and Balbo et al.'s model essentially have two functions to complete with each time step, collecting resources or moving depending on previous success or projected success, this is more complex in the Thoughtful Foragers model. This is largely due to the purpose of the model and the array of factors which are taken into account when making decisions during hunting. In this model, rather than agents being assigned resources based upon the quality of the environment, the amount of resources they may collect are determined by the utility quality of the prey they capture. This prey is encountered through a probabilistic function, as described above. Once encountered agents must decide whether to pursue the prey. This decision accounts for several different factors including the expected probability of successfully killing the prey (derived from the success of the agent and its associates in killing the prey previously, which is weighted to increase the significance of recent days), pursuit time, the utility of the animal, the amount of resources already collected that day, the amount of time left during the day, as well as their hunting strategy or goal (either to stalk everything, to be selective of what prey to stalk according to the previously stated factors, or to be selective of what to kill but increase the probability of stalking the prey if it is later in the day so that the risk of returning with nothing is reduced). While it is beyond the scope of the current paper to address all of the complexities of decision making within this model, it can be seen that resource gathering and the functions of the agents is much more complex in this model than those previously discussed.

Also relevant to these types of models due to their impact in archaeology and similarity of topic are Mithen’s (1988, 1990, 1991) Deer Models, which are not agent based models, but are simulations derived from Leslie Matrices (these estimate the future demography of a population based upon the reproductive and survival rates of a species) (see also Mithen 1997). Mithen used this method to explore the effect of hunting intensities upon red deer and reindeer populations. This also explored the demographic characteristics of deer exploited by humans under a catastrophic mortality profile (where the mortality profile is similar to the demography of the living population, due to hunting occuring in chance encounters (Discamps and Costamagno 2015)). Two models were produced, one for reindeer and one for red deer. These incorporated different complexities. While the reindeer model included wolf predation, the red deer model included yearly fluctuations in environmental quality. This fluctuation affected calf survival rate, as well as the future survival and reproductive rate of deer born in a particular year (those born in a year where the environmental quality was good had a higher survival probability and fecundity than those born in a bad year). While this is not an agent based model, the results of this model and the Thoughtful Foragers model were discussed simultaneously (Mithen 1990).

The results of each of the models described above is summarized here to explore their similarities. Balbo et al. (2014) found that changing the average yearly precipitation did not have a significant effect on the extinction of hunter gatherers on a regional and continental scale. Nevertheless, on a local scale it had a large effect. However, the primary impact on the success of agents was the short term (decadal and annual) variance in yearly precipitation, which causes fluctuations in resource abundance. This led to agents constantly moving their home and revising their subsistence strategies. They argue this could have led to the extinction of hunter gatherers in Kutch Saurashtra.

The Anasazi model found that environmental pressures significantly influenced where agents selected to locate their farms, and that agents' site distributions were similar to those of archaeological data and replicated real world responses to environmental change. This suggests that environmental factors were paramount in deciding where to farm within the valley. However, while there is a population collapse, the exodus from Long House Valley, which is seen in the archaeological data, is not replicated by the model. The authors suggest that sociocultural variables were therefore important in the agriculturalists' decision to abandon the valley.

Mithen (1990) compared virtual faunal assemblages produced by the Thoughtful Foragers model to Scanian and German Mesolithic assemblages. By doing so he has inferred that Scanian sites were very selective of their prey and did not place importance on the risk of procuring no resources from hunting that day. In contrast, the assemblages from Germany were indicative of a much more risk avoidant approach, either stalking everything or increasing the probability of stalking less desirable prey through the day. Mithen suggests this is due to the Scanian hunter gatherers having other marine resources available and consequently the risk of a failed hunt is less severe than in landlocked Germany, where no other resources are available.

Finally, Mithen's (1988, 1990, 1991) Deer models showed that as hunting intensity increased, fluctuations in deer population size increased. This grew further when accounting for wolf predation of elderly and juvenile reindeer. Further, when the population density of the red deer decreased in response to more intense hunting, the profiles of deer exploited by humans in the model included a greater proportion of juveniles due to an increase in the fecundity of female deer, which would increase the ratio of juveniles to adults within the population. This simulated finding was replicated in the real world when comparing age profiles to the La Riera assemblage, where there was an increase of juvenile relative to adult deer in the assemblage through time. Consequently, Mithen hypothesised that this is due to an intensification of hunting deer through time at the site. Further, Mithen suggested that as hunting intensity increased and yields became more variable, the value of information gathered through experience about potential yields would be less valuable. Not only this, but the results suggest that being more selective when hunting deer, while decreasing energy expenditure, increases the fluctuation of yield. This therefore accounts for the catastrophic mortality profiles of deer assemblages, which are indicative of less selective hunting to reduce the risk of insufficient yield.

As stated above, this last example is not an agent based model. Nevertheless, some interesting observations were made when discussing the results of these Deer models and the Thoughtful Forager model together. Mithen states that when two mathematical models produce similar conclusions it increases the reliability of the results (Mithen 1990, 259). The results of these models converge in showing that selective hunting patterns increase the risk of yield shortfall. This may help indicate the economic and ecological challenges past hunter gatherers faced. For example, if a selective hunting pattern is being used, it suggests that either the variability in yield from prey was low or that other resources were being utilized (for example the Scanian hunter gatherers utilizing coastal resources). Alternatively, if a catastrophic mortality profile is seen in an assemblage, it suggests that the hunters were attempting to reduce the risk of shortfall due to the difficulty of obtaining other resources. This is significant because it allows a deeper understanding of the economics of past hunter gatherer groups, which may not have been apparent without agent based simulation.

As well as exploring the advantages, disadvantages and past uses of ABM this paper has shown what may be learned when comparing the results of similar and dissimilar ABMs in a similar way to how Mithen has compared the results of these two models. From the results outlined above we can see that environmental pressures have significant effects on both hunter gatherers and agriculturalists. Mithen (1988, 1990, 1991) has argued that red deer and reindeer populations would significantly fluctuate in response to hunting intensities leading to pressure upon the population and reliance on alternative resources. Similarly, Balbo et al. (2014) have shown that short term variations in resources significantly affect the survival of hunter gatherer populations. Taken together we may suggest that, following optimal foraging theory, within optimal conditions, hunter gatherers are selective of prey to reduce the number of prey which must be processed in order to attain suitable resources, and to reduce the energy expended in doing so. Once resource abundances fluctuate, either due to hunting intensity or climatic change, hunter gatherers broaden to exploit less desirable prey and different species of animal. They expend more energy in the process, but reduce the degree of variance in resource yield. Finally, if resource fluctuation continues to increase, hunter gatherers become extinct within that landscape. As expected, these results support the optimal foraging theory the models are based upon. However, these models provide an insight into the behavioural changes which would be expected when resource stability decreases.

Naturally, similar critiques and responses apply to these models as those discussed previously. There are however additional factors of significance. For example, Balbo et al.'s (2014) model has issues with the calculations of resources, which illustrates the importance of clear methodology and verification. Their resources are calculated using Kelly's (1983) calculations. However, while Kelly states that the primary biomass of the environment is largely inedible Balbo et al. use this as their resource. The use of primary product would have been more suitable, as Kelly argues that this is the edible portion. Additionally, Balbo et al. use Kelly's method to calculate what proportion of resources would be accessible to hunter gatherers, by dividing the amount of primary production in the biome by the amount of primary biomass. This has the added issue that Kelly used these values as rough estimates, which may not be suitable for a practical use such as this. An alternative way to check Kelly's calculations are suitably accurate for use in an agent based model is to use modern hunter gatherer data, divide the total range size for a hunter gatherer to get an approximate area per individual, then calculate the total amount of primary product within that area and how much of a percentage humans need to survive. This gives a good indication of the accessibility of primary product within that hunter gatherer's landscape (both through primary and secondary consumption) and may be compared to Kelly's calculations in order to test whether similar results have been produced (a method used in this thesis, see chapter 5). It is possible that if Balbo et al. had used primary product rather than biomass, their agents may have been much more vulnerable to variations in precipitation, which may have led to an effect being seen at a regional and continental scale.

This raises an issue which is not exclusive to ABM but applies to all forms of research. The outcomes and inferences drawn from a model are only as valid as the data which is put into it. While in this case it is due to human error, in other cases uncertainty is not explicitly addressed. An example of this which is not an ABM is Timmerman's (2020) diffusion model, exploring the extinction of Neanderthals and dispersal of modern humans. This extrapolates from Harris and Nielsen's (2016) results that, due to population bottlenecks leading to the accumulation of deleterious mutations, Neanderthals had 40% less genetic fitness than humans, to reduce the carrying capacity of landscape cells for Neanderthals relative to humans by half. The logic behind this is uncertain and seems arbitrary as genetic fitness does not directly relate to resource acquisition and carrying capacity. Rather, this is a factor which would affect life expectancy which then may affect population size and density. While other evidence, such as analysis of Neanderthal habitat range has been used, which does support a competitive advantage for humans, this figure may have benefitted from a parameter sweep rather than assuming Neanderthals were at such a large disadvantage.

This would have the added benefit of assessing the extent to which this determines Neanderthal extinction.

These examples emphasise the importance of ensuring the data input into ABMs is correct, although this is important for all input-output methodologies and is not unique to ABMs. If the data are uncertain it is important to highlight this fact. While assumptions are an inherent part of research, when producing an ABM it is important to highlight when assumptions are made and if possible to use parameter sweeps in order to assess the importance of parameters for the outcomes of the model. This mirrors what has been said above - ABMs should not be created to represent reality, but rather to explore the functioning of a particular mechanism. While models may be produced with mechanisms that seek to explore real-world processes and may provide results that inform us of the causes of real-world features, even these models should not be viewed and scrutinized as representing reality, because they can only account for a finite number of processes. By exploring the mechanisms in this way, it will increase confidence in the results of agent based simulations.

Summary and Conclusions

This paper has explored the advantages and limitations of using Agent Based Modelling (ABM) in archaeology. These limitations were discussed with reference to why ABMs were used less frequently in archaeology than in other subjects. It has then presented some examples of how ABMs have been used to explore two topics: hominin dispersal and land use. This was done not only to introduce archaeologists who have not explored ABMs to their methods, but also to explore how the results of models that have been constructed in different ways may complement each other.

The advantages of ABM are its ability to help us understand complex non-linear causal relationships, combine both quantitative and qualitative data, aid in producing new theories and hypotheses, highlight gaps in the data for future research, investigate the relative significance of different conditions on the outcome of events, and provides a structured way to present theories which makes all assumptions and uncertainties obvious to the reader.

By comparing several ABMs it was shown that vastly different models may produce congruent results, which strengthens their validity and reliability. These models were also critiqued to highlight several points. Firstly, we must be careful not to bias the mechanisms of the model towards particular results. Secondly, the model is only as good as the data put into it. Where data pertaining to an aspect of the system is unavailable or uncertain, a parameter sweep may be used to assess the relative importance of the parameter on the outcome of the model and how it impacts the results using sensitivity analysis. We may then infer which value creates data most representative of what is seen in the archaeological record. Thirdly, a common critique of ABMs in archaeology, which may be applied to each of the models described above, and is not specific to ABM but is a critique of all forms of modelling, is that they are reductionist. Critiquing them based upon this point misunderstands the purpose of ABMs. Rather than creating realistic representations of the past, computer simulations simplify aspects of reality into a more manageable state in order to assess specific systems. As shown above, most models have very specific purposes. Meanwhile, most critics who suggest models are reductionist expect ABMs to incorporate complexities which are beyond the purpose of the model. Further, as has been noted above, in other subjects the complexity of ABMs is considered a challenge, with researchers aiming to reduce the number of parameters to the minimum. Therefore, when critiquing models we must make sure to critique them within the context of their purposes.

In conclusion, while ABMs are applicable to a wide range of subjects, in which context and for what questions may ABMs be particularly suitable? 1) Where environmental factors or complex interactions are important influences. 2) Where variables are well known or are suitable for parameter sweeps, to assess the impact of a range of situations. 3) Where questions and mechanisms may be simplified or divided into smaller, more manageable systems.

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Chapter 5: Resource Accessibility And Human Dispersal

Abstract

The rapid dispersal of our species out of Africa is a subject of great interest. While this topic has been researched extensively, the timing, route and causes of this dispersal are still uncertain. This chapter seeks to explore the impact resource accessibility and fluctuation may have had upon the final out of Africa dispersal. The accessibility of resources in different biomes for contemporary hunter-gatherers is estimated. This is then used to create a map of accessible resource distribution, using the PRISM 4 reconstruction. Modern environmental data are used to estimate how resources fluctuate in different biomes. This was applied to an Agent Based Model (ABM) to explore the effect these fluctuations may have upon a simulated population. Implications for early human migration are then discussed. It is found that Eurasia likely had a higher amount of usable resources, and consequently, these resources may have been a pull factor encouraging dispersal. Further, the high variability of resources in tropical forests, coupled with a low resource accessibility for hunter gatherers, may have led to this biome inhibiting dispersal and contributing to African population subdivision. The accessibility and stability of resources within terrestrial environments likely had a large impact on human dispersal.

5.1 Introduction

Modern Human Dispersal

The dispersal of our species, *Homo sapiens,* out of Africa following their origin approximately 300 ka has been a contentious area of debate (e.g. Boivin et al. 2013; Oppenheimer 2009; Schillaci 2008). Whilst the earliest dispersals of our species remains an enigmatic subject, there is a general consensus that the main wave of expansion responsible for modern populations occurred after 75 ka (Mellars et al. 2013). Nevertheless, researchers have extensively questioned the timing of dispersal, whether there was a single or multiple dispersal events which have meaningfully affected modern populations, and the route taken by our ancestors.

The timing of final dispersal is suggested and widely accepted to have been ~50-75 ka (Malaspinas et al. 2016; Mellars et al. 2013). However, the archaeological sites Skhul and

Qafzeh are dated to ~100-130 ka (Grün et al. 2005). Additionally, a *Homo sapiens* maxilla was discovered in Misliya Cave, Israel, dated to 180 ka (Hershkovitz et al. 2018). This demonstrates dispersal occurred before the 50-75 ka expansion. Some argue this to be a 'failed' expansion (Oppenheimer 2009), while others argue it suggests a more protracted, gradual expansion or even an early successful expansion propagated by a second lineage of *Homo sapiens* (Boivin et al. 2013; Schillaci 2008). It has been suggested that these early expansions did not greatly contribute to contemporary human genetic diversity (Groucutt et al. 2015; Mallick et al. 2016). Further, it has been argued that fossils in southeast Asia, including the mandible found in Zhirendong and human teeth in Fuyan and Luna Cave, China dating to >80 ka, have characteristically modern features (Bae et al. 2014; Liu et al. 2010, 2015; Reyes-Centeno et al. 2017). This has been argued to suggest gene flow or an early population dispersal occuring into this area before this time. More controversially, there is evidence for multiple earlier failed dispersals. Most recently, the cranial proportions of a skull found in Apidima Cave, Greece (Apidima 1), dated to ~210 ka have been suggested to be most similar to modern human proportions (Harvati et al. 2019). Consequently, this has led to the suggestion that an early *Homo sapiens* dispersal occurred at this time and reached further than previously thought (ibid). Despite suggestions that this may represent a population transitioning from *Homo erectus* to Neanderthals (de Lumley 2019), genetic evidence supports the concept of earlier, far-reaching expansions. Posth et al. (2017) suggest that introgression of African mtDNA into Neanderthals occurred between ~460-219 ka. Pagani et al. (2016) found that 2% of Papuan DNA is derived from an earlier extinct out of Africa dispersal.

However, genetic data is complex to interpret. For example, while earlier genetic studies have suggested that Aboriginal Australians may be descendents of an earlier migration (Rasmussen et al. 2011), supporting that at least two out of Africa (OOA) events took place which significantly contributed to the contemporary human genome, this finding has been found to be the effect of admixture with archaic hominins such as Denisovans (Mondal et al. 2016). When this admixture is corrected for, these results suggest a single wave of expansion ~50-75 ka (Malaspinas et al. 2016).

Clearly, the evidence for modern human dispersal is incomplete (Villa and Roebroeks 2014), and even possible to misinterpret. For example, as noted by Boivin et al. (2013), the earliest fossil evidence for modern humans outside of Africa could be misinterpreted to suggest dispersal from the east rather than from Africa. If, as has been suggested by Stringer (2000), a coastal route was taken out of Africa, this would accentuate the limitations of the archaeological record to explore human dispersal. Loss of the coastline due to sea level change makes it difficult to gain access to sites which are now submerged.

Part of this debate is uncertainty over which route was taken out of Africa, or whether multiple routes were used. Two primary routes have been suggested, which modern humans may have used to expand out of Africa. Firstly, humans may have migrated coastally from east Africa across the Bab al-Mandab strait into southern Arabia (Armitage et al. 2011). Alternatively, they may have migrated across the Sinai peninsula (Pagani et al. 2015). While a route from Maghreb to Iberia has also been suggested, it has not gained much support due to the high current of the Strait of Gibraltar, and the persistence of Neanderthals in southern Iberia, which would suggest invasive modern humans arrived from one of the eastern routes, rather than through Iberia (Derricourt 2005; Straus 2001). Therefore, this paper will focus upon the two more probable routes. A full critique of these theories is beyond the scope of this paper (see Dennel and Petraglia (2012) for a comprehensive analysis of the limitations of skeletal, artefactual and DNA evidence). While both theories are supported by genetic data (Pagani et al. 2015, 2016; Quintana-Murci et al. 1999), it is clear that both have their disadvantages. The coastal route hypothesis relies on the assumption that coastal routes provide a stable food source in contrast to fluctuating terrestrial food sources. This assumption has been criticised due to a lack of field data (Groucutt et al. 2015). However, evidence from historical hunter gatherers in California suggests this may be a stable, year round resource used for 3000 years (Jones et al. 2008). Groucutt et al. (2015) have also argued that sites used as evidence for the coastal hypothesis would have been ~600 km from the coast on average. Likewise, the genetic data supporting movement across the Sinai peninsula has also been criticised for not accounting for more modern back-migrations into Africa, an issue which may affect multiple genetic studies as more modern migrations overwrite evidence for ancient population movements (Vyas et al. 2016). Due to the difficulty this presents, Vyas et al.'s (2017) attempt to assess the probability of both migration routes within a single study found no preference for one migration route over the other.

As has been previously noted, it is likely that dispersal out of Africa was a complex process involving multiple populations and routes (Dennell and Petraglia 2012; Wurz and Van Peer 2012). Early dispersals likely took place, as evidenced by the archaeological record. However, the dispersal primarily responsible for non-African heritage likely occurred in a single wave ~50-75 ka. Due to more modern admixture, it is uncertain which route was taken during this wave. However, dispersal may have occurred across both the Sinai peninsula and the Bab al-Mandab strait.

There are several pressures cited as possible causes of dispersal. (1) Climatic causes, such as pulses in rainfall creating favourable conditions for migration from Northern Africa (Hoffmann et al. 2016; Osborne et al. 2008), or climatic changes leading to increased aridity pushing populations out of Africa (Carto et al. 2009). (2) Technological innovations, leading to increases in productivity that may have allowed populations to disperse into previously uninhabitable environments (Mellars 2006). (3) Disease rates (Reed and Tishkoff 2006), and in particular zoonotic disease rates that do not rely on population density for transmission (Bar-Yosef and Belfer-Cohen 2013), are very high in tropical Africa and may have been a push factor when climatic conditions or technology facilitated the habitation of new areas. This is supported by evidence showing that malaria prevalence has a large effect on Middle Palaeolithic site distribution (Trájer, Sebestyén and Domokos 2020). (4) Moral dispute (conflict between allies) and the social characteristics of dispersing groups may have been a powerful pressure for dispersal (Bar-Yosef and Belfer-Cohen 2013; Spikins 2015). Thus far, the pressures cited are more related to dispersal success. However, Spikins (2015) suggests that for dispersal to have occurred at the rate seen in the archaeological record a further motivator was needed. The speed of dispersal cannot be explained through demographic factors such as population increase. Therefore, as noted above, she suggests that following a conflict between allies, individuals attempt to distance themselves from their previous friends. This may have instigated dispersal at a rapid rate (from an evolutionary perspective).

This paper will explore the effects of resource availability on modern human dispersal, focusing on the accessibility of resources in different biomes and how this changes our perceptions of the global landscape. This will firstly introduce previous attempts to estimate the accessibility of resources for hunter-gatherers and outline the aims of the chapter.

Hunter-Gatherer Resource Accessibility

Several authors have suggested that hunter-gatherers use approximately 0.01-0.001% of the resources within their environment (Boyden 1992, 80; Haberl 2001; Weisz et al. 2001). This estimate provides no indication of its origin, is seemingly not based on ethnographic data, is excessively low, and provides no indication of variation determined by biome. In comparison, contemporary humans use ~25% of global NPP (Krausmann et al. 2013).

The amount of resources able to be exploited in an environment likely differs based upon the accessibility of those resources. Kelly (1983) suggested that of the resources available in the environment, Standing Biomass (SB) is largely inedible, while Net Primary Product (NPP) represents the amount of consumable plant material. He suggested that the accessibility of these resources to hunter-gatherers correlates with the ratio of Net Primary Product (NPP) to Standing Biomass (SB). This is because plants within an area of high biomass have high evolutionary competition. Therefore, more energy is devoted to capturing sunlight, meaning the area where the most energy is invested is high above the ground, or for structural maintenance, which largely produces inedible biomass. Further, Kelly (1983) proposed that secondary biomass would similarly be located in difficult to reach areas, as animals would remain close to the location of edible primary biomass. By assessing the ratio of NPP to SB Kelly found that the environments with the largest NPP are not necessarily the environments with the most resources available to be exploited by humans. Rather, in comparison to more open landscapes (grasslands, savanna, deserts and tundra) more closed forested landscapes had a considerably lower proportion of their resources (both primary product and secondary biomass) available to humans. As a consequence, the suitability of biomes for human survival, and the carrying capacity of a particular biome, is determined by how much NPP is accessible, rather than the overall NPP.

Kelly’s exploration of accessibility highlights that more resources do not directly equate to more accessible resources. However, despite Kelly’s results having been used in a previous agent based model (Balbo et al. 2014), Kelly’s study was correlational and did not provide any precise figures of the percentage of resources humans were able to exploit in each biome. This could be important for our broader understanding of how modern humans dispersed. While particular focus has been placed on the ‘coastal highway’, it may be the case that other, more open biomes with abundant accessible resources also provided an easy route out of Africa.

Binford (2001) provides a dataset of 339 hunter-gatherer groups, which is suitable to produce more accurate estimates of resource usage. This dataset provides estimates of: the size of groups’ area of occupation, NPP and SB available within this area, the biome of groups’ habitats, and population sizes.

Further, Kelly’s analysis does not account for the impact of annual fluctuations in resources. By using modern estimates of biome specific variation in NPP (Mohamed et al. 2004), the effect this may have upon habitat suitability will be explored.

Palaeoreconstructions

The estimations of accessible NPP will be applied to a model of Mid-Upper Pliocene (~3 Ma) biome distribution, PRISM4 (Dowsett et al. 2016; Salzmann et al. 2008). This is a reconstruction of a particularly warm period, created to aid in projections of modern global warming (Dowsett et al. 2016). Other reconstructions primarily focus upon the last glacial maximum (LGM) or the early Holocene. For example, the CLIMAP (CLIMAP Project Members 1976), and BIOME4 reconstructions (Kaplan et al. 2003) have a focus of 18 ka and 21 ka respectively. During and leading up to these time periods conditions were particularly harsh, as evidenced by the extinction of more cold adapted Neanderthals (although other factors also had a significant impact upon this).

Conditions when humans were initially expanding out of Africa, during the last interglacial period, were less severe and warmer than the LGM and early Holocene (Kukla 1997; Nikolova et al. 2013). Although, due to the astronomical causes it is not strictly analogous, the climatic effects are similar to what is projected for the future (Lunt et al. 2013). Unfortunately, comprehensive global data sets and reconstructions of the last interglacial period are largely lacking; particularly reconstructions of past biome distribution. Creating these reconstructions is a priority of the third and fourth phases of the Palaeoclimate Modelling Intercomparison Project (Lunt et al. 2013; Nikolova et al. 2013). Despite the lack of data, climatic simulations have been produced to predict the conditions of the last interglacial. Interestingly, these models do not always show agreement with the proxy data available. For example, Lunt et al. (2013) have shown a discrepancy between estimates of Eurasian warming. Proxy data suggests a 15°C warming of Eurasia (relative to modern data), while the ensemble results of simulations suggest a 2°C warming (relative to preindustrial data). Similar discrepancies were found when assessing each simulation individually and are not due to seasonal biases in proxy data. A more recent comparison showed greater agreement, although there were exceptions (Otto-Bliesner, Brady and Zhao 2021). As of yet however, these models have focused upon global temperature, precipitation and ice coverage. While the models' effects on vegetation have been explored, current proxy reconstructions of vegetation are of low coverage and considered unreliable (Otto-Bliesner et al. 2017; Otto-Bliesner, Brady and Zhao 2021). Attempts to assess vegetation differences between the pre-industrial period and the last interglacial period have shown increased precipitation in the Sahara and Sahel, increased expansion of forested areas, a reduction in deserts within the northern hemisphere, and an increase in grasslands at mid latitudes (Nikolova et al. 2013; O'ishi et al. 2021).

The PRISM4 model of the Pliocene has been compared to an extensive proxy dataset and shown to have a good fit, although there is a bias towards cooler conditions, which could be improved by focusing on more specific time slices (Salzmann et al. 2008, 2013). Ultimately, this reconstruction shows a northward shift of temperate forests and shrinkage of tundra, with a spread of warm forests. Further, it shows a decrease of desert biomes and replacement with tropical savannas and woodland. When comparing models and proxy data of the Pliocene and last interglacial, temperature and precipitation differences are shown to be more accentuated during the Pliocene (Zhang et al. 2021). Therefore, while both models of the last interglacial and the Pliocene show similar features qualitatively (increased expansion of grasslands and forested biomes), the Pliocene was warmer and wetter than the last interglacial, and therefore the difference in biome distribution relative to pre-industrial conditions is greater.

While there are difficulties in using simulations for the last interglacial, a recent dispersal model of modern humans has utilized the LOVECLIM model in a particularly effective way to create a simulation of the last 408 thousand years of climate change, with a focus on the last 125 ka (Timmermann and Friedrich 2016; Vahdati et al. 2019). As may be expected from the discussion above, this simulation shows high agreement with proxy data for the last glacial maximum (although there were discrepancies in precipitation when compared to other models) and the early Holocene, while the degree of warming for the last interglacial was underestimated (Timmermann and Friedrich 2016). While this model does not completely agree with proxy data, the use of the simulation to create a holistic model of past climate change will provide significant opportunities for future models, particularly as more proxy data becomes available and it is refined. However, given the inconsistencies of the time slices assessed by Palaeoclimate Modelling Intercomparison Project (PMIP) and the limitations of the proxy data, more specific, time defined proxy data needs to be collected to test the validity and reliability of this model.

Due to the large amounts of proxy data available, the high agreement between the model and the proxy data (Salzmann et al. 2008), and the explicit development of a biome distribution dataset which is easily applicable to this ABM, the PRISM4 model was selected for use in this study. While this model uses a reconstruction of a warmer phase, it is important to note that the PRISM4 model also has a bias towards cooler conditions relative to proxy data, particularly in northern latitudes (Salzmann et al. 2008, 2013). The aim of this paper is not to use an exact reconstruction of past conditions. Each model, for each time period, and in particular the last interglacial, has their limitations. This paper aims to use a palaeoreconstruction to highlight the impact accounting for the differential ability of hunter gatherers to collect resources in different biomes may have upon the results of a dispersal model, so that this may be accounted for in future studies.

Aims

This chapter has two aims:

1) To use Binford's (2001) ethnographic data to produce estimates of the proportion of resources hunter-gatherers can use in different biomes, and apply this information to a reconstruction of a past environment.
2) To assess the impact annual fluctuations in resources may have upon hunter-gatherers' ability to survive in different biomes.
3) Following on from 1 and 2 above, the implications of this research for human dispersal and population division are then explored and discussed.

5.2 Methods

The estimates of usable resources available in each biome were calculated as follows. (1) Using Binford's (2001) extensive data of 339 hunter-gatherer groups the area each individual uses within their environment was estimated, by dividing the group's total area of occupation by their total population. (2) The total number of resources within this area was then calculated (NPP/km^2/yr × Area of Individual). Binford's ethnographic data was used as it is the most comprehensive data available to estimate resource usage and accessibility. However, caution must be used when inferring the behaviour of our ancestors from ethnographic data, as some modern ethnographic groups may not have reached their landscapes carrying capacity (see section 5.5). (3) The percentage of resources in the area that would need to be consumed for a human to survive was calculated. To do this the amount of biomass needed for a human to survive was calculated by converting Boyden's (1992, 80) Human Energy Equivalent (3500 MJ/yr) into dry weight biomass (g) using Mitsch and Jorgensen's (2003, 70) conversion chart, and also compared against McDaniel and Borton's (2002) estimate. Both of these estimates provided similar results (188,000g and 180,000g respectively). Therefore, the amount of biomass needed per year was estimated to be approximately 185,000g. The proportion of biomass needed to survive relative to the total NPP available in each individual's area was then calculated to estimate the proportion of resources hunter-gatherers can use in each biome (accessible NPP). By subsetting the results by the biome each group inhabits, the mean proportion used by each group provides an estimate of the amount of accessible NPP in each biome.

This dataset was used to produce a realistic environment for an agent based model of out of Africa population dispersal. The model was used to aid the exploration of the effect of resource accessibility and resource variability on the ability of agents to inhabit different biomes. This model used the PRISM4 Pliocene reconstruction to identify the biomes of latitude/longitude coordinates to produce a global simulation (Dowsett et al. 2016; Salzmann et al. 2008). The simulation was produced at a resolution with each cell representing 1° of latitude/longitude, allowing for differences in cell size with latitude (see supplementary section 1.2.1). Data from Whittaker and Likens (1973) were then used to relate these biomes to their annual NPP. The method above was used to calculate the amount of accessible resources in each biome (the proportion hunter-gatherers can actually use). To simulate inter-annual variation in NPP, coefficients of variation (COV) in NPP across an 11 year period for each biome were used to provide variations in NPP around the means provided by Whittaker and Likens (1973) (Mohamed et al. 2004) (see table 1). These variations are largely caused by differences in precipitation (Mohamed et al. 2004). This was applied in a simple way to each cell with no spatial autocorrelation. This allows the effects of a simple form of interannual variability in NPP on population dispersal and biome habitation to be explored.

10,000 agents, representing asexual individuals, were initialized into the model at the approximate location of lake Turkana, Ethiopia. Agents begin within a two landscape cell radius of this location within a Moore neighbourhood. Lake Turkana was chosen due to the high presence of hominin and human fossils in this region (Spoor et al. 2007; Stringer 2016; White et al. 2003), suggesting it is a focal region for the origin of modern humans. Agents are initialized with full health and resources, and a random age between 1-50. Each iteration of the model represents a single year, with the model running for 15,000 years. Each year agents may move, collect resources, reproduce, and die. Realistic reproduction (6%) and mortality rates (1.2%) were taken from ethnographic data for use in the model (Gurven and Kaplan 2007; Hill, Hurtado and Walker 2007; White 2014, 2016; Wood 1990). However, these estimates do not account for disaster events, and the possible increased dangers of the Palaeolithic environment. Therefore, mortality rates were inflated to a level where it produced a realistic population growth rate (<0.1%), according to ethnographic and archaeological data (Hassan and Sengel 1973; Hassan 1975). Agents hold a series of information about themselves: health, age, resources, location. The amount of resources agents are able to gather from an environment is based upon the calculated accessible portion of NPP within the biome they are in (table 1). Further, resources are divided between the population of agents within a cell. Therefore, if the cell's carrying capacity is reached agents may collect fewer resources than they require to survive. If agents are unable to collect enough resources they lose health, which increases their probability of death by 10%. This chance of death is independent of the ethnographically determined mortality rate. Therefore, agents were less likely to successfully disperse into areas where resources were scarce or uncertain (see supplement 1 for a complete description of the model).

5.3 Results

The estimates of accessible NPP for each biome were similar to Kelly's (1983) expected proportions. A higher percentage of resources were accessible in more open grassland and desert environments (table 1). The larger percentage of harvestable resources available in open environments reflects our ancestors' evolutionary adaptations to more open environments. In particular, and in contrast to desert environments which still only provide a small amount of harvestable resources, the larger amount of accessible NPP available in grasslands may reflect our species' preference for grassland environments (Falk and Balling 2010). Many Palaeolithic sites of both modern humans and earlier hominins are located in what would have been grassland environments (Finlayson et al. 2011). For example, the earliest archaeological sites in the Nefud desert were occupied during a humid phase when the location would have been grassland (Petraglia et al. 2012). In this study, grasslands were found to have the highest amount of exploitable resources once the accessible fraction of resources was taken into account (table 1).

Comparing the distribution of accessible NPP per km^2 to the total NPP per km^2 in the PRISM4 reconstruction provides a very different picture of the landscape (figure 1). Biomes with a higher amount of harvestable resources are more prevalent in Europe and the near east when compared to Africa. This is contrary to expectations and may have significance for future dispersal theories and models. In particular, the smaller amount of resources available in tropical forests, in comparison to grasslands, has a large effect on this distribution.

Further, the agent based model showed that, when there was annual variation in NPP, agents were unable to inhabit tropical forests in Africa (figure 1). This was replicated each time the model was run with a different random seed (N= 10) and was due to a combination of factors. Firstly, despite tropical forests having the highest NPP per km^2, the amount that is harvestable is proportionally the smallest. This still leaves a considerable amount of resources available to exploit. However, tropical forests also have the most variable NPP per year (table 1). When this variation was applied to the model, agents were no longer able to survive in this biome, due to the NPP being exceptionally low in some years of the model.

The results here relate to the accessibility of resources in different biomes. This suggests that the amount and variability of accessible resources in different biomes may have considerably impacted the ability of past humans to inhabit them. While these results have implications for modern human dispersal, the model presented did not aim to evaluate different possible dispersal rates and routes. However, the findings of this paper may contribute to future models of dispersal. For example, if this research is combined with topographical and palaeolithic fluvial data, it may help reveal whether a within land route out of Africa is actually more constrained or improbable than previously thought. The implications of these results will be discussed with regard to two topics. Firstly, whether tropical forests may have been a challenging biome for past hunter gatherers to survive in. Secondly, whether the distribution of accessible resources may have had implications for past dispersal events.

Table 1. Biome resource characteristics: NPP (Whittaker and Likens 1973), Usable NPP calculated using mean resource usage percentages, Mean resource usage (original data from Binford (2001)), COVs in NPP (Mohamed et al. 2004).

Biome	**NPP (kg/km^2/yr)**	**Usable NPP (kg/km^2/yr)**	**Mean Resource Usage (%)**	**NPP COVs (%)**
Grassland	500	72.432	14.5	11
Temperate Forest	1300	67.952	5.2	21.6
Tropical Forest	1500	37.097	2.5	36.5
Boreal Forest	800	33.589	4.2	14.9
Tropical Savanna	700	19.440	2.8	15.9
Desert	70	7.441	10.6	20.3
Tundra	140	7.230	5.2	10.1
Land Ice	0	0	-	-

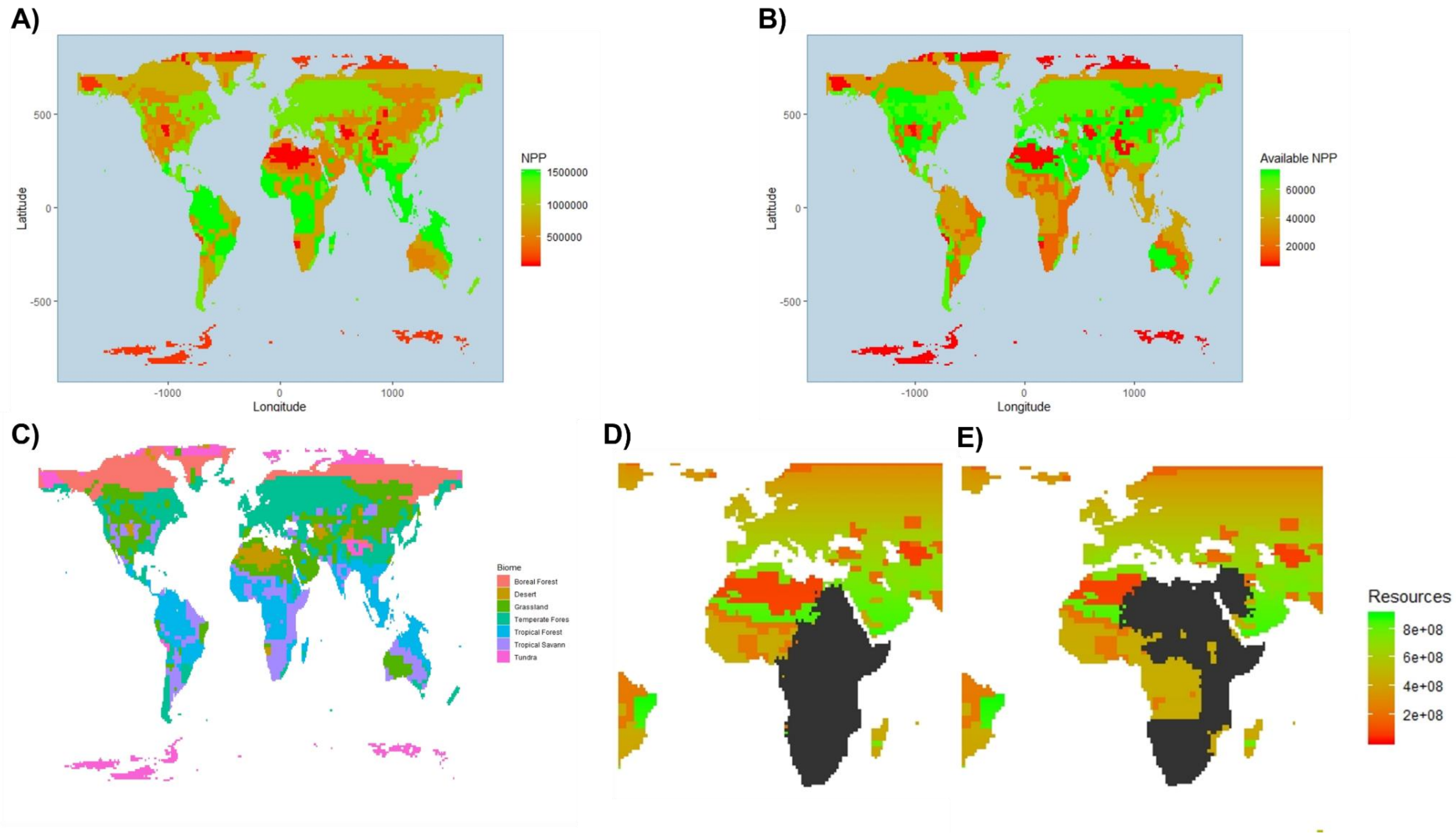

Figure 1. A) Global distribution of NPP (g/km^2/year) during the Pliocene; B) Global distribution of available NPP (g/km^2/year); C) Biome distribution; D) Showing occupied locations in Africa (black) when there is no annual variation in resources (in one realisation of the model); E) Showing occupied locations in Africa (black) when there is annual variation in resources (in one realisation of the model).

5.4 Discussion

Tropical Forests

The ABM showed that when the model included interannual variability in resources, which reflected the COVs found by Mohamed et al. (2004) in their 11 year study, agents were unable to colonise tropical forests. Due to the starting location of agents being in the approximate location of Lake Turkana, Kenya and the distribution of tropical forests in the PRISM 4 reconstruction (in particular, in central and eastern Africa), this constrained the area through which agents could reach northern Africa and the Sinai peninsula from eastern Africa. If humans evolved across Africa or within western or southern Africa, rainforests still would have been a considerable barrier. Due to the high density of forests in western Africa, it is unlikely that our ancestors would have been able to survive the variability in resources. Further, if they evolved in southern Africa, they would still be limited to the same route towards northern Africa. As a consequence, this may have been an important barrier to movement, making it difficult for humans to pass through the northern route. A simple consideration of watercourses and topography would be unable to recognise this barrier to movement. This demonstrates that without modelling the ecology of the environment we may fail to understand potential constraints to dispersal.

Various lines of evidence indicate that hunter-gatherers struggled to survive in tropical forests, particularly without access to farmed foods (Headland and Bailey 1991), which provide a stable source of resources. Similar to Kelly (1983) (see above), Bailey et al. (1989) and Headland (1987) have argued that the majority of edible material would be above ground and difficult to reach, difficult to process for consumption, and highly variable seasonally. In addition, high energy plants found in tropical forests today which are suitable for human consumption are suggested to have dispersed from agricultural settlements (Headland and Bailey 1991). This suggests that without an ‘artificial’ source of food, which is both accessible and stable, humans would not be able to survive in tropical forests.

However, alternative viewpoints have been put forward. More modern research suggests that hunter-gatherers are able to colonize rainforest environments. Mercader (2002) has cited a diverse range of evidence suggesting that Middle Stone Age (~280-50 ka) humans were able to inhabit African rainforests and that this intensified in the Later Stone Age. In addition, several authors have noted the importance of rainforest resources for humans in southern Asia. In particular, in Sri Lanka isotopic evidence has shown an extended reliance on rainforest resources from ~36-3 ka (Roberts et al. 2015, 2017). While Roberts and Petraglia (2015) recognise the limitations of African and Australian data suggesting occupation of rainforests (e.g. the use of indirect pollen records) and argue that there is no direct evidence for rainforest coverage at sites in these regions, they have argued that evidence from Melanesia and Southeast Asia conclusively demonstrates specialized use of rainforests. The use of microlith tools and the ability to capture small prey are argued to be the technological adaptations which facilitated the habitation, or at least exploitation, of this biome (Wedage et al. 2019a, 2019b). Additionally, the collection of wild yams, where available, may have provided sufficient energy for survival in tropical forests. Yasuoka (2013) observed that the Baka obtained 65% of their caloric intake from wild yams when within forests. Largely, this was achieved through unintentional cultivation of the plants, where discarded waste from the collected yams would grow into new plants, leading to clusters of yams. This would provide a stable source of food during times of uncertainty, and may counteract the uncertainty of this biome, suggested by the low amount of accessible resources indicated by this research and by the COVs in NPP found by Mohamed et al. (2004), making it more habitable. Hence, these researchers have suggested that it is possible that early modern humans were able to inhabit rainforests and that they were ‘generalist specialists’, able to specialize to a range of extreme environments (Roberts and Stewart 2018), though they may still be dependent on resources external to tropical forests, or resources gathered through exchange.

It is therefore clear that modern hunter-gatherers are able to inhabit tropical rainforests with the use of semi-cultivated plants, although the archaeological evidence suggests this is unlikely to be characteristic of early phases of dispersal. Further, it is important to note that as groups were dispersing and coming into contact with new environments, such as tropical forests, they would have needed to learn how to exploit them, and therefore would not have been able to effectively inhabit them initially, although this is unlikely to have had a big impact on the large timescale this section discusses. Nevertheless, Upper Palaeolithic inhabitants of Sri Lanka were intensively utilising tropical forests. However, taphonomic bias in the archaeological record has led to only sites that would have been on the forest border being found or securely dated (Mercader 2002; Roberts and Petraglia 2015). This bias is also exacerbated by the difficulty of finding archaeological materials where these biomes have persisted. Genetic research partially fills the gap left by the archaeological data, as will be discussed below.

While tropical forests may not have been uninhabitable or completely prevented dispersal they do appear to have been a significant barrier. Findings of long term population divergence and subdivision (Choudhury et al. 2018; Gunz et al. 2009), as well as morphological differences among forest groups within Africa (Perry and Dominy 2009; Shea and Bailey 1996), provide further support that tropical forests would have been a barrier to dispersal. Population divergence within Africa is thought to have occurred over the last 100 ka. As reviewed by Choudhury et al. (2018), the initial divergence differentiated the southern Khoesan populations. Following this, there is genetic differentiation of modern rainforest foragers (60-75 ka), and northern and eastern African populations (50 ka). Notably, modern-day rainforest foragers (Baka and Mbuti) are genetically distinct. This confirms that, despite a lack of archaeological evidence, Palaeolithic hunter-gatherers were able to specialize and inhabit rainforests. However, the biological adaptations seen in modern forest hunter gatherers may be responsible for their long term success. Rainforest foragers have been classified as ‘pygmies’ due to their small body size. This small body size enables foragers to survive on a smaller caloric budget and is also associated with early maturation, which promotes faster reproduction (Perry and Dominy 2009; Shea and Bailey 1996). As a result, as the ‘pygmy’ groups adapted by becoming smaller they were able to inhabit rainforests, but they still may have presented a considerable barrier to other hunter-gatherer groups. This is further supported by growing evidence that the Bantu dispersed late upon their advent of agriculture (~5 ka) from the north through the central rainforests and then towards the east and south, rather than circumventing the rainforests (Campbell and Tishkoff 2010; Choudhury et al. 2018). If this is the case, this group may have only been able to disperse through the rainforests due to their use of agriculture, and up until that point rainforests may have been a barrier constricting the dispersal of this group.

Authors have previously suggested that environmental barriers may have contributed to population isolation, leading to the genetic differentiations discussed above (Campbell and Tishkoff 2010; Scerri et al. 2018). For example, on a smaller scale, the Kalahari desert has considerably affected the population structure of southern Africa (Uren et al. 2016). Similarly, while it is clear that other factors played a role in the population structure of Africa (e.g. cultural and linguistic differences, as well as other climatic factors), the ABM suggests that tropical rainforests may have been a biome which significantly contributed to population fragmentation. Future research should explore whether this barrier divided the northern and southern routes out of Africa, as may be suggested by the late southern dispersal of the Bantu. Future palaeoreconstructions of the last interglacial, which integrate more proxy data, as well as more local scale studies (Pederzani et al. 2021), could be used to determine the extent of prehistoric rainforests and how they have fluctuated in their coverage. Once this is determined, traditional populations above and below the Pleistocene rainforest belt could be assessed for their genetic similarity.

Distribution of Resources as a Pressure for Migration

It could be argued that assumptions about the distribution of available resources for prehistoric hunter-gatherers need to be reassessed in light of the analysis presented in this paper. Rather than directly using NPP to represent resources as other researchers have done (e.g. Vahdati et al. (2019) and Timmermann and Friedrich (2016)), this paper utilised ethnographic data to estimate the amount of resources hunter-gatherers would be able to use in different biomes. This revealed that the greatest amount of exploitable resources were available in grasslands, followed by temperate forests. These biomes are characteristic of Eurasia and may have led to increased survival for groups who moved there. Therefore, once groups moved out of Africa, population growth and dispersal rates may have increased due to favourable conditions.

The hypothesis that the colonization of grassland in Asia would have been beneficial has been suggested previously for early hominin expansions (Dennell, Petraglia and Korisettar 1998; Dennell 2003; Holmes 2007). Further, the use of temperate forests by early Asian hominins has also been suggested (Belmaker 2018). Therefore, this research supports theories that dispersal success and speed was largely determined by the distribution of hominins' preferred habitats, both grasslands and temperate forests. These findings are significant for early *Homo* dispersals. However, they may also be applied to the later dispersals of *Homo sapiens*.

A large focus has been placed upon the idea that humans utilized the coast to provide themselves with a stable supply of resources, and that due to this they were able to disperse at a relatively rapid pace along the coastline (Stringer 2000). While this study does not challenge this route of dispersal, it indicates that other high yield biomes may also have provided a corridor out of Africa. In particular, the extension of grassland into southern Asia (Parton et al. 2015), in comparison to more temperate forested environments within western and central Europe may have provided a more appealing pathway out of Africa during the last interglacial period (although temperate forests were also a preferred biome). This may partially explain the discrepancy between dates of the earliest occupation in Asia, and dates of earliest occupation in Europe. However, as has previously been suggested, assimilation of smaller human groups within Neanderthal groups likely also played a large role (Timmermann and Friedrich 2016). The importance of grasslands has been noted before, with regard to expansion through the Arabian Peninsula. Boivin et al. (2013), for example, have suggested that movement across the Arabian Peninsula during MIS 5 (130-75 ka) was only possible due to the replacement of desert environments with grasslands. This may have occurred every ~23 ka since MIS 6 (160-150 ka) (Parton et al. 2015). Further, Boivin et al. (2013) have argued that coastal environments would have been adjacent to desert environments during MIS 4 (~74–59 ka), while more inland grasslands may have provided a better pathway out of Africa. While it is unlikely that grasslands provided the only pathway out of Africa, their impact upon our dispersal deserves more recognition. More research needs to be undertaken to explore the effect of resource accessibility on habitat suitability. In particular, future dispersal models need to take accessibility into account.

5.5 Limitations and Future Research

The method used within this chapter has several limitations, some of which are mentioned above. This section will describe these limitations and suggest what future research may be done to further this work.

Firstly, while this paper has attempted to highlight resource accessibility as an issue which requires more attention within archaeological research, and therefore it only required the use of realistic example reconstruction, the use of more advanced climatic models reconstructing the last interglacial period should be used as they become more reliable and available. This would help establish the extent to which the distribution of tropical forests may have constricted movement across Africa and may provide a greater understanding of how the evolving landscape affected population subdivision and dispersal.

Secondly, as noted above, the use of ethnographic data has limitations, both generally and specifically in relation to this study. Generally, the predictive ability of the ethnographic record is limited according to the groups which are used for analysis (Burke et al. 2017), and are also subject to observer bias (Hollowell and Nicholas 2008). Further, it must be acknowledged that ethnographic groups are not analogous to our ancestors. Modern hunter gatherers have had many millennia to develop their techniques and technologies for living within their environments and also use technology our ancestors would not have had access to (e.g. iron arrowheads) (Marlowe 2005). Many have access to markets to mitigate risks (Donders and Barriocanal 2020). Also, they may live within constricted bounds which does not allow for group expansion and fission, with many being displaced (Bankoff and Perry 2016; Cernea and Schmidt-Soltau 2006), and they may not have reached their landscape’s carrying capacity. Therefore, the population growth rates and ability to access resources likely differs from our ancestors.

Associated with this, data limitations within this paper may have affected some of the results. For example, Tropical Savanna was estimated to have a low amount of usable resources, in contrast to expectations. This is likely due to the data focusing on more wooded areas within the groups area of habitation, rather than the more open areas. Further, the impact of more modern causes of NPP variability, for example deforestation, may have had an effect on estimates of global NPP variability (Mohamed et al. 2004). Due to the different goals of researchers, biases such as this are difficult to avoid when using others' data. Further study should seek to conduct sensitivity analysis upon the model presented in this chapter in order to assess how robust the results of this study may be to inaccuracies in the data. Additionally, a study specifically targeted at collecting data from hunter gatherer groups within different biomes, with an active attempt to assess the broader distribution of resources within their areas of occupation when groups are living in mosaic environments, would greatly benefit this research. Further, the collection of long term, specific data on fluctuations in NPP within these areas, rather than using generalized global estimates, may reveal nuances which this study was unable to identify.

By conducting high detail ethnographic studies on resource acquisition, we may gain a deeper understanding of why groups use complex tools, why particular mobility patterns are used, as well as how this affects demographic and intra and inter group social interactions (including cooperation and warfare). These results may then be applied to the archaeological record to understand more about how changing climates may have impacted, not only our ancestors' dispersal, but their lifestyles.

Conclusion

The implications of this study are twofold. Firstly, the accessibility of resources within different biomes may have a large impact on their suitability. This should be taken into consideration when generating future theories and models of dispersal. This research has revealed that Eurasia likely had a higher amount of usable resources than Africa during our evolutionary past. Accordingly, this may have been a significant factor in dispersal success when modern humans and earlier hominins migrated out of Africa. This presents an alternative view of dispersal than is available when just assessing resource distribution using NPP.

Secondly, this study supports previous claims that modern humans would not have been able to survive in tropical rainforests. This is due to tropical forests having such a low accessibility and a high annual variability in resources. Nevertheless, if humans were able to find (or semi cultivate) a reliable food source, then tropical forests would not have been a barrier. Currently, evidence suggests that, with the exception of ‘pygmy’ populations, humans developed the ability to survive in tropical forests after the final out of Africa dispersal. As a result, tropical forests may have contributed to population subdivision in Africa.

The results of this study should be used to inform future ABMs and theories more broadly. While there is recognition that some biomes are more preferable to others, these suitabilities are either not being recognized (Timmermann and Friedrich 2016; Vahdati et al. 2019), or are being arbitrarily assigned (Romanowska 2015), in computer simulations. While this study does not completely rectify this problem, it hopes to highlight this as an important issue. Future research should aim to practically explore these issues further ethnographically.

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Chapter 6: An Agent Based Model of Extraversion and Human Dispersal

Abstract

The evolution of cognitive diversity is largely a neglected topic. Despite this, a few studies have attempted to explore the effects of behavioural and cognitive diversity on our evolution, but these have stopped short of suggesting their impact upon specific events in our evolutionary history. This chapter explores how variations in human personality, specifically introversion/extraversion, may have affected past humans' ability to adapt to new environments in the Palaeolithic, and how this may have impacted their dispersal out of Africa. It has been found that dopamine receptor genes associated with extraversion increase with distance from Africa. This has been suggested to be due to these genes promoting behaviour that confers either a reproductive advantage, a better ability to adapt to new environments, or a greater propensity to disperse. This paper presents an agent based model to explore how variations in introversion/extraversion, may have affected our dispersal out of Africa, and tests the hypothesis that a reproductive advantage may have led to this distribution of dopamine receptor genes. Reflecting the psychological literature, this model provides extraverts with a reproductive advantage, but also a higher mortality rate. The model supports the suggestions that the observed distribution of DRD4 genes associated with extraversion may entirely be the result of sexual selection. Selection for extraversion in the model was found to be density dependent, with the most extraverted agents being in less densely populated areas at the front of the wave of expansion, in scenarios where extraverts' reproductive advantage outweighs their greater mortality rate. The implications of this density dependent selection will be discussed in relation to *Homo sapiens* dispersal events.

6.1 Introduction

Our cognitive diversity is a defining feature of our species and has likely increased through our lineage (see chapter 3). Despite this, the evolutionary effects of this variety have largely been ignored. A few studies have attempted to explore the implications of psychological and cognitive diversity on our evolution (Armstrong 2015; Buss 1991; Ehardt 2009; Horrobin 1998; Jensen et al. 1997; Kershner 2020b, 2020a; Kuttner, Lorincz and Swan 1967; Nettle 2005, 2006; Polimeni and Reiss 2002; Spikins 2013; Spikins and Wright 2016; Spikins, Wright and Hodgson 2016; Spikins, Scott and Wright 2017, 2018; Stevens and Price 2015;

Stone, Shackelford and Buss 2012; Williams and Taylor 2006). However, the impact this may have had upon specific events during our evolution has not been widely discussed. This paper aims to explore the impact of the extraversion continuum on humans' ability to adapt to different environments and expand out of Africa during the Palaeolithic, using Agent Based Modelling (ABM).

ABM is a method of computer simulation used to assess how the results of a system are the product of their parts (agents; see chapter 4). Agents within a model generally represent either individuals or groups who are autonomous within their environment, have goals, and are reactive to the world around them. Their reactions to the environment around them are determined by rules. These rules combine to produce a system which attempts to replicate a simplified version of reality. By creating these simplified models it helps the researcher understand how each part of the system affects the outcome (Costopoulos 2008; Lake 2015). This allows researchers to explore how changing the scenarios of a situation may lead to different outcomes. Researchers are then able to identify which scenario produces results similar to what is observed in reality, and therefore support or propose theories that seek to explain the causal mechanisms behind those observations. This model will explore how variations in human personality, specifically introversion/extraversion, may have affected human dispersal out of Africa, and compare the findings to the distribution of dopamine receptor genes associated with extraversion.

The Genetics and Evolution of Extraversion

Extensive psychological research has been conducted to explore the behavioural differences associated with extraversion and how these may be associated with life history differences (see chapter 1 and 2). Extraverts are more social (Anderson et al. 2001; Ilmarinen et al. 2015; Krämer and Winter 2008; Ong et al. 2011; Pollet, Roberts and Dunbar 2011; Slee and Rigby 1993), more successful in forming short term sexual relationships (Brown and Sacco 2017), and have been found to have more children, both in western societies and in polygynous populations in Senegal (Alvergne, Jokela and Lummaa 2010). However, extraverts are also more risk taking and prone to injury and mortality (Hajek, Bock and König 2017; Horvath and Zuckerman 1993; Jonah 1997; Lajunen 2001; Nettle 2005). This evidence suggests that introversion and extraversion represent K and r specialised phenotypes (Rushton 1985). Relative to introverts, extraverts are likely to reproduce quickly, produce more offspring and die early (r specialised). While introverts are likely to reproduce later, produce less offspring, but survive longer (K specialised).

There is no simple relationship between genes and what we classify as “extraverted” behaviour. Further, it is important to remain cautious when interpreting genetic research. New methodologies for assessing genetics may lead to revisions of current interpretations of the genetic causes of personality, as has occurred in Neanderthal research (Peeters and Zwart 2020). Nevertheless, up to 50% of extraversion is thought to be genetically, rather than environmentally, determined (Eaves and Eysenck 1975; Rettew et al. 2008; Van Den Berg, De Moor and McGue 2014; van den Berg et al. 2016). Genetic research suggests that the heritable component of extraversion is highly polygenic, with any single gene having a small effect size (Turkheimer, Pettersson and Horn 2014; van den Berg et al. 2016). Despite this several genes have been associated with more extraverted behaviour (Golimbet et al. 2007; Smillie et al. 2010). In particular, a significant association has been found between dopamine receptor genes and extraverted behaviour (Benjamin et al. 1996; Ebstein et al. 1996; Faurie et al. 2017).

This is significant because the dopaminergic system may have had important implications for our evolution. For example, DeLouize et al. (2017) and Previc (1999, 2009) have suggested that the expansion of the dopaminergic system is responsible for some of the evolved abilities and features of *Homo erectus*, such as novelty seeking and sociality, as well as handedness, REM sleep, thermoregulation, enhanced executive functions (e.g. working memory, mental flexibility and impulse control), and an enhanced reward system. They argue that this may have adapted through two avenues. Firstly, through increased consumption of meat leading to reduced cell death in the dopaminergic system. Secondly, through increases in exercise leading to a greater need of thermoregulation, which leads to selection for an enhanced dopaminergic system. These theories suggest that the social and motivational functions of the dopaminergic system were just one of multiple reasons for the selection of an increased dopaminergic system. Nevertheless, they also stress the importance of the rapid evolution of this system, which is directly related to extraverted characteristics. This suggests that, as well as the effects on modern human dispersal, which will be assessed in this paper, changes in the levels and variance of extraversion may have had broader impacts on our evolution.

Dopamine receptor genes have been shown to have a significant impact on behaviours associated with extraversion. In particular, the 7 and 2 repeat (7R and 2R) alleles of the dopamine receptor D4 gene (DRD4) have been shown to increase novelty seeking and risk taking behaviour (Benjamin et al. 1996; Ebstein et al. 1996; Faurie et al. 2017), including sexual promiscuity (Garcia et al. 2010), and have been associated with attention deficit/hyperactivity disorder (ADHD) (Faraone et al. 2001; Gizer, Ficks and Waldman 2009; Hamarman et al. 2004). While DRD4 is associated with ADHD, it acts in conjunction with other genes and environmental factors to cause the condition (Altink et al. 2012). Therefore, while the 7R allele increases the likelihood of developing ADHD, not everyone with the allele has this condition. More generally the 7R variant has been associated with aggression and possible antisociality (Bachner-Melman et al. 2005). However, long DRD4 variants have also been associated with increased prosocial behavior, but only in response to particular environmental conditions (e.g. parenting style, religious priming and peer relationships) (Buil et al. 2015; DiLalla, Elam and Smolen 2009; Jiang, Chew and Ebstein 2013; Knafo, Israel and Ebstein 2011). Therefore, it has been suggested that the 7R variant is a plasticity gene, the result of which (at least for prosocial behaviour) is significantly impacted by environmental interaction (Jiang, Chew and Ebstein 2013). This likely explains the inconsistent results when associating DRD4 variants with the more social aspects of extraversion, although it must be noted that few genes have a completely determinative effect on phenotype. Additionally, Faurie et al. (2017) found that individuals living in dangerous areas around Mount Merapi volcano were heterozygous (4R-2R) for the DRD4 gene. This heterozygosity produced more risk averse behaviour, which they argue provides heterozygotes with an advantage in these conditions. Consequently, they suggest that, due to the negative effects of overdominance (leading to more risky behaviour), there is negative frequency dependent selection for the 2R allele in more risky environments (Faurie et al. 2017). This may suggest that selection for the 2R allele reduced risky behaviour by increasing heterozygosity, and that risk aversion led to rapid selection for this allele. More research is needed to explore the effects of heterozygosity on the 7R allele.

The 7 repeat allele of DRD4 is thought to have originated during the Upper Palaeolithic (~40-50ka) at a time of rapid global colonisation and technological innovation (Ding et al. 2002; Wang et al. 2004). The geographical distribution of DRD4 alleles reflects an increase of extraversion associated alleles (7R and 2R) further from Africa (Chen et al. 1999). These findings cannot be attributed to stochastic neutral selective processes, but rather are a function of selection (Matthews and Butler 2011). The advantages leading to the rapid selection for these genes have been hypothesised to be either sexual-selective, due to a better ability to adapt to environmental changes, or due to an increased propensity for dispersal (Wang et al. 2004).

6.2 Methods

Overview

Here we present an agent based model (ABM) of human dispersal, written in C#. Agents (representing individual humans) within this model are provided with an extraversion score, which is genetically determined and transmitted from parents to offspring. This score affects the reproductive ability of agents and their mortality risk, with these characteristics being positively associated with extraversion. Within a simulated Pliocene landscape the relationship between ecology and extraversion is explored. In particular, the impact of extraversion on agent dispersal and survival is assessed. This section will provide a brief overview of the model. For a more complete description, following the Overview, Design concepts and Details (ODD) protocol, see supplementary section 1.

Purpose

The purpose of this model is to explore how variations in human personality, specifically introversion/extraversion, may have affected human adaptability to new environments in the Palaeolithic. Questions this model seeks to address are:

- Are different personality types adapted to specific ecological settings?
- How does the spatial distribution of personality types differ as populations spread?
- Are there advantages to a population having diversity in extraversion?

Entities and Scales

This section provides a description of the entities within the model (agents and the environment), with a description of the time and spatial scale at which the model takes place.

Agents: Each agent in the model represents an individual within the landscape. These agents hold information about themselves: location, age, health, resources, and extraversion score. The extraversion score of agents is on a scale from 1-100. Higher scores indicate extraversion (more likely to reproduce but also more likely to die spontaneously), while lower scores indicate introversion (see supplement 1.2.2 for more information on how this affects agents' functioning). Agents move through the landscape attempting to collect resources. They move through continuous space in a random direction along both the x and y axes of the model, either 12km, 6km, or do not move at all. Agents may move along both axes simultaneously to move diagonally. The speed of movement is not affected by extraversion, and therefore differences in dispersal are directly related to selection. If agents do not collect enough they die due to lack of resources. They may also die spontaneously according to hunter gatherer mortality rates, with this being moderated by their extraversion score. The remaining agents then attempt to reproduce, with their probability of reproduction being affected by their extraversion and age.

Agents are hermaphrodite. However, they produce offspring in pairs, with the offspring inheriting the average extraversion score of their parents, plus a random factor that represents non-inherited and environmental effects. This is intended to reflect the polygenic nature of extraversion. However, this also produces a blending mechanism, which makes the maintenance of diversity more unlikely than if a more particulate test was used. Therefore, it is a sterner test for the maintenance of population diversity. However, this method is also more likely to reduce within group diversity than between group diversity. Due to the population-level scale of this model, this method was deemed sufficient, however future studies should also explore the effect of a more particulate method upon within group diversity. Finally, reproducing agents move to be with one another with equal probability, following evidence of mate exchanges and extensive mating networks in hunter gatherer groups (Lovis, Whallon and Donahue 2006; Wobst 1976; Zilhão and Pettitt 2006).

Parameters set upon initialization determined the general probability of accidental death (*Safety*), and the degree to which reproductive ability (*BirthDiff)* and probability of death (*DeathDiff)* differ according to agents' extraversion scores (see supplement 1.2.1 for further information on ethnographic data used to inform the demographic characteristics of the model). These parameters are varied to test different conditions.

Environment: As described further below, the environment is split into a grid of cells that contain resources agents may use. The size of these grid squares and the resources they hold differs between scenarios of the model.

Three scenarios were modelled ranging in environmental complexity from more simplistic to more complex:

- *Homog* - the net primary product (NPP) of the environment is homogenous without continents or inter annual variability in NPP.
- *PRISM 4* - uses the PRISM4 reconstruction to construct a realistic NPP distribution.
- *P4 Var* - uses the PRISM4 reconstruction but adds inter annual variability in landscape cell NPP.

In the *PRISM 4* and *P4 Var* tests the environment agents inhabit is a global approximate reconstruction of the distribution of resources available to humans in the Mid-Upper Pliocene environment (~ 3Ma). Following Romanowska (2015), the Mid-Upper Pliocene environmental reconstruction (PRISM 4) was used (Dowsett et al. 2016; Salzmann et al. 2008), rather than a Pleistocene reconstruction, as it is a more comprehensive simulation of a warm period than any available for the Pleistocene, and at a continental scale may represent similar conditions to what was experienced during the Pleistocene interglacials (see chapter 5). The environment is composed of cells which represent 1° latitude/longitude (see supplement 1.2.1), and hold an estimate of the amount of resources which would have been available to hunter gatherers in that location (see chapter 5). This was derived from the PRISM 4 reconstruction, with the available amount of resources calculated using contemporary environmental and ethnographic data (chapter 5; figure 1). The *P4 Var* test also includes estimates of annual variation in resource availability, taken from Mohamed et al. (2004). The *PRISM 4* and *P4 Var* tests were assessed together, with annual variation in resources being termed *Fluctuation Level* and treated as a further parameter during the analysis. The *Homog* test uses the same techniques as the other tests to estimate the amount of resources available, but is a more simplistic homogenous environment (see supplement 1.2.1 for details).

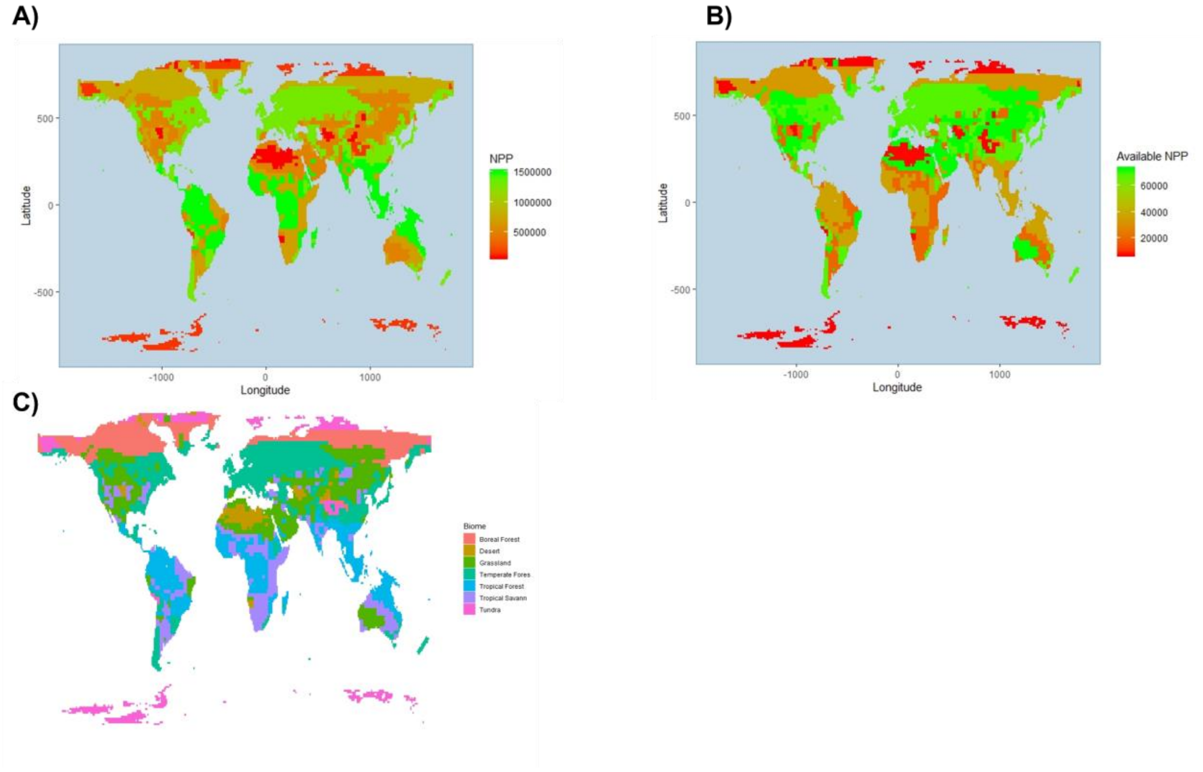

Figure 1. A) Global distribution of NPP (g/km^2/year) during the Pliocene; B) Global distribution of available NPP (g/km^2/year; calculated in chapter 5); C) Biome distribution; Derived from the PRISM 4 reconstruction (Dowsett et al. 2016; Salzmann et al. 2008).

This method provides a model with an approximation of biome and resource distribution, though obviously the environment and environmental changes occuring at the time were much more complex than this model allows. For example, biome distribution may change over time, opening and closing potential dispersal routes (Vahdati et al. 2019), annual fluctuations in resources are spatially related rather than randomly determined, and changes in sea level may also have had significant effects on dispersal during the Upper Pleistocene. While justified above, it is also important to reiterate that the reconstruction used models from an earlier time period than the target time.

Scale: Each timestep of the model represents a single year. The model runs for 15,000 years. However, it also ends if it reaches the maximum population size of 1.8 million individuals. The map in the model is at a coarse global scale, with cells representing a latitude/longitude coordinate. For the functions of the model this is converted into a km scale allowing for the curvature of the Earth. 1° of latitude is approximately converted into 110.57Km. However, the size of 1° of longitude varies with latitude. 1° of longitude at the equator is 111.32Km. By multiplying this by the cosine of the latitude this may be adjusted to account for the curvature of the earth (Coyne, Casey and Milliken 2003; Pojee et al. 2017). This is accounted for when calculating environmental yields (see supplement 1.2.1).

Initialisation and Process Scheduling

Initialisation: At the start of the model 10,000 agents are initialised into the map. Within the *Homog* test agents originate in the centre of a fully homogenous landscape with no continents. In the *Prism4 and P4 Var* tests the agents all begin within a cell in Eastern Africa, using the coordinates of Lake Turkana (3.6268° N, 36.0023° E) as a basis for their starting point. Agents begin within two landscape cells (latitude/longitude cells) of this location. Agents’ initial values are as shown in table 1.

Table 1. The starting values of agents and relevant environmental characteristics when the model is initialised.

Characteristic	**Value**
Age	Random between 1 - 50
Location	3.6268° N, 36.0023° E
Extraversion	50

Resources	185000g
Health	100
Birth Probability Difference	High/Medium/Low
Death Difference	High/Medium/Low
Safety	High/Low

The approximate location of Lake Turkana was chosen due to the presence of hominin fossils in this region. In particular, both the finding of *Homo sapiens* remains (Stringer 2016; White et al. 2003) and the finding of earlier hominins in this region supports the location being a focal region for the origin of modern humans (Spoor et al. 2007). Nevertheless, this is not a suggestion that modern humans exclusively evolved in this region. There is considerable evidence that the speciation of *Homo sapiens* took place in a number of interlinked groups across Africa (Scerri et al. 2018). However, by starting with a small confined population within an area where hominins were clearly present, the emergent spatial distribution of agents and extraversion across Africa itself may also be explored.

The effect agents' extraversion scores have upon their probability of reproduction and mortality are determined upon initialisation by the parameters Birth Probability Difference (*BirthDiff*) and Death Difference (*DeathDiff*). These parameters increase the chance of reproduction and mortality for each point of extraversion above 50 and decrease it for each point below 50, relative to the default. The slope of this difference is set upon initialisation (see supplementary figures 2 and 3; this causes differences in slope as follows. *BirthDiff*: Low = 0.03, Med = 0.06, High = 0.12. *DeathDiff*: Low = 0.025, Med = 0.05, High = 0.075; see supplementary section 1.2.2 for more information).

Process Scheduling: The processing of the model takes place as shown in figure 2. A more complete description of the model is presented in supplementary section 1, providing the remaining sections of the ODD protocol (Grimm et al. 2006, 2010, 2020; Polhill 2010).

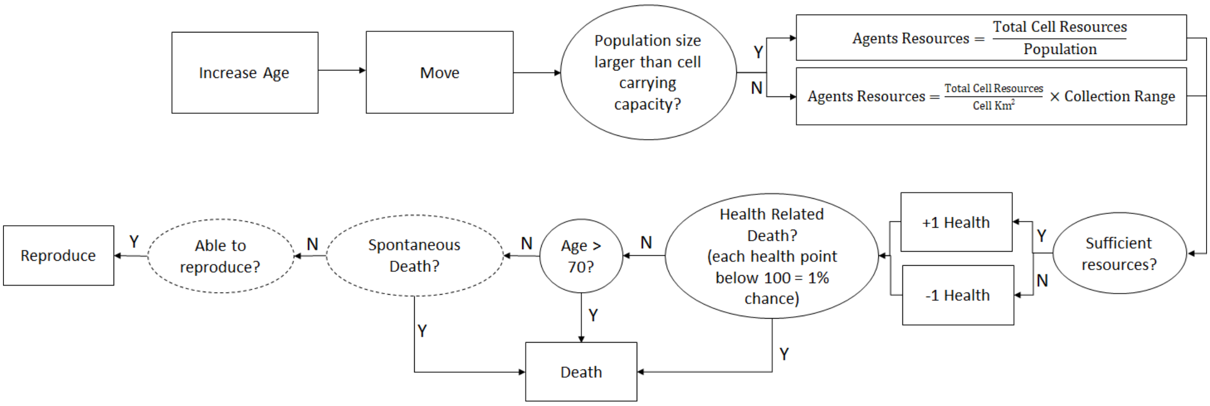

Figure 2. Process schedule of one year of the model.

6.3 Summary of Results

The results of this model allow us to explore the effects different conditions have upon personality distribution (see supplement 2 for the complete results).

As expected, different parameterisations of *BirthDiff* and *DeathDiff* led to different directions of selection for extraversion (figure 3). Type 3 ANOVA was used to assess the relative effects of the parameters upon the mean extraversion of agents in the model. Significant effects were found ($p < 0.05$) for *BirthDiff*, *DeathDiff* and their interaction. When measuring the effect sizes (η^2), *BirthDiff* was consistently found, in all tests, to have the largest effect on mean extraversion (table 2). *DeathDiff* also had a large effect size, while their interaction, although significant, had a small effect. Likewise, in the P4 Var test, all other effects were either not significant or small. Further, when parameterising the model, in order to achieve a mean extraversion level with very little directional selection, the proportional increase in mortality chance per year (relative to the default) applied by each point of extraversion had to be higher than the proportional change in reproductive chance. For example, when *BirthDiff* is low the reproduction rate is proportionally increased by 0.5% for each point of extraversion. In contrast, when *DeathDiff* is low there is a proportional change in mortality of 0.83% for each point of extraversion. However, the mean extraversion of agents remains stable. As will be discussed further below, this suggests that within this model reproductive ability was a more important determinant of evolutionary success.

To get an indication of how the effect of the parameters may change at different times in the model, the effect sizes were plotted over time. Due to limitations of the data, type 1 ANOVA was used for this test. To standardise this method, parameters were input into the ANOVA according to the size of the effect found using the time slices (largest effects first). *BirthDiff* was found to have had the largest effect size early in the model, while *DeathDiff* had a larger effect later in the model (see figure 4 and supplementary figure 16). However, interpretation of this result must be done with caution as parameter loss (as runs reach the maximum population size or go extinct) and the order parameters are input into the type 1 ANOVA may affect the output (for example, see supplementary figure 16).

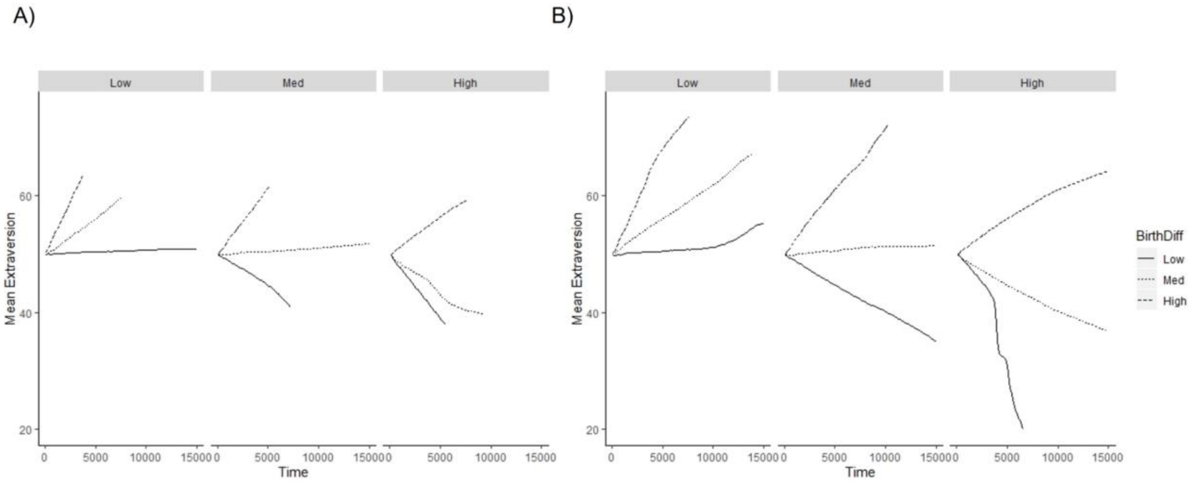

Figure 3. Mean Extraversion of runs of the model faceted by DeathDiff. A) Fluctuation Level = 0 (PRISM 4), B) Fluctuation Level = 1 (P4 Var).

Table 2. The effect sizes (η^2) of parameters on mean extraversion, tested over all observations for each run and for a specific time slice at the last point before parameter variation is lost (NS = not significant).

Response Variable	**Homog**		**P4 Var**	
	All Observations	*Time Slice (2000)*	*All Observations*	*Time Slice (3000)*
BirthDiff	0.500	0.723	0.414	0.711
DeathDiff	0.192	0.270	0.174	0.284
BirthDiff:DeathDiff	0.05	<0.001	0.050	<0.001
Fluctuation Level	-	-	<0.01	NS
Fluctuation Level:BirthDiff	-	-	0.039	NS
Fluctuation Level: DeathDiff	-	-	0.014	NS
Fluctuation Level: BirthDiff: DeathDiff	-	-	0.003	NS

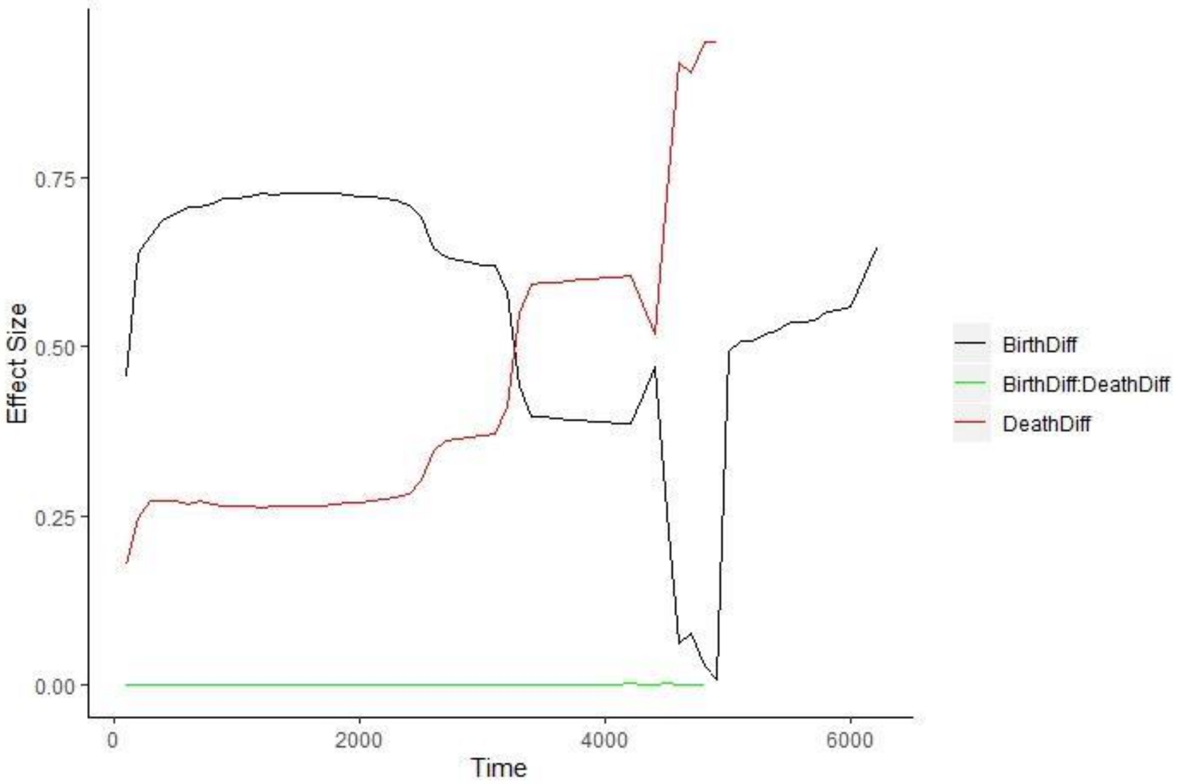

Figure 4. The effect size (η^2) of parameters on the mean extraversion of agents over time, showing that BirthDiff has the largest effect on mean extraversion at the start of the model. Following 4000 years, there is a loss of parameter variation which affected the results (Homog test).

The spatial distribution of extraversion within model runs was not uniform (see figures 5, 6 and 7 for example maps from each test). Within the tests, there was a correlation between the distance of a landscape cell from the point of origin and the mean extraversion of the agents in that cell. This correlation's direction and strength was associated with the direction and strength of selection for extraversion in the model (figure 8). If selection favoured extraversion, due to extraverts' reproductive advantage outweighing their increased risk of mortality, then the correlation would be positive, and vice versa. A negative correlation was also found between the mean extraversion of agents in a landscape cell and the size of the population within that cell (figure 9). Using the same example scenario as above, this negatively correlated with extraversion, showing that the most extraverted agents were in more sparsely populated areas. Using type 3 ANOVA and extracting the effect sizes for the time slices (the last point before parameter variation was lost), it was found that *BirthDiff* and *DeathDiff* had a significant effect on the strength of these correlation (see supplementary tables 2 and 3). In particular, a higher *BirthDiff* led to a more positive correlation between extraversion and distance from the point of origin, while a higher *DeathDiff* consistently led to a more negative correlation in the PRISM 4 test. However, this was not the case in the P4

Var test (when the model incorporated fluctuation in resources; figure 8). For example, when *BirthDiff* was high, increasing *DeathDiff* led to a more positive correlation than expected. This was due to the combination of conflicting selective pressures and resource fluctuation decreasing population sizes in the model. Therefore, when agents were dispersing, the lower population sizes meant there were even fewer potential mates at the front of the wave of expansion, which led to increased selection for the most extraverted individuals at the wave front, due to their increased probability of seeking a mate. Therefore, these results suggest that selection for extraversion is density dependent. In particular, the advantaged population (depending on the direction of selection) was more likely to reproduce when they were in sparsely populated regions, extraverts due to their reproductive advantage, and introverts due to their reduced mortality (meaning they had more time to find a mate), leading to increased selection for these phenotypes in sparsely populated areas. Additionally, extraverts having a higher reproduction probability may also increase their probability of dispersal towards neighbouring cells, due to mates moving to be together (see section 6.2). This may increase the probability of extraverts being in more sparsely populated areas and at the wave front (in scenarios where the direction of selection favours extraversion). Therefore, extraverts being more active in mate exchange networks may be an alternative explanation for the distribution of extraversion related genes seen in reality.

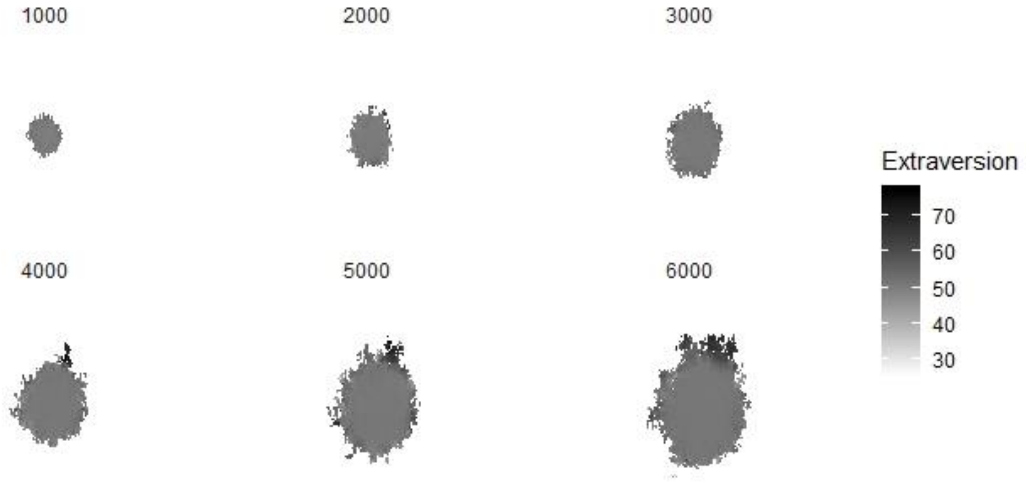

Figure 5. A time series of the mean extraversion of agents in landscape cells in an example run; BirthDiff = Mid, DeathDiff = Mid (in a homogenous landscape - Homog test)

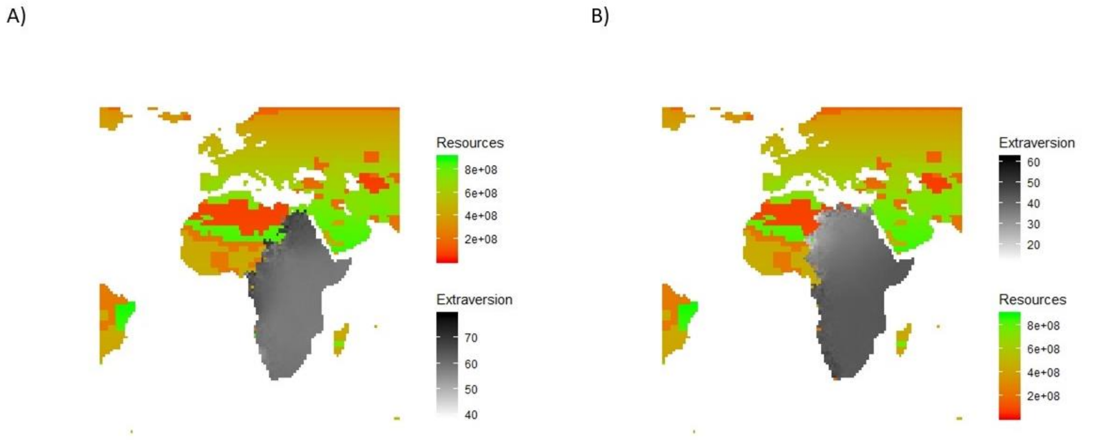

Figure 6. The mean extraversion of agents within landscape cells in example runs (A) BirthDiff = Mid, DeathDiff = Low; B) BirthDiff = Low, DeathDiff = Mid) when the model reached its end (7000 years in these cases) (PRISM 4 test).

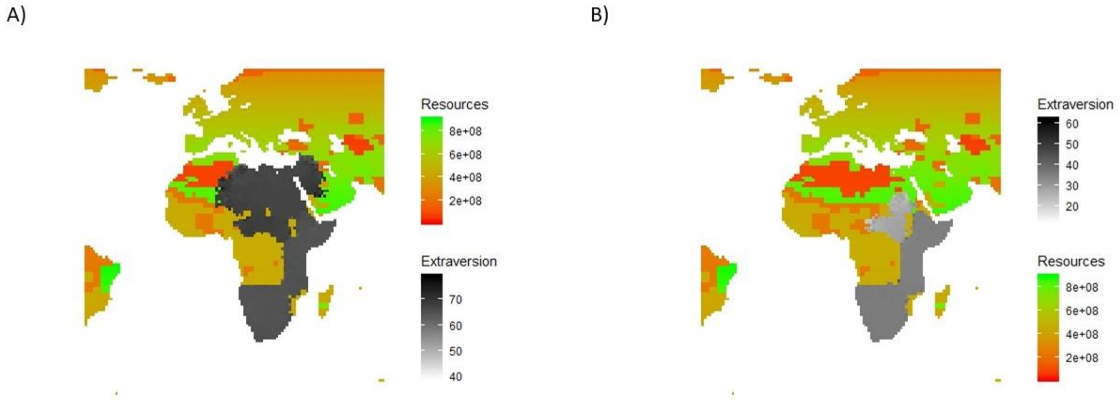

Figure 7. The mean extraversion of agents within landscape cells in example runs (A) BirthDiff = Mid, DeathDiff = Low; B) BirthDiff = Low, DeathDiff = Mid) when the model reached its end (13,000 and 15,000 years in these cases respectively) (P4 Var test).

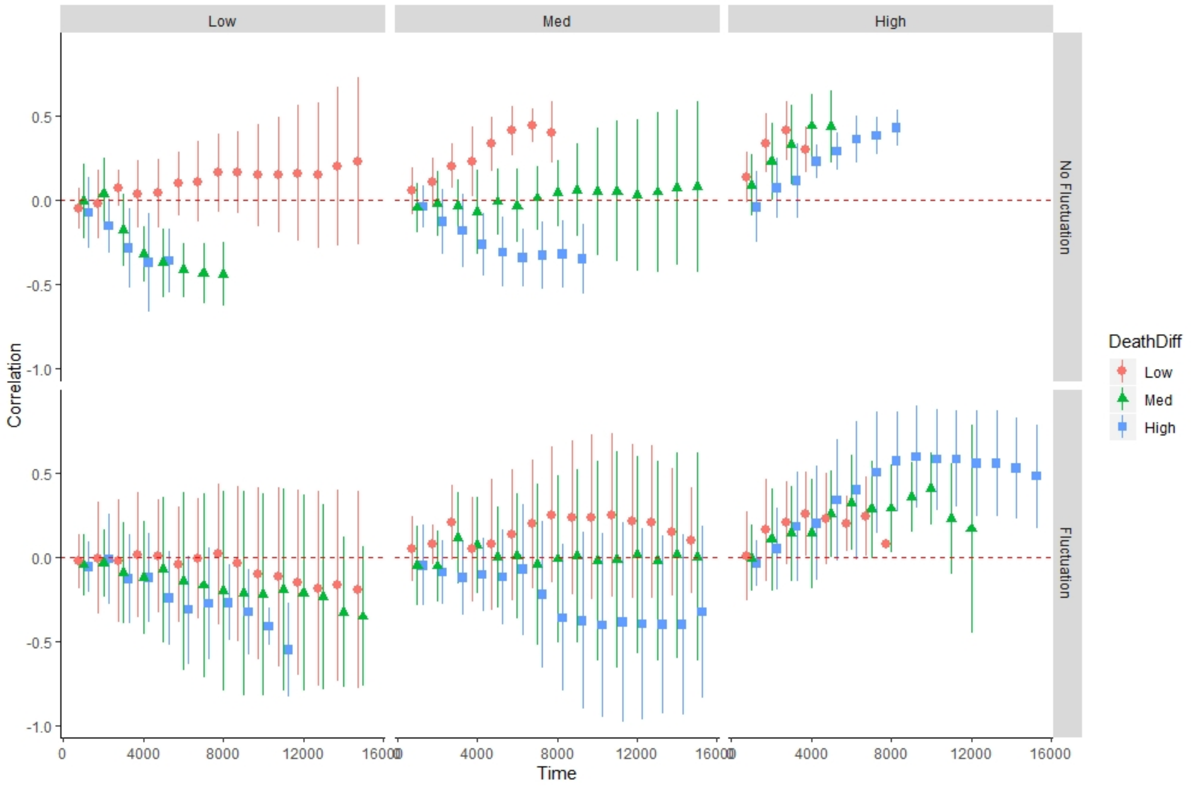

Figure 8. The mean correlation coefficient (Pearson's r) between distance from the point of origin and extraversion through time (error bars = standard deviation). Faceted by BirthDiff (horizontally) and Fluctuation Level (vertically).

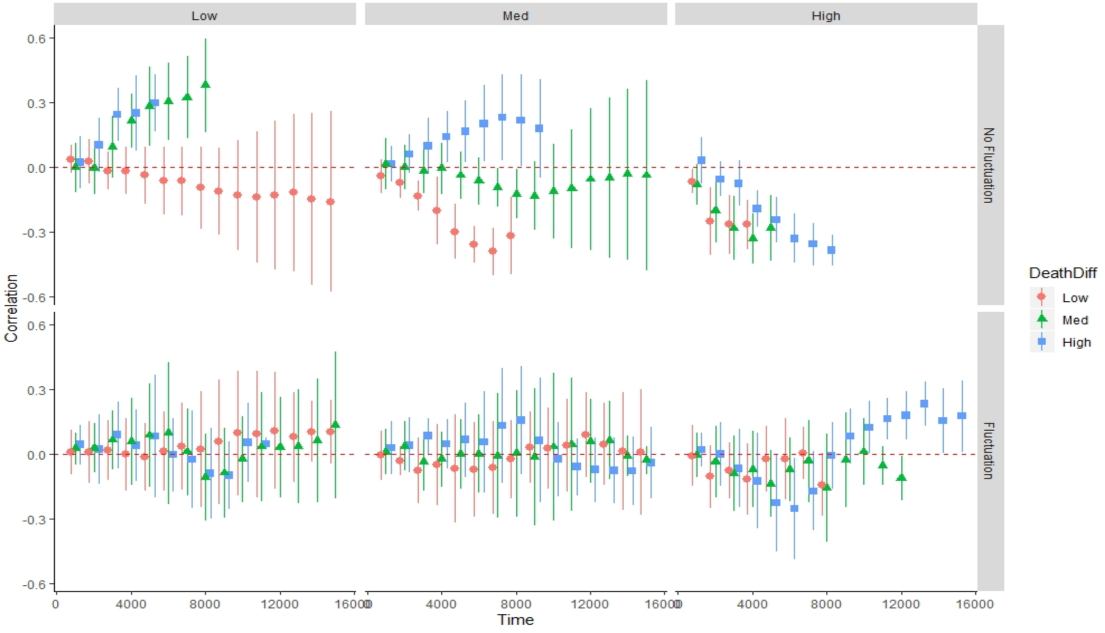

Figure 9. The correlation coefficient between cell population size and extraversion, through time. (error bars = standard deviation). Faceted by BirthDiff and Fluctuation Level (as figure 5).

When assessing the effect sizes of the parameters on the correlation between the mean extraversion of agents in a landscape cell and distance that cell is from the point of origin, over time, using the same method as above, *BirthDiff* was found to have the highest effect throughout the model (see figure 10). This suggests that the ability to disperse is largely associated with extraverts' reproductive advantages. Although, as was also shown above, *DeathDiff* and the pairwise interaction between these parameters also had a significant effect. The effect of this interaction also increased during the middle of the model run.

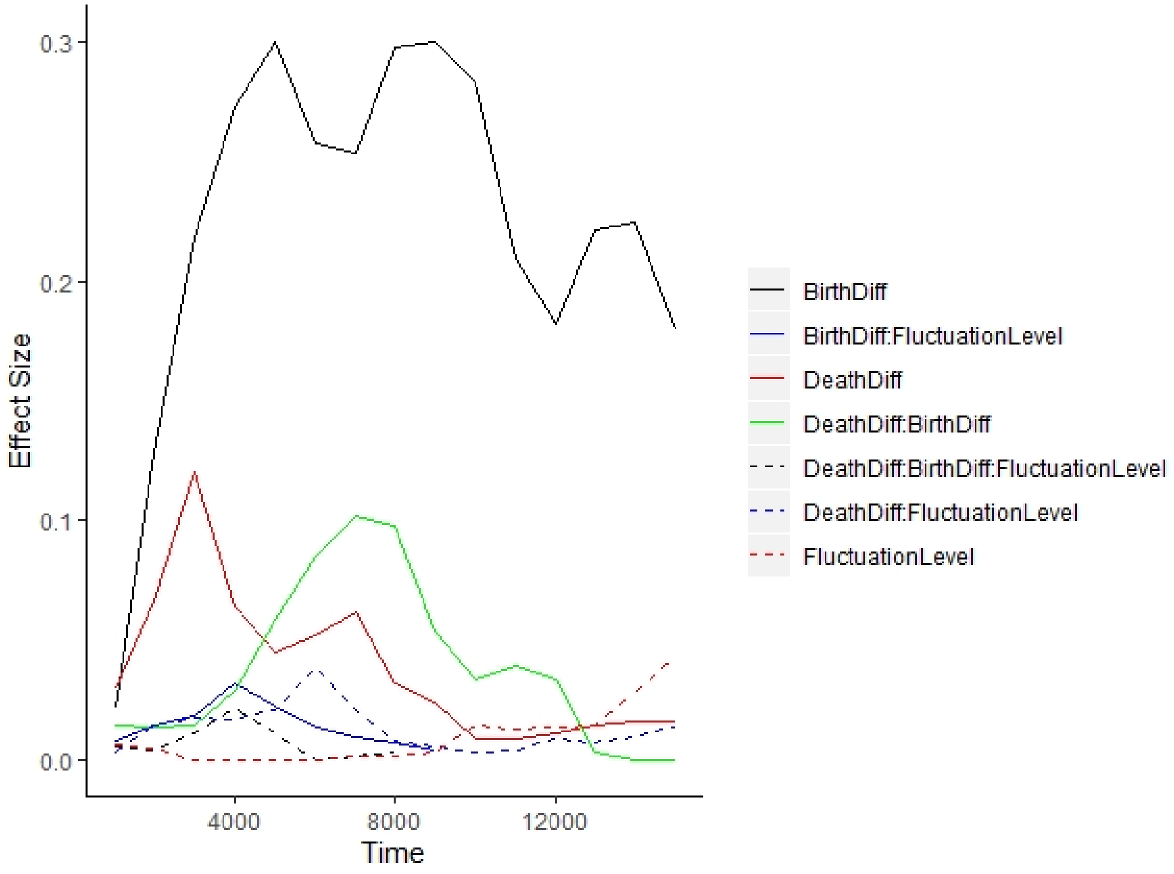

Figure 10. The effect size of parameters on the correlation coefficient between extraversion and distance from the point of origin (P4 Var test - PRISM 4 test with interannual variability in NPP).

Two further sensitivity tests were conducted to assess whether selection for extraversion was density dependent (supplementary section 2.3). Firstly, the effect of reducing the *Safety* of the environment (increasing the general mortality rate for all agents in the model) was tested. This led to an increase in the severity of selection. For example, in a scenario which led to selection for extraversion (*BirthDiff* = Mid, *DeathDiff* = Low), mean extraversion levels were even higher than usual in the scenario with lower *Safety* (supplementary figure 27).

Secondly, a direct test of the effect of cell population size on selection was tested. Two scenarios, one with a larger starting population size (n = 10,000) and one with a smaller starting population size (n = 100), were used. All other parameters were identical, using a scenario which led to selection for extraversion, and movement was turned off to remove the effects of dispersal on selection. This test found that runs which started with a smaller population size had greater selection for extraversion and reached higher mean extraversion scores. Suggesting that, while the direction of selection was determined by the input parameters, the strength of that selection was density dependent. This supports the results above which suggest that the distribution of extraversion may be caused by a density dependent selection for the phenotype more likely to reproduce within a sparsely populated area, independent of the movement function associated with reproduction.

6.4 Discussion

The effect of cognitive diversity upon specific moments in our evolutionary history is rarely explored. However, the retention of phenotypes with different adaptive strengths and their spatial sorting may significantly increase a species’ adaptability and success, particularly during periods of dispersal. This model has sought to investigate whether variation along the introversion/extraversion continuum may have had a direct impact on the ability of modern humans to disperse out of Africa during the Palaeolithic.

This model suggests that, when the reproductive advantages of extraversion outweigh the mortality costs, extraverts are more likely to be at the expanding wave front due to their better ability to reproduce within low density populations.

Within particular scenarios of the model, the mortality costs of being an extravert outweighed the reproductive advantages. This led to selection against extraversion. Within these scenarios, the distribution of extraversion reversed due to introverts being more likely to survive long enough in sparsely populated areas to reproduce. However, as discussed above, proportionally the difference in mortality probability per point of extraversion had to be larger than the difference in reproduction probability for extraversion to remain relatively stable in the model. In other words, mortality differences caused by extraversion had to be larger to have a similar effect on selection. While it is difficult to compare these parameters in this way, this result seems counterintuitive. Failing to reproduce may be considered trivial compared to failing to survive, as agents may attempt to reproduce again the following year. Therefore, it would be expected that a smaller change in mortality probability would have a larger effect. Nevertheless, in this dispersal model, missing chances to reproduce had a larger effect on selection. This may be due to the high impact of dispersal on selection for individuals with a reproductive advantage.

Other factors that are not represented in this model would also affect the direction of selection toward increased reproduction (r specialisation) or reduced mortality (K specialisation). In the real world the evolutionary route towards an increased reproductive rate is easier than towards a decreased mortality. While a decreased mortality may be accomplished by changing behaviour, this change may only reduce mortality so far, as many extrinsic causes compound to determine an individual's probability of mortality, many of which can not be avoided. In comparison, reproductive rates are much more responsive. This is evidenced by the fact that animals under high mortality generally increase their rate of reproduction (Gasser et al. 2000; Stearns et al. 2000). This is also observed in humans when they are subjected to high infant mortality rates (Quinlan 2010), or juvenile stress (Belsky et al. 2010; Mell et al. 2018; Webster et al. 2014). This increase in reproductive rate is both biologically determined, through faster maturation rates, as well as behaviourally determined. Therefore, while the results of scenarios leading to selection for introversion show that, under conditions where a reproductive advantage is unable to develop and where mortality protection may develop at both an unrealistic rate and to an excessive level, selection may lead to agents with increased longevity dispersing, this is less likely to occur in reality. Accordingly, this discussion will primarily focus upon the scenarios which led to selection for extraversion.

Spatiotemporal Selection for Extraversion

Whilst focus often has been on the life history and evolutionary implications of traits generally, changes in the prevalence and distribution of these traits may have been more significant. Within the ABM developed for this chapter a negative correlation between extraversion and population density was found when the reproductive advantages associated with extraversion outweighed the disadvantages of an increased mortality. This suggests that the strength of selection for extraversion differed in relation to emergent characteristics of the model, in particular population density. Therefore selection for extraversion varies spatiotemporally.

Spatiotemporal selection for extraversion has previously been suggested by Nettle (2005, 2006). He argued that the optimal balance between the advantages of extraversion and the disadvantages would change in response to the environment, the density of the population, and the frequency of extraverts within the population. Such spatiotemporal mechanisms have also been suggested to maintain personality variation more broadly within humans (Penke, Denissen and Miller 2007). As will be discussed further below, spatiotemporal and density dependent selection for risk taking, aggression and sociality has been observed within birds, lizards and cane toads (Cote and Clobert 2007; Duckworth 2008; Gruber et al. 2017; Haage et al. 2017; Nicolaus et al. 2016; Rodriguez, Hausberger and Clergeau 2010), and more broadly is regarded as a general mechanism affecting a range of species either phenotypically or genetically (Erm and Phillips 2020; Phillips, Brown and Shine 2010; Wolf et al. 2013). This model supports these ecological studies, suggesting that selection for extraversion is density dependent, with the more risk taking phenotypes (extraverts) being selected for when local population density is lower or when forming a new population. Counterintuitively, this also suggests that selection would favour more risk taking extraverts, than cautious introverts in dangerous environments. Within the model this occurred due to the reproductive advantages of extraversion outweighing the increased probability of accidental death. This contrasts with Hintze et al.'s (2015) findings, which may suggest that in reality the cost of losing an opportunity to reproduce when dispersing outweighed the increased chances of mortality. Further, it may suggest that when populations have the opportunity to expand (which was not included in Hintze et al.'s (ibid) model), or when agents have the opportunity to take risks multiple times, the outcomes may favour risk taking in less dense populations.

Distribution of Extraversion

This model predicts two features of the distribution of extraversion. Firstly, the most extraverted individuals within the population will be at the front of the wave of expansion. Secondly, as the population size increases in newly inhabited territories the strength of selection for extraversion will decrease. This is the result of the density dependent selection described above. The mechanisms behind these two features are discussed presently, with reference to the dopamine receptor gene distributions. Comparable examples from animal behaviour studies and ecological research will also be discussed to highlight that these personality distributions should be an expected result of natural selection and are not specific to humans. Additionally, this model allowed agents to move to be with their partners during reproduction, to represent a mate exchange network. This provides agents with an increased reproductive rate with an opportunity to move more often. This represents an alternative process by which extraverts may have been more likely to populate more sparse regions and the front of the wave of dispersal upon leaving Africa. However, further sensitivity analysis seeking to explore whether extraversion was under density dependent selection (i.e., extraversion is selected for to a greater extent when the population size is lower) supports the idea that this distribution may also occur when this movement function is removed.

The results of this model predicted (on the basis of the parameters used in the model) the geographic distribution of dopamine D4 receptor genes associated with extraversion, when extraverts' reproductive advantage outweighed the increased mortality probability (Chen et al. 1999; Matthews and Butler 2011). Agents towards the front of the wave of expansion in the model were more extraverted. In reality this distribution was hypothesised to be the result of individuals with the 7R variant being more adaptable to new environments, more likely to disperse, or due to the result of sexual selection (Matthews and Butler 2011; Wang et al. 2004).

The parameters within this model which had the largest effect on the distribution of extraversion were *BirthDiff* and *DeathDiff*, with interactions between these parameters also having a moderate effect. *BirthDiff* is a parameter which determines the reproductive advantage given to more extraverted agents. This is based upon psychological research showing extraverts have more children (Alvergne, Jokela and Lummaa 2010). In contrast, *DeathDiff* determines the increased likelihood of mortality extraverted agents are subjected to relative to more introverted agents, based upon evidence that extraverts are more prone to injury and mortality (Hajek, Bock and König 2017; Horvath and Zuckerman 1993; Jonah 1997; Lajunen 2001; Nettle 2005).

The high effect of *BirthDiff* suggests that reproductive selection may have been a significant factor contributing to the current distribution of extraversion. As discussed above, extraversion was subject to density dependent selection. As a consequence of this density dependent selection, extraverts were significantly more likely to successfully disperse into new, uninhabited environments due to their increased fecundity, suggesting that the observed distribution of DRD4 genes is not necessarily due to extraverts' increased exploration or adaptability. While this model suggests that this reproductive advantage may have had a large effect on extraverts’ success when dispersing, it is unlikely to be the only aspect of extraverted behaviour which has led to this distribution. For example, this model in no way negates the theory that their exploratory nature may have increased their propensity for dispersing and success when adapting to new environments. This model also suggests that extraverts’ increased reproduction rate may mean they are more active within mate exchange networks, therefore this may make them more likely to move to sparsely populated regions or regions at the front of the wave of expansion, merely because of this extra movement. Further, extraverts’ increased leadership abilities and social success may have increased their probability of being high status individuals in newly formed groups. Therefore, while the current model suggests that extraverts’ reproductive advantages would have increased their success in newly dispersed groups, other aspects of their behaviour would also have contributed to their ability to disperse.

Comparing this finding to animal behaviour research, it is expected that particular personality types would be better able to disperse than others. Animal behaviour researchers and conservationists are increasingly recognising the importance of personality for welfare, breeding and reintroduction programmes (Powell and Gartner 2011), as well as the impact of personality on animal dispersal (Nilsson et al. 2014). This research has shown that altering partner selections and enclosure environments to allow for animals’ unique personality traits may aid breeding efforts (Martin-Wintle et al. 2017; Powell and Svoke 2008; Tetley and O’Hara 2012). Considering the personality of animals being used in reintroduction programs, studies of multiple different species have shown that particular phenotypes are more likely to disperse and/or are more successful dispersers than others. Lizards (*Lacerta vivipara*) were found to differ in their social tolerance, which influenced their dispersal patterns. Some lizards were repulsed by densely populated areas, while others were attracted by them. Based upon these preferences lizards dispersed to different areas, with less socially tolerant lizards being more likely to colonise sparsely populated areas (Cote and Clobert 2007). Foxes (*Vulpes velox)* which were classified as ‘bolder’ were less likely to survive reintroduction (Bremner-Harrison, Prodohl and Elwood 2004). More aggressive western bluebirds (*Sialia mexicana*) were better able to disperse and had a higher fitness in newer populations than less aggressive bluebirds (Duckworth 2008). Once new areas were colonised there was significant negative selection for aggression. As population density increases, and the population ages, kin cooperation becomes an important factor which decreases the selective advantages of aggression. Similarly, density dependent selection for exploratory behaviour was observed in great tits (*Parus major*). Faster explorers were selected for in less dense populations, but slower explorers were selected for in more dense populations (Nicolaus et al. 2016). Genetically determined differences in longevity and reproductive rate are associated with dispersal rate in Colias butterflies (Saastamoinen, Ikonen and Hanski 2009). Cane toads were seen to be more social at their expansion front (Gruber et al. 2017), although invasive cane toad tadpoles have also been found to have developed a tendency to cannibalise cane toad eggs to reduce intraspecific competition (DeVore et al. 2021). Starlings inhabiting novel environments were more responsive to social cues (Rodriguez, Hausberger and Clergeau 2010). Further, in contemporary humans differences in migration based upon temperament are also seen. Sociability was associated with long distance migration in Finland (Jokela et al. 2008), while extraversion was associated with intra-state migration in the US (Jokela 2009). Further, in the UK extraversion was associated with movement in the last 5 years (Shuttleworth et al. 2021). Interestingly however, sociability was associated with increased migration to urban rather than rural areas in Finland, when compared to individuals with high emotionality or activity (Jokela et al. 2008). This suggests that extraverts may be more likely to disperse towards more densely populated areas. This is incompatible with the model outcome that extraverts were more likely to be at the front of the wave of expansion, because they would be more likely to disperse towards established, densely populated areas. If this is the case, extraverts may not have been more likely to be at the front of the wave of dispersal, however other aspects of their behaviour (such as a reproductive advantage) may have increased their success relative to others when they were in these sparsely populated areas. However, Crown et al. (2020) found the opposite result, suggesting that extraversion is associated with migration towards less densely populated areas. Therefore, more research is needed exploring the effects of extraversion on migration and dispersal.

This discussion shows that dispersing individuals face unique challenges. Hence, developing characteristics to improve fitness in these circumstances is essential (Wolf and Weissing 2012). These characteristics appear to be species specific, relating to the individuals' own ecological challenges. Importantly, the genetics associated with dispersal are highly polygenic and context dependent (Saastamoinen et al. 2018).

There is little disagreement that social pressures have significantly affected human evolution. Our species has also managed to disperse across the world - an achievement accomplished by few animals. Doubtless, this is influenced by cultural changes, however it would be understandable if the phenotype better able to disperse is socially distinct. While this model provides a simplified functioning of extraversion, other characteristics such as leadership abilities would likely lead to a relative increase in fitness in a newly established group rather than an older one. Consequently, it is likely that more extraverted individuals, due to their generally higher status within groups, would be likely to survive in new environments due to their greater access to resources (see chapter 3). However, this model suggests that, even without this possible increase to fitness, the increased fecundity of extraverts seen in the psychological literature (section 6.1) could solely account for the distribution of extraverted genes seen in genetic research.

The second feature predicted by the model was a reduction in selection for the extraverted phenotype once the expanding front had passed and population sizes increased. This is supported by the negative correlation between extraversion and cell population size, and further sensitivity analysis that showed selection was more severe in a smaller population (supplementary section 2.3). As populations became larger in newly occupied territories the pressures to become more extraverted were reduced, due to the increase in potential reproductive partners making it more likely that more introverted agents can reproduce.

This is similar to observations made in evolutionary ecology, which have not previously been applied to human evolution. Travis and Dytham (2002), identified using ABM that species are subject to spatial sorting when dispersing, with the agents with a propensity towards dispersal being situated at the wave front. The current study also found spatial sorting of phenotypes. However, this study explored the effect of a tradeoff between mortality and reproductive rate. The model showed that agents with an increased fecundity were more likely to be at the dispersal front. There are two reasons for this. Firstly, like Travis and Dytham (2002), these agents had a higher movement rate due to a function representing mate exchange. However, further sensitivity analysis suggests that a similar distribution may be found if this function was removed due to agents with a greater reproductive rate being more successful in smaller populations. Therefore, our model suggests that a similar spatial sorting may be produced as a result of other life history traits. It has been argued by Phillips et al. (2010) that members of a species at the expanding front are subject to vastly different selective mechanisms to those in the core of the population. Consequently, they may evolve to have a faster rate of reproduction due to lower population densities. This may reduce the negative impact of Allee effects (positive correlation between population density and fitness) observed in other dispersal models (Shaw and Kokko 2015; Travis and Dytham 2002), by offsetting the decrease in fitness experienced in small populations (Erm and Phillips 2020). Further, they have suggested that, due to the best dispersers being at the expanding front, this may lead to a runaway effect increasing the dispersal rate of subsequent generations, if traits (both life history traits and traits directly related to probability of movement) increasing dispersal are heritable (Ochocki and Miller 2017; Perkins et al. 2013; Travis et al. 2009). These traits may then be maladaptive following the passing of the dispersal front, and therefore would reduce in prevalence until they are no longer present (Phillips, Brown and

Shine 2010; Travis and Dytham 2002). This is supported by empirical evidence. Cote et al. (2010) reviewed evidence for ‘personality dependent dispersal’ in different species and found that dispersers were generally more sociable, bold or aggressive. However, following initial dispersal they are joined by individuals with alternative phenotypes as the ecological conditions of the newly settled area change. For example, Duckworth’s (2008) study of bluebirds shows this form of change (see above). The fact that dispersers behaviour may be maladaptive in non-dispersing populations has also led to the suggestion that these populations may be pulled towards sparsely populated regions, rather than pushed from densely populated areas, which would further increase their rate of dispersal (Erm and Phillips 2020). Therefore, in ecology there is recognition that the conditions associated with dispersal considerably affect selection pressures for genetically determined traits, and that derived differences between dispersing and core populations are important determinants of a species’ dispersal ability (Miller et al. 2020).

The discussion above may partially explain what has been observed by geneticists exploring human dispersal. When dispersing, selection favoured extraversion, which reduced the impact of Allee effects. Selection for extraversion may have been further enhanced due to serial founder effects and population bottlenecks. This is supported by genetic evidence supporting a loss of genetic diversity during dispersal (DeGiorgio, Jakobsson and Rosenberg 2009), and was observed within the P4 Var test, when agents were passing through narrow pathways in central and eastern Africa (figure 10). However, in reality, following the passing of the wave front, less extraverted phenotypes were likely selected for in more densely populated areas (or areas with broader social networks). This appears to be observable in Asia where there was a reduction in the prevalence of the DRD4 7R variant (associated with extraverted behaviour), while a derived 2R variant (associated with a less ‘extraverted’ phenotype) increased in prevalence (Matthews and Butler 2011; Wang et al. 2004). Further, the creation of a new genetic variant may increase heterogeneity which, as discussed above, may lead to less risk taking phenotypes (Faurie et al. 2017). The model presented in this paper, and the ecological evidence cited above, suggests that a reduction in sexual selective pressures as local population sizes became larger and a concomitant selection for reduced risk taking (increased longevity) could have led to this change. However, in reality other important factors may have also had an effect on this. For example, increases in cultural complexity and social network size may have provided distinct niches where different types of personality would thrive (Smaldino et al. 2019).

Evolutionary anthropologists often conceptualise the dispersal of modern humans as the movement of an homogenous population. Findings from evolutionary ecology do not seem to have been broadly applied to Out of Africa human dispersal, which may lead to significant effects on interpretation. For example, Romanowska et al. (2017) developed a model to test the hypothesis that the simpler technology observed east of the Movius line during the Lower Palaeolithic may be the product of small population densities further from Africa as a result of dispersal. Their study found that, based upon ethnographic estimates of population growth and biome carrying capacities, biome capacities would be reached quickly and not produce this effect. However, as seen in the current paper, ethnographic data is not easily applied to dispersing modern humans and must be much more cautiously applied to *Homo erectus*. Population growth rates were likely much lower, and therefore the argument that the simpler technology east of the Movius line was due to small population densities may still be valid. Further, their model used biome-determined, static dispersal rates, which may have precluded this result as a dispersal phenotype was unable to evolve. Hence, many of the features observed in evolutionary ecology, such as dispersal acceleration, spatial sorting, and runaway selection towards dispersal phenotypes, which may be disadvantageous in a static setting, were unable to emerge from Romanowska et al.’s (2017) model. Therefore, it was unlikely to produce the density distributions observed in ecology. From this, it is clear that attention needs to be given to the effects of phenotypic diversity when constructing Out of Africa dispersal models. The evolution of extreme phenotypes subject to runaway selection for dispersal may provide a partial answer for why modern humans dispersed so quickly around the world.

The wider implications of this research suggest that, rather than looking at uniform changes through our evolution, we need to also focus upon changes in our diversity. The current research supports previous literature suggesting that our psychological and behavioural differences may have had significant effects on our evolution (Armstrong 2015; Buss 1991; Ehardt 2009; Horrobin 1998; Jensen et al. 1997; Kershner 2020b, 2020a; Kuttner, Lorincz and Swan 1967; Nettle 2005, 2006; Polimeni and Reiss 2002; Spikins 2013; Spikins and Wright 2016; Spikins, Wright and Hodgson 2016; Spikins, Scott and Wright 2017, 2018; Stevens and Price 2015; Stone, Shackelford and Buss 2012; Williams and Taylor 2006), rather than be a neutral or detrimental byproduct of it as some have suggested (Bednarik 2016; Pickard, Pickard and Bonsall 2011; Tooby and Cosmides 1990). Related to this, Potts (1998, 2013) has argued that humans have developed ‘versatile adaptations’, such as bipedality, encephalization and tool use, which increase survival in variable environments. While these adaptations may increase survival in times of instability, they may then be used to colonise new regions in times of stability (Grove 2014; Grove et al. 2015). Similarly, the current paper suggests that in dangerous or fluctuating environments, selection increases for the advantaged phenotype (due to lower population densities). This phenotype may then be better suited to disperse within stable conditions. However, this is not necessarily a product of versatility, but rather may be due to a period of increased selective pressure increasing the uptake of traits particularly beneficial within low density populations, which may then be useful upon dispersal.

The model presented in this paper explored the implications of differences in extraversion upon dispersal within a hermaphrodite population. However, mate selection differs depending upon sex (Buss 2003). Despite this, within Western, educated, industrialized, rich and democratic (WEIRD) populations extraverts have been found to have a greater sexual frequency (Whyte et al. 2019), and number of children and grandchildren (Berg et al. 2014; Dijkstra and Barelds 2009; Jokela 2012; Jokela et al. 2011). While most studies found the association between extraversion and number of offspring did not differ by sex, Whyte et al. (2019) did not find this association in women. Within a more traditional, polygynous population in Senegal, extraversion was positively associated with social status, number of wives and number of children in males (with no effect on offspring quality) (Alvergne, Jokela and Lummaa 2010). However, in females neuroticism was associated with the number and quality of offspring, with intermediate levels of neuroticism being optimal. Extraversion in males was also associated with the number of offspring in the Ache (Bailey et al. 2013). Nevertheless, extraversion did not have an effect upon reproductive success in women within these populations. Therefore, it is possible that the association between reproductive success and extraversion may differ between the sexes. This difference may also be affected by culture, leading to inconsistencies when comparing the results of studies using different populations. Future research should aim to explore the effects that sexual differences in this association may have upon the dispersal of personality phenotypes.

In addition to this several further avenues of research could be pursued with this model. Firstly, the effects of mate exchange upon the distribution of extraversion genes, including different sizes of mate exchange networks and a model with no mate exchange, could be explored. This may provide more of an indication of how much of an effect this function had, not only upon this model, but upon our genetic landscape in general. Secondly, further investigation of the spatiotemporal distribution of extraversion throughout the landscape within the model may be explored. For example, measurements of extraversion either side of a particular point in the landscape may reveal further details, such as local differences in extraversion and bottleneck effects. Finally, while extraversion was represented and transmitted as a continuous, blended variable with a random element, to represent the polygenic nature of extraversion, experimenting with a more particulate transmission mechanism in the model may allow further inferences to be made about effects on local diversity. For example, while the blended model was able to explore population level diversity on a broad scale, it would be unlikely to preserve diversity at a local scale. Further, while in reality gene flow is needed to maintain adaptability, within this model a randomly determined element was added to offspring's extraversion, which may allow sub-populations to adapt towards an optimum regardless of gene flow. Therefore, exploring the effect of different ways of representing the genetics of extraversion may be particularly interesting.

Conclusion

This paper has presented an agent based model to explore how variations in human personality, specifically introversion/extraversion, may have affected our ability to disperse during the Palaeolithic. This model supports the hypothesis that the distribution of DRD4 genes could be accounted for through the reproductive advantages associated with extraverted behaviour, rather than any increased likelihood of dispersing. Therefore, rather than dispersal success being directly related to dispersal probability, it may actually be the product of a less obvious tradeoff mechanism. However, this does not dispute the possible effect of an increased propensity towards dispersal. Yet, more research is needed to explore whether extraversion increases dispersal to sparsely populated areas (Crown, Gheasi and Faggian 2020), or to more densely populated areas (Jokela et al. 2008). Regardless, I would argue that the 7R variant of the DRD4 gene influences behaviour to create a 'dispersal phenotype' in humans (phenotypes better equipped or with a greater predilection to dispersal). This phenotype is characterized by increased novelty seeking, risk taking, promiscuity and also increases social success. As the populations in newly inhabited regions became more established and densely populated, selective pressures for extraversion likely reduced. In reality this reduction in selective pressures may increase selection for 'residential phenotypes' (phenotypes specialised for living within pre-established groups). This was seen in the genetic literature, where the more risk averse 2R allele originated following migration. Potentially, this would also increase heterogeneity in the DRD4 gene, which also promotes risk aversion. Within the model it was found that this was a result of reduced reproductive selection pressures, due to an increase in potential mates. Similar results are seen in animal behaviour studies, and this process closely follows what would be expected based upon work in evolutionary ecology. More broadly, the results of this model and the subsequent discussion suggest that, similar to discussions in evolutionary ecology, more attention needs to be given to the impacts of phenotypic diversity when discussing human dispersal, as this may significantly impact the rates and causes of dispersal.

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Supplementary Information For Chapters 5 and 6

Supplement 1 – Methods

This supplementary section provides a more detailed description of the construction of the model used in chapters 5 and 6. The dispersal model used in chapter 6 only differs from that used in chapter 5 by the addition of an extraversion function. This will provide readers with the remaining sections of the Overview, Design concepts, Details (ODD) protocol that were omitted from the paper, and will highlight where differences arise between the two models (Grimm et al. 2006, 2010, 2020; Polhill 2010).

S1.1 Design Concepts

S1.1.1 Emergence

Several emergent results of the model are expected to vary in response to the initialization parameters of the model, and also in response to complex derived features of the model. In response to how the model is parameterized (see section 2.1.2), the demographic features of the population are expected to change (e.g. population size, density, mean age, mean extraversion). Within chapter 6 the emergent extraversion scores of agents are expected to affect their ability to disperse into different environments. Further, the ecological characteristics of agents' locations is expected to impact the selective pressures for or against extraversion. Likewise, these local ecological characteristics will also impact local demography.

Some results of the model will be determined by imposed rules in the model. For example, if one run of the model has a low *Safety* (high mortality rate), compared to a run with a high *Safety* it is expected that the first model will have a lower population size (where other parameters remain constant). When presenting the results of this model any findings which are expected and are directly determined by the rules of the model, such as this, will be highlighted.

S1.1.2 Stochasticity, Interaction, Adaptation and Observation

Stochasticity: Multiple aspects of agent and environment behaviour are stochastic (subject to random effects), as will be explained further below:

- Movement distance
- Movement direction

- Death
- Reproduction
- Mate selection
- Landscape cell resource fluctuation (*P4 Var* only)
- Agents’ extraversion is also influenced by a stochastic addition at birth (chapter 6)

Interaction: Agents interact with their environment and each other in three ways: 1) Agents are able to extract resources from their environment. The amount they are able to extract is determined by the environment cell’s accessible NPP. 2) Agents may share the resources available within a landscape cell. 3) Agents reproduce with one another and produce offspring which in chapter 6 have an extraversion score that is a mean of the two parents plus a random effect.

Adaptation: In the model presented in chapter 5, agents are able to adapt to their environment through movement from less suitable environments to more preferable environments, although this movement is determined stochastically. Additionally in chapter 6 populations of agents are able to adapt through selection and spatial sorting of extraversion scores. Over time this enables agents to adopt a phenotype that has a greater chance of reproducing, but is subject to an increased chance of mortality (extraversion), or vice versa (introversion), depending on their environmental pressures.

Observation: Data was collected from the model in two ways. Firstly, at the end of each century general demographic data was collected, such as population size, mean extraversion (chapter 6), mean age, mean health. Secondly, at the end of each millennium more detailed spatial data, such as the mean extraversion (chapter 6), mean health, mean age, and the population size within each landscape cell, was collected.

S1.2 Details

S1.2.1 Input Data

The environment used in the model was synthesised from the PRISM 4 reconstruction (Dowsett et al. 2016; Salzmann et al. 2008), which provided information on the distribution of biomes during the past (described below), and utilized Whittaker and Likens (1973) estimates of Net Primary Production (NPP), to estimate the amount resources that would have been available in those biomes. Mohamed et al.’s (2004) estimates of NPP variability were then used to calculate resource fluctuation. Ethnographic data was then used to calculate the amount of resources hunter gatherers would have been able to use in these environments (see chapter 5).

Data was also required to determine the speed at which agents moved into new environments, their probability of death each year and their reproductive rate. Ethnographic and archaeological data on the population growth rates of hunter gatherers was also used to inform the parameter assumptions.

Environment Resources: In the *PRISM 4* and *P4 Var* tests the simulated environment was created using the PRISM 4 reconstruction to identify the biomes of latitude/longitude coordinates (Dowsett et al. 2016; Salzmann et al. 2008). The environment was split into cells. These cells represented 1° latitude/longitude of the Pliocene reconstruction. Data from Whittaker and Likens (1973) was then used to associate the biomes with an estimated Net Primary Production (NPP) per km^2. The NPP of the environment reflects the amount of resources available for consumption within an environment (Kelly 1983). NPP has been used to reflect resource availability in several other ABMs (Timmermann 2020; Vahdati et al. 2019). The amount of resources hunter gatherers would be able to exploit within this landscape cell was then calculated (see chapter 5). The NPP of each landscape cell was calculated to account for differences in the area (km^2) of each cell as latitude changes. This was also accounted for in the movements of the agents. The same methods were used for the *Homog* test. However, all landscape cells were assigned the same biome type.

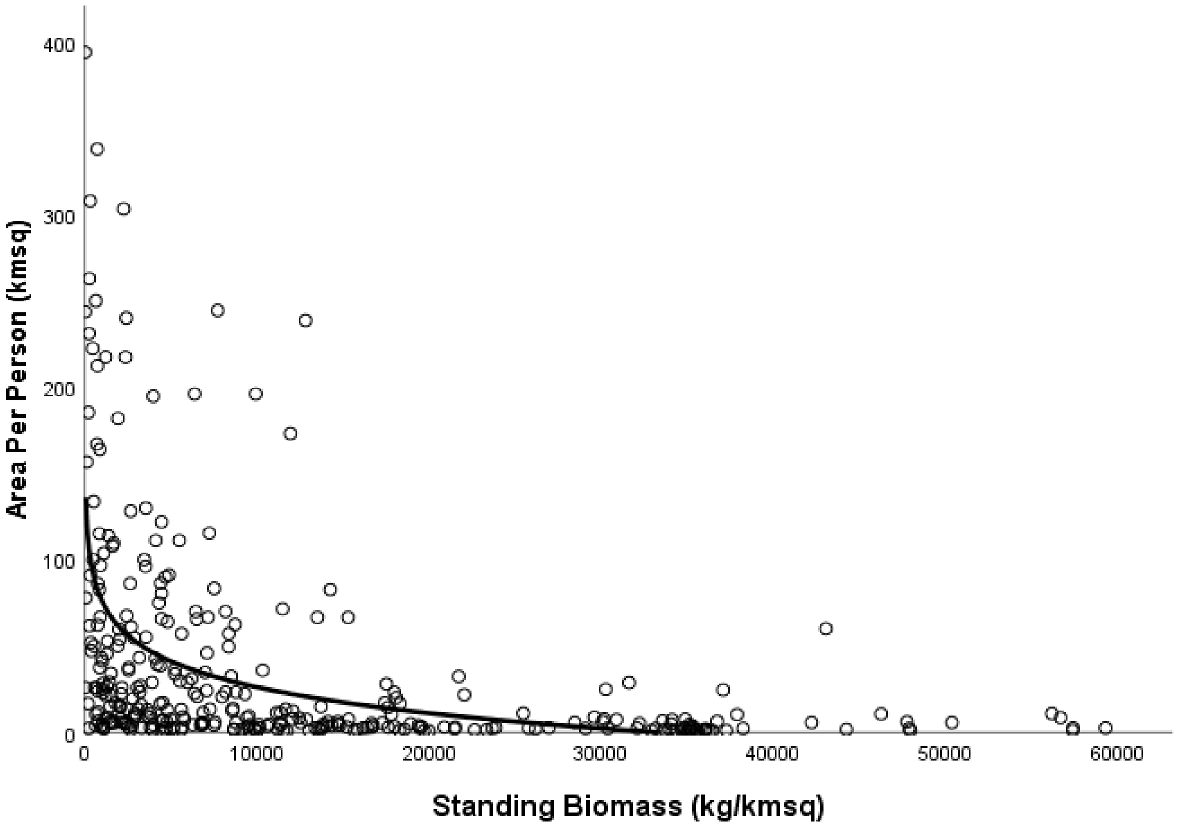
Inter annual variability: Inter annual variability in resources was calculated for the *P4 Var* test by using data from Mohamed et al. (2004). Their data provides coefficients of variation (COV) in global NPP across an 11 year period for each of the biomes in this study. These COVs were used to provide variations in NPP around the means provided by Whittaker and Likens (1973). This variability was modelled stochastically for each landscape cell, with no autocorrelation of variation. Each landscape cell could therefore provide more or less resources than Whittaker and Likens' values suggest. For example, grassland has a mean NPP of 500,000g per km per year (units simplified to NPP). This may vary from 555,000 - 445,000 NPP according to the variance of 11% calculated by Mohamed et al. (2004). This provides the values for how much the resources available in the environment should fluctuate from year to year. One limitation of this method is that Mohamed et al.'s (2004) global averaged data loses spatial variability, which may be more extreme than temporal variability. This can be seen when Mohamed et al.'s (2004) COVs are compared to COVs produced using Binford's (2001) data, which focuses on the NPP available within particular regions occupied by modern hunter gatherers (table 2). However, Binford's data does not provide information on temporal variation and focuses on spatial variation, therefore Mohamed et al.'s data (2004) was considered more generalisable and suitable for this study. Environmental variability is thought to have had a large effect on human evolution and the development of phenotypic plasticity (Grove 2011; Potts 2013; Trauth et al. 2010), therefore it is an important aspect to include in this model. Plasticity, which has been interpreted as having developed in response to increased climatic variability, has been argued to enable expansion into new environments during times of limited variability (e.g. Grove 2014; Grove et al. 2015). Therefore, the *P4 Var* test provides an opportunity to see how inter annual variability in resources affects the resulting distribution of extraversion, relative to the more static environments of the other tests.

Supplementary Table 1. Mohamed et al.'s (2004) COVs in NPP compared to COVs derived from Binford's (2001) data.

Biome	**Mohamed et al.'s COV (%)**	**Binford's COV (%)**
Boreal Forest	14.9	55.3
Desert	20.3	91.3
Grassland	11	36.9
Savanna	15.9	38.3
Temperate Forest	21.6	5.7
Tropical Forest	36.5	40.6
Tundra	10.1	83.1

Gathering Range: The size of the area that agents gather from is dependent on the Standing Biomass (SB) of the biome they are in, as well as the size of the population around them.

The SB of the environment determines the range agents may collect resources from. Using Binford's (2001) data a significant association was found between the area an individual occupies and the SB of their environment ($P < 0.01$). A linear regression was then produced to predict how large an area an agent would occupy within an environment with a particular SB ($226.21 + -21.72 * \log(x)$; $R^2 = 0.248$; $P < 0.001$ figure 3):



Supplementary Figure 1. Standing Biomass plotted against the area an individual occupies, with the line representing the predictive logarithmic regression.

SB was used rather than NPP as it provided more predictive power (NPP, $R^2 = 0.172$). However, when SB was greater than 30,000kg per km^2 negative values were produced by the equation. This is due to the low sample size of hunter gatherer groups living in areas of extremely high SB. This relates to a problem noted by Burke et al. (2017), that the predictive ability of the ethnographic record is limited according to the groups which are used for analysis. Therefore, in order to rectify this, the average area occupied by individuals in an environment with an SB above 30,000kg per km^2 was used. This produced an area per person of 5.8km, which was reduced to 4.8km when an outlier of 60km was removed. For simplicity this was rounded to 5km and used for biomes of high SB in the model (temperate and tropical forests).

Limitations of the environmental reconstruction: It is important to recognise the limitations of the ethnographic record. The ethnographic record is limited by a difficulty to obtain data from groups within particularly harsh environments and the differential survival of hunter gatherer societies. Hunter gatherers are not suspended in time (Cummings 2013, 131–141). Selective pressures have and are acting on them. Consequently, the generalised, shared features we see between hunter gatherer groups may be the result of shared selective pressures which would have been less common in the past (Kelly 1995; Schrire 1984).

Further, in reality not every environment of the same biome has the same NPP, and there are yearly fluctuations within the same location. This leads to high standard deviations in NPP within the same biome. However, the aim of producing this environment was to create realistic carrying capacities within the environment. By using the means for each biome it ensures they are realistic, however as a simplification to limit the number of variables to be assessed and increase the understandability of the model, the variation within biomes is lost. Nevertheless, as discussed above, intra-biome variation was introduced in the *P4 Var* test using data from Mohamed et al. (2004) to assess whether the added complexity of inter-annual variation affected the results of the model.

This method provides us with simplified but realistic estimations of resource usage and procurement ranges in different biomes for use in the model.

Movement: Agents movement speed is determined upon initialisation (see section 2.1.3 in the main paper). However, this movement speed is also stochastic. Agents may move the full distance, half the distance or not at all. This movement speed does not reflect the everyday movement individuals would undertake (e.g. movement to procure resources), as this is determined below by their collection range. Rather, this reflects the movement of the centre of their home range and their expansion into new territories. This movement speed is informed by archaeological data. Estimates of the rate of hominin dispersal are very low, ranging from 3 km per generation for modern humans (Eswaran 2002), to larger estimates of 16 km per generation for *Homo erectus* (Prat 2018; Lewin and Foley 2004, 340). Other estimates suggest a modern human movement speed of 0.4-0.5 km/yr from the Levant across Western Europe (Fort, Pujol and Cavalli-Sforza 2004; Mellars 2006a), and 1 km/yr from Africa across the coastal route into Australasia (Mellars 2006b). The total range of expansion speeds is between 0.4-1.1 km/yr (Fort, Pujol and Cavalli-Sforza 2004; Prat 2018). However, for the purposes of the model it must be remembered that these estimations of group movement speed are in one direction only, reflecting the wave of colonization rather than the movements of individuals who may move in any direction each year and reverse their direction. Within this model an agent’s direction of movement each year is stochastic, it is therefore expected that the movement speed of the agents in the model should be larger than that of these estimates.

Death, Reproduction and Population Growth Rate: Ethnographic and archaeological data was used to inform how reproductive and mortality functions were constructed. The aim was to produce a realistic population growth rate which could be manipulated in different runs of the model to reflect the possible ecological differences of the past.

Death probabilities (determined by *Safety*) were initially constructed to be similar to ethnographic results showing a 1.1-1.3% mortality chance per year (Gurven and Kaplan 2007; Hill, Hurtado and Walker 2007). However, when assessing mortality profiles, Trinkaus (2011) found that ethnographic and palaeolithic modern human mortality profiles are significantly different. Ethnographic data shows that between 52-80% (mean = 65%) of ages at death were over 40. In comparison, only 26% of upper palaeolithic modern humans and 23% of Neanderthals had an age at death of over 40. Therefore, showing that palaeolithic mortality profiles differ from ethnographic mortality profiles. Nevertheless, as noted by Trinkaus (ibid), these differences are likely in part due to taphonomical and sampling biases in the archaeological record, which would decrease the proportion of older individuals in the record, and also biases associated with skeletal aging of individuals over 40 which frequently predict a younger age (Hens, Rastelli and Belcastro 2008). By using the 1.2% mortality probability and turning off the extraversion-determined parameters *DeathDiff* and *BirthDiff*, age at death was similar to Trinkaus' results with ~60% of agents dying over the age of 40. In comparison, when *Safety* was reduced (and mortality was increased to 3%), this produced reduced values more reflective of the palaeolithic data (~45% respectively). Due to the biases mentioned above, it was not deemed necessary to reach the excessively low values of Trinkaus' paper, especially as this would likely lead to population extinction. Although, this may be an avenue for future research.

Similarly, a realistic reproduction rate was informed by ethnographic data. The aim was to produce a realistic rate of reproduction without incorporating those who would die before reaching a reproductive age in order to increase the efficiency of the model. In order to reproduce, agents must be between the ages of 15 and 50. Agents have a 6% chance of reproduction between these ages. This produces a rate of reproduction where agents have approximately 2.1 children each. Sex is not included in the model, therefore per 'mother' this is 4.2 children. Ethnographic literature has shown that hunter gatherers have approximately 5.4 children per mother (White 2014, 2016; Wood 1990). However, between 20-30% of these children do not reach a reproductive age (White 2014, 2016), although some sources claim it is as much as 50% (Gurven and Kaplan 2007). By limiting the chance of reproduction each year to 6% it allows for a 23% juvenile mortality rate. A child spacing gap of 2 years is also used in the model, reflecting ethnographic findings (Hassan and Sengel 1973).

Hunter gatherer population growth is thought to be exceptionally low, with estimates ranging from a maximum estimate of 2.7% per year, to a more restrained but arguably realistic estimate of 0.1% per year (Hassan 1975). This difference from the maximum is thought to be accounted for by the use of ‘birth control methods’, such as infanticide and abortion, in order to artificially control population levels. This ensures that population levels don’t rise to a level that would lead to resource shortages. Further, population growth during the Palaeolithic is thought to have been much lower, ranging between 0.0007% to 0.002% per year (Hassan and Sengel 1973; Hassan 1975). Hassan (ibid) believes this is due to greater levels of infanticide and abortion. However, this reduction relative to modern hunter gatherers may also be due to a higher adult mortality rate during the Upper Palaeolithic relative to modern hunter gatherers. As seen above there were considerably fewer individuals over the age of 40 in Upper Palaeolithic samples (26.5%) than in the ethnographic records (65%) (Trinkaus 2011). Further, the values produced by Hassan were extrapolated from population size estimates for the late Palaeolithic, which despite decades of further research since Hassans’ work remain inconsistent and vary widely (see section S1.2.3). This estimate of population growth also relies on the assumption that there were only 2 individuals 2 million years ago. Consequently, while it is highly probable that growth rates were lower due to higher mortality rates, the Palaeolithic estimates of growth rate produced by Hassan are not valid. Further, none of these estimates capture the effects of catastrophic events. Nevertheless, varying the *Safety* of the model may be used to explore the effects of different mortality rates.

While a wide range of parameter combinations were run within chapter 6 to explore the effects of different pressures and population growth rates on extraversion, the data above was used to inform a realistic parameterisation of the model.

S1.2.2 Submodels

Using the input data outlined above, several submodels were produced that have not been fully explained thus far, and will be outlined here in the order they take place during an iteration of the model:

- Resource Acquisition
- Death
- Reproduction

Resource Acquisition: Using the input data outlined in section S1.2.1, the collection range and amount of exploitable resources were calculated for each agents' location. Initially, agents collected the resources which were available to them within their collection range. However, if the population size within the landscape cell was large, and the combined collective size of agents areas was larger than the landscape cell, agents collected all of the available resources within the cell and shared them equally.

Agents collecting more resources than necessary had no impact on the model as the extra resources were not stored and did not provide any health advantages. Thus, when the carrying capacity of the cell was reached, agents began to receive less resources and lose health.

Death: When agents reached the age of 70 they died of old age. Alternatively, they may die if they have not collected enough resources (termed a health related death), or spontaneously through an accident.

Health related deaths are caused when agents do not collect the required 185,000g of NPP from the environment. As resources were distributed equally to agents within a cell, in order to inhibit the extinction of a cell's entire population when they did not collect enough resources, agents lost a point of health for each year they had not collected enough resources. Each point of health lost increases their chance of death by 10%. When agents collect enough resources, they may restore a point of health which they have lost in a previous year up to the maximum of 100.

The likelihood of an agent dying spontaneously is calculated as follows:

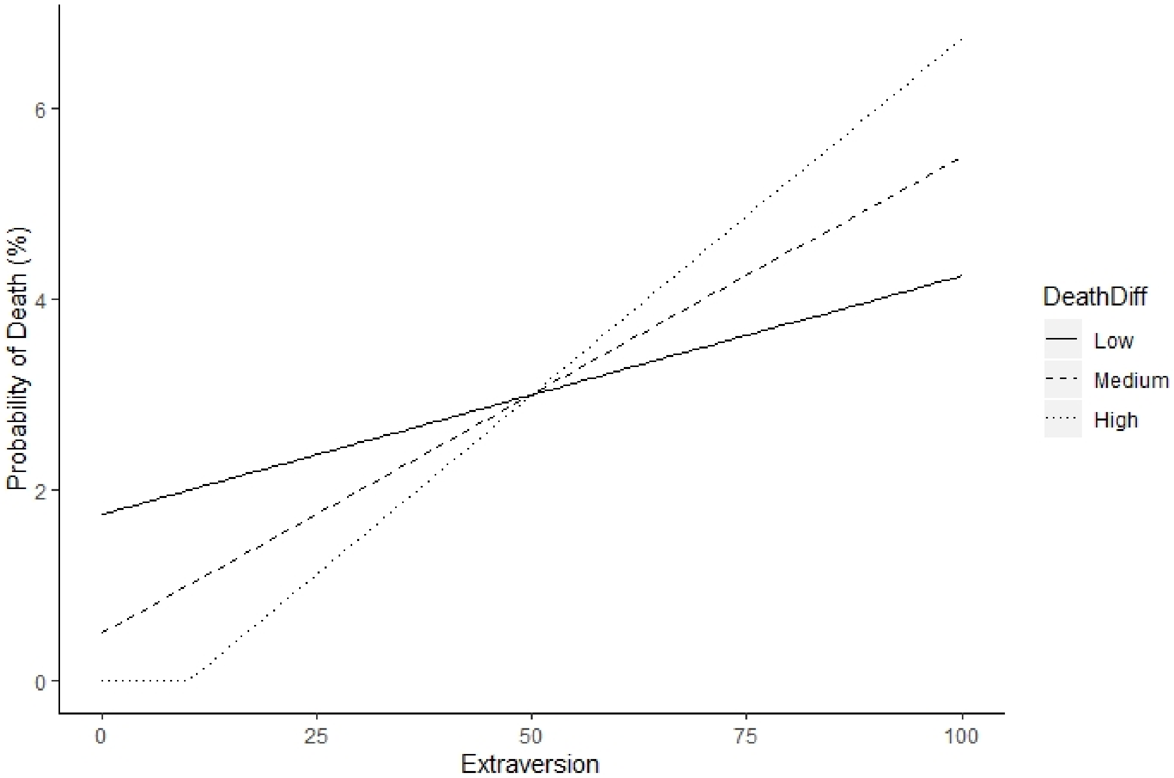
Chance of spontaneous death = 120 [the median ethnographic mortality probability (%) multiplied by 100] + ((Extraversion - 50) × DeathDiff [difference caused by extraversion])

```
if (Chance of spontaneous death > Random number between (0, Safety))
                  {
                      Agent dies;
                  }
```

When the *Safety* level is higher the average mortality rate within the environment is lower. Following the discussion above, and preliminary testing, the *Safety* level was reduced to produce mortality levels of 3%, to reflect the palaeolithic data. During further sensitivity analysis (S2.3), this was lowered further to test the effect of a more dangerous environment upon selection for extraversion. As mentioned above, the palaeolithic environment was likely to be more dangerous than a modern environment.

Carnivore attacks have been a pressure throughout our evolutionary history (Camarós et al. 2016; Treves and Naughton-Treves 1999). Victims of predation are visible throughout the archaeological record, from early examples such as the *Australopithecus africanus* Taung child (Berger and McGraw 2007), to frequent Neanderthal and early modern human skeletal modifications, seen to be the effect of carnivore predation and scavenging (Camarós et al. 2016, 2017), to modern day attacks on humans (Treves and Naughton-Treves 1999). However, for the majority of this history the biodiversity of predators was larger than at present (Hoare 2019). For example, predators such as wolves, who are considered top predators today, would have had to compete with 11 species of predator larger than or as large as themselves (Wang et al. 2004). Wang et al. (2004) have also argued that predator density was larger, with high competition. This pressure ultimately may have led to the extinction of the largest carnivores (e.g. cave lions). Further, Spotted hyena (*Crocuta crocuta*), cave lions (*Panthera spelaea*), cave bears (*Ursus spelaeus*) and hominins would have been in direct competition for both food and shelter (Dusseldorp 2013; Spikins et al. 2019; Stiner 2004). This is reflected in the frequent finding of hyena activity at hominin sites and the difficulty differentiating hyena and early hominin assemblages (Pickering 2002). Discamps (2014) has also noted a large increase in hyena population sizes during the Middle-to-Upper Palaeolithic transition. Hence, early modern humans were in direct competition with a greater range of predators living at higher population levels than today, which would have led to a higher mortality rate.

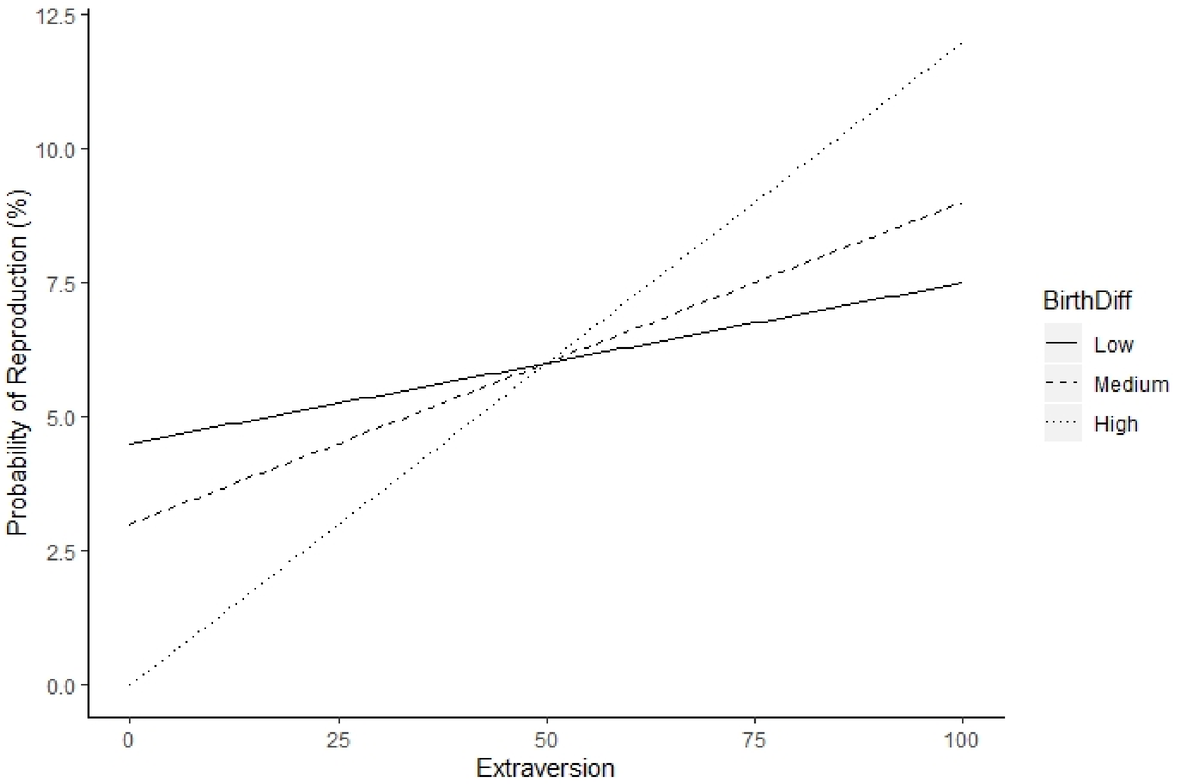
In the model for chapter 6 an additional function was added so that the *Safety* of the environment in the model interacts with a parameter called *DeathDiff*, input upon initialisation, which changes an agent’s chance of spontaneous death according to their extraversion (see supplementary figure 2). Therefore, this produces a mean mortality rate which reflects the ethnographic and archaeological data, while individual mortality rates vary according to agents’ extraversion. If an agent has an extraversion score of 50, they acquire the default mortality rate of 3%. However, if their extraversion score is higher or lower than 50, their chance of mortality increases or decreases respectively. The slope of this difference is determined by *Deathdiff*, which has three levels (Low = 0.025, Med = 0.05, High = 0.075). This allows us to assess the impact increasing the mortality difference between introverts and extraverts may have upon the output of the model.



Supplementary Figure 2. Showing the effect of DeathDiff on agents' probability of spontaneous death, modified by extraversion.

Reproduction: Agents reproduce in pairs. A reproducing agent randomly selects another agent to reproduce with. The selected agent must either be from their own landscape cell or the next closest one to it. The addition of a second landscape cell reflects the larger size of mating network distances than resource procurement distances, with Wobst (1976) suggesting that maximum reproductive distances for hunter gatherers are approximately 300km, although they are unlikely to reach this size often. Thus, in this model the maximum reproductive distances are approximately 150km.

As mentioned above, agents have a 6% probability of reproducing each year. Within chapter 6 this is then influenced by their extraversion scores. The agent's extraversion interacts with the parameter *BirthDiff*, input upon initialisation, to either increase (higher extraversion) or decrease (lower extraversion) their probability of reproducing, following psychological data (see section 1.1). The *BirthDiff*, similar to *DeathDiff,* has three levels, which determine the impact this has upon reproductive ability (see supplementary figure 3; this causes differences in slope as follows: Low = 0.03, Med = 0.06, High = 0.12). In other words, this produces a mean reproductive rate which reflects the ethnographic data, while individual reproductive rates vary according to extraversion.



Supplementary Figure 3. Showing the effect of BirthDiff on agents' probability of reproduction, modified by extraversion.

In addition to the probabilistic test outlined above, both agents must pass several checks in order to reproduce:

- Age 15 > 50
- Health > uniform random number between (0 - 100)
- Not had a child in the last 2 years

Following evidence of mate exchanges and extensive mating networks in hunter gatherer groups (Lovis, Whallon and Donahue 2006; Wobst 1976; Zilhão and Pettitt 2006), the agents then relocate randomly (with equal probability) either to the location of the mother or father to be together and the child is born at their location. The offspring inherits the average extraversion score of their parents, plus a random factor that represents non-inherited and environmental effects.

S1.2.3 Model Tests

Three environmental conditions, here termed as separate 'tests', were completed using the model. These tests built up the complexity of the model from a simple homogeneous environment with a fixed NPP (*Homog; see 'Appendix File A' for the model code*), to a more complex continental environment utilizing the PRISM 4 reconstruction (*PRISM 4: see ‘Appendix File B’ for the model code*), to a model which incorporated yearly fluctuation in resources (*P4 Var: see ‘Appendix File B’ for the model code*).

Within chapter 5 the *PRISM 4* and *P4 Var* tests were run 10 times (only changing the seeding of the random number generator, and allowing consistent outcomes to be identified from these two scenarios) without the extraversion related parameters *BirthDiff* or *DeathDiff* settings to explore the effects of resources accessibility and variability on agents’ ability to inhabit different biomes.

Within chapter 6 the *Homog* test was additionally used. The effects caused by changing parameters’ values within the model were tested. *BirthDiff* and *DeathDiff* were varied by three levels for a total of 9 parameter combinations, to explore different selective pressures on extraversion. Each test was repeated 10 times for a total of 90 runs for each test. The *PRISM 4* and *P4 Var* tests were analysed together, with the inter annual variability in resources introduced by the *P4 Var* test being treated as a further test parameter (*Fluctuation Level*). The use of 10 runs for each parameter combination was deemed sufficient to capture the variability of the large-scale results of the model assessed in these chapters, while also ensuring computational time was not too large. This allowed the consistent and mean outcomes of the model to be assessed.

Runs of the model reached completion when the population either reached the maximum time limit (15,000 years), the maximum population size (1.8 million), or became extinct. This led to different end times for each run. This maximum population size attempts to compromise between previously modelled estimates of population size for the Old World within the Upper Palaeolithic. These estimates range from an extreme minimum of 5500 people occupying Europe to an excessively high value of 8.3 million occupying the whole world (Bocquet-Appel et al. 2005; Gautney and Holliday 2015; Wren and Burke 2019). The latter value produced by Gautney and Holliday (ibid) suggests that all occupiable land is used, which is unlikely. Further, these results were produced using modern hunter gatherer estimates, which as a result of differing population growth rates (discussed above) may be much higher than was present in the Palaeolithic. This same study produced lower human population estimates of 2,117,000-2,955,000 based upon medium to large carnivore population densities (Gautney and Holliday 2015). These estimates also assumed that all habitable land was occupied. Consequently, a lower estimate was used. This likely better reflects the past and decreases processing times.

S1.2.4 Data Analysis

Analysis was completed using R studio (version 1.2.5019). Graphics were created using the ggplot2 package (version 3.2.1). Type 3 ANOVA (car package, version 3.0-10) was used and the eta squared effect sizes extracted, for tests of the entire dataset and time slices (sjstats package, version 0.17.9; correlation coefficients were also calculated using this package). Where data was subsetted by time, gaps in the data meant type 3 ANOVA was no longer suitable. Therefore, type 1 ANOVA was used (stats package, version 3.6.1), with effect sizes extracted. This type of ANOVA is sensitive to the order of data input. This was allowed for by inputting the variables with the highest effect size for the type 3 ANOVA first. This limited the effect of the order of input. The subsetted data was then merged for use in figures (e.g. figure 7).

Supplement 2 – Chapter 6 Supplementary Results

This supplementary section will provide a more in depth report of the results of each test conducted on the model, to support the summary provided in the main paper.

S2.1 Test 1 - Homogenous Environment (Homog)

This test explored the effects of extraversion on agent dispersal under different conditions within a homogenous environment.

<u>Population size and growth</u>

As expected, different parameterizations of the model led to different population sizes (supplementary figure 4), growth rates and ending times for each run. This leads to parameter variations being lost throughout the run of the model (see supplementary table 2). This was seen in all tests of the model.

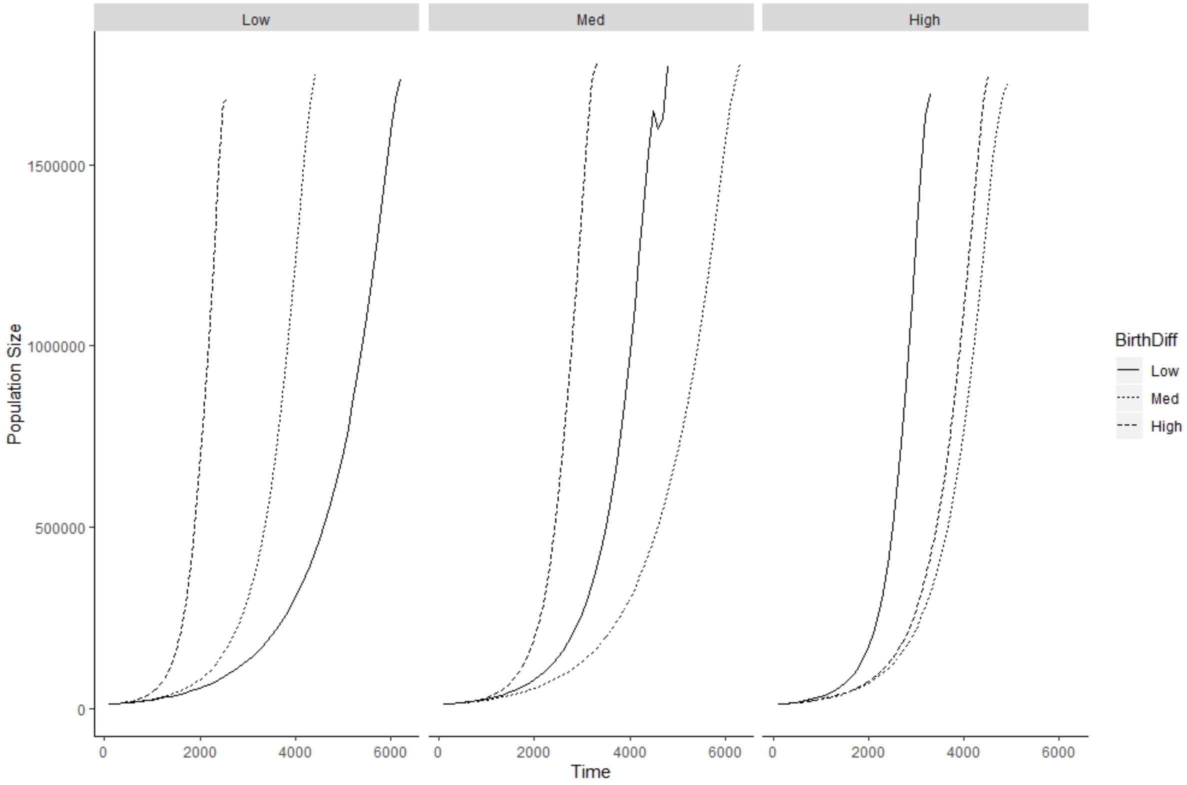
Supplementary Table 2. Frequency tables of the number of runs retained at different times during the model, showing how parameter variation is lost through time - A) BirthDiff, B) DeathDiff (Homog test). Each parameterization was repeated 10 times, with loss of variation being uniform across repetitions.

A)

	BirthDiff		
Time	Low	Med	High
1000	30	30	30
2000	30	30	30
3000	30	30	20
4000	20	30	10
5000	10	10	0
6000	10	10	0

B)

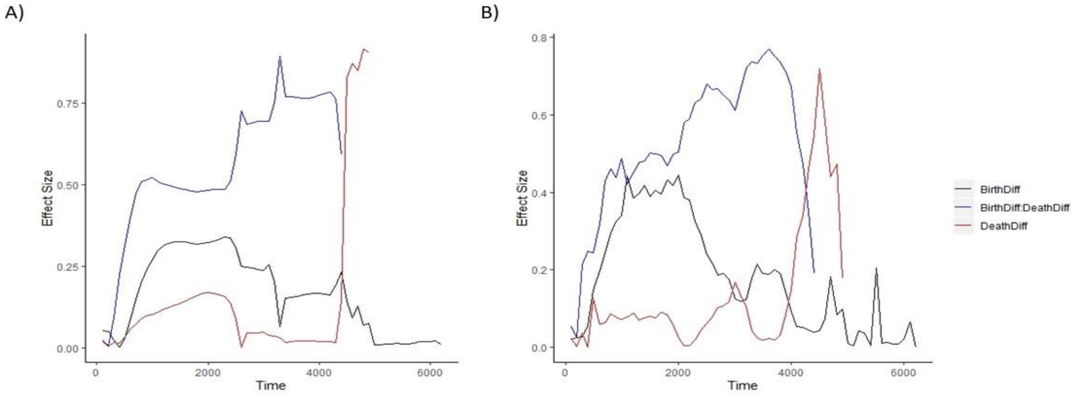
	DeathDiff		
Time	Low	Med	High
1000	30	30	30
2000	30	30	30
3000	20	30	30
4000	20	20	20
5000	10	10	0
6000	10	10	0



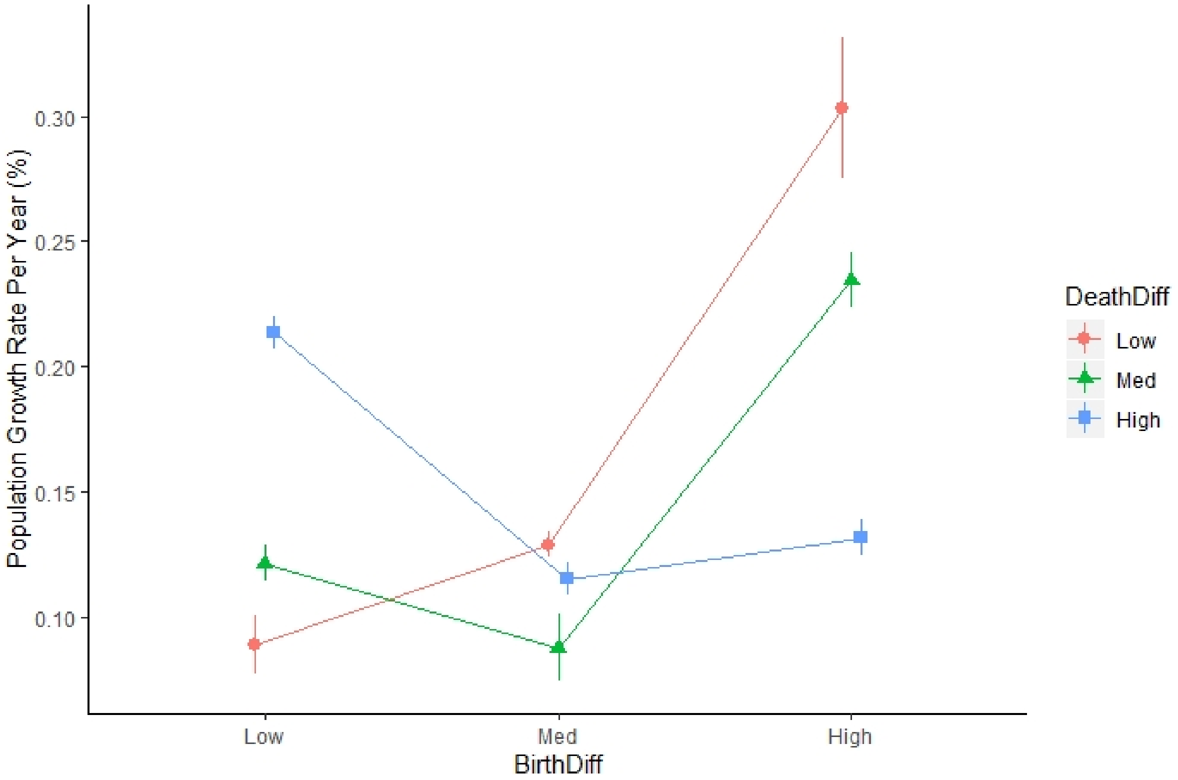
Supplementary Figure 4. Population sizes of runs of the model faceted by DeathDiff. (Homog).

Exploring the effects of the parameters on the outcomes of the model, three tests of effect size (η^2) were used. Firstly, the effect size on all observations from the model regardless of time was used. Secondly, due to the effect the amount of time that has passed has on population size and other outputs of the model, the effect of the parameters at a time slice was used. The time slice used for this test was the last point where all parameter combinations were present (2000 years). Both of these methods extracted effect sizes from type 3 ANOVA. The third test of effect size utilized type 1 ANOVA, due to limitations of the data, to assess effect sizes over time. To standardise this method, parameters were input into the ANOVA according to the size of the effect found using the time slices (largest effects first). This test provides an indication of how the effect of parameters may change at different times in the model. However, this should be used with caution and in conjunction with the previous tests, because it is affected by the order the parameters are input into the model and by the loss of parameters through time.

As expected, *BirthDiff, DeathDiff* and their interaction have an impact on the mean population sizes within the model (when using a time slice; supplementary table 3). However, due to the relationship between population size and the amount of time that has passed in the model, ANOVA was not significant when assessing the mean population sizes of every observation at once. When assessing the effect sizes using the time slice at 2000 years, which were significant, we can see that *BirthDiff* and the interaction have a much larger effect size than *DeathDiff*. Nevertheless, the effect size of parameters may change over time as agents are more dispersed, therefore it is useful to assess the effect sizes over time. As noted above, when testing effect sizes over time it is important to recognise that as factor levels of the parameters are lost, as runs of the model end, this leads to parameters' effect sizes being reduced. The interaction between *BirthDiff and DeathDiff* has the largest effect before significant amounts of parameter variation was lost. During this time, *BirthDiff* has a larger singular effect on the population size than *DeathDiff* (supplementary figure 5a). This was also replicated when exploring which parameters had the largest effect on population growth rate (percentage increase in population size per year) both for the overall effect sizes (supplementary table 3) and the effect sizes over time (supplementary figure 5b). As can be seen from supplementary figure 6, increasing the *BirthDiff* or *DeathDiff* alone does not necessarily lead to a higher population level. This is due to the disadvantages associated with increasing each, for a portion of the population (either introverts or extraverts). For example, when *DeathDiff* is set to 'Med', increasing *BirthDiff* from 'Low' to 'Med' leads to a decrease in population growth rates. This is due to selection being less directional in this run and introverts being subjected to lower reproduction rates. Consequently, population growth rates are reduced rather than increased.



Supplementary Figure 5. The effect size (η²) of parameters on the population sizes (A) and population growth (B) within the model over time (Homog test), showing that the interaction between the parameters has the largest effect, while BirthDiff has the largest singular effect, on both population size and growth. Note: there is significant loss of parameter variation after 4000 years.



Supplementary Figure 6. Interaction plot showing the effect of BirthDiff and DeathDiff on mean population growth at 2000 years, showing that there is an interaction between the *parameters affecting population growth rates (n = 10; error bars = standard deviation; offsetting is used to avoid error bars overlapping; Homog).*

Mean Extraversion

As expected, the two test parameters have a large effect on the mean extraversion of agents both when using every observation and when using a time slice (supplementary table 3). Additionally, the interaction between these parameters had almost no impact on mean extraversion (see supplementary table 3 and figure 7).

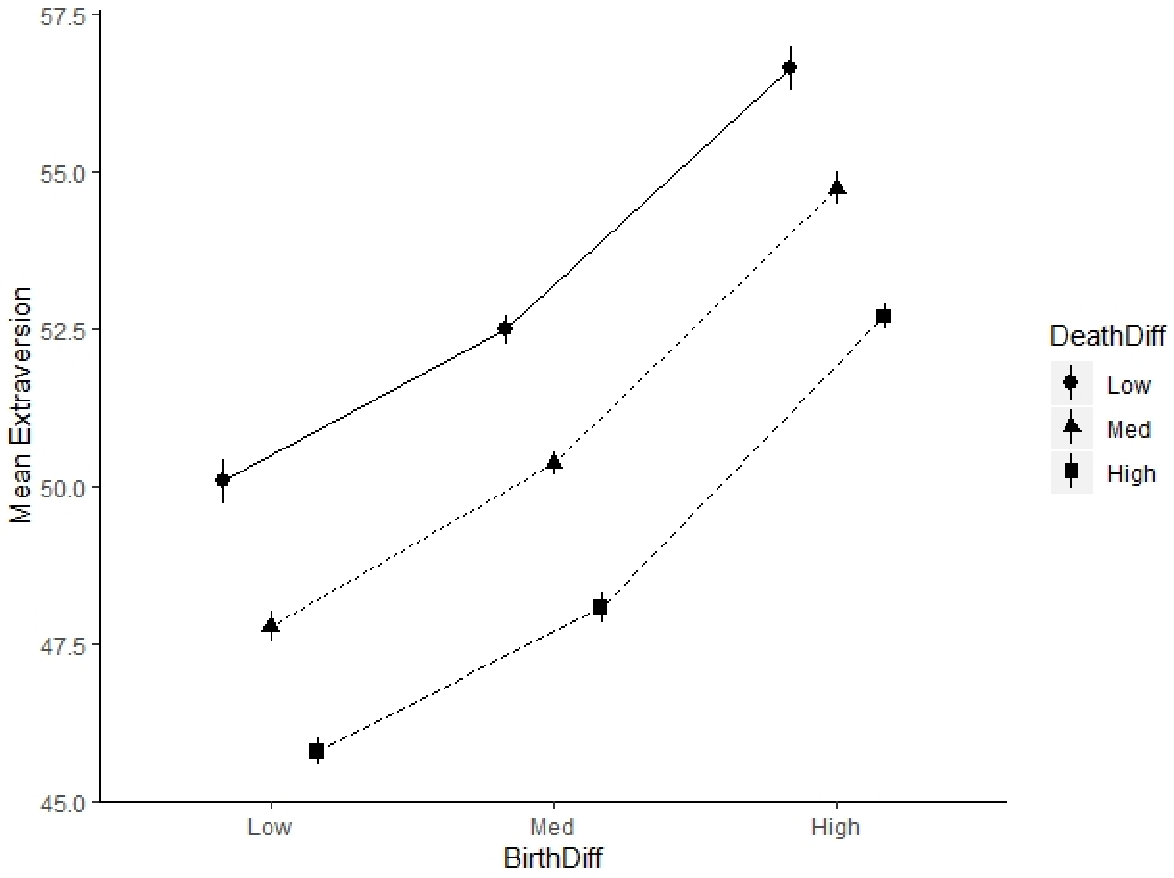
When assessing the effect size over time, it can be seen that at the beginning of the run *BirthDiff* almost entirely determines mean extraversion (supplementary figure 8). However, *BirthDiff* then reduces to have a minimal effect. Through the remainder of the model *DeathDiff* had the largest effect on mean extraversion, although this may be due to runs where *BirthDiff* had a large effect being lost earlier in the model. However, there seems to be an equal loss of factor levels (see supplementary table 2). Alternatively, during expansion reproduction may be more important, whereas when populations are more static staying alive may be more important. This would cause *BirthDiff* to have a higher effect size earlier in the model. The differences in mean extraversion in response to different parameters can also be seen in the example runs of the model (supplementary figure 9).

The correlation between the mean extraversion of agents in a landscape cell and the distance of that landscape cell from the point of agent origin varies according to how the model is parameterized and varies over time within a run (supplementary figure 10; see supplementary figure 11 for a time series of extraversion distribution in an example run). While there is a high amount of variance in this correlation, differences in the mean correlation overall are associated with the direction of selection within each run, which is determined by how the model is parameterized. The phenotype that is favoured by selection is more likely to disperse further than the other phenotype. For extraverts, this is because a higher reproduction rate enables extraverts to expand out into the expanded range. Alternatively, for introverts a lower death rate enables them to survive for longer in these areas waiting for an opportunity to reproduce. Therefore, when *BirthDiff* is high and *DeathDiff* is low, extraverts are more likely to expand, due to their reproductive advantage. However, if *DeathDiff* is high and *BirthDiff* is low, despite extraverts still having a minor reproductive advantage, they are more likely to die before they can reproduce in the expanded range and start a new population. Due to this being so closely associated with the direction of selection, the parameters with the largest effect on this correlation were similar to the effects on mean extraversion (see supplementary table 3).

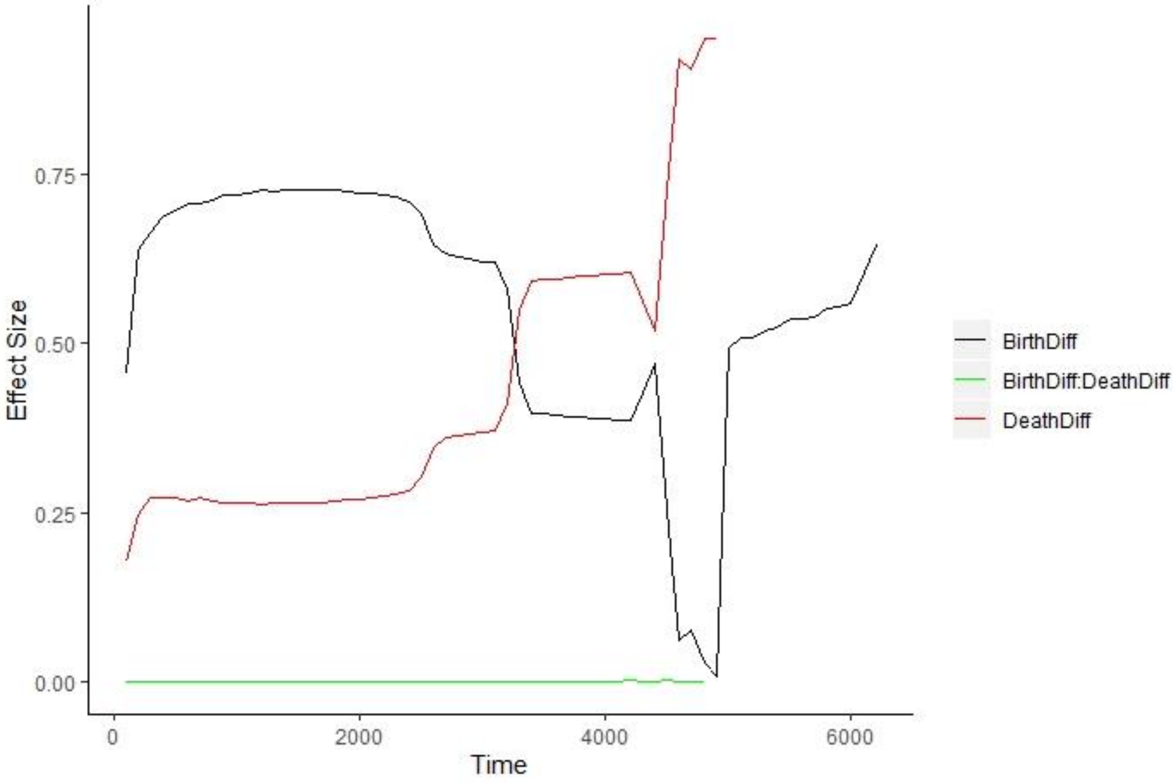
Supplementary Table 3. The effect sizes (η^2) of parameters on response variables (NS = not significant; Homog).

Response Variable	BirthDiff		DeathDiff		Interaction	
	All Observations	*Time Slice (2000)*	*All Observations*	*Time Slice (2000)*	*All Observations*	*Time Slice (2000)*
Population Size	NS	0.588	NS	0.017	NS	0.375
Population Growth	0.240	0.444	0.023	0.024	0.342	0.503
Mean Extraversion	0.500	0.723	0.192	0.270	0.05	<0.001
Correlation Between Cell Mean Extraversion and Distance From Africa	0.204	0.259	0.136	0.220	0.027	0.012

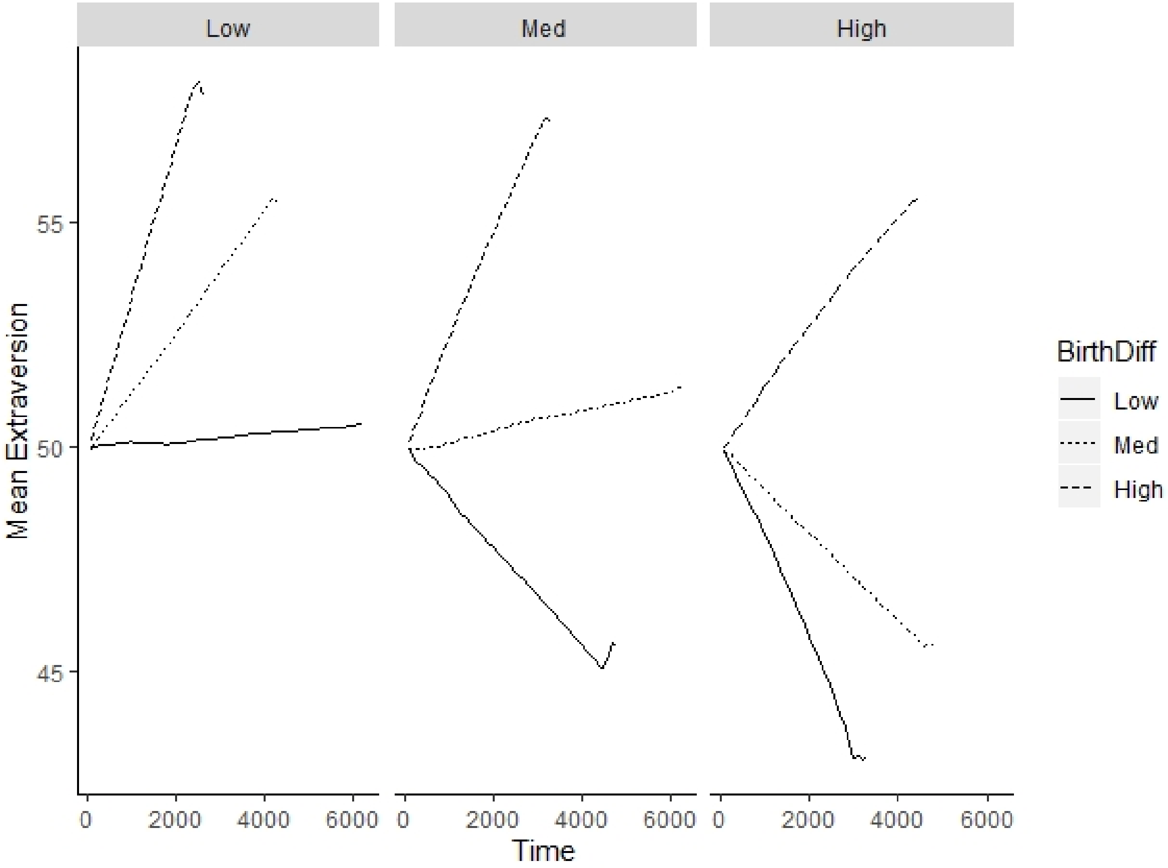
Variance in the strength of the correlation between extraversion and distance from the point of origin over time may be due to agents moving into new areas, where the favoured population are more successful at reproducing in areas of low population density, whether this is due to longevity or a reproductive advantage. Following this, the prevalence of the disadvantaged population may increase in areas as population density increases, due to a relaxation of selective pressures. Supporting this hypothesis, a negative correlation was found between extraversion and the population size within landscape cells during runs that showed positive selection for extraversion, and the reverse when extraversion was under negative selection (supplementary figure 12). Once the density increases this also increases the probability that agents attempting to move to a different location will be successful as more agents are attempting to move around them, increasing the number of agents they may reproduce with in the new location. This would create a pattern where (when extraversion is selected for) extraverts move and then introverts follow (either through the movement of introverts or selection for more introverted genes), causing fluctuation in how much correlation there is between distance from the point of origin and extraversion. As this is density dependent, if the density decreases closer to the point of origin then the correlation may even reverse. Another cause of variance may be the difference between the actual distance agents (and their ancestors) have travelled and the euclidean distance. Agents may have taken a much longer path, to reach a place not too far from the point of origin. While this may be a source of variation, it should not significantly affect the results, because if the dispersal ability is higher for an agent, they are still more likely to move further from the point of origin than an agent who is less successful at dispersing.



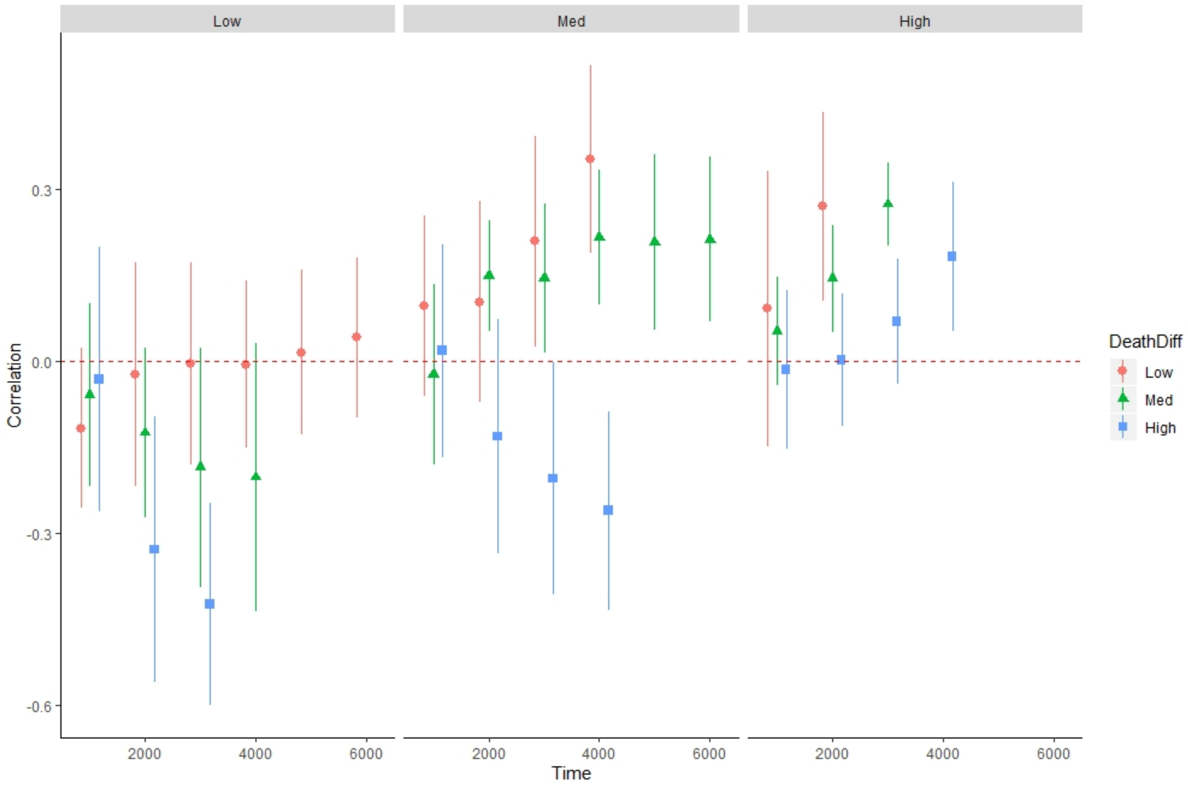
Supplementary Figure 7. Interaction plot showing the effect of BirthDiff and DeathDiff on mean extraversion at 2000 years, showing that there is no interaction effect between the parameters on mean extraversion (error bars = standard deviation; Homog).



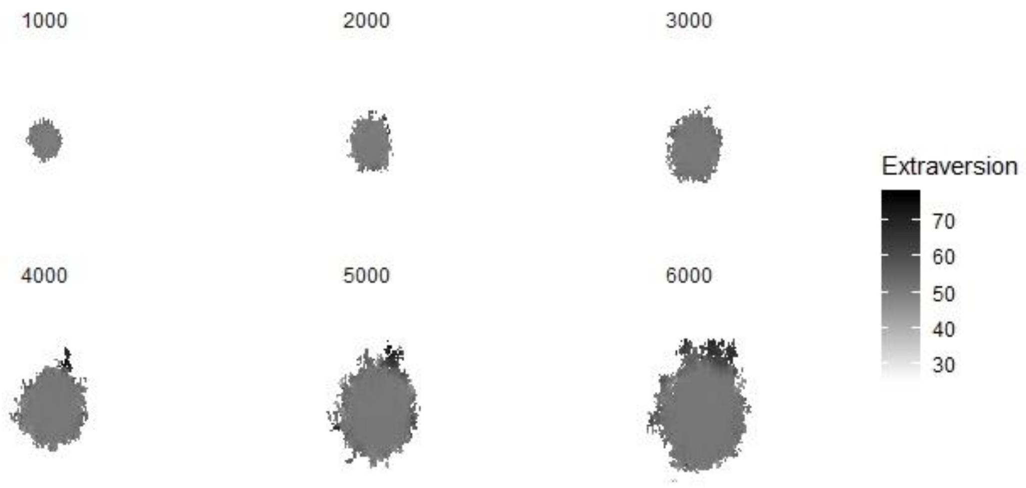
Supplementary Figure 8. The effect size (η^2) of parameters on the mean extraversion of agents over time, showing that BirthDiff has the largest effect on mean extraversion at the start of the model. Following 4000 years, there is a loss of parameter variation which affected the results (Homog test).



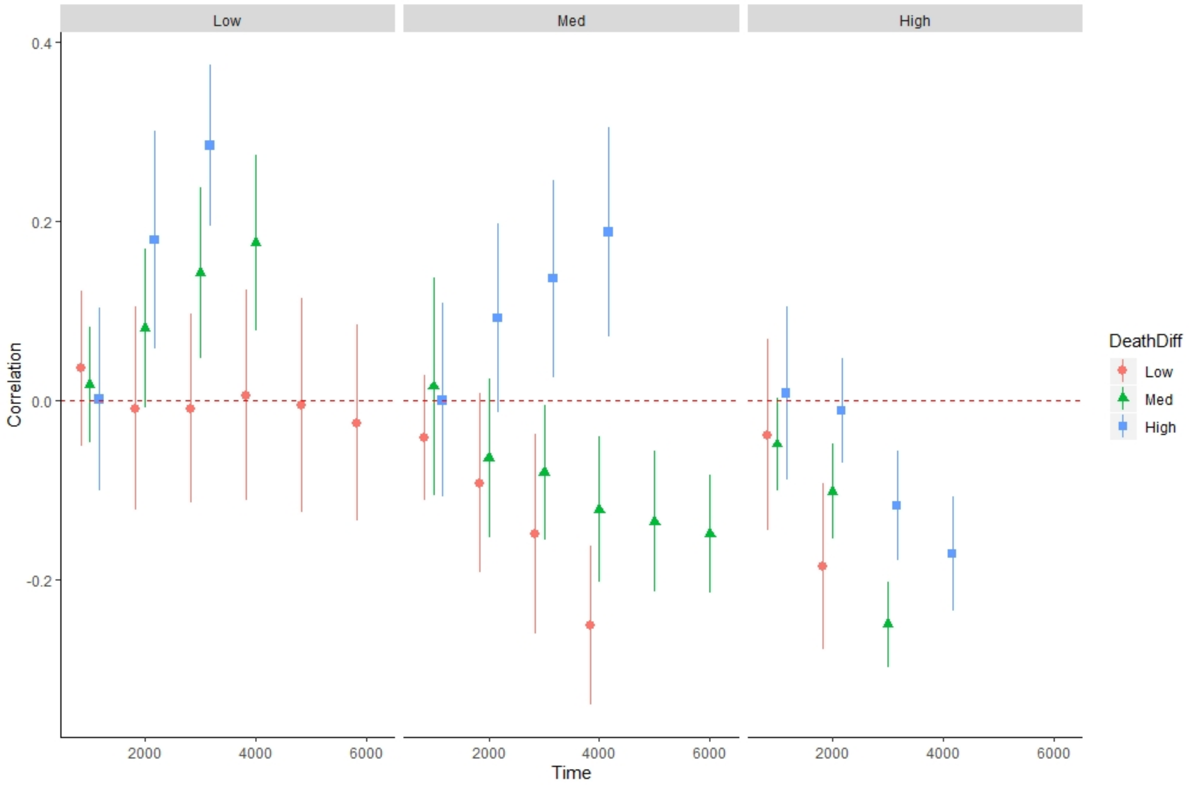
Supplementary Figure 9. Mean extraversion of all runs of the nine parameterisations of the model, faceted by DeathDiff (Homog).



Supplementary Figure 10. The mean correlation coefficient between distance from the point of origin and extraversion, through time. Faceted by BirthDiff (error bars = standard deviation; offsetting is used to avoid error bars overlapping; Homog test).



Supplementary Figure 11. A time series of the mean extraversion of individuals in landscape cells in an example run; BirthDiff = Mid, DeathDiff = Mid (Homog test)



Supplementary Figure 12. The mean correlation coefficient between the population size of landscape cells and mean extraversion in those cells, through time. Faceted by BirthDiff (n = 10; error bars = standard deviation; offsetting is used to avoid error bars overlapping; Homog test).

S2.2 Test 2 and 3 - PRISM 4 and P4 Var

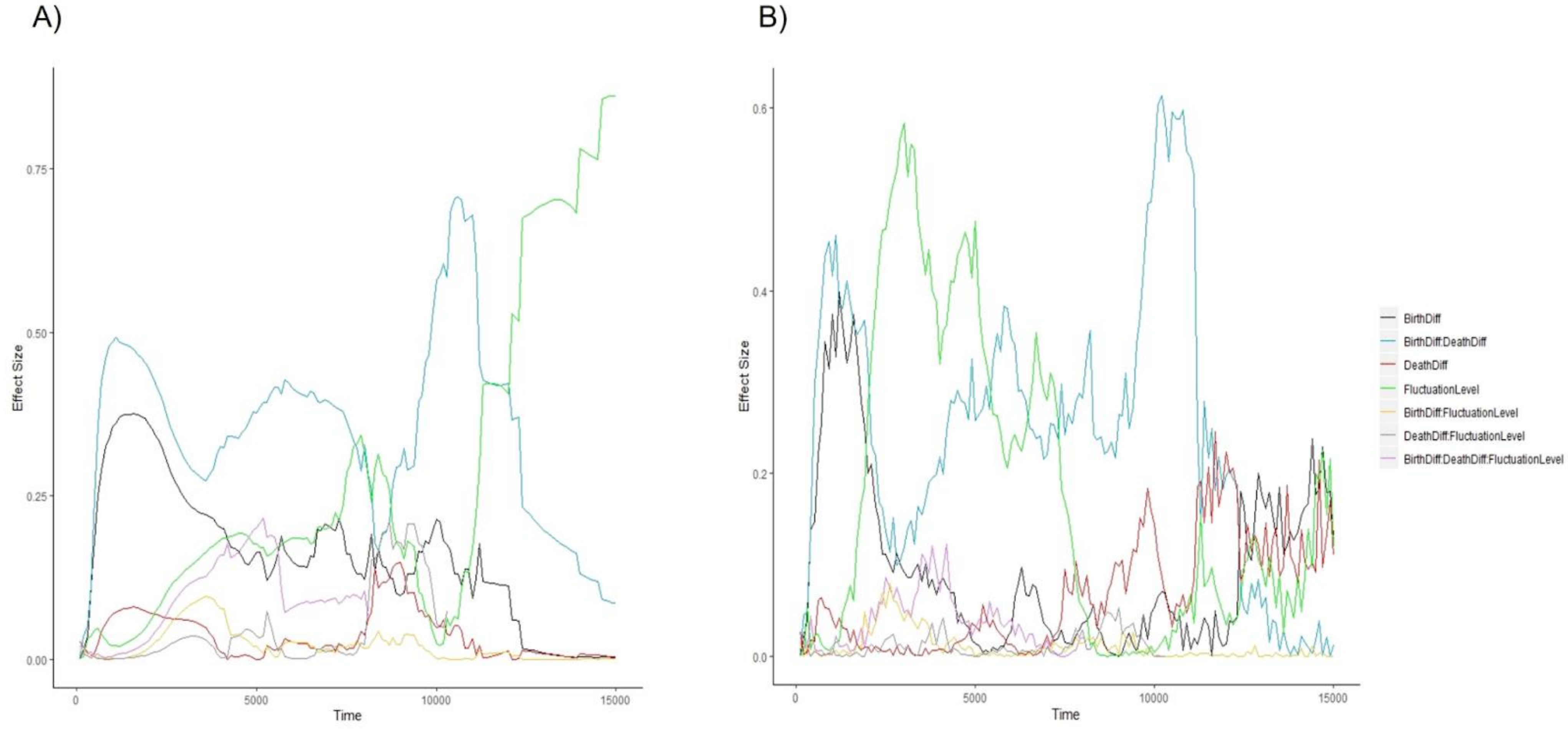
Tests 2 and 3 explored the effects of extraversion on agent dispersal under different conditions within the PRISM 4 reconstruction of the Pliocene environment (test 2: *PRISM 4; figure 1*) and explored the effect of fluctuating interannual variability in resources (*Fluctuation Level*) within this environment (test 3: *P4 Var*).

Population size and growth

Similar to the Homog test the *BirthDiff, DeathDiff* and their interaction had a small effect on population size when assessing all observations (see supplementary table 4), due to the relationship between time passed in the model and population size. This was significantly higher when assessing a time slice. Once again, the last point at which parameter variation is maintained was selected as the time slice (3000 years). In contrast, *Fluctuation Level* had the largest effect of the parameters when assessing all observations, rather than a time slice, due to its effect on the carrying capacity of landscape cells. Its interactions with the other parameters and it's pairwise interaction with *BirthDiff* also had a relatively high effect.

The growth rates in the model were still highly affected by *BirthDiff* and *BirthDiff*'s interaction with *DeathDiff*. However, *DeathDiff* had the smallest singular effect on population growth rates in this test. *Fluctuation Level* had the highest effect on the population growth rates.

When this was assessed over time these findings were maintained (supplementary figure *13*). However, the *Fluctuation Level* had a higher effect on population sizes later in the model, while *BirthDiff* and *DeathDiff* had a higher effect earlier. In contrast, the population growth rate was affected by the *Fluctuation Level* earlier in the model, with periods where the *Fluctuation Level* had a greater or equal effect on population growth as the interaction between *BirthDiff* and *DeathDiff.* While these results need to be interpreted with caution, due to the effect of loss of factor combinations later in the model (which may be a cause of the steep rise in the effect of *Fluctuation Level* on population sizes later in the model), these findings may be due to variability in resources creating geographical barriers which decrease population growth and expansion. Further, the variation in the carrying capacity of landscape cells may lead to population decrease (during times of low resources) where previously there would have been a steady increase. This is shown in the graphs of population size (supplementary figure 14) and population growth rate (supplementary figure 15) and is further demonstrated by a negative correlation between *Fluctuation Level* and population growth when assessing all runs of the model (r = -0.35). Therefore, *Fluctuation Level* constrains the rate of population growth. Further, resource fluctuation in the *P4 Var* test also decreased the area agents were able to disperse to. This highlights the increased difficulty of population dispersal when resource acquisition is unstable. Furthermore, when interannual fluctuations were added agents were unable to survive in tropical forests. The survival of hunter gatherers within tropical forests may therefore be precluded by this fluctuation, although possible in static conditions (see chapter 5). This drastically reduces the amount of liveable space available within Africa and also constrains the size of the route out of Africa within the *P4 Var* test.

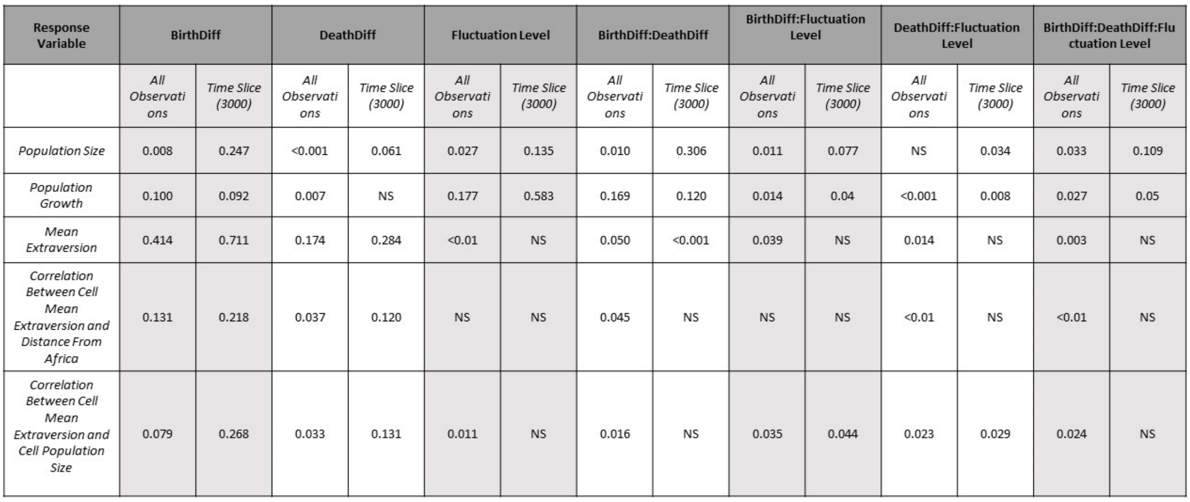


Supplementary Figure 13. The effect size (η^2) of parameters on the population sizes (A) and population growth (B) within the model over time (PRISM 4 test).

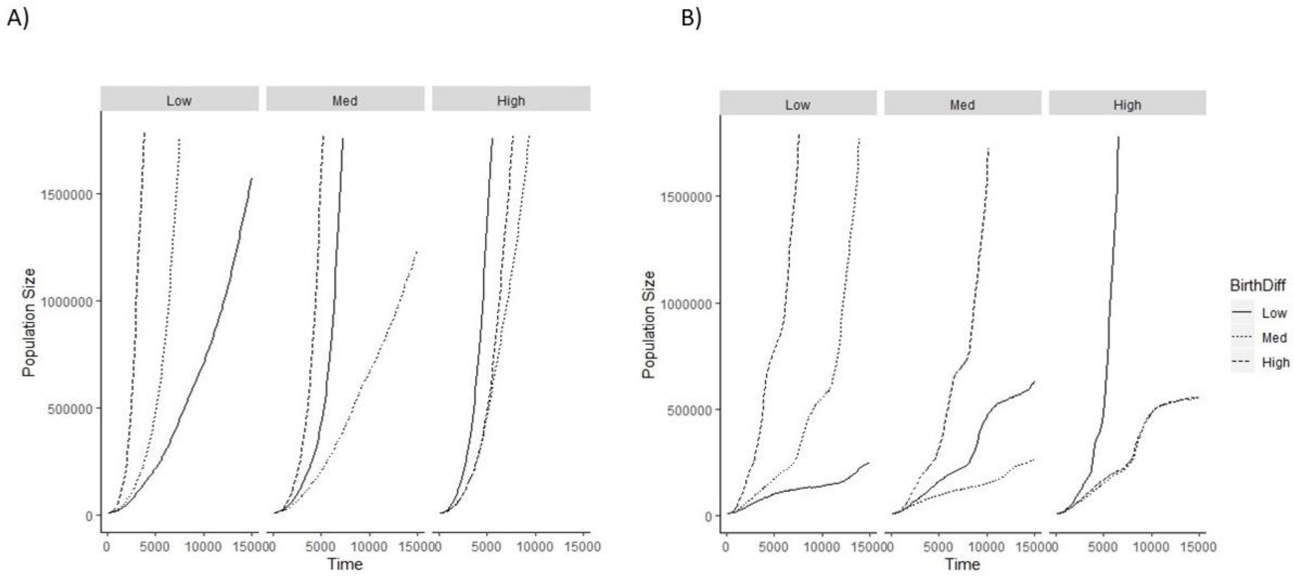
Mean Extraversion

The mean extraversion levels within this test were similar to those observed in the Homog test. As seen in the Homog test, *BirthDiff*, *DeathDiff* and to a lesser extent their interaction almost entirely account for the differences in mean extraversion between runs (see supplementary table 4). Although *Fluctuation Level* did not have a significant effect size, the pairwise interactions of the other parameters with *Fluctuation Level* did have a small effect when assessing all observations, but not the time slice at 3000 years. Therefore, while *BirthDiff* and *DeathDiff* are important determinants of mean extraversion, the interactions between these parameters and the stability of the environment only had a minor effect. Nevertheless, it is important to note that these results are confounded by not accounting for the variation in effects through time. When assessing the effect sizes through time, it can be seen that *BirthDiff* is highly determinative of mean extraversion. However, as noted above, an issue of using type 1 ANOVA is that the order the parameters are input impacts the results. When the parameters are reordered it suggests that *DeathDiff* may have a greater effect size during the later stages of the model (supplementary figure 16). Therefore, the importance of the selective advantages/disadvantages of extraversion may differ at different times in the model. Although, this may also be due to a greater loss of factor levels for *BirthDiff* than *DeathDiff* during the later stages of the model, which makes this suggestion uncertain. Further, as seen in supplementary figure 17, *Fluctuation Level* seems to have an observable effect on the mean extraversion of agents, increasing the extent to which it may fluctuate through the model. Increasing the *Fluctuation Level* also enlarged the range of mean extraversion values emerging from the models (supplementary figure 18). This may be due to population bottlenecks, caused by the narrower routes of expansion, leading to founder effects.

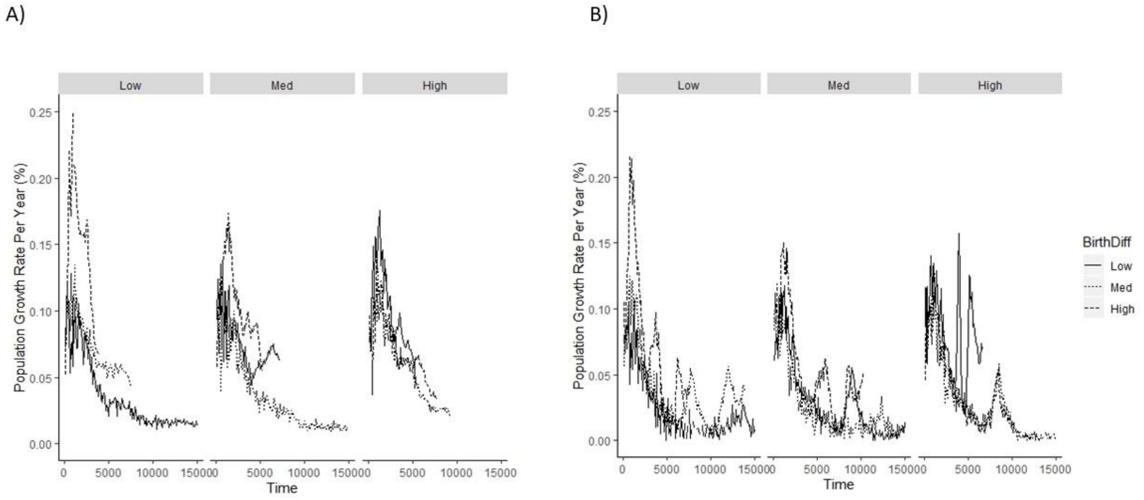
Supplementary Table 4. The effect sizes (η^2) of parameters on response variables (NS = not significant; P4 Var).



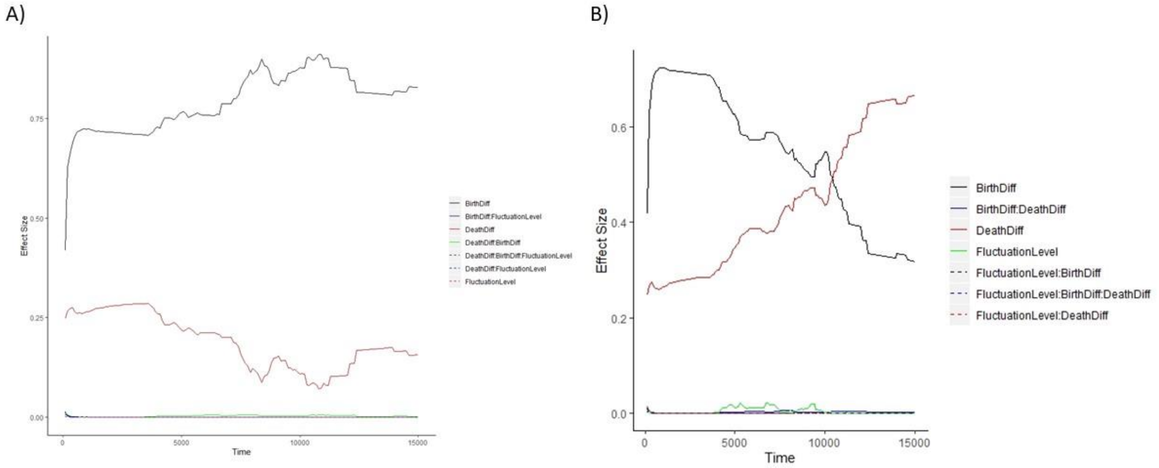
Response Variable	BirthDiff		DeathDiff		Fluctuation Level		BirthDiff:DeathDiff		BirthDiff:Fluctuation Level		DeathDiff:Fluctuation Level		BirthDiff:DeathDiff:Fluctuation Level	
	All Observations	*Time Slice (3000)*	*All Observations*	*Time Slice (3000)*	*All Observations*	*Time Slice (3000)*	*All Observations*	*Time Slice (3000)*	*All Observations*	*Time Slice (3000)*	*All Observations*	*Time Slice (3000)*	*All Observations*	*Time Slice (3000)*
Population Size	0.008	0.247	<0.001	0.061	0.027	0.135	0.010	0.306	0.011	0.077	NS	0.034	0.033	0.109
Population Growth	0.100	0.092	0.007	NS	0.177	0.583	0.169	0.120	0.014	0.04	<0.001	0.008	0.027	0.05
Mean Extraversion	0.414	0.711	0.174	0.284	<0.01	NS	0.050	<0.001	0.039	NS	0.014	NS	0.003	NS
Correlation Between Cell Mean Extraversion and Distance From Africa	0.131	0.218	0.037	0.120	NS	NS	0.045	NS	NS	NS	<0.01	NS	<0.01	NS
Correlation Between Cell Mean Extraversion and Cell Population Size	0.079	0.268	0.033	0.131	0.011	NS	0.016	NS	0.035	0.044	0.023	0.029	0.024	NS



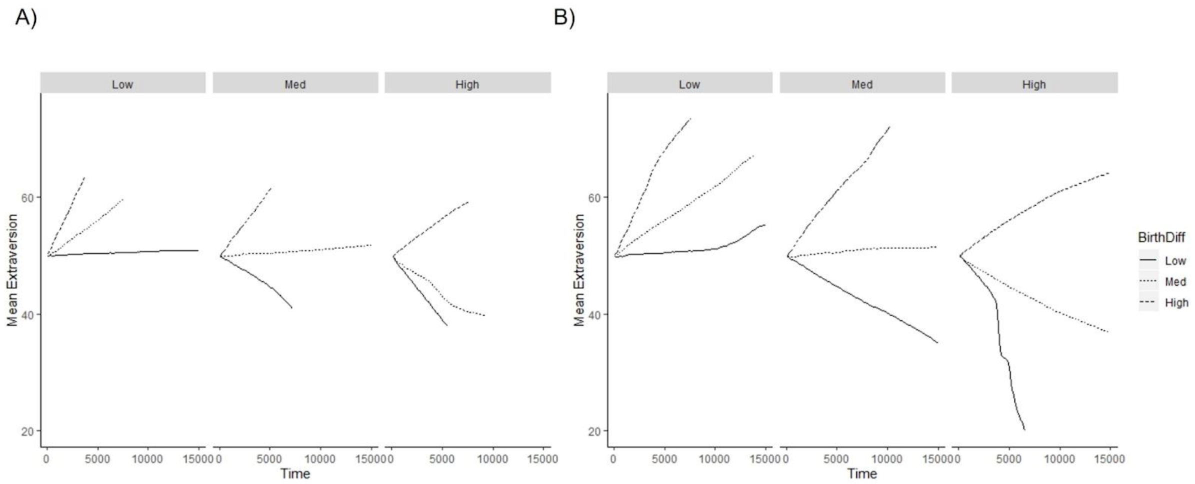
Supplementary Figure 14. Population sizes of runs of the model faceted by DeathDiff. A) Fluctuation Level = 0, B) Fluctuation Level = 1 (PRISM 4).



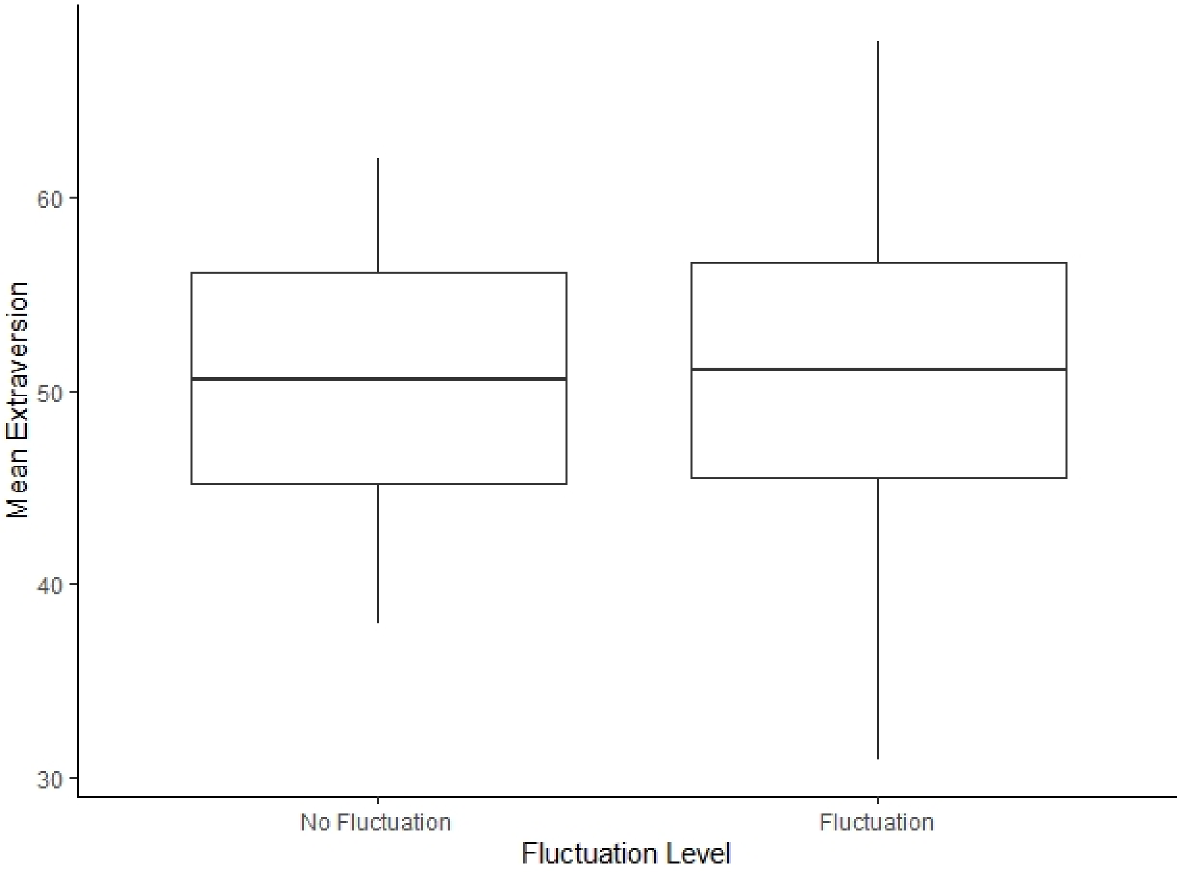
Supplementary Figure 15. Population growth rates per year of runs of the model faceted by DeathDiff. A) Fluctuation Level = 0, B) Fluctuation Level = 1 (PRISM 4).



Supplementary Figure 16. The effect size (η^2) of parameters on the mean extraversion of agents over time (PRISM 4 test). A) ordered according to the method above, B) ordered the alternate way.

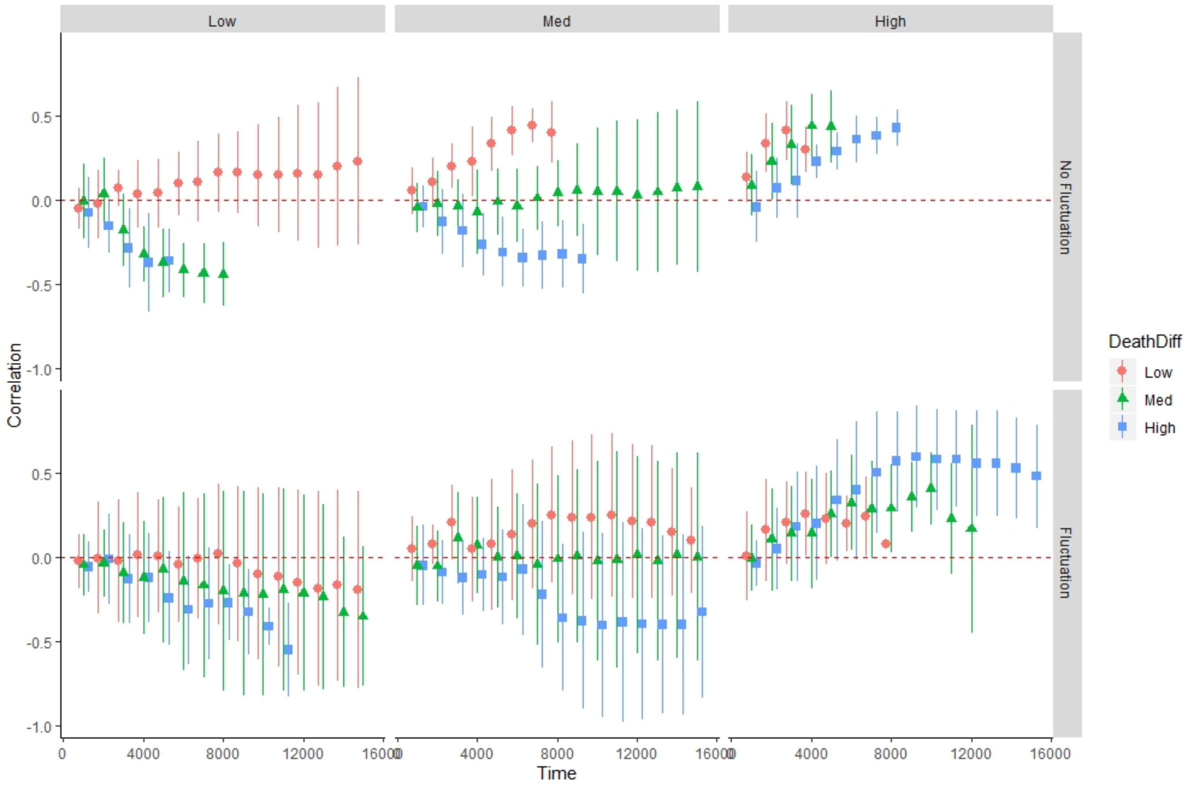


Supplementary Figure 17. Mean Extraversion of runs of the model faceted by DeathDiff. A) Fluctuation Level = 0 (PRISM 4), B) Fluctuation Level = 1 (P4 Var).

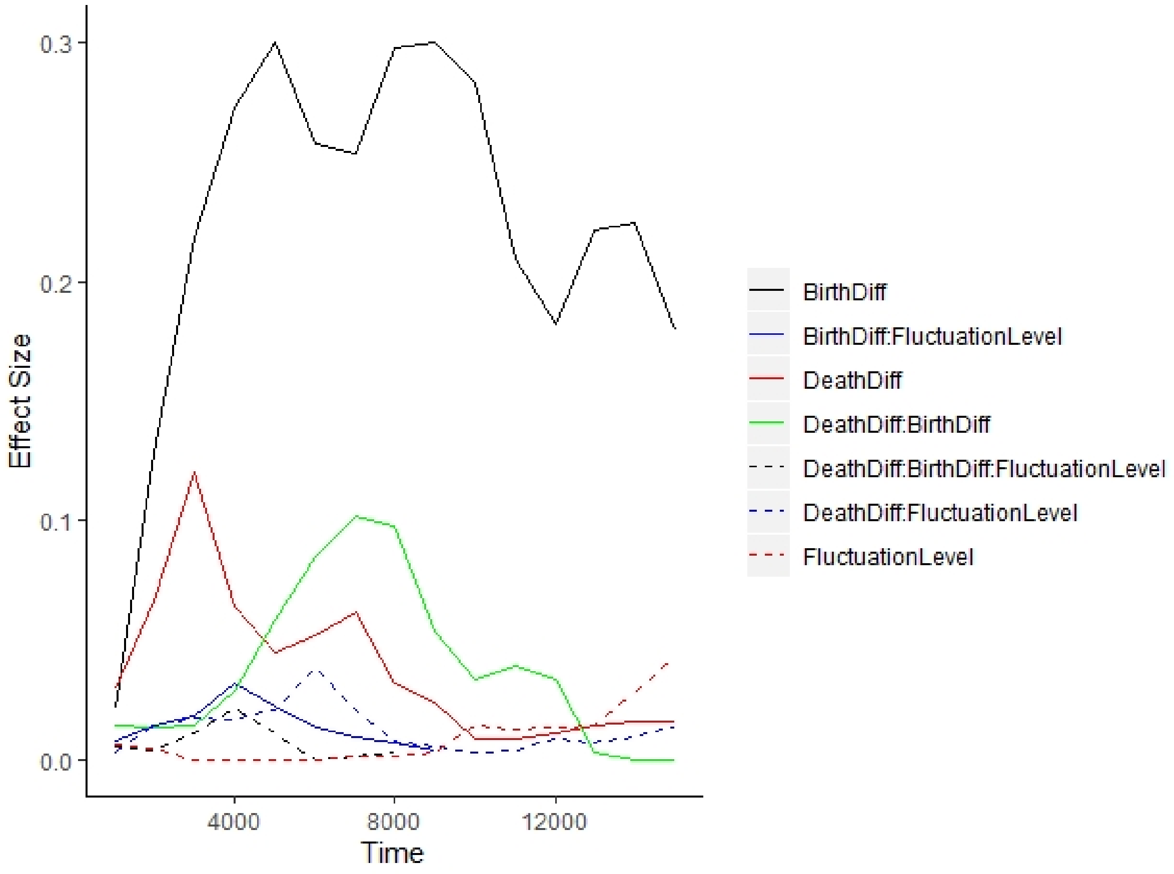


Supplementary Figure 18. Showing the effect of Fluctuation Level on the mean extraversion of each run of the model at 5000 years (P4 Var test).

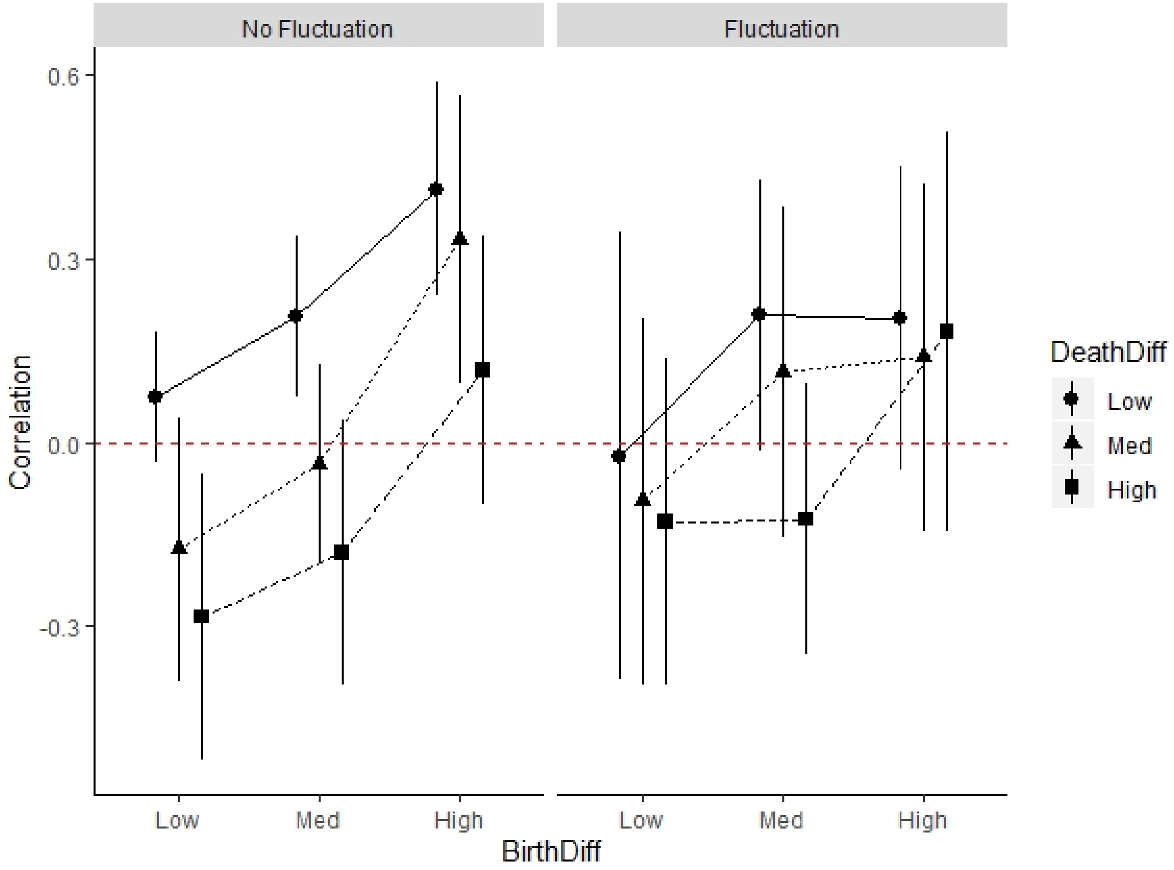
The correlations between extraversion and distance from the point of origin seen in the Homog test were replicated in the PRISM 4 and P4 Var tests (supplementary figure 19). Throughout the model this was primarily affected by *BirthDiff* (see supplementary table 4) and to a lesser extent *DeathDiff,* and their interaction, while the interaction between all three parameters and the pairwise interaction between *Fluctuation Level* and *DeathDiff* reached significance when assessing all observations (not when assessing the time slice), the effect sizes were small. Other effects did not reach significance. When assessing this over time *BirthDiff* also had the highest effect throughout the model (see supplementary figure 20), suggesting that the ability to disperse is associated with extraverts' reproductive advantages (see supplementary figure 22 and 23 for example maps of extraversion distribution). Reflecting the strength of its effects, within the PRISM 4 test (not including fluctuation in resources), the correlation clearly becomes more positive as the *BirthDiff* is increased (supplementary figure 21). Although as seen in supplementary figure 21, this correlation is also highly related to *DeathDiff*. Supplementary figures 19 and 21 also show that, similar to what was seen above with mean extraversion, adding fluctuation in resources increases the variability in the strength of this correlation. This is likely due to the increased stochasticity introduced by fluctuating resources, which may lead to founder effects occurring for populations with the disadvantaged phenotype. Further, there seems to be a greater interaction between *BirthDiff* and *DeathDiff* when there is fluctuation in resources in the model (supplementary figure 21). For example, a run with high *BirthDiff* and *DeathDiff* leads to a more positive correlation than expected when fluctuation is included in the run. This may be due to fluctuating resources reducing the routes agents may expand through, and decreasing population sizes in these areas. Meanwhile, high *DeathDiff* also causes reduced population sizes. While this would be protective within a scenario with selection for introversion, as extraversion is selected for in this scenario, this increases the average agent's probability of death. Therefore, this may reduce the amount of potential mates available at the front of the wave of expansion and may lead to increased selection for the most extraverted individuals. This effect becomes even more pronounced later in the model, with the association between *DeathDiff* and the correlation reversing for runs with a high *BirthDiff* (supplementary figure 19). This supports the hypothesis that the correlation is density dependent.



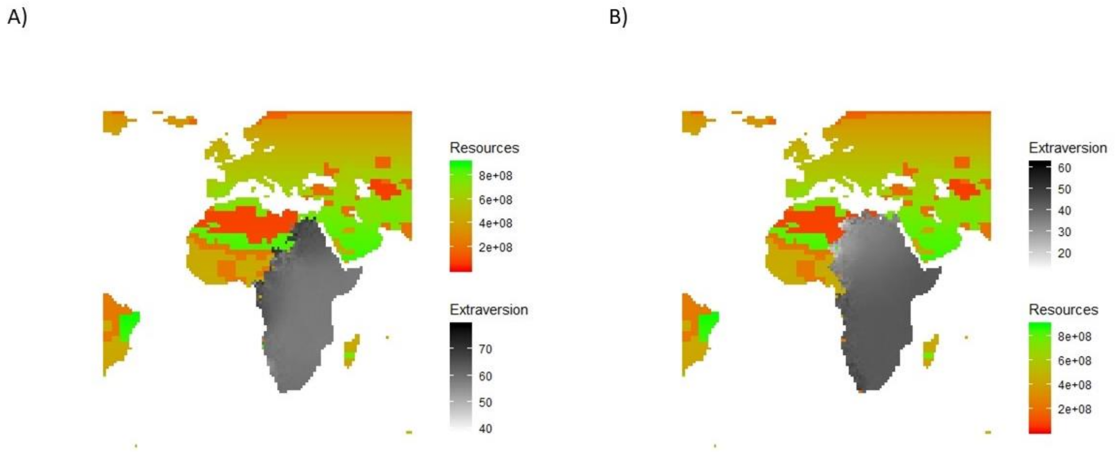
Supplementary Figure 19. The mean correlation coefficient between distance from the point of origin and extraversion through time (error bars = standard deviation). Faceted by BirthDiff and Fluctuation Level.



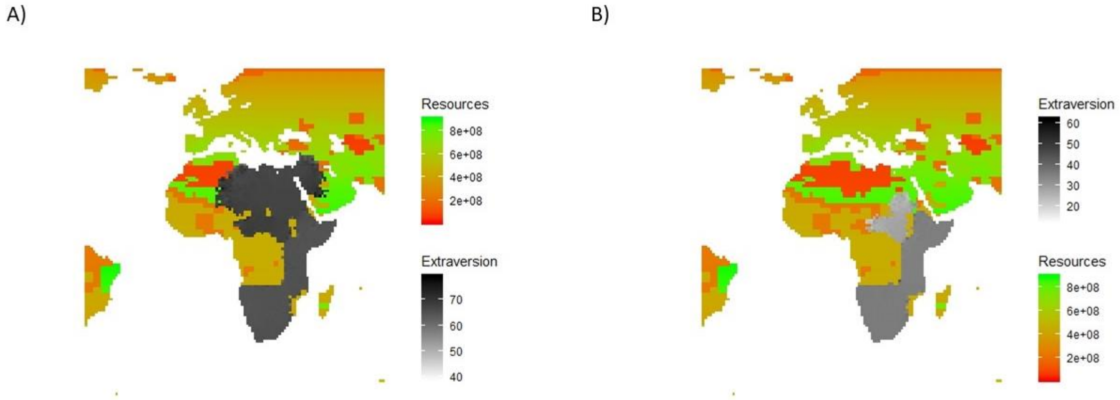
Supplementary Figure 20. The effect size of parameters on the correlation coefficient between extraversion and distance from the point of origin (P4 Var test).



Supplementary figure 21. Interaction plot of BirthDiff and DeathDiff, faceted by fluctuation level, showing the effect of the parameters on the correlation coefficient between extraversion and distance from the point of origin at 3000 years (error bars = standard deviation)*.*

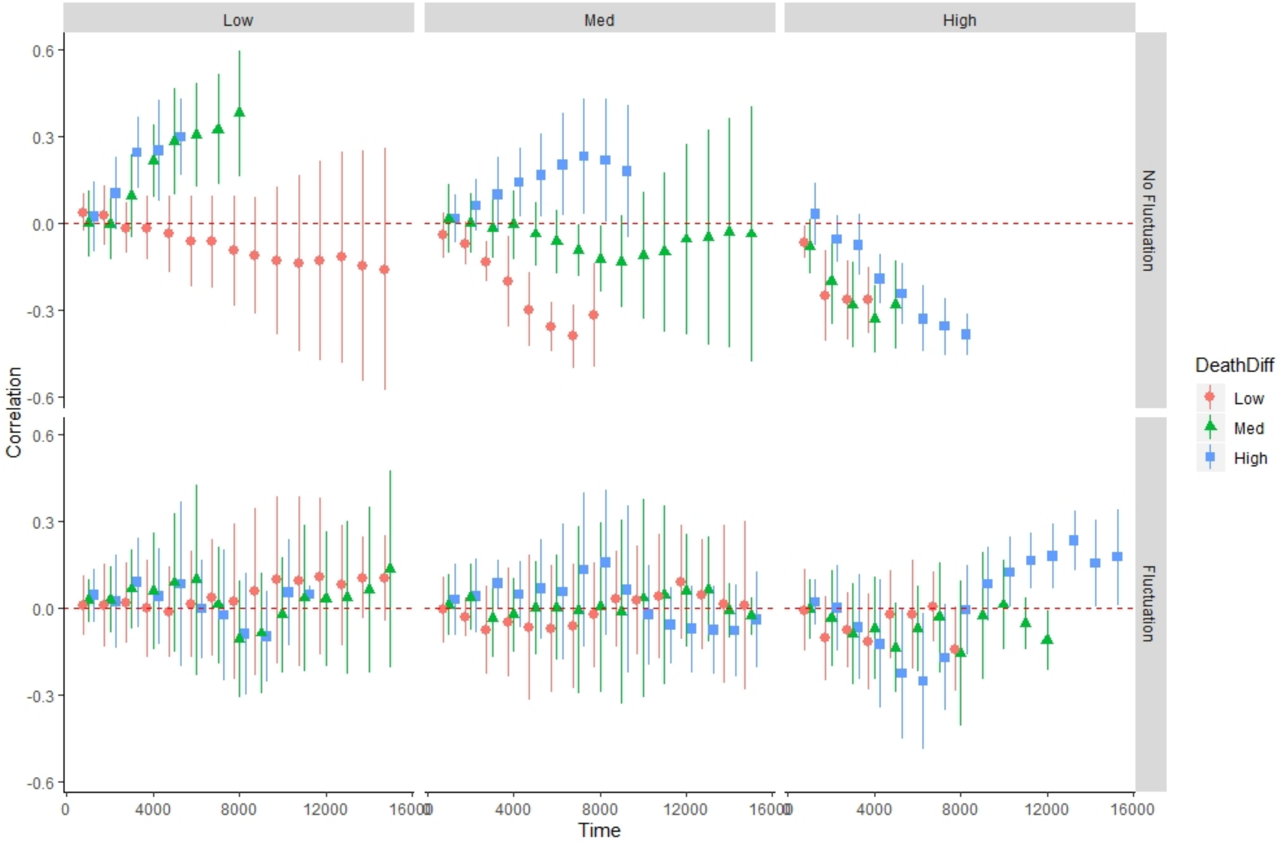


Supplementary Figure 22. The mean extraversion of landscape cells in example runs (A)BirthDiff = Mid, DeathDiff = Low; B) BirthDiff = Low, DeathDiff = Mid) when the model reached its end (7000 years in these cases) (PRISM 4 test).

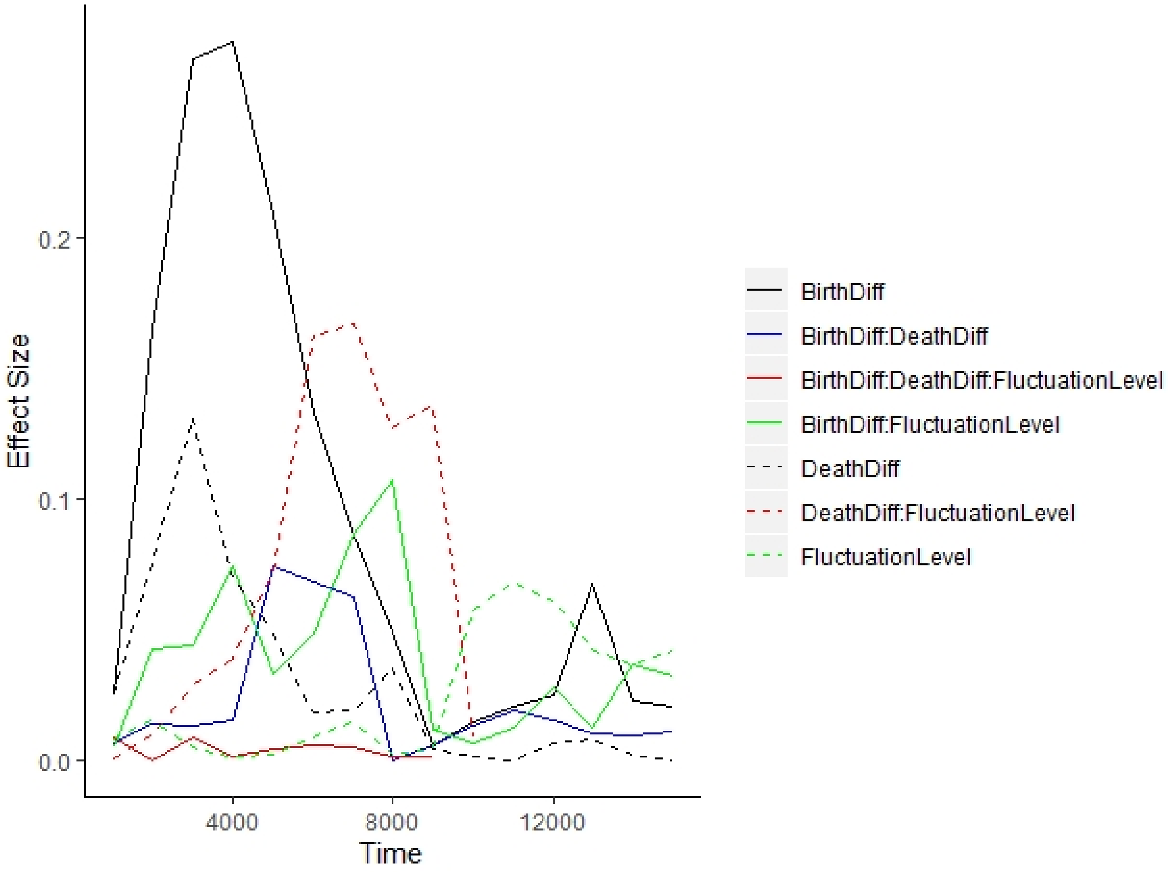


Supplementary Figure 23. The mean extraversion of landscape cells in example runs (A) BirthDiff = Mid, DeathDiff = Low; B) BirthDiff = Low, DeathDiff = Mid) when the model reached its end (13,000 and 15,000 years in these cases respectively) (P4 Var test).

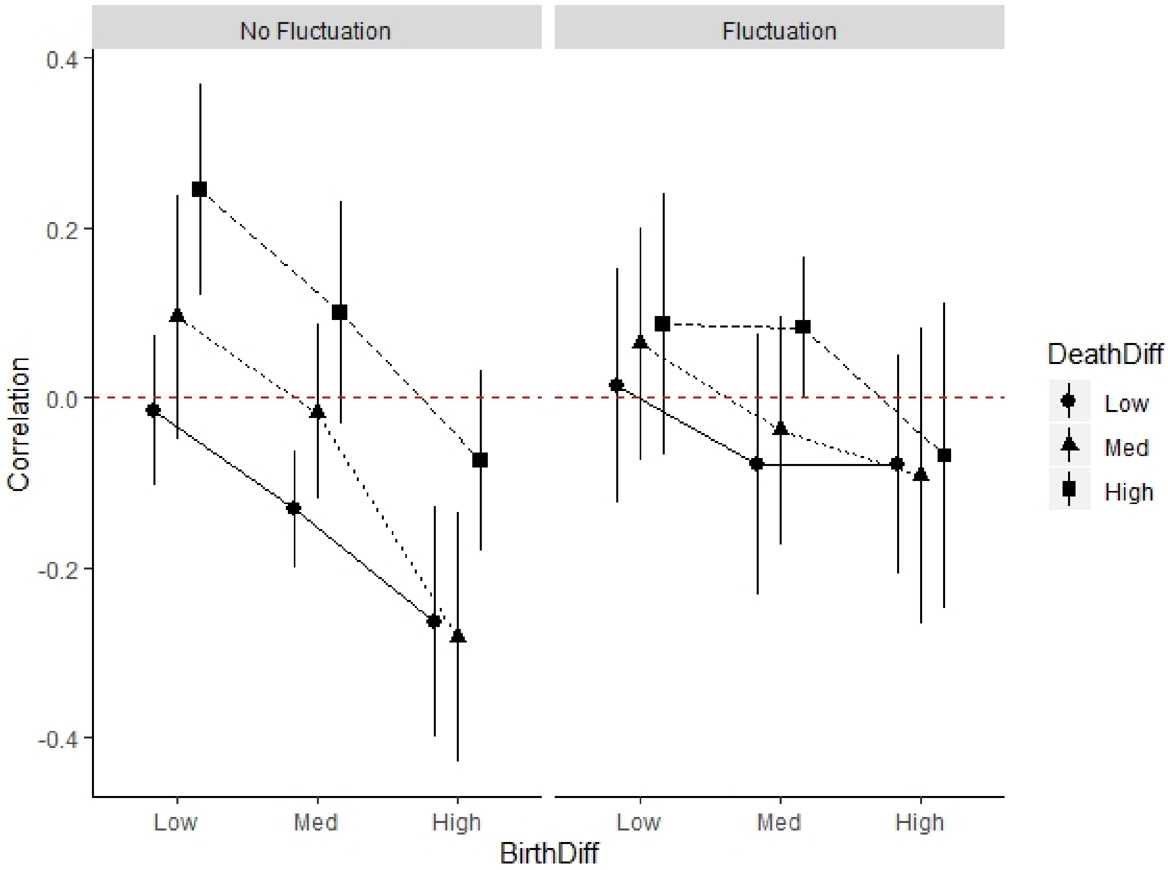
The hypothesis suggested in the Homog test as a cause for this relationship, that the favoured population, for example extraverts during runs where extraversion is selected for, are the initial migrants with introverts following when the population density has increased, is supported by similar correlations between the population size in landscape cells and extraversion during the PRISM 4 test (supplementary figure 24). However, while this correlation is retained in the early years of the *P4 Var* test (supplementary figure 26), it became more complex during the later years of the model (supplementary figure 24). This may be due to the increased stochasticity produced by the variability in resources, which causes variability in local population sizes. Further, the increased difficulty of dispersal may lead to the more successful phenotype having denser populations within the occupied area rather than smaller but more dispersed populations across the landscape. This is supported by the larger effect of the pairwise interactions between *Fluctuation Level*, *BirthDiff* and *DeathDiff* during the middle of the model (supplementary figure 25), at which time agents may have filled the occupiable areas in easter and southern Africa and not yet found a route out of this region. During runs that lead to lower population sizes, this correlation may also reverse, suggesting that groups do not reach a high enough density to produce the correlation, and in these cases population density is determined by the success of the advantaged phenotype. Nevertheless, the *P4 Var* test results still suggest that the advantaged phenotype is more likely to disperse.



Supplementary Figure 24. The correlation coefficient between cell population size and extraversion, through time. (error bars = standard deviation). Faceted by BirthDiff and Fluctuation Level.



Supplementary Figure 25. The effect size of parameters on the correlation coefficient between extraversion and cell population size for all runs (P4 Var test).



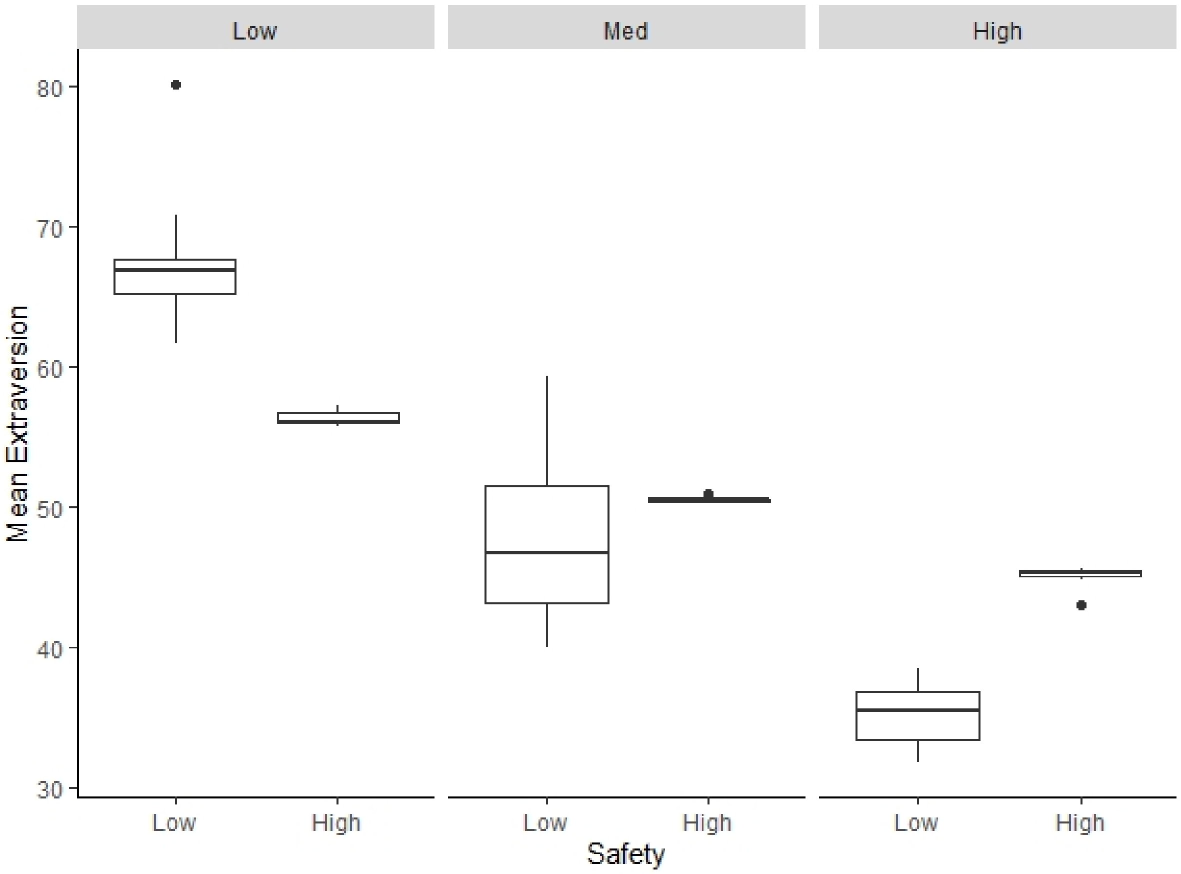
Supplementary figure 26*. Interaction plot of BirthDiff and DeathDiff, faceted by fluctuation level, showing the effect of the parameters on the correlation coefficient between extraversion and cell population size at 3000 years* (error bars = standard deviation)*.*

S2.3 Further Sensitivity Analysis

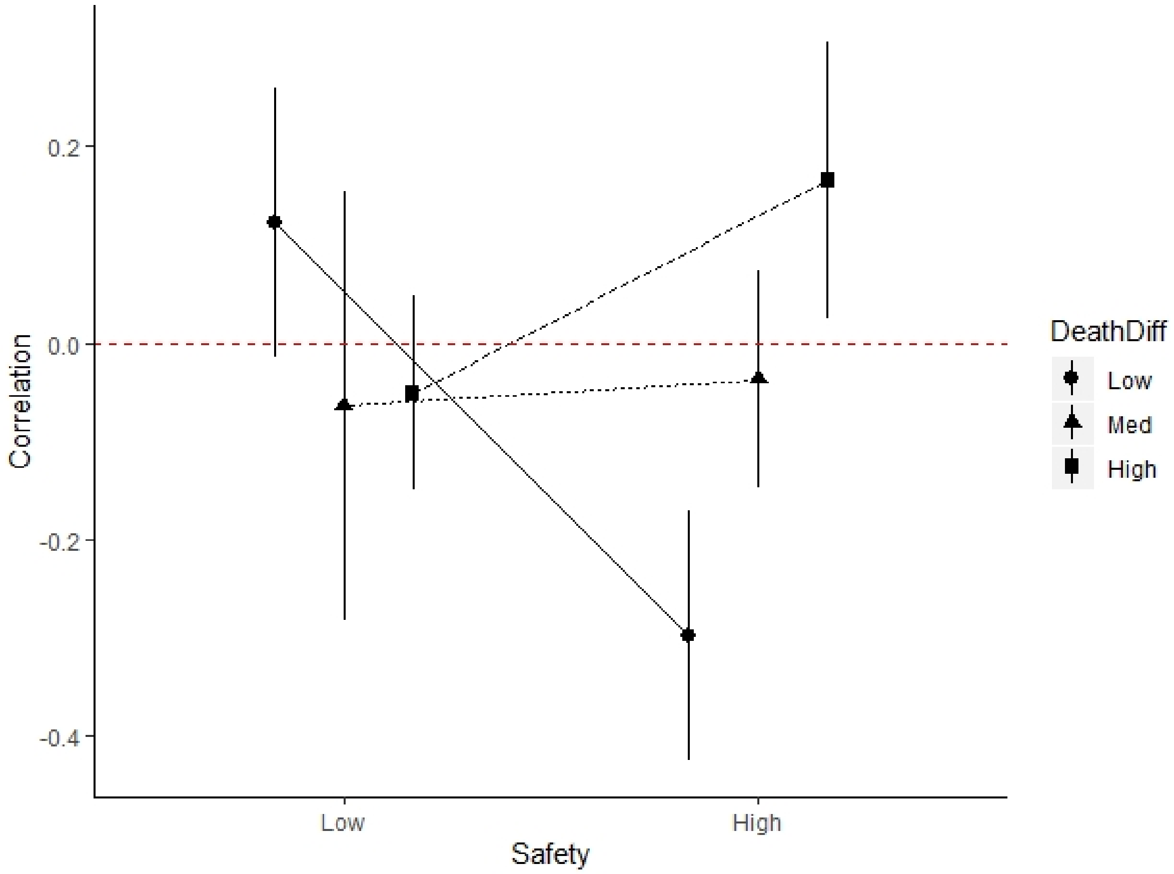
Two further sensitivity tests were performed on the model. Firstly, the effect of lowering the *Safety* within the model was assessed. Secondly, a test was performed to explore the effect of population size on selection for extraversion.

When testing the effect of reducing the *Safety* within the model (increasing the mean probability of mortality in the model for all agents, regardless of extraversion), all *DeathDiff* levels were used, while keeping *BirthDiff* at a constant ‘Mid’ value, to assess its effect when selection for extraversion was in different directions. These parameter combinations were repeated 10 times. It was found that a lower *Safety* led to a greater level of selection for the advantaged phenotype, and a greater range of mean extraversion values (supplementary figure 27). While this did not have a significant effect on the correlation between extraversion and distance from the point of origin, it did have a significant effect on the correlation with the cell population size (supplementary figure 28). Similar to what was seen with *Fluctuation*

Level above, when population sizes were reduced in the model due to the increased chance of mortality, this led to the correlation being the opposite of what was expected from the analysis above, with the mean extraversion of landscape cells being positively correlated with their population size, when extraversion was positively selected for. As above, this was likely due to population density being associated with the success of the advantaged phenotype, while in contrast to other runs, density levels hadn't reached the threshold where it significantly reduced the selective pressures on the disadvantaged phenotype. Therefore, rather than extraversion being selected for at a greater rate in the more sparsely populated areas of the model (e.g. in newly colonised areas), the low population levels meant that the selective pressures for their reproductive advantage was still high even in the more densely populated areas in these runs. Hence, the higher population sizes were a reflection of their success rather than due to density dependent differences in selection. However, in these runs, when that threshold was reached later in the model, the correlation became more negative. Therefore, counterintuitively in a scenario with positive selection for extraversion, if a population becomes large, the average extraversion of the population will be larger in the more sparsely populated areas, due to increased selective pressures for extraversion. This likely accounts for the increased selection for the advantaged phenotype in more dangerous environments, which are more sparsely populated.

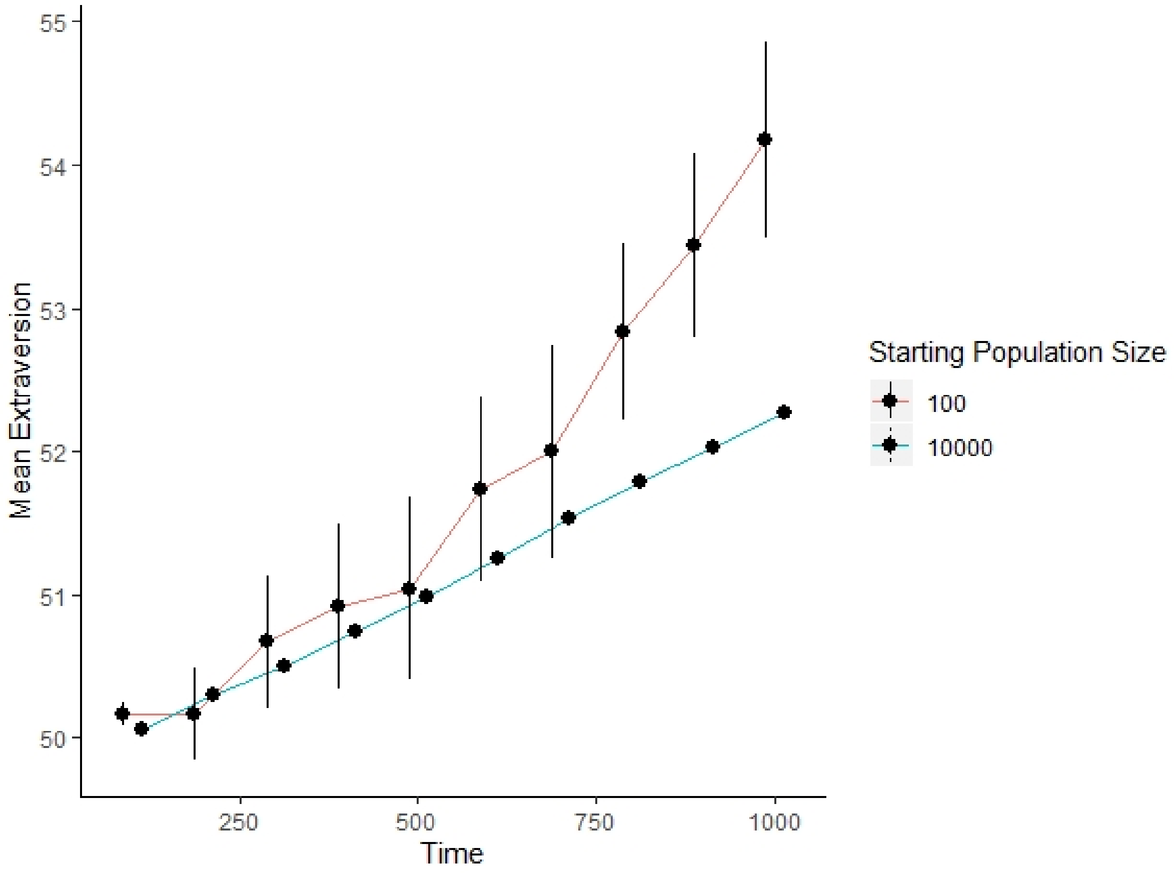


Supplementary Figure 27. Boxplot showing the effect of Safety level on the mean extraversion within runs of the model at 5000 years (the last point at which parameter variation is maintained), faceted by DeathDiff (N = 10 for each parameter combination).



Supplementary Figure 28. Interaction plot showing the effect of Safety level on the correlation coefficient between extraversion and cell population size at 5000 years. Due to overall population sizes being low in scenarios with low Safety, pressures for reproduction are high, and only the most extraverted agents are able to produce larger cell population sizes. Hence, there is a positive correlation between extraversion and cell population size. In contrast, when Safety is high, cell populations are already larger and selective pressures are only accentuated in less densely populated areas, leading to a negative correlation between extraversion and cell population size (error bars = standard deviation).

To test the effect of population size upon the strength of selection for extraversion, two sets of 10 runs were completed using the Homog environment. The first set started with a lower population size (n = 100), while the second set started with a larger population size (n = 10,000). All other parameters were identical (*BirthDiff* = High, *DeathDiff* = Med). In order to remove the effects of dispersal, agent movement was turned off. This test found that runs which started with a smaller population size had greater selection for extraversion (supplementary figure 29), further showing that extraversion is selected for to a greater extent in smaller populations, and that this selection is density dependent.



Supplementary Figure 29. Mean extraversion over time for two starting conditions (n = 10) of the model, one with a smaller starting population (n = 100), one with a larger starting population (n = 10,000). Showing that selection for extraversion is increased in the smaller population (error bars = standard error).

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Discussion and Conclusion

Introduction

Humanity is characterized by a wide variety of psychological and cognitive differences. As has been noted through this thesis, the evolutionary importance of this variability is a subject which has not been extensively discussed, and has been met with resistance. Further, previous attempts have largely focused upon individual examples of our diversity. While this thesis also focuses upon particular examples (e.g. extraversion), it has attempted to broaden the discussion and investigate the causes and possible advantages of personality and cognitive differences simultaneously. By using an interdisciplinary approach, applying information from archaeology, ethnography, psychology, evolutionary ecology, and using computer simulation methods, this project has approached this subject in a new way.

This thesis has explored how individuals with different psychological traits, and consequently life history traits, may be differently adapted to their environments, and the evolutionary implications of this difference. Chapter 1 explored the diversity of one aspect of our psychological variability, our personality. This reviewed how personality traits may affect an individual's life history, and any associated selective advantages and disadvantages. Chapter 2 then explored extraversion in more depth as a case study of personality difference. Chapter 3 explored the broader evolutionary mechanisms which may have increased cognitive and psychological diversity, and specifically how they may have evolved in humans. The selective benefits of two examples of psychological diversity (autistic traits and extraversion), and their possible contribution to our evolutionary success within the Palaeolithic, were then discussed. Chapter 6 then explored an example of how the life history differences associated with extraversion may have impacted a specific event in human history, dispersal out of Africa. To accomplish this, a review of previous ABMs was conducted (chapter 4), and a dispersal model was created with a realistic environment and resource usage, building upon previous methodology (chapter 5). Life history differences to reproduction and mortality, based upon the psychological literature (chapter 2), were then applied to agents, based upon a score reflecting how extraverted they are (chapter 6). This revealed that the increased reproductive rate of extraverts may make them better dispersers and may be responsible for the global distribution of genes associated with extraversion (described by Chen et al. 1999; Matthews and Butler 2011; Wang et al. 2004).

This thesis has allowed us to gain a new understanding of how individual differences in personality and cognition may have contributed to our evolution. It accomplished this by investigating the effect of personality and cognitive difference on our evolution both broadly, and by focusing upon specific case studies of types of difference and specific past events, using an interdisciplinary perspective. In particular, this thesis has significant implications for three areas of research, which will be expanded upon in the current discussion. Firstly, how our psychological diversity may have affected our dispersal out of Africa. Secondly, how our psychological diversity evolved and may be partially responsible for our species' success and ability to adapt to different environmental conditions. Thirdly, the implications of this thesis for our broader understanding of human dispersal, and how ABM may be particularly useful for investigating this.

1. The Impact of Psychological Diversity on Dispersal

This thesis has provided a new perspective of the dispersal of our species. By creating an agent based model (ABM), exploring the effects that variation in extraversion may have had upon the out of Africa dispersal (~75 ka), and the mechanisms which may have affected the distribution of genes associated with extraversion, this thesis has highlighted the impact our diversity may have had upon a specific event in our evolutionary history (chapter 6).

The results of this model have shown that the reproductive advantage associated with extraversion may lead to an increase in extraversion towards the wave front of a dispersing species, despite the costs of an increased mortality risk (up to a threshold). This is due to this advantage reducing the negative impacts from Allee effects (in this case caused by a reduction in potential mates at the sparsely populated wave front). Therefore, this model has shown that if extraverts had a reproductive advantage, as the psychological literature reviewed in chapter 2 suggests, this alone may cause the increased prevalence of dopamine receptor genes associated with extraversion further from Africa (Chen et al. 1999; Matthews and Butler 2011; Wang et al. 2004). While in the model reproducing agents had an increased chance of movement due to a function representing mate exchange, sensitivity analysis in chapter 6 suggested that the reproductive advantage causes increased selection for extraversion in sparse populations. Therefore, this spatial distribution may occur independent of increased mobility. As discussed in chapter 6, within the context of evolutionary ecology, this type of diversity within a dispersing species is not unexpected. As will be discussed further below, the ability to form disperser/resident phenotypes may have significant implications for dispersal. Within the real world this may increase dispersal in two ways: 1) It may lead to runaway selection, leading to more accentuated dispersal phenotypes; 2) it may lead to dispersers being pulled towards sparsely occupied regions as they experience less success in large populations (Erm and Phillips 2020). Consequently, not only may dispersal have an impact upon phenotype distribution, but our diversity may also have had a significant effect on our dispersal. The implications of this will be discussed further below.

It has been difficult to ascertain why modern humans dispersed as rapidly as the archaeological evidence suggests. The points made above may provide a new perspective on this debate. Thus far, theories have focused upon social or ecological explanations for this dispersal speed (Mellars 2006; Spikins 2015; Stringer 2000). However, Bar-Yosef and Belfer-Cohen (2013) have argued that behavioural differences within and between human populations may have had a significant impact on the success of those groups dispersing. They have argued that differences in intuition and emotion affect decision making, and therefore may have had a significant impact upon key moments in our evolutionary history. While they focus upon personal experience and social codices and how they affect the emotional system, personality differences, as well as other psychological and cognitive differences, significantly affect decision making and should also be considered. It is important to note that, while extraversion has been a focus of this thesis, it is only an example. Other behavioural and cognitive differences have likely also had a large effect on our species’ ability to disperse.

Acknowledging our differences may add considerably to existing theories of dispersal, help generate new theories, and provide a greater understanding of the motivations behind movement. For example, Spikins (2015) has suggested that expulsion events due to conflict may have caused humans to disperse rapidly. She highlights that even major barriers to dispersal, such as sea crossings, were surmounted. Risky environments seem to have been attractive despite large disadvantages (e.g. cold northern environments). Meanwhile, no ecological push factors are sufficient to account for the rate of dispersal. Therefore, Spikins has suggested that moral dispute may have been a push factor motivating dispersal. It is probable that personality differences and their associated life history differences (see chapter 1) may have had a significant impact upon this process. Firstly, people with high extraversion are more likely to engage in criminal and sexually risky behaviour which may lead to moral disputes. Further, as shown in this thesis, they have attributes which may make them more successful dispersers. Finally, their better leadership and social abilities may make them better at gathering followers to establish a new group. Consequently, moral dispute may be another factor which led to the current distribution of extraversion. Beyond extraversion, other personality types may have increased the likelihood of moral disputes.

Psychoticism is associated with behaviours (e.g. aggressiveness and sexual deviance) that decrease social reputation and may increase conflict. Further, while psychoticism may increase impulsivity and lead to faster reproduction, many of the advantages of psychoticism function through deceptive cheating. As a result, while people with high psychoticism may be more likely to be ostracized in the way Spikins (ibid) describes, they may be less likely to construct new groups and be successful dispersers if they have been caught in acts of deception and have a low social reputation. Rather, they would be most successful when taking advantage of an established, ignorant population. Individuals who have a high openness to experience may also be a phenotype more likely to disperse in this way. They may experience resistance to their new ways of thinking from traditionalists, which may lead to disputes. Additionally, their innovative abilities may increase their success in new environments relative to their conspecifics. In contrast, individuals who are highly conscientious and agreeable are less likely to be involved in moral disputes and therefore are unlikely to disperse in this way. In summary, personality types that are more likely to be engaged in disputes may have been more likely to disperse in the way Spikins describes, particularly if they were also able to maintain their social status.

Whilst we should be careful in making generalisations about differences between populations, as expected from this discussion, extraversion and openness are elevated and agreeableness is lower in European and American populations in comparison to Asian and African populations (Allik and McCrae 2004; Schmitt, Allik and McCrae 2007). Although these results are also likely related to the modern cultural characteristics of these populations, such as political beliefs (McCrae and Terracciano 2005), and research into cross cultural differences in personality are challenging (see chapter 1), this may also suggest that these traits in particular had an impact upon our dispersal from Africa (and vice versa). Olson (2007) has argued that selective emigration of individuals with these phenotypes may have led to this distribution, due to them being most attracted by new environments. However, this distribution is likely the result of multiple pressures and occurred in multiple ways (Rentfrow, Gosling and Potter 2008; Rentfrow 2020), including through moral dispute. Further, multiple island populations were found to have lower extraversion and openness to experience and higher conscientiousness compared to mainlanders, emigrants and immigrants, suggesting that these phenotypes are less dispersive (Camperio Ciani et al. 2007; Ciani and Capiluppi 2011). Several other studies have also associated high extraversion and openness to experience with movement (Crown, Gheasi and Faggian 2020; Jokela 2009; Jokela et al. 2008; Shuttleworth et al. 2021). While this has previously been suggested to be the result of individuals with these personality traits leaving isolated populations, or searching for more suitable environmental niches for their traits, or just generally being more attracted to novel environments, it may be that people with these personality types are also more likely to be involved in disputes that lead to population fission or movement.

A second theory which may benefit from a psychological diversity perspective is Dennell's (2017b) naive prey hypothesis. Dennell suggested that hominins dispersed so fast because they were coming into contact with naive prey that didn't know the danger a primate could present. Once prey became aware of the danger of humans, the humans would then move on and return when the prey were naive again. Interestingly, Dennell (2017a) argued, following Meltzer (2009, 235), that there are two colonising strategies employed by hunter gatherers. "Bolder" colonists move between places with lower resource productivity/stability which are unsuitable for long term occupation, and move when yields decline, using a more risky strategy that leads to a faster rate of dispersal. "Cautious" colonists occupy areas of high productivity/stability and disperse to similar areas at a much slower rate. He has argued that bold dispersers would be much more likely to capitalize on naive prey. While these terms characterize groups, it is likely that the strategies those groups utilize are determined in part by the personality of their members and their collective personality (Ogunfowora and Schmidt 2015). Therefore, we may speculate that this is another theory that would benefit from explicit integration with personality theory. While explicit research is needed, we may suggest from the discussion above that members of more bold groups would be characterized by increased extraversion and openness to experience. Extraverts' impulsivity, and the attraction to novel situations shared by extraverts and those with high openness, may increase the likelihood of adopting a bold strategy, which increases their likelihood of moving to novel environments. Further, individuals with high openness to experience may be more willing to adapt to exploiting different prey and environments, making them more successful at using this strategy. Consequently, Dennell's suggestions may highlight another aspect of the dispersing niche that may particularly favour extraverts and individuals with high openness to experience, or even may be a manifestation of the behaviour associated with these traits.

A final example where a psychological perspective may add to existing theory is Bar-Yosef and Belfer-Cohen (2013) disease prevalence theory. They have argued that high rates of disease would have been a push factor out of Africa. We may suggest that, due to their increased social contact, extraverts may be more likely to contract diseases. This is true in a modern context and is supported by a reduction in preference for extraverted faces when people believe they may become infected with a disease (Brown and Sacco 2016; Brown et al. 2019), and a greater difficulty for extraverts to abide by social distancing rules during the covid-19 pandemic (Wijngaards, Sisouw de Zilwa and Burger 2020). Historic disease prevalence is also negatively related to modern reported levels of extraversion and openness to experience, which is likely the result of selective pressures reducing the prevalence of phenotypes that are susceptible to disease (Schaller and Murray 2008). Therefore, it is highly likely that as populations moved out of Africa people with high levels of extraversion and openness to experience would have experienced a greater benefit when colonising areas with low pathogen rates.

There are other debates to which personality differences may contribute. People high in neuroticism may be disproportionately affected by disease prevalence. They are more likely to have developed psychopathologies during the covid-19 pandemic (Lee and Crunk 2020; Mazza et al. 2020a, 2020b, 2021), suggesting that they are more distressed by the conditions of high pathology than those low in neuroticism (Chin 2020). While this may be due to other factors, such as isolation caused by lockdown, it is likely that this is due to an increased fear of catching the virus. As has been noted by Chin (2020), this distress may have negative consequences, such as feeling overwhelmed, which may decrease performance on tasks. However, it also increases the likelihood of reporting symptoms (either real or imagined) to others, which may have positive outcomes in a highly pathogenic environment. Therefore, neuroticism may be protective in a pathogenic environment. Schaller and Murray (2008) found evidence that neuroticism was positively correlated with disease prevalence. However, this finding was not statistically significant. Individuals with high neuroticism also avoid ambiguous stimuli and adopt a “better safe than sorry” strategy (Lommen, Engelhard and van den Hout 2010). This may mean that they are less willing to leave a known region to explore the unknown. Hence, it is uncertain whether neuroticism levels would change in dispersing populations, and this is one area which might benefit from future research.

Whilst we should be careful not to place too much emphasis on population differences in average personality traits, there are some interesting and notable patterns. Population personality has been associated with broader social, political and geographic conditions. For example, on a smaller scale in the United States, personality was associated with geographical topography (Götz et al. 2020; Oishi, Talhelm and Lee 2015). Further, personality has been associated with temperature, with more clement environments being inhabited by more extraverted and open individuals (Wei et al. 2017). Individuals also spatially sort themselves based upon neighbourhood characteristics and urbanisation (Jokela et al. 2015; Oishi 2015). For example, people with high conscientiousness tend to live in suburban areas, while people high on openness live in the city centre, with life satisfaction being associated with personality-environment matching. Therefore, more specific environmental factors may have influenced the choices of our ancestors when deciding whether or not to disperse.

The discussion above has shown that broader factors than those accounted for in the ABM may have also contributed to the current global distribution of personality factors. This section suggests that extraversion and other personality traits may have been under positive selection during dispersal for several reasons. As shown in chapter 6, the reproductive advantage associated with extraversion would likely have mitigated the reproductive pressures associated with low population densities when dispersing. Further, by exploring the ways psychological and cognitive variation may have affected the mechanisms suggested by other theories, several further implications of this research may be suggested.

Firstly, we may suggest that phenotypes that are likely to be involved in moral disputes would be more likely to disperse. Secondly, we may suggest for future research that “bold” strategists’ behaviour is more similar to what would be expected from more extraverted or high openness groups. Thirdly, phenotypes more susceptible to disease would benefit most when dispersing from Africa into more northern latitudes. The different causes of dispersal outlined above have likely simultaneously impacted populations to different degrees across time and space. Although extraversion has been used as an example of difference within this study, this review suggests that it is the phenotype most impacted by both push factors of dispersal (e.g. disease, moral dispute), and most advantageous in a dispersed or highly mobile population.

However, there are areas for further study. Other personality traits may have also been advantageous when dispersing. For example, openness to experience has been shown to have a similar geographic distribution to extraversion, which may suggest it too was under positive selection during dispersal. As seen above, this may be due to the same push factors as extraversion. However, the advantages associated with openness are likely associated with a better ability to exploit their new environment. Other personality traits, such as neuroticism, may also be associated with dispersal and further research should be conducted to explore this. In particular, whether neuroticism provides protection against transmissible diseases, which would lead to highly neurotic individuals gaining less of an advantage from dispersing away from pathogenic environments, or whether the increased distress experienced by neurotic individuals during pandemics/epidemics would be a push factor leading to dispersal. Additionally, other geographic factors have an effect on habitat selection and how this relates to personality, which may impact global personality distributions. Therefore, beyond what has been assessed in this thesis, personality distributions were likely affected by a wider range of pressures as well as opportunities during dispersal, and other traits were probably significantly impacted by and had an effect on our dispersal. This section also shows that peoples' success in the different ecological and environmental settings associated with dispersal was likely to be influenced by their psychological traits.

2. The Evolution of Cognitive and Behavioural Diversity

Our psychological and cognitive diversity has likely enabled our species to adapt to a wide range of environments and ecological settings. This section reviews the findings of several relevant chapters of this thesis and discusses them more broadly. In particular, how individuals' psychological traits affect their preference for different working and living conditions is discussed. Following niche construction theory, the evolutionary implications of these preferences are discussed. Their significance for theories of division of labour and specialisation is considered. How this may have increased our ecological niche, and ability to adapt to changes in climate is also discussed. Two examples of technologies that would have required specialisation, which increased our niche width, are discussed.

Chapter 1 explored the diversity of personality types and the ways in which they have been taxonomised. As well as enabling the identification of extraversion as a reliable example of difference for use in this thesis, it highlighted the extent of our behavioural variability. This variability has been reduced into a small number of factors. However, it is important not to dismiss the importance of the lower level traits (i.e. facets) which are subsumed by these factors. The fact that our species is characterized by such a large amount of lower level traits highlights the complexity of our psychological diversity. The life history implications of personality traits and their associated behaviours were also explored, identifying multiple evolutionary tradeoffs. Our diversity, however, goes beyond these personality and trait differences, with members of our species exhibiting a wide range of cognitive differences. This diversity has been argued to be either selectively neutral or detrimental (Bednarik 2013, 2016; Pickard, Pickard and Bonsall 2011; Tooby and Cosmides 1990). In contrast, chapter 3 has argued that this diversity may have had significant advantages for our species. Within particular contexts, different traits may thrive. In particular, as populations increased in size, cultural complexity, and niche diversity, a wider range of cognitive and behavioural differences may have been beneficial. Therefore, selection would have favoured diversity rather than uniformity. Chapter 3 used extraversion and local processing bias as examples to explore how this may have developed. This section will discuss the evolution of this diversity, and its adaptive benefits more broadly, with particular attention paid to the importance of niche assortment.

Within the context of the previous section it is easy to see that different personality types are better adapted to certain contexts. The primary example from this thesis is that extraverts are better adapted to disperse. Beyond this, individuals with high openness may be more drawn to areas with more opportunity or uncertainty. Within the past these environments may have been uninhabited landscapes, where extraverts and people with high openness may set up new groups and become high ranking. Hence, the mean level of these traits would increase along our path of dispersal out of Africa (Olson 2007). This needs to be explored within traditional groups. However, within a modern WEIRD context (Western, educated, industrialized, rich, and democratic), cities seem to take the role of uncertain places of opportunity (Jokela et al. 2015).

Patterns of dispersal influenced by diverse personality types are also evident in a modern context. For example, people living within the same postal district tend to have similar personality types, suggesting that niche assortment is a feature of modern living (Jokela et al. 2015; Oishi 2015). This is further supported by findings that some personality types are better at working alone (openness, conscientiousness) than others (extraversion, neuroticism) (Neal et al. 2012). Further, various authors have suggested that personality types are associated with different RIASEC interest types (Realistic, Investigative, Artistic, Social, Enterprising, Conventional). Extraverted and agreeable people are suggested to be more interested in Social vocations, with extraverts also being interested in Enterprising vocations, while openness has been associated with having Artistic and Investigative interests (Barrick, Mount and Gupta 2003; Larson, Rottinghaus and Borgen 2002). Conscientiousness was associated with Enterprising and Conventional interests (Armstrong and Anthoney 2009). Similar results were found when assessing the lower facets of personality traits (Armstrong and Anthoney 2009). Importantly, people doing the same job tend to have similar personality traits (King et al. 2017). It has even been suggested that if an individual is in a working environment that does not match with their personality, they may need to find ways to change their workplace, or the individual may need to change jobs in order to find an occupation which suits their personality (Brown and Hirschi 2013). For example, if people differ significantly from the mean level of neuroticism and openness found in their occupation, this predicts lower job satisfaction (Törnroos, Jokela and Hakulinen 2019). People select environments they find attractive, and are selected out of environments which do not suit them (Schneider 1987). Törnroos et al. (2019) found that mean personality levels differ for different occupations. For example, extraverted people tend to work in management and public services. Construction, managerial and healthcare workers have the lower mean levels of neuroticism. Conscientious people work in skilled trades and management, while agreeable people work in personal care, leisure and teaching. People with high openness work in the media, sports, research and teaching. Today, our personality differences are very influential when deciding where to work and live. While research of this nature needs to be applied to more traditional societies, we should expect that peoples' personality types played a significant part in determining their roles within groups within the past. This would have been increasingly important as cultures became more complex and task diversity increased.

Looking at wider cognitive differences, individuals with autism spectrum conditions or traits of autism are often drawn to STEM careers or educational programs due to their enhanced understanding of complex systems, and high attention to detail (Baron-Cohen et al. 1998; Janšáková and Kyselicová 2020; Wei et al. 2013). Supporting this, individuals with Asperger's are also more frequently employed in Investigative or Conventional vocations (Lorenz and Heinitz 2014). It has been shown that this may provide considerable benefits for companies. For example, a neurodiverse software-testing team, incorporating people with ASC, in Australia's Department of Human Services, was found to be 30% more productive than other teams (Austin and Pisano 2017). People with ASC also frequently exhibit artistic and musical skills, as well as other special isolated skills that may provide them with advantages within particular occupations (Meilleur, Jelenic and Mottron 2015). However, it is important to appreciate the diversity of interests of people with ASC, as they can go beyond the stereotyped interests often ascribed to them (Bury et al. 2019). Similarly, Marwaha et al. (2007) found that Individuals with schizophrenia are also more likely to be employed in 'Elementary' jobs requiring simple manual tasks (e.g. cleaning), or skilled trades (e.g. construction and electrical trades), with few working in managerial roles. Marwaha et al. (ibid) suggested that this may be because these jobs do not require as much interaction with others. Willoughby (2013) found that people with ADHD were more interested in Enterprising vocations. Some of the symptoms of ADHD, such as impulsivity, may also be advantageous for entrepreneurs, particularly in uncertain environments (Antshel 2018; Wiklund et al. 2017), and are associated with self employment (Verheul et al. 2016). Lasky et al. (2016) found that individuals' symptoms of ADHD were either intensified or reduced depending upon their working environment, and that in highly stimulating environments their symptoms became strengths. In particular, within fast-paced, physical, challenging workplaces, which provided novelty, symptoms of ADHD were reduced. Whereas, within jobs without these features, the symptoms of ADHD may be more affecting.

The discussion above shows that individuals are most successful within particular working environments that emphasise the strengths of their traits, and are generally attracted to those environments. This supports the ideas put forward in chapter 3. As our ancestors' technology and culture became more complex and labour was divided into more niches, rather than selection favouring generalists who may be able to do each job to a satisfactory level, specialist cognitive types predisposed towards particular roles may have been advantageous.

Humans are thought to have constructed a cognitive niche (Pinker 2010; Whiten and Erdal 2012). This is characterized by complex technology, cooperation, and language. These features likely coevolved and were subject to feedback which led to rapid development of these skills (Pinker 2010; Whiten and Erdal 2012). Not only is this 'human niche' characterised by a change in behaviour, but following niche construction theory it involves changing the environment, either to suit or further enhance individuals' skills, which may change selective pressures (Bertolotti and Magnani 2017; Fuentes 2017; Laland, Kendal and Brown 2007; Laland and O'Brien 2010). While we may suggest that we developed a 'human niche', characterised by cognitive and social skills and pressures, this should be perceived as a broad niche subsuming other smaller niches. For example it has been suggested by Hiscock (2014) that humans created a niche of lithic production. This niche required complex learning environments. We are regarded as powerful niche constructors (Laland and O'Brien 2010). While niche construction theory can be applied to broader concepts such as intelligence, it has also been applied to more specific changes, such as sickle-cell protection in response to malaria prevalence, or lactase persistence in response to dairy farming (O'Brien and Laland 2012). Therefore, niche construction theory is multileveled and applying it at different scales may help reveal important aspects of our evolution.

The evidence for the assortment of individuals with different personality and cognitive traits into different types of vocation and living conditions (urban vs suburban) may be viewed in a similar way to the above examples of niche construction. This evidence suggests that humans have constructed multiple cognitive/psychological niches. Individuals are not equally adapted to these niches, but rather are behaviourally or cognitively specialised towards particular roles. As argued in chapter 3, this likely developed in response to social network population sizes increasing. However, while archaeologists have argued that division of labour and task specialisation would have been particularly advantageous to our species and may be responsible for our success over other hominins (Kuhn and Stiner 2006; Nakahashi and Feldman 2014), little research has explored how this may have affected individual success. Further, most of this research has focused upon sexual division of labour, when other factors such as age (Bird and Codding 2015), or as this thesis suggests psychology, may also be dividing factors. Spikins et al. (2016) have already explored the effects of prosociality on the creation of a niche for individuals with traits of ASC. Beyond this, division of labour and specialisation seems to have created multiple niches where individuals with different psychological specialisations may flourish.

Niche construction theory suggests that there should be a feedback between the newly constructed environment and selection upon the individual. Therefore, not only will individuals assort themselves into the roles that most suit their traits, but they may also develop new traits which aid in their role. For example, the agent based model in chapter 6 has shown that when agents relocate, which is a form of niche construction (Laland, Matthews and Feldman 2016), they enter less densely populated areas. This then leads to increased selection for more extraverted phenotypes who can reproduce faster. Therefore, by changing their context it has led to a change in selective processes. Further, this may lead to runaway selection and possible incompatibility with pre-dispersal conditions (Erm and Phillips 2020; Ochocki and Miller 2017; Perkins et al. 2013; Travis et al. 2009), to the point where a phenotype may experience considerable disadvantages when taken out of their constructed niche. Similarly, the establishment of different roles within groups, may have had a similar effect. Not only could niche diversity provide places for existing types of psychological difference, but it may also have led to increases in psychological diversity through selective mechanisms. For example, social specialisation (e.g. leadership or management) may be considered an extraverted niche. Within this setting selection may have occurred for more socially adept individuals, better at communicating and controlling peoples’ perception of them. However, as shown above, extraverts taken out of this setting and put into a setting where they work alone may struggle considerably. They are to some degree tied to their niche. As reviewed above, this may influence decisions on where to work, live and may also have implications for partner selection, with people preferring partners with similar personalities to themselves (Botwin, Buss and Shackelford 1997). Individuals may even migrate to particular niches or environments where their personality type is tolerated/valued (Rentfrow, Gosling and Potter 2008). This may be geographically (Camperio Ciani et al. 2007; Ciani and Capiluppi 2011), or in terms of job role. Further, if there are fewer types of roles available we would expect diversity to decrease. As discussed in chapter 1, this has been found across multiple cultures (Durkee et al. 2020; Lukaszewski et al. 2017), and has been predicted using agent based modelling (Smaldino et al. 2019). While these results are concerned with personality diversity, it is likely that this also applies to broader psychological and cognitive differences. Similar characteristics would be expected in an ancestral setting. Therefore, niche diversity and niche specific selective mechanisms may have had a significant effect on the evolution of psychological diversity in the past.

Following this, it could be argued that as human culture and social organisation became more complicated and division of labour developed, people separated into particular roles according, in part, to their behavioural and cognitive predispositions. Once this division occurred, selection likely favoured more and more specialised individuals (Ridley 2009). Individuals were subject to different selective mechanisms to one another, enabling their different skills, including psychological traits, to develop further. Consequently, our personality differences may have both contributed to and been the result of our division of labour and specialisations.

Returning to a suggestion made in the introduction of this thesis, that the psychological diversity of our species has enabled us to survive within a range of environments, withstand environmental change, and colonise new regions, the discussion above suggests that personality differences may have been pivotal in developing division of labour. This may have provided groups with significant benefits and increased economic efficiency if skilled individuals were able to focus upon particular tasks (Horan, Bulte and Shogren 2005; Nakahashi and Feldman 2014), which may have enabled groups to survive in more diverse ecologies.

This may be viewed in a similar way to the plastic adaptations suggested by Grove and colleagues (2014; 2015) and Potts (1998, 2013). Our ability to specialise and have preadaptations towards particular ways of thinking, feeling and behaving, even from birth (Kelsey, Farris and Grossmann 2021), likely allowed groups to more easily develop a range of skills for interacting with their environment. For example, as suggested in chapter 3, someone with a local processing bias may develop a new method of manufacturing that may not occur to others, due to their cognitive biases. However, more socially adept individuals may be better at transferring that information (von Hippel and Suddendorf 2018). The value of having individuals with different personality and cognitive types, suited to different roles, within a group is not new when discussing employment and vocation (see above), and personality type is also important for personnel selection in business (Seibert and DeGeest 2017). However, this has not been applied to the ancestral groups in which this diversity likely developed.

Chapter 3 has provided a mechanism of how this may have developed, which ultimately leads to an increase in the human environmental niche. Following Grove and colleagues (2014; 2015), periods of climatic instability may have provided pressure for new biological, material and socio-cultural developments. These developments may then have been used during times of stability to inhabit new territories and disperse. Bolnick et al. (2003) have shown that individuals of multiple species are differently adapted to their environment, compared to their conspecifics. They are specialised to different ecological settings and this individual specialisation vastly increases the width of their species' niche. In contrast to other species, humans may share in the profits gained as a result of others' abilities and inventions. Therefore, this may increase niche width even further. Therefore, as a consequence of individual specialisation, groups may become better adapted to a wider range of environments.

Middle Stone Age (MSA) industries may be an example of this. Transitions to MSA technology are suggested to have taken place during periods of climatic or resource instability to reduce the risk of shortfall (McCall 2007; Potts et al. 2018, 2020). This may be the reason behind the development of the Howiesons Poort industry, a South African MSA blade industry (~80 - 65 ka) (Wadley 2008). This industry has been suggested to be similar to northern Japanese microblade industries (McCall and Thomas 2012), characterised by the 'batch' production of microblades, done by specialists (Bleed 2002), which were hafted into more expensive and complex composite tools. The lithics themselves were highly standardised, small, heat treated (Brown et al. 2009), and are suggested to have reduced uncertainties in resource acquisition (Hiscock, Clarkson and Mackay 2011). The adhesives used for hafting were complexly manufactured with heat control, use of ochre to control ph, and the use of beeswax or fat to increase workability (Wadley, Hodgskiss and Grant 2009; Wadley 2010). Spikins and Wright (2016) have previously argued that the technological changes taking place at this time represent a shift in thought towards a more analytic, detail oriented view of the world. They suggest this represents a use of autistic traits. Simultaneously, there was a shift towards increased symbolism and social networking. Shell beads (d'Errico and Backwell 2016; Vanhaeren, Wadley and d'Errico 2019) and ostrich shells (Texier et al. 2010), may have been used to form and maintain information-sharing networks across an uncertain landscape (McCall and Thomas 2012). Technology and social life was more complex. This complexity may have led to, and been the result of, task specialisation and conditions under which more technically focused and less socially oriented individuals may focus on manufacturing, while more socially adept individuals focused on hunting and maintaining social networks. While this is speculative and difficult to prove, it has been suggested that pressure flaking, used by Still Bay and Howiesons Poort industries, would have required extensive apprenticeship to learn (d'Errico et al. 2017). Combined with the complexities of hafting, the advantages of batch production, and the evidence of overproduction of blades (McCall and Thomas 2012), it is unlikely that all members of the group contributed equally to each task. Rather, it is likely that task specialisation became more important in these MSA cultures. This may have provided an environment where individuals' differences may be capitalised on, to increase group efficiency and success. New innovations may also be more probable when people specialize because the costs may be taken by the group rather than the individual, and the individual has more time to think about improving the method being used. The behavioural innovations cited above have been argued to account for the population increase and dispersal of our species (Mellars 2006). While this was a tentative suggestion, it would support the argument that individual specialisation promotes group plasticity and that the development of this under climatic uncertainty increases niche width.

A second example where specialization increased niche width is the use of fitted clothing. This development undoubtedly increased the ecological niche of modern humans, by enabling them to inhabit colder environments. Complex clothing is argued to have developed during the MSA, with intensification in Europe during the Upper Palaeolithic (Gilligan 2007). Collard et al. (2016) have suggested that this was a point of difference between Neanderthals and modern humans, which may have contributed to the former's replacement. Collard et al. (ibid) suggest that Neanderthals used loose fitting cape-like clothing, while modern humans used more specialised, fur trimmed, cold weather clothing. As Collard et al. (ibid) have reviewed, the manufacturing of cold weather clothing would have required the targeting of mustelids and canids, and the use of specialized tools such as endscrapers and bone needles. While it is unlikely that the division between Neanderthal and modern human clothing industry is as extreme as this (Ocobock, Lacy and Niclou 2021), modern humans seem to have had a more specialised industry for clothing production, which may have given them an advantage or at least enabled them to inhabit the same environments as their more cold adapted cousins. Similar to hafting, the creation of complex clothing would likely have required specialist individuals with a more detail oriented view of the world.

In archaeology we need to appreciate that division of labour goes beyond sex. Within a modern context we appreciate that we all have characteristics that make us good (or bad) at particular tasks. If a task is required to be completed we attempt to select the best person for the job, either through formal interview processes in an attempt to learn a person's skills, or through an informal consideration of past interactions with that person to see whether they may be good at that job. This is not a new, human-specific skill but rather is something seen throughout nature in mate selection. The extrapolation of this skill beyond mate selection may have provided humans with a particular advantage. As noted above, the ability to recognise others were good at particular tasks and allow them to focus on those tasks increases the efficiency of the group and may enable these people to invent new methods of production. Specialists in particular tasks are then subject to different selective pressures, which may lead to an increase in their cognitive and behavioural differences. This individual specialisation leads to new, often more complex, ways of interacting with the environment, which groups may use to increase their efficiency and widen their ecological niche. Therefore, counterintuitively, individual specialisation may have been a ‘plastic’ adaptation enabling groups to survive in a wider range of conditions. As a result, our psychological diversity may have had a more indirect effect on our dispersal as groups benefited from the inventions of specialists with psychological predispositions towards particular tasks and different ways of thinking.

While the changes in the material culture of the MSA and the proliferation of cultural objects during the Upper Palaeolithic cannot be wholly ascribed to changes in our psychological diversity, this section has argued that it likely had an impact when our species began dividing tasks amongst themselves and specialising. However, while this may have provided additional characteristics by which labour could be divided, other than just sex, the benefits of specialisation and task division do not rely on psychological difference. Rather, psychological differences and selection for these differences may have increased the advantages gained from specialisation and division of labour.

3. Understanding Human Dispersal More Generally

This thesis has several implications for our understanding of dispersal more generally. Firstly, determining how accessible resources were in different biomes for our ancestors may significantly change our view of the Palaeolithic landscape and our dispersal. Secondly, recognising that evolution was not static during dispersal, but that the encountered ecological conditions likely led to new phenotypes at the expansion front, may help us understand why our dispersal was so rapid. Thirdly, when creating the ABM several gaps in the literature were identified. Filling these gaps may help refine future iterations of this model, as well as other dispersal models.

Chapters 5 and 6 have highlighted important features which should be taken into account when discussing human and hominin dispersal. Firstly, chapter 5 has shown that resource accessibility should be considered in future theories of human dispersal. While biomes may have more resources in general, these may not always be accessible to hunter gatherers. This may significantly alter our perspective of global resource distribution. Further, a lack of stability in accessible resources may cause geographical barriers to expansion. These are both factors which need to be taken into account when modelling dispersal. Using and refining the methods used in chapter 5 may offer a more reproducible and less arbitrary method for determining habitat suitability than has been previously used in some models. For example, as noted in chapter 4, many ABMs either regard habitat suitability as a parameter to be varied (Mithen and Reed 2002; Nikitas and Nikita 2005), or attempt to use archaeological data or literature to assign habitat suitability (Burke et al. 2017; Romanowska 2015; Wren and Burke 2019). By exploring how accessible resources are in different biomes for modern hunter gatherers, it may help us infer how accessible they may have been for our ancestors. While there are limitations to this method, for example modern hunter gatherers may have developed novel methods for dealing with the environment which our ancestors did not have, it may help improve our understanding of how our ancestors related to their environment. Further, it may help us determine whether the lack of archaeological sites in biomes such as tropical rainforests is due to practical and preservational issues, or due to their unsuitability for our ancestors’ occupation, as suggested by chapter 5.

The ABM and ecological literature discussed in chapter 6, highlighted the importance of a population’s ability to evolve for their ability to disperse. They showed that different phenotypes, particularly those with more rapid reproduction or dispersal rate, are better suited or more likely to occupy the wave front when a species is dispersing (Phillips, Brown and Shine 2010; Travis and Dytham 2002). This may lead to spatial sorting and a runaway effect that increases dispersal rates each generation (Ochocki and Miller 2017; Perkins et al. 2013; Travis et al. 2009). These individuals may then be specialized for living at low population densities at the expansion front, but their behaviour may be maladaptive in the core of the population (Duckworth 2008; Phillips, Brown and Shine 2010; Travis and Dytham 2002). This may lead to even faster population dispersal as these populations are then pulled towards less densely populated areas (Erm and Phillips 2020).

As has been discussed above, this may explain why humans dispersed so rapidly. Rapid dispersal may have occurred in multiple ways, which are not mutually exclusive. For example, following Spikins (2015) dispersers may have been increasingly more prone to conflict and group fission. Alternatively, they may have become more adapted towards “Bolder” strategies (Dennell 2017b). While theories such as this suggest a dichotomy in behaviour between dispersers and residents, they do not explicitly suggest evolution during dispersal. While we have an appreciation that our dispersal has led to genetic drift and reduced genetic variability outside of Africa (Campbell and Tishkoff 2010; Gomez, Hirbo and Tishkoff 2014), we have not explored the functional implications this may have had upon the behaviour of dispersing people. Therefore, similar to what has been shown in this thesis, as well as by evolutionary ecologists (Duckworth 2008; Ochocki and Miller 2017; Perkins et al. 2013; Phillips, Brown and Shine 2010; Travis and Dytham 2002; Travis et al. 2009), researchers studying human dispersal need to acknowledge that individuals and cultures evolved in response to ecological selective pressures during dispersal.

Thus far, this section has argued that findings from ecological research may inform us of characteristics of our dispersal which are not immediately obvious from the archaeological record. In contrast, Dennell (2017b) has argued that more attention needs to be paid to the behaviour of humans in comparison to past hominins. Humans significantly changed their behaviour over the course of their evolution and are much more cooperative than other hominins, both within and between groups, and he argues that this may have allowed humans to function as a ‘super-organism’. Not only does he suggest that this may have played a large role in our ability to colonise the world, but he also argues that due to this humans should not be treated the same as other animals when discussing dispersal. This thesis shows that applying techniques and thought processes from animal behaviour and ecological research to human dispersal can lead to new perspectives of the problem. It can help generate new hypotheses, and reveals explanations for seemingly difficult to explain problems. Additionally, it may help explain the origins and implications of some of the behavioural changes Dennell suggests make humans incomparable to other animals. Archaeologists seem to have explored the issue of dispersal in isolation, despite the species of interest either being extinct or globally dispersed. Meanwhile, evolutionary ecologists have been utilizing real world data, experimental data, and computer simulations to explore dispersal both as a general process, and in relation to specific extant species. By utilizing findings from other disciplines, such as evolutionary ecology, we may better understand our ancestors’ dispersal.

This thesis has also highlighted several advantages of using ABM in archaeology (chapter 4). Firstly, its ability to help investigate the processes which have led to the formation of a feature observable in the archaeological record. Secondly, its ability to account for individual differences between agents within the system. Thirdly, ABM helps identify gaps within the literature.

As well as highlighting the importance of evolvability during dispersal, constructing the ABM for this thesis has helped identify other gaps within the literature, which may be areas for future research. For example, it has brought to attention the need to explore in more detail the impact of resource accessibility on biome suitability and the impact this may have had on dispersal. This will require field work exploring how biomes vary in NPP, both seasonally and annually, as well as spatially. How this affects hunter gatherer subsistence strategies should then be assessed. This fine scale research may then be used to inform future dispersal models and theories. The construction of the ABM also highlighted gaps and disparities in the ethnographic demographic data. In particular, estimates of hunter gatherer population growth have a large range (2.7-0.1%) (Hassan 1975). Further, these estimates do not appear to directly relate to reproduction and mortality rates estimated for hunter gatherers, which lead to much higher population growth rates. More long term quantitative demographic data of multiple groups, incorporating reproduction, mortality and growth rate within one study needs to be conducted to rectify these issues. Additionally, it is thought that Palaeolithic population growth rates were much lower. This is likely because the landscape was more dangerous. Additionally, it is likely that population extinctions due to climate, disease, or other disasters reduced long term population growth rates even further. More research is therefore required to explore hunter gatherer population growth rates and how this relates to Palaeolithic population growth rates.

Conclusions

This thesis has explored whether the emergence of cognitive and psychological variability had a significant impact upon our ability to adapt to new, changing or fluctuating environments. An agent based model (ABM) was used to investigate whether an example of psychological difference, variance in extraversion, may have had an effect upon a key event of our evolutionary history, our dispersal out of Africa. The results of this study suggest that our psychological differences likely had a large impact upon both our ability to adapt to new environments, and our dispersal.

The results of the ABM suggest that as our species dispersed, behavioural phenotypes more likely, or more successful at dispersing were selected for (chapter 6). The ABM showed that extraverts are better able to disperse due to their reproductive advantage, even with an inflated chance of mortality (up to a threshold). Within the model their reproductive advantage allowed agents with high extraversion to move more often due to a function representing mate exchange. Further the most extraverted agents also had an advantage in less populated areas, where the number of potential mates was low, as they were more likely to reproduce. Therefore, agents at the dispersal front were more extraverted. As shown in chapter 6, this second cause would likely also lead to the observed spatial distribution of extraversion genes if they were not part of a mate exchange network. This supports the hypothesis that dopamine receptor genes associated with extraversion may be more prevalent further from Africa due to sexual selection during dispersal. However, this does not negate a second hypothesis, that individuals with this allele are more likely to disperse (Chen et al. 1999; Matthews and Butler 2011; Wang et al. 2004). It may be that individual differences in probability of dispersal led to assortment, while sexual selection aided the success of dispersers. However, this distribution does not rely on an increased probability of movement or ability to adapt to novel environments, and may independently be the result of sexual selection. The discussion of these results, within the context of ecological research, suggests that these differences between dispersing individuals and resident (not dispersing) individuals is a common result of selection, and may lead to an increase in dispersal speed. As discussed above, other psychological differences may be associated with dispersal (openness), while others may increase success in resident groups (agreeableness). Therefore, we may expect to find other genes associated with psychological traits distributed globally in similar ways to dopamine receptor genes.

More broadly, this thesis has suggested ways in which our psychological and cognitive diversity may have increased our species niche width, which would have increased our ability to adapt to changing and novel environments. As an example of psychological difference, chapter 1 explored just how much personality variability our species possesses and reviewed the life history effects of a range of personality differences. The life history traits, genetic and neurological causes of extraversion were explored in more depth in chapter 2, as a case study. These chapters identified the tradeoffs associated with different personality traits, and show that peoples' traits lead them to interact with their environment in different ways. This may predispose individuals to be successful in different ecological settings or group roles. Chapter 3 explored the evolutionary mechanisms which may have led to our cognitive and psychological variability. This chapter suggested that as our cultural complexity increased to facilitate larger social networks, the social conditions which enable individuals to specialise into particular roles developed. As individuals with different cognitive and psychological strengths were able to specialise, this led to a widening of our psychological niche. Individuals with more severe psychological differences were able to thrive, and selection likely favoured a wider range of cognitive and behavioural types. As has also been argued in the current discussion, this likely led to an increase in the types of environments our species was able to survive in. This may both be a product of direct selection, such as selection for extraverts and people with high openness upon dispersal, and due to selection for difference within groups when there is a variety of niches individuals may specialise into and occupy.

This thesis therefore suggests that our species' cognitive and psychological diversity is an important aspect of our evolutionary history. It is a feature of our species that likely had a large impact upon our ability to adapt to changing and new environments. Recognising this diversity may offer new perspectives to longstanding problems within archaeology. It may allow us to better understand our dispersal, and the proliferation of material culture and inventiveness during the Middle-Upper Palaeolithic. The increase in our psychological and cognitive diversity was likely a defining change that occurred within our species, widening our ecological niche, improving our ability to adapt to new ecological conditions, and increasing our success when dispersing into new environments.

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