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 decline and fall of the Roman Empire have been subjects of extensive debate and scholarly inquiry for centuries. Edward Gibbon, an English historian in the 18th century, delved into this issue with meticulous detail (Gibbon, 1776). Multiple theories have emerged to explain this historical event. One such theory proposes that the collapse was influenced by immigration from the empire's periphery to its center, resulting in conflicts and challenges in maintaining complex systems reliant on trust (Heather, 2010). Another theory suggests that the decline can be attributed to a decrease in average intelligence. This model argues that intelligence, with an estimated heritability of 80% in modern societies (Plomin & Deart, 2015), is highly selected for under harsh conditions, where complex problem-solving skills are crucial (Lynn, 1987).

The development of complex societies initially favors intelligence, as evidenced by studies showing positive impacts of socio-ecological complexity on the brain size and neocortex of non-human primates, resulting in increased intelligence due to competition for limited resources, larger home ranges, and intricate social relationships (Shultz & Dunbar, 2022). During the rise of human civilization, increasing social complexity imposes higher demands for intelligence due to larger group sizes. However, when living conditions become relatively comfortable, the selection pressure on intelligence weakens, as observed in the case of Rome, where improved living conditions, including amenities like plumbing, clean water, basic medical care, and abundant food, diminished the relationship between wealth and fertility (Dutton & Woodley of Menie, 2018; Clark, 2007).

Under more favorable conditions, individuals with higher intelligence and socioeconomic status tend to exhibit declining fertility rates, as observed in the West since the mid-nineteenth century and in developing countries over the past half-century (Meisenberg, 2009). This phenomenon may be attributed to factors such as increased use of contraception by individuals with high intelligence (Lynn, 2011) and a weakened positive relationship between wealth, intelligence, and completed fertility (Clark, 2007; Lynn, 2011). Historical accounts from the time of Christ in the Mediterranean region, including Ovid's commentary on higher-status young men eschewing fatherhood and Polybius' observations, provide suggestive evidence of declining fertility among the upper classes. The Roman Emperor Augustus even attempted to address this issue by imposing taxes on childlessness, which many individuals simply paid (Dutton & Woodley of Menie, 2018; Dixon, 2005, p.212).

Frost (2022) proposed three causes for the decline in cognitive ability during Classical Antiquity: a decline in fertility and family formation, an increase in female hypergamy among freed slaves, and an increase in the slave population, particularly foreign slaves. Consequently, intelligence levels within nations and civilizations are expected to follow cyclic patterns of increase, peak, and decline. Furthermore, successful societies often experience widespread immigration from the periphery, potentially leading to a dilution of the overall cognitive abilities of the population. Empirical evidence has indicated the existence of this pattern in Western countries compared to migrant populations (Rindermann & Thompson, 2016; Sørensen et al., 2016; Kirkegaard, 2013). Ancestry analyses of ancient Romans have also demonstrated significant shifts, aligning with documented migratory movements (Antonio et al., 2019). However, it is essential to consider that ancestry shifts can lead to changes in polygenic scores, reflecting population stratification related to environmental factors not accounted for in the original genome-wide association studies (GWAS) (Zaidi & Mathieson, 2020). Therefore, controlling for the effect of ancestry on polygenic scores through principal component analysis becomes crucial.

In light of these theories and observations, this study aims to investigate the relationship between cognitive decline and the fall of the Roman Empire using polygenic score analyses. To date, no genetic data from a representative sample of Roman citizens across multiple centuries have been used to examine changes in polygenic scores for intelligence concurrently with the historical rise and fall of Roman civilization. Previous studies have successfully employed polygenic scores to detect evolutionary changes in various traits, such as skeletal stature and immunity-related traits (Cox et al., 2022; Kerner et al., 2023). However, due to the lack of GWAS studies on intelligence with satisfactory predictive validity, we relied on GWAS of educational attainment as a proxy for intelligence, despite its tapping into other non-cognitive traits (Okbay et al., 2022; Mõttus et al., 2017).

In the subsequent sections, we will present the methodology employed in this study, discuss the limitations arising from the use of GWAS of educational attainment, and provide a comprehensive analysis of the findings. By exploring the fluctuations in polygenic scores for intelligence over time and their potential correlation with the rise and fall of Roman civilization, we aim to shed light on the complex relationship between cognitive abilities and the decline of empires.

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.

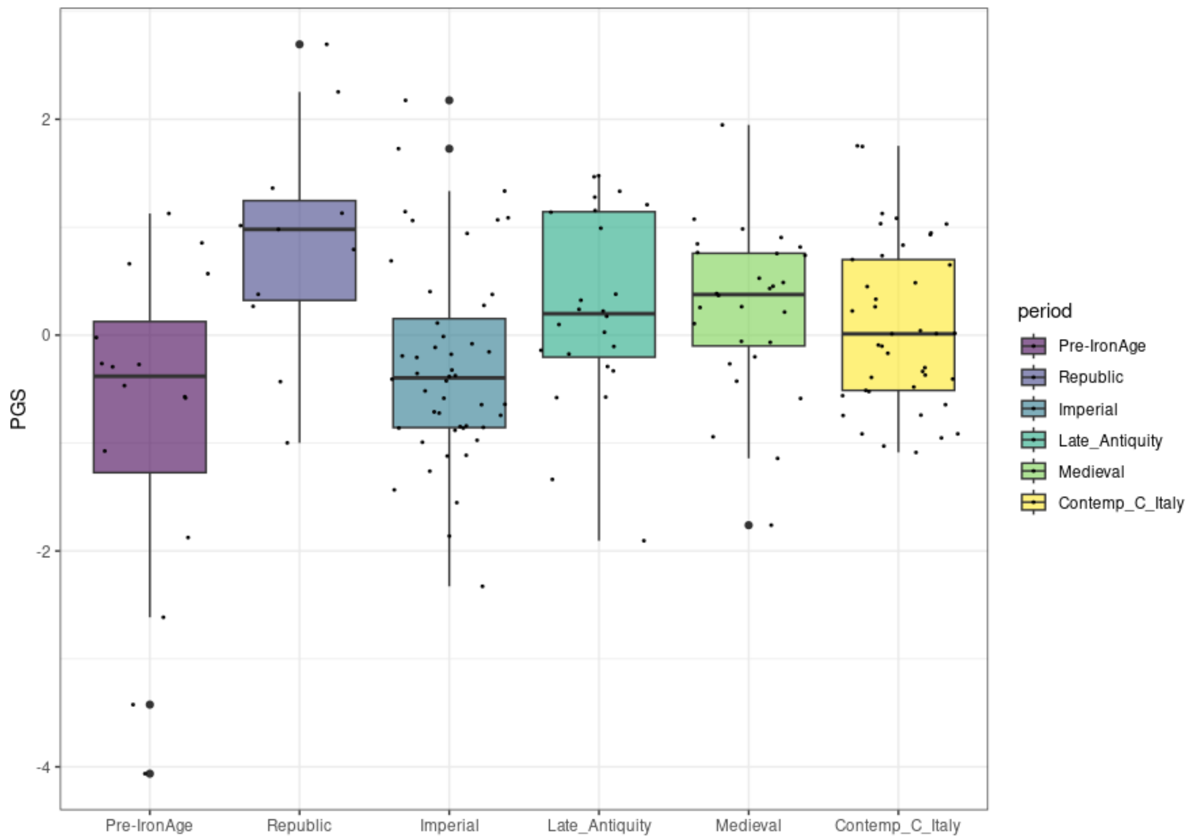
The summary statistics from the two largest GWAS of educational attainment (EA3 and EA4) were used to compute PGS for ancient Roman genomes (Lee et al., 2018; Okbay et al., 2022). Allele frequencies and principal component analysis (PCA) were calculated using Plink 2.0 (https://www.cog-genomics.org/plink/2.0/).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

Results

There were 3741 SNPs in the sample out of the 3951 SNPs that were significant ($p< 5 \times 10^{-8}$) 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.

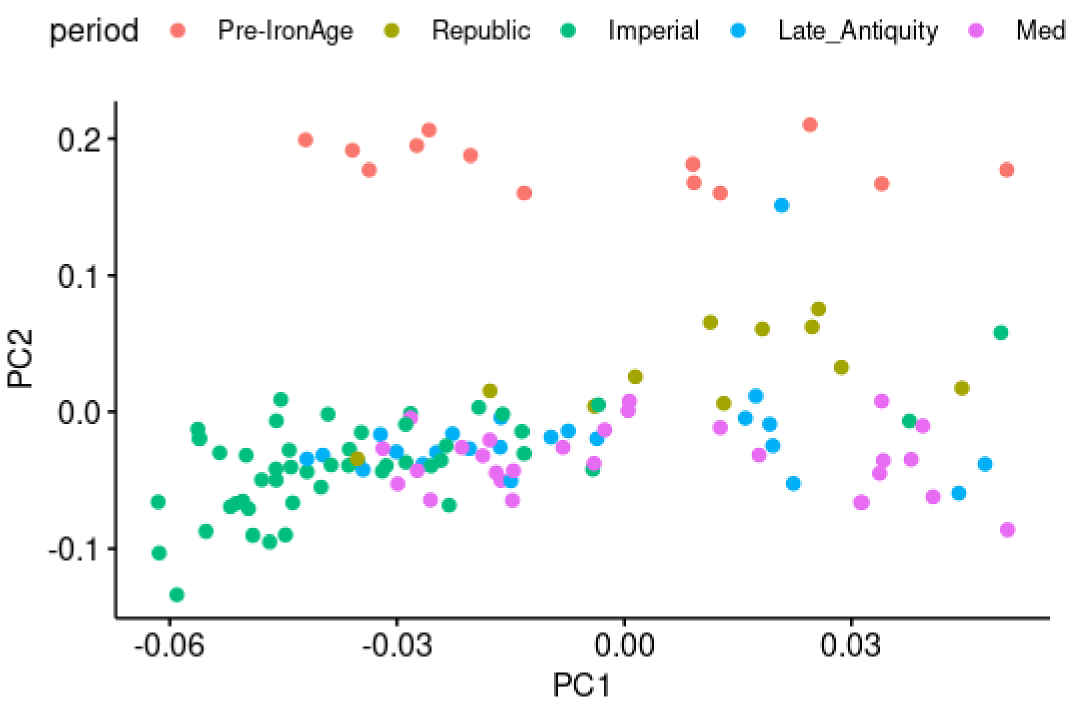
Period	N	PGS (Z)
Pre-Iron Age	16	-0.77
Republic	11	0.86
Imperial	48	-0.27
Late Antiquity	24	0.25
Medieval	28	0.25
Contemporary	41	0.08

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 Western 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. Effect of period and ancestry on PGS.

	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
R^2	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. Standard errors are shown below the Beta coefficient.

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). 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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