Intelligence Trends in Ancient Rome: The Rise and Fall of Roman Polygenic Scores

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Abstract

We analysed 127 Ancient Roman genomes with a view to understanding the possible reasons for the fall of the Roman Empire. Taking the polygenic score for educational attainment (EA4) as a proxy for intelligence, we find that intelligence increased from the Neolithic Era (Z= -0.77) to the Iron Age (Z= 0.86), declines after the Republic Period and during the Imperial Period (Z= -0.27) and increases in Late Antiquity (Z= 0.25) and is approximately at the same level today (Z= 0.08). We show that this is congruent with a cyclical model of civilization based around intelligence, with the documented history of Rome, and also with patterns of immigration into Rome.

Key words: GWAS; Polygenic Scores; Rome; Civilization Cycles; ancient Rome; Roman empire

Introduction

The causes of the Fall of the Roman Empire have long been debated, with English historian Edward Gibbon (1737-1794) providing a detailed treatment of the issue as early as the 1770s (Gibbon, 1776). One theory is that the collapse was caused by immigration from the imperial periphery to the centre of the empire, with this leading to conflict and, perhaps, difficulty maintaining complex systems based around trust (Heather, 2010). Another theory is that the decline can ultimately be understood in terms of a decline in average intelligence. According to this model, intelligence, which has a relatively high genetic component of about 80% in adulthood (Plomin & Deart, 2015), is strongly selected for under harsh conditions due to the need to solve complex problems relating to keeping warm (Lynn, 1987). This leads to the development of complex polities. Initially, living in complex societies selects for intelligence. The size of the brain and the neocortex in non-human primates have been shown to be positively impacted by socio-ecological complexity, leading to increased intelligence due to competition for limited resources, greater home ranges, and more complex social relationships (Shultz & Dunbar, 2022). This demonstrates that a larger group size leads to higher intelligence demands. However, when the conditions become “too comfortable,” selection pressure on intelligence weakens by, in the case of Rome, providing relatively healthy living conditions including plumbing, clean water, basic medical care and an abundance of food. Under harsher conditions, wealth predicts fertility, indirectly selecting for intelligence, but this pressure is weakened in a context of relative luxury (Dutton & Woodley of Menie, 2018; Clark, 2007). Thus, the intelligence of nations and civilizations is expected to follow a pattern of cycles, initially increasing to reach a peak and then decreasing again. The height of Roman Civilization also coincided with a warm period, the Roman Warm Period, which would have weakened selection for intelligence even further (Nunn, 2007).

For various reasons, in these relatively developed conditions, those who are more intelligent, and who tend to have higher socioeconomic status, appear to increasingly limit their fertility. This phenomenon has also been observed in the West since the mid-nineteenth century. These reasons may include those with high intelligence being more efficient users of contraception (Lynn, 2011) that is itself developed at this stage (Harvey, 2016, p.80). In addition, under harsh conditions there tends to be a positive relationship between wealth, and thus its robust corollary intelligence, and completed fertility (Clark, 2007; Lynn, 2011). This is weakened under more lenient conditions (Lynn, 2011). Consequently, there develops a negative relationship between intelligence and fertility. There is some suggestive evidence that this was happening at around the time of Christ. The poet Ovid commented on the fact that higher status young men were eschewing fatherhood, something on which the Greek historian Polybius was commenting a century earlier. The Emperor Augustus tried to deal with this problem by taxing childlessness among the higher classes and many of them simply paid the tax (Dutton & Woodley of Menie, 2018; Dixon, 2005, p.212). Unfortunately, the Romans did not appear to keep any statistics that would allow us to verify such tendencies.

In addition, there will be widespread immigration into such successful societies from the periphery of the empire and the average IQ of such people may be lower than that of the group who founded the civilization in the first place. There is some evidence for the veracity of this theory with regard to Western countries as compared to those who migrate to them (Rindermann & Thompson, 2016; Sørensen et al 2016; Kirkegaard 2013).

The ancestry profile of the ancient Roman shows dramatic changes that corresponded to documented migratory movements of people (Antonio et al., 2019). The Neolithic/Copper Age population carried a predominant Anatolian farmer ancestry, following the spread of agriculture from the Near East. During the Bronze Age, there was a major shift in ancestry with the introduction of 30-40% ancestry from Bronze and Iron Age nomadic populations from the Pontic-Caspian Steppe (Antonio et al., 2019). Linguistically these people belonged to the Indo-European family and spoke Italic languages, including Latin. During the Imperial period, ancestry shifted toward the eastern Mediterranean. Very few individuals were primarily of western European ancestry. This shift was likely caused by immigration from megacities, such as Athens, Antioch, and Alexandria. There was also an influx of slaves, predominantly from Greece, Syria, North Africa and Gaul. Slaves amounted to about 30% of the population of imperial Rome (Goldhill, 2006). After the fall of the Western Roman empire, during Late Antiquity, there was an overall decline in Rome's population, accompanied by a sharp decline in eastern Mediterranean ancestry. There was a corresponding larger proportion of individuals of central European origin, which may also reflect settlement by Gauls, Goths and Lombards. The medieval period saw a further increase in northern and central European ancestry. These major ancestry shifts could have caused a change in the genetic potential for cognitive abilities which could be reflected in the polygenic scores. However, ancestry shifts can cause changes in polygenic scores that reflect population stratification correlated to environmental factors not perfectly controlled for in the original GWAS, without being directly related to the traits via genetic mechanisms (Zaidi and Mathieson, 2020).

Thus, the general genetic theory of rise and fall of empires is that they begin by evolving high intelligence and other pro-social psychological traits, termed *Asabiyyah* by the Medieval philosopher Ibd Khaldun (Wazir et al., 2022). As they achieve greatness, internal selection for intelligence reverses due to the upper classes using contraception and preferring entertainment to family-making. External selection for intelligence reverses as large numbers of immigrants with below average intelligence arrive to enjoy the offerings of the empire, while also serving as replacement children for the locals who are forgoing them. This double-relaxed selection leads to a quick decline in the average intelligence of the empire, thus causing its demise (Nyborg 2012). After the decline of an empire, the population may or may not enter another eugenic phase where intelligence is rising. Thus, to test such a theory for Rome, one needs to obtain genetic data from a representative sample of citizens across hundreds of years. These should show a rise and fall in the polygenic scores (PGS) for intelligence at the same time as history shows the empire rose and fell. In this study we report the first such analyses.

Previous studies have employed polygenic scores computed to detect evolutionary change in several polygenic traits. Cox et al. (2022) used a polygenic score derived from modern samples to predict skeletal stature under ancient DNA, predicting 6.3% of femur length. Another recent study used polygenic scores to detect changes in immunity-related traits in Europe after the Neolithic (Kerner et al., 2023) and an increase in general cognitive ability in Europe after the Neolithic has been reported using polygenic scores derived from older GWAS (Woodley et al., 2017).

Because there is a lack of GWA studies of intelligence with a satisfactory predictive validity, we relied on GWAS of education which is a proxy for intelligence. The most recent GWAS of educational attainment explains about 15% of the variance in the outcome as well as predicting cognitive performance (Okbay et al., 2022). However, it also taps into other non-cognitive traits such as conscientiousness and emotional stability that increase an individual's chances of completing higher education. In fact, Neuroticism and Conscientiousness were found to be correlated (negatively and positively, respectively) to the polygenic score for education (Mõttus et al., 2017). The implications of this limitation will be discussed.

Method

A dataset of 127 genomes of the ancient Roman samples were obtained from a public dataset (Antonio et al., 2019). All the individuals were from central Italy and the majority (109) were from Lazio, the current administrative region where Rome is located. The rest of the sample was from other regions in Central Italy (Marche, Abruzzo and Umbria). A sample of 33 modern individuals from matching regions in Central Italy was obtained from another study (Raveane et al. ,2019). Following the subdivision employed by Antonio et al. (2019), the ancient individuals were divided into five groups corresponding to (pre)historical periods: 1) pre-Iron Age, comprising individuals from the Neolithic, Copper Age and Bronze Age (about 10K to 2K BCE); 2) Iron Age and Republic, from 900 to 200 BCE; 3) Imperial, from 0 to 400 CE; 4) Late Antiquity, from 400 to 700 BCE; 5) Medieval/Early Modern, from 470 to 1770.

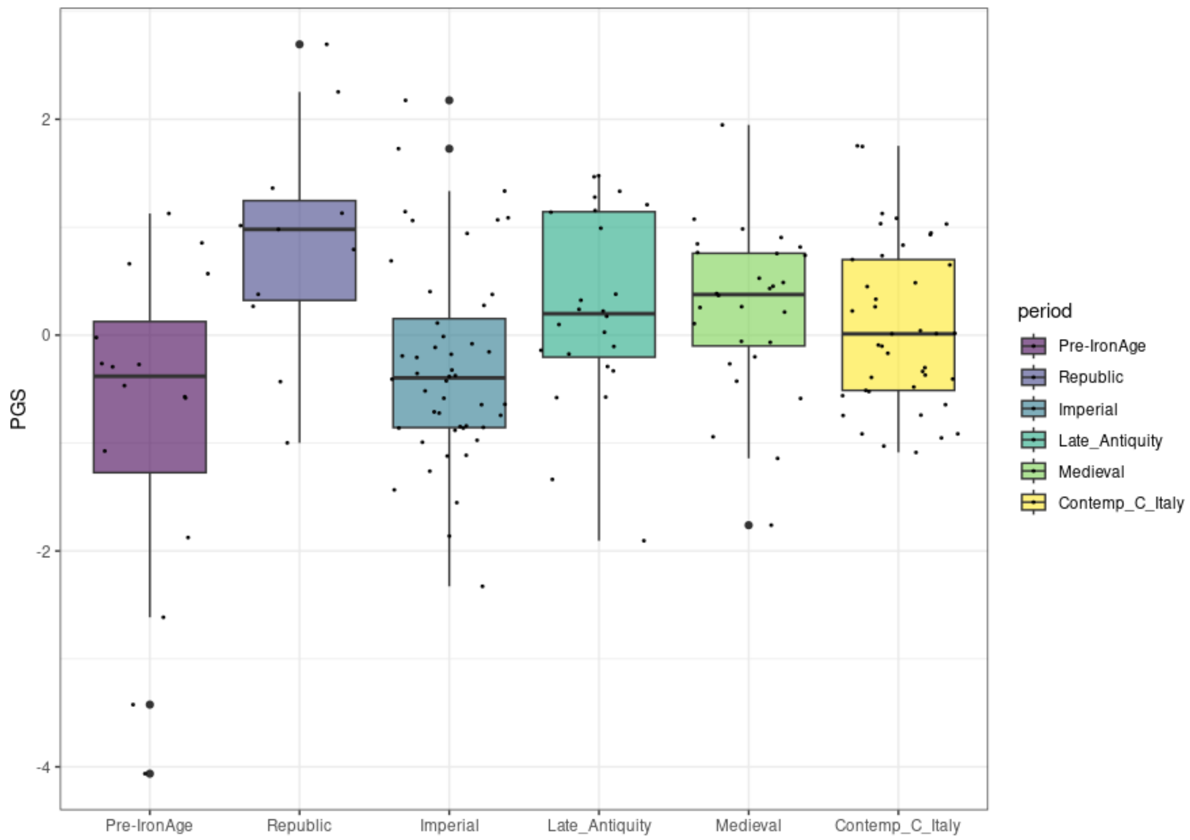
The summary statistics from the two largest GWAS of educational attainment (EA3 and EA4) were used to compute PGS for ancient Roman genomes (Lee et al., 2018; Okbay et al., 2022). Allele frequencies and principal component analysis (PCA) were calculated using Plink 2.0 (https://www.cog-genomics.org/plink/2.0/). R was employed to perform the statistical analyses.

Results

There were 3741 SNPs in the sample out of the 3951 SNPs that were significant (p< 5 × 10-8) in the GWAS (Okbay et al., 2022). Since the goal here is to minimise bias and not to maximise within population validity, it is appropriate to rely only on the most significant variants which have higher signal-to-noise and signal-to-bias ratios.

The education PGS (eduPGS) were lowest in the Neolithic/pre-Iron Age and highest in the Iron Age/Republican Era (Figure 1). The transition from the neolithic to the Iron age saw a sharp increase in eduPGS. After the Republican Era, there was a sharp decline during Imperial times, followed by a moderate increase in Late Antiquity and the Middle Ages. The results using the eduPGS from the older GWAS (Lee et al., 2018) were similar (suppl. Figure 1) so they are not reported here.

Figure 1. Educational attainment (EA4) polygenic scores by period.



The Z-transformed polygenic scores are shown in table 1.

Table 1. PGS (Z) for different periods.

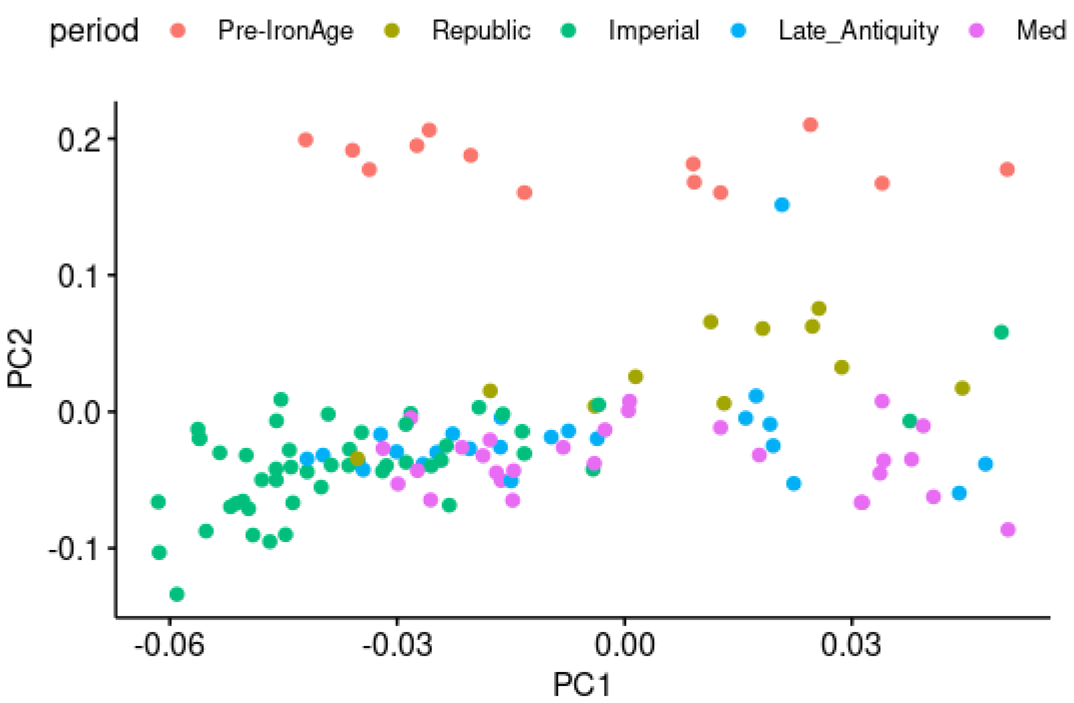
Period	N	PGS (Z)
Pre-Iron Age	16	-0.77
Republic	11	0.86
Imperial	48	-0.27
Late Antiquity	24	0.25
Medieval	28	0.25
Contemporary	41	0.08

OLS regression was run with PGS as the dependent variable and period as the categorical independent variable (Table 1). A significant model emerged (adj. R2= 0.17, p = 0.0002), suggesting that the polygenic scores among the periods were significantly different.

The effect of ancestry

A 2-component principal component analysis was run on the individual genomes.Three outliers at the far extreme of PC1 were identified and removed from the analysis. There was significant overlap between the time periods, although the second component clearly differentiated the pre-iron age period from the others (Figure 2).

Figure 2. Principal Components Analysis plot.



The PC1 scores were lowest in the imperial period, and higher in the republican and mediaeval periods. Thus, they can be interpreted as European ancestry, which was lower during the imperial period but higher in the republican and mediaeval periods (Antonio et al., 2019). PC1 was significantly correlated to EA4 ($r = 0.36$, $p= 3.5 \times 10^{-5}$) but there was no correlation between PC2 and EA4 ($r= 0.05$, $p= 0.558$).

OLS linear regression was run to test the model that polygenic scores are significantly different between groups after accounting for population stratification (first principal component, PC1). A significant model emerged ($R^2= 0.18$, $p= 0.0002$). PC1 was a significant predictor of the eduPGS (Beta= 0.28, $p < 0.008$), but among the periods, only the Republican period was a significant predictor (Beta= 0.96, $p< 0.01$) (Table 2).

Table 2.

	Model 1	Model 2
(Intercept)	-0.70 **	-0.33
	-0.23	-0.26
Period: Republic	1.52 ***	0.96 *
	-0.36	-0.38
Period: Imperial	0.47	0.18
	-0.27	-0.31
Period: Late Antiquity	0.94 **	0.46
	-0.3	-0.32

Period: Medieval	0.94 **	0.37
	-0.29	-0.31
PC1		0.28 **
		-0.1
N	127	124
R2	0.17	0.18

All continuous predictors are mean-centred and scaled by 1 standard deviation. *** p < 0.001; ** p < 0.01; * p < 0.05.

Comparison with contemporary Italians

Genomes from contemporary inhabitants of central Italy (Raveane et al., 2019) were added to identify more recent trends in the evolution of cognition. The genomes from southern and northern Italy were excluded because they belong to populations from different geographical areas and with different histories. The contemporary eduPGS has not significantly changed from the Medieval levels (Figure 1).

A simple pairwise comparison shows that Cohen's d 95% confidence interval includes 0, with a range of -0.27 to 0.71.

Conversely, the Republican period PGS is 0.94 SDs higher than the contemporary PGS (95% C.I= 0.24 - 1.65, p = 0.008).

Seeing as the non-Republic periods were similar in average eduPGS, we also ran a simpler contrast between Republic vs. non-Republic. This gap was d = 0.94 [0.23 - 1.64], p= 0.003.

Discussion

Our results are congruent with the intelligence-based model of the rise and fall of the Roman Empire discussed earlier. In addition, we see that intelligence appears to increase from the Neolithic (c. 10,000 to 2200 BC) to the Iron Age, as has been found before (Kuijpers et al 2022). This is consistent with evidence from Huebner's (2005) analysis of per capita major innovation across time. He finds a peak of per capita major innovation in about 300 BC, this being shortly after the end of the Iron Age and, also, the height of Classical Greek Civilization. The increase in population density and social complexity could have selected for higher cognitive ability, a phenomenon that occurs also among non-human primates (Shulz and Dunbar, 2022). The migration of Proto-Indo-European people from the Yamnaya culture at the start of the Bronze Age (around 3300 BC) may have been a contributing factor to the increase in polygenic scores for intelligence (education proxy). These people moved from the Eastern European steppes into the Danube valley, eventually separating into Pre-Celtic, Pre-Italic and Pre-Germanic populations. The split between Proto-Germanic and Proto-Italic speakers is believed to have happened around 3500 BC (Russell et al., 2011). The Italic tribes mixed with the natives and this is reflected in the dramatic change in ancestry, which shifted from being entirely Anatolian Neolithic/Sardinian during the Neolithic to mostly (72%) central European in the Iron Age/Republican sample (Antonio et al., 2019). At the same time, the new immigrants established Latin as the language of the rising Mediterranean power.

We also find that intelligence declines after the end of the Roman Republic. As power transfers from Greece to Rome in about 100 BC, people who have been subject to more intense selection for longer (the Romans), initiate a new age of innovation and per capita major innovation increases between 50 BC and 150 AD before going into decline (Huebner, 2005). In addition, the end of the Roman Republic was a time of civil war and general catastrophe (Chrystal, 2019), consistent with evidence that a certain level of intelligence, and its corollary trust, is necessary in order to hold together a stable and democratic system of government (Vanhanen, 2004). Congruous with the theory that intelligence was in decline in ancient Rome, the rate of innovation declined starting around the year 200 BC (Dutton & Woodley of Menie, 2018; Rindermann, 2018; Huebner, 2005).

However, returning to the easy conditions created by civilization, the “cura annonae” was a government-run program that was initially introduced in 123 BC by Gaius Gracchus with a grain law. This program provided free or subsidised grain and bread to the poorest 40,000 citizens of Rome, eventually reaching around 200,000 by the time of Augustus (around the time of Christ) until the end of the Western Roman Empire. The corn-dole began as an emergency measure to feed the increasing number of destitute and indebted citizen-farmers. By the end of the Republic, it had become a permanent institution. Later emperors added olive oil (Septimius Severus), wine and pork (Aurelian) to the dole (ca. 270-275 AD), besides converting the dole to bread from the more perishable grain. The grain was primarily imported from Sicily and North Africa, requiring hundreds and even thousands of ships to deliver the grain to Rome. The introduction of this program had a potential dysgenic role due to its accessibility and permanence combined with the negative relationship between low socioeconomic status and intelligence.

However, a parallel interpretation is that our results reflect changes in the ethnic composition of the people living in Rome. Our sample shows a clear shift in genetic ancestry components between the Iron Age and the Imperial Period, where the former was characterised by a preponderance of Central European ancestry and the latter by Near-Eastern-like ancestry (Antonio et al., 2019). This change may be attributed to the substantial immigration from other parts of the Roman empire, where selection pressures may not have been as strong. The collapse of the Roman Empire was accompanied and accelerated by an influx of Germanic people which settled in Italy and changed its genetic landscape (Antonio et al., 2019). This influx can explain the slow rise in the polygenic scores of Late Antiquity and into the Medieval period, which partly reversed the decline observed in the Imperial Period. The effect of ancestry on polygenic score differences however, must be interpreted with caution because it could reflect “residual environmental stratification”, in other words, environmental factors that are correlated to ancestry in the GWAS (Zaidi & Mathieson, 2020).

Our comparison of contemporary genomes from central Italy have demonstrated that polygenic scores have not significantly altered from the Middle Ages to the present day. During the Republican period however, polygenic scores were higher than they are now, nearly one full standard deviation higher.

Regrettably, we were unable to separate the impacts of cognitive and non-cognitive genetic factors on the educational polygenic score. Indeed, efforts have been made to distinguish these two elements through a technique known as GWAS-by-subtraction. This approach conducts a GWAS on the residual 'noncognitive' genetic variation in educational achievement that cognitive abilities do not account for (Demange et al., 2021). The "NonCog" component demonstrated a positive genetic link with Conscientiousness (exhibiting diligence and orderliness), Extraversion (displaying enthusiasm and assertiveness), and Agreeableness (showing politeness and empathy), as well as a negative rg with Neuroticism (experiencing emotional instability). It is plausible that selection pressures on these characteristics affected the trend in polygenic scores in ancient Rome. Nonetheless, the complexity of the "non-cognitive" genetic factor, coupled with its dependence on a negative definition (i.e., "everything that X does not explain in Y), renders it inappropriate for use as a valid indicator of polygenic adaptation. A further significant concern is that both "non-cog" and "cog" factors exhibit enrichment for analogous neural tissues, and the "non-cog" factor maintains a positive, albeit modest, connection with cognitive ability (Demange et al., 2021).

In summary, our findings demonstrate rises and falls in education-related abilities across the history of Rome consistent with the impact of the relatively luxurious conditions of civilization but also, potentially, consistent with the impact of immigration from areas of low (or high) average intelligence. Hopefully, future research, with larger samples, will be able to engage in a finer grained analysis of this issue.

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