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MACROEVOLUTIONARY ORIGINS OF COMPARATIVE DEVELOPMENT*

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Advances in evolutionary theories (the Extended Synthesis) demonstrate that organisms systematically modify environments in ways that influence their own and other species' evolution. This paper utilises these theories to examine the economic consequences of human dispersal from Africa. Evidence shows that early humans' dispersal affected the adaptability of animal species to human environments and, through this, the extinction of large mammals during *Homo sapiens*' out-of-Africa migration. Empirical analyses explore the variation in extinction rates as a source of exogenous pressure for cooperation and innovation among hunter-gatherers and examine the impact of extinction on long-run development. The results indicate that extinction affects economic performance by driving continental differences in biogeography, disease environments and institutions. Eurasia's location along the out-of-Africa migratory path provided human and animal populations with co-evolutionary foundations for domestication and agriculture, which gave Eurasians technological and institutional advantages in comparative development.

Human dispersal from Africa and the domestication of plants and animals are among the core historical processes of comparative development (Diamond, 1997; Ashraf and Galor, 2018; Riahi, 2020). *Homo sapiens*' out-of-Africa migration caused genetic changes in human populations, led to the isolation of human societies and contributed to varying cultural evolution. Domestication fundamentally altered human interactions with nature and led to the transition to agriculture. Identifying the evolutionary processes involved in dispersal and domestication is essential to understanding the deep determinants of development.[1]

Recent advancements in evolutionary biology, the Extended Evolutionary Synthesis, suggest that organisms modify their environments and influence the evolution of themselves and other species through niche construction (ecosystem engineering). This evolutionary process has been identified as a primary driver of macroevolutionary changes such as co-evolution and extinction during human dispersal and domestication, as shown in recent empirical and theoretical studies (e.g., Laland *et al.*, 2015; Boivin *et al.*, 2016). Despite its potential relevance for understanding comparative development, economic literature has yet to explore the implications of this new way of thinking about evolution.[2]

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[1] Section 1 provides an overview of various evolutionary processes involved in evolutionary change.

[2] The standard evolutionary theory (the Modern Synthesis) maintains that evolution matches organisms to random environments, i.e., niche construction does not affect the direction of evolution. Section 1 reviews different approaches to evolution.

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This paper utilises the Extended Synthesis and evaluates the economic consequences of human evolution in, and dispersal from, Africa. It finds that human dispersals and the extinction of megafauna (large mammals) during *Homo sapiens*' out-of-Africa migration contribute to continental divergence in economic performance.[3] Intriguingly, the regions that experienced more megafauna extinction in the past 100,000 years had faster growth rates in the last 500 years. Even after accounting for other deep-rooted determinants of long-run growth, extinction explains almost the entire growth gap between sub-Saharan Africa and other regions. However, this is not a direct causal effect, and the paper explores how various historical and evolutionary processes link extinction to economic growth.

Megafauna were dominant niche constructors of the last ice age; humans, plants and pathogens heavily depended on megafauna for survival (Boivin *et al.*, 2017; Galetti *et al.*, 2018; Doughty *et al.*, 2020).[4] *Homo sapiens* were particularly potent ecosystem engineers; their dispersal from Africa threatened the survival of megafauna, and many species went extinct soon after *Homo sapiens*' arrival (Koch and Barnosky, 2006).

The primary source of variation in extinction rates is archaic human dispersal patterns (Sandom *et al.*, 2014). A shorter history of co-evolutionary interactions between humans and animals corresponds to higher extinction rates. In Africa, where humans and animals intensely co-evolved, extinctions were negligible. Outside Africa, extinction monotonically increases with migratory distance from East Africa, i.e., Eurasia's extinctions were moderate, and the Americas and Australia underwent mass extinction. The paper's empirical analyses exploit the variation in extinction rates as a source of exogenous pressure on humans to change their interactions with nature (constructed niches) and each other (societal institutions) and examine the impact of extinction on long-run development.

In regions experiencing extinction, decreasing megafauna populations required megafauna-dependent species to form new co-evolutionary partnerships and restore ecological stability. In human societies, subsistence strategies shifted to ensure the stability of the supply of common resources, and other species needed to adjust their strategies to ecosystems dominated by humans. Hence, extinction rates inform us about the pressures humans encountered to practice common resource management and species' adaptability to humanly modified ecosystems—factors affecting the evolution of domestication and agriculture (Diamond, 1997; Zeder, 2017a; Riahi, 2021).

Africa's low extinction rates signal stable ecologies that did not require changing strategies from foraging to resource management, while mass extinction in the Americas and Australia indicates animal species without the evolutionary potential to adjust to human environments, and neither of these is conducive to domestication and agriculture. Moreover, evidence shows that extinction affected mammal-based pathogen dispersal, and is related to variation in disease environments (Doughty *et al.*, 2020), with important implications for economic development (e.g., Acemoglu *et al.*, 2003).[5]

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[3] *Homo sapiens*' out-of-Africa migration started around 100,000 years ago and ended with their occupation of South America around 15,000 years ago (Nielsen *et al.*, 2017).

[4] The last ice age (Pleistocene Epoch) is the most recent period of widespread glaciation. It occurred between 2.6 million and 11,700 years ago.

[5] The abundance of megafauna in Africa facilitated pathogen dispersal, and megafauna scarcity in the Americas disrupted pathogen dispersal (Doughty *et al.*, 2020). Continental differences in disease environments were important in the Holocene's economic divergence. For example, sub-Saharan Africa's disease environment was hostile to Eurasian animals and humans and provided a natural barrier to the dispersal of Southwest Asian domesticates (e.g., cows, sheep and horses) and European colonisers after 1500. Section 4 discusses these issues further.

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Eurasia's regions occupied by archaic humans early in the Pleistocene (from Southwest Asia to China) experienced moderate extinction, and empirical analyses show that this gave Eurasians biogeographical and institutional advantages for the climatic stability of the Holocene (the past 11,700 years). In those regions, the threats to the survival of megafauna were the impetus for human resource management and institutional change (e.g., towards polycentric institutions governing the commons; Ostrom, 1990). Moreover, Eurasian megafauna co-evolved with different human species before *Homo sapiens*, and some responded well to human management, which supported the robustness of the emerging institutions. These transformations laid the foundation for domestication, agriculture and, subsequently, the emergence of Eurasia's hierarchical institutions and epidemic diseases that facilitated European colonisation after 1500 CE (Diamond, 1997).

Thus, extinction is related to economic growth because it spurs continental divergence in biogeography, disease environments and institutions.[6] An important contribution of the paper is demonstrating that the geographical position of Eurasia along the out-of-Africa migratory path provided its populations with co-evolutionary foundations that facilitated economic development. Other regions experienced suboptimal co-evolutionary conditions, which deprived their human populations of the advantages Eurasians enjoyed.

This paper contributes to the literature by integrating the latest evidence from evolutionary biology, evolutionary anthropology, palaeontology and economics into a novel framework for studying deep determinants of long-run development. It shows how historical and evolutionary processes underlying ecosystems and institutions interact with critical junctures (e.g., climate change; Acemoglu and Robinson, 2012) in creating economic divergence. This framework offers a fresh perspective on the root causes of continental economic divergence and provides valuable guidelines for interpreting statistical associations between cultural or genetic variables and social outcomes, particularly in causal inference.

Smith (1975) and North and Thomas (1977) first proposed that megafauna extinction in the Americas is related to the emergence of plant-based agriculture on this continent. Diamond (1997) suggested that the mass extinctions in the Americas and Australia may explain the absence of domesticable megafauna in those regions. Riahi (2020; 2022) are the first studies that provide empirical evidence of the impact of extinction on plant and animal domestication. However, he does not identify extinction as a fundamental determinant of economic divergence or articulate the mechanisms connecting human dispersal and extinction to macro-level development outcomes, which are the focus of the current paper.

The macrogenoeconomics of comparative development focuses on the impact of *Homo sapiens*' out-of-Africa migration on human genetic variation and maintains that Eurasians' genetic features (genetic diversity and distance) explain their economic success.[7] The assumption underlying these theories is that *Homo sapiens*' out-of-Africa migration only changed humans, i.e., they rely solely on microevolutionary processes responsible for genetic variation (natural selection and genetic drift) and ignore the macroevolutionary aspects of human dispersal. This paper shows that dispersal changed many aspects of human environments, notably the traits of animal species and their diversity, through niche constriction and co-evolution. Eurasian economies developed

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[6] See contributions of Engerman and Sokoloff (1994; 2002), Diamond (1997), La Porta *et al.* (1997; 1998), Acemoglu *et al.* (2001; 2002; 2003; 2005), Olsson and Hibbs (2005) and Putterman (2008) for the importance of biogeography, endowments, institutions and disease environments in development. Nunn (2009) provides a review of this literature. Dow and Reed (2022) present a comprehensive discussion of economic prehistory.

[7] Ashraf and Galor (2013) and Spolaore and Wacziarg (2009; 2013) are prominent examples.

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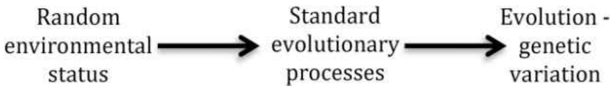

Fig. 1. *Change in Populations in the Modern Evolutionary Synthesis.*

earlier and grew faster than their counterparts primarily because they were better endowed biogeographically, not because of Eurasians' genetic composition. Evidence points to human niche construction as the first-order evolutionary process in continental economic divergence.[8]

Five sections constitute the remainder of this paper; each uses the preceding section's arguments and results to advance its thesis. Section 1 discusses approaches to evolution and their implications. Section 2 examines the relationship between human dispersal, extinction and domestication. Section 3 discusses the impact of extinction on historical inequalities in comparative development. Section 4 reformulates deep determinants of development with the help of Acemoglu and Robinson's (2012) critical juncture framework, revises Diamond's (1997) 'Factors Underlying the Broadest Pattern of History', and compares the current paper's framework with alternatives. The last section presents conclusions and directions for future research.

1. Approaches to Evolution

Various evolutionary processes work at different levels and shape the organic world's diversity.[9] Microevolutionary processes (mutation, natural selection, genetic drift and gene flow) cause evolutionary change *within* a population.[10] These processes are central to the standard evolutionary theory (the Modern Evolutionary Synthesis, hereafter, MES), a synthesis of Darwinian natural selection, Mendelian inheritance and population-level thinking.

In this approach, natural selection shapes organisms to pre-existing random environmental templates (environmental background conditions). Genes are the target of selection, and evolution consists of changes in gene frequencies (prevalence) from one generation to the next. Inheritance happens solely through genetic channels; evolution has a gradual pace and is driven primarily by natural selection.

Figure 1 presents the causes of diversity in the MES. Random changes in environments (e.g., climate change, volcanic activities, extraterrestrial impacts) result in changes in allele (variation in the form of the genes) frequencies, with various forms of natural selection acting on these variants and causing evolution. Along with genetic drift and gene flow, these processes change populations. Cultures evolve similarly, i.e., exogenous pressures require selection to identify the most adaptive and valuable cultural attributes (beliefs, ideas and behaviours).

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[8] Riahi (2017; 2021) shows that macrogenoeconomics' empirical evidence suffers from omitted variable bias. The current paper deepens Riahi's (2017; 2021) criticisms of macrogenoeconomics and pins down the evolutionary and historical processes responsible for the bias. Section 4 discusses these issues further.

[9] The following discussions of evolutionary processes and different approaches to evolution are adapted from multiple sources, including Laland and Boogert (2010), Laland (2015), Laland *et al.* (2015), Zeder (2015; 2017a; 2018) and Laland *et al.* (2017). I refrain from excessive referencing to save space.

[10] Mutation is a random (environmentally triggered) genetic change in a population. Natural selection is the process whereby organisms better adapted to their environment tend to survive and produce more offspring. Genetic drift occurs when a fraction of a population moves away, forming two genetically distinct groups. Gene flow is the transfer of genetic material from one population to another (migration and mating).

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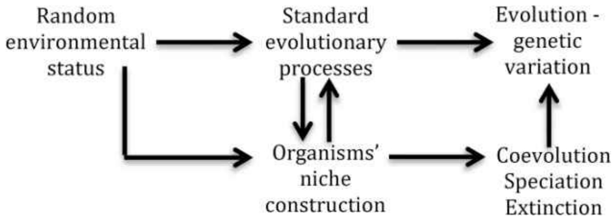

Fig. 2. *Change in Populations in the Extended Evolutionary Synthesis.*

Other evolutionary processes are used to study populations' co-evolution and evolutionary changes with deep-time perspectives (e.g., human evolution).[11] These processes are central to the Extended Evolutionary Synthesis (henceforth, EES), which extends the structure of the MES to include broader definitions of evolution, evolutionary processes and inheritance mechanisms.

In particular, the EES maintains that organisms' modification to their environments (niche construction) is an evolutionary process more fundamental than the standard evolutionary processes. Figure 2 presents the mechanisms of change in populations in the EES.[12] Here, the processes of the MES are still at work. However, niche construction affects evolution's direction and pace. Through their metabolism, activities and choices, organisms shape their environments in ways that increase their fitness in those environments. These modified ecosystems trigger co-evolutionary responses affecting life diversity within and without the ecosystem (e.g., co-evolution and extinction). Thus, apart from random environmental changes, non-random differences in environments resulting from the organisms' activities affect genetic and cultural evolution. The feedback from the standard evolutionary processes indicates that organisms more effective in niche construction produce more offspring, i.e., they evolve by natural selection.[13]

All organisms engage in niche construction to harvest energy. A famous example is the beaver building dams. Laland and Boogert (2010) argue that beavers' dams modify nutrient cycle and decomposition dynamics, change riparian zones' structure, influence the water's character and the materials transported downstream, and modify plant diversity. These developments ultimately modify natural selection's pattern and strength, acting on beaver traits and thousands of other species. Therefore, beavers' niche construction affects more than the prevalence of genes for dam-building in beaver populations.

In the EES, inheritance happens through a broad range of internal (genetic, epigenetic and maternal) and external (ecological and cultural) channels.[14] Niche construction has persistent ecological impacts that affect multiple generations of all organisms involved in the constructed niche. Ecological inheritances alter selective environments (the environments in which natural selection operates) and can change the patterns of evolution.

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[11] Macroevolutionary processes describe evolutionary patterns above the species level. Examples of macroevolutionary processes are co-evolution, speciation and species selection. Co-evolution occurs when two or more species reciprocally affect each other's evolution through natural selection or other evolutionary processes. Speciation is the formation of new and distinct species through successive microevolutionary changes. Species selection is large-scale natural selection in which an entire species is the target of selection; this process can result in extinction.

[12] This framework is simplified to fit the purpose of the current paper. See Laland *et al.*'s (2015, tbl.1, figs.1, 2) for extensive descriptions of the mechanisms of the EES.

[13] However, in the EES, the target of selection could be genes, genome (the complete set of the genetic material of an organism), tissues, organisms, groups of organisms (clade and kin) and even species.

[14] Unlike genetic changes, epigenetic changes do not change the DNA sequence; they affect the translation of the DNA sequence.

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In short, change in populations in the EES happens through cyclical and reciprocal interactions between micro- and macroevolutionary processes and multiple inheritance channels. The standard evolutionary processes are not the ultimate causes of genetic or cultural evolution; no single factor by itself is the prime cause of evolution.

The MES recognises niche construction as a universal phenomenon, but assumes its impacts are similar to random environmental changes. Therefore, the MES does not elevate niche constriction to the rank of an evolutionary process. The following example is cited in Laland (2015) and helps clarify the difference between the MES and the EES, particularly regarding their applications to social sciences.

The frequency of alleles for adult lactose tolerance correlates with whether that culture has a history of dairy farming. Lactose-tolerant alleles were selected in populations that adopted dairy farming and relied on dairy products. For the MES, this is equivalent to a lactose-rich asteroid crashing into the planet, creating a nutritional environment favouring genetic variants that thrive in this new ecology. The EES sees the adoption of dairy farming (a cultural niche construction) as a manifestation of the general propensity of humans to systematically modify their environments towards states that otherwise are not attainable. The process that triggered the increase in the frequency of lactose-tolerant alleles is human niche construction, a non-random event generated by human *choice*, influencing the direction of evolution by natural selection.

Because of this emphasis on the interplay between environments and evolutionary processes, the EES provides valuable guidelines for social scientists studying evolutionary and historical processes involved in cultural and institutional change, or the relationships between human genetic or cultural variation and socioeconomic outcomes. For example, the fundamental assumption of economic theory is that preferences guide choices, and the influential literature on the biological foundations of preferences provides evolutionary rationales for preferences.[15] This literature relies on the MES and assumes that natural selection shapes preferences in response to environmental background conditions, with genes as the sole inheritance channel. The EES maintains that choices could be evolutionarily consequential, suggesting a richer dynamics of interactions between preferences and choices: systematic environmental changes resulting from human choice could merge with genetic, cultural and ecological inheritances and change the direction of evolution (by natural selection) of human preferences. Utilising the EES could help these theories examine how genetic and cultural evolution interact in shaping preferences, a question that remains unresolved in this literature (Robalino and Robson, 2019). Other applications of the EES are considered in the remainder of the paper.[16]

1.1. *General Framework*

The paper's conceptual framework connects human dispersal to macro-level development outcomes through the niche construction process, with attention to the external inheritance mechanisms. The argument can be schematically summarised as

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[15] This literature provides evolutionary explanations for hedonic and adaptive utility, risk aversion and theory of mind. See Robalino and Robson (2019) for a review.

[16] Examining the full implications of the EES's framework, even only for the economic literature, is beyond this paper's scope and the author's knowledge. Interested readers are referred to a recent issue of the Royal Society's *Interface Focus* (2017: volume 7, issue 5), which discusses the EES's structure and its implications for various scientific disciplines, including social sciences.

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[human dispersal]⇒[niche construction/co-evolution]⇒[extinction/resource management]
⇒[prehistoric/pre-colonial environments]⇒[historic/current inequalities]

As humans dispersed globally, they affected other species by their behaviours (and vice versa; archaic human–flora–fauna niche construction and co-evolution; Boivin *et al.*, 2017). With *Homo sapiens*' out-of-Africa migration, the duration of human–fauna co-evolution became crucial in the severity of megafauna extinction (Sandom *et al.*, 2014), the need for resource management by *Homo sapiens*, and other species' responses to human control (modern human–flora–fauna co-evolution; domestication; Riahi, 2020; 2022). Megafauna extinction and animal domestication are related to historical disease environments through various channels (Wolfe *et al.*, 2007; Doughty *et al.*, 2020). Through these, dispersal is related to pre-colonial environments (e.g., factor endowments and disease environments), which, in turn, influence comparative development through well-known historical processes (e.g., Diamond, 1997; Acemoglu *et al.*, 2001).

A novel aspect of the above framework is its emphasis on the ecological consequences of human dispersal. The economic literature has overwhelmingly ignored this aspect of human dispersal and focused solely on the role of *Homo sapiens*' out-of-Africa migration in causing human genetic variation primarily through genetic drift (e.g., Ashraf and Galor, 2013). The paper returns to this issue in Section 4. Sections 2 and 3 describe and show evidence of the above argument step by step.

2. Ecological Consequences of Human Dispersal

2.1. *Human Dispersal, Human–Fauna Co-evolution and Megafauna Extinction*

Humans appeared around 5 to 7 ma (mega-annum, one million years before 1950 CE) in an area known as the Wall of Africa, spreading south–north from South Africa to Ethiopia.[17] Human dispersal from Africa began 1.9 ma and involved successive waves of different species of humans. All human migrations follow similar geographical patterns, i.e., they were all out-of-Africa migrations with Southwest Asia or the Arabian Peninsula as the gateways of Eurasia (Lopez *et al.*, 2015).

Homo erectus first left Africa at 1.9 ma and were dispersed across most of Eurasia's lower latitudes by 1.4 ma.[18] Late forms of this species (*Homo antecessor* in Europe and *Homo heidelbergensis* in Africa) survived until 0.5 ma in different regions. *Homo heidelbergensis* spread across East Africa and Eurasia, giving rise to Neanderthals and Denisovans. These species occupied warmer and more ecologically diverse areas of this continent below the 50th parallel. Neanderthals ranged from the Middle East to Europe, while Denisovans spread across Central to Southeast Asia and Oceania. With the retreat of ice sheets in the late Pleistocene, these species eventually pushed human boundaries beyond the 50th parallel (Harvati *et al.*, 2019).

Our ancestors, *Homo sapiens*, appeared in Africa more than 300 ka (kilo-annum, 1,000 years before 1950 CE). They migrated from Africa between 60 and 90 ka and reached South America by around 15 ka. They were the first humans to set foot in Oceania and the Americas.[19]

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[17] The dates are approximates based on the latest evidence. Humans split from chimpanzee lineage between 5 and 7 ma in Africa (Steiper and Young, 2006).

[18] Fossils suggest *Homo erectus* were present in Georgia by 1.85 ma, in North China by 1.66 ma, in Java by 1.6 ma and in Spain by 1.4 ma. This species had limited cranial capacity (brain size of 660–750 cc), a small body frame and limited bipedal abilities (Dennell, 2017).

[19] *Homo sapiens* were believed to have originated in East Africa approximately 250,000 years ago (Henn *et al.*, 2012; Nielsen *et al.*, 2017). However, a recent discovery of 350,000-year-old human fossils from Jebel Irhoud in Morocco

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Humans, animals and plants continuously affected each other's behaviour and evolution during these episodes (Boivin *et al.*, 2017). These co-evolutionary interactions created four distinct human paleo-biogeographical regions (Sandom *et al.*, 2014). These regions are sub-Saharan Africa—the birthplace of the genus *Homo* (human evolution region)—Eurasia below the 50th parallel, which was occupied by archaic humans early in the Pleistocene (archaic-early region); Eurasia above the 50th parallel, which was occupied by archaic humans later (archaic-late region); and the Americas and Oceania (sapiens region).

A source of disparities between these regions was the duration of human–fauna co-evolution. When *Homo sapiens* started their dispersal from Africa, there were vast differences in animals' familiarity with humans. African animals co-evolved with multiple human species and became highly familiar with human behaviour, i.e., they became 'predator-savvy' concerning humans (e.g., they evolved long flight distances from humans). Animals of the Americas and Australia, who evolved in the absence of humans, were 'predator-naive' (unfamiliar with the tool-making bipedal ape). Eurasian mammals co-existed with large-brained humans since *Homo erectus* dispersal. They were neither as savvy as African mammals nor as naive as those of the Americas and Oceania.[20]

Homo sapiens dispersal heightened these ecological differences. Their dispersal accompanied the extinction of around a quarter of large, mainly herbivore mammals globally in an event known as the Late Quaternary Extinction, henceforth, the LQE (Koch and Barnosky, 2006). These extinctions did not affect all regions uniformly. Figure 3(a) shows that the LQE is negligible in the human evolution region and almost all African megafauna survived into the Holocene. In other areas, the LQE is considerable, with the archaic-early region experiencing relatively moderate extinction (albeit with considerable variation). Other regions underwent severe extinctions. Figure 3(b) uses *Homo sapiens*' migratory distance from East Africa as a proxy for general human dispersal patterns. The positive correlation between the two variables indicates higher extinction where humans arrived later.

The literature proposes four main explanations for the LQE: human-driven extinction, climate-driven extinction, hyper diseases and extraterrestrial impacts (Koch and Barnosky, 2006). Human- and climate-driven extinction have the most reliable empirical support and are most compatible with the observed patterns in Figure 3.

Homo sapiens dispersal and the LQE coincide with the climatic fluctuations of the Pleistocene–Holocene transition. Dansegard–Oeschger (D-O) and Heinrich events were two primary drivers of these fluctuations.[21] The D-O events caused rapid warming followed by cold periods lasting a few hundred years, and Heinrich events resulted in the melting of icebergs and the global rise in sea levels. From 60 to 11.7 ka, the Earth witnessed six Heinrich events and 17 D-O events. These fluctuations, which climaxed during the Last Glacial Maximum (LGM, 21 ka), disproportionately impacted higher latitudes, where more animal species went extinct.

Human-driven extinction concerns the impact of *Homo sapiens* niche construction, particularly their hunting methods and the scope of their environmental modifications. Compared to other

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(Hublin *et al.*, 2017) points to possible pan-African origins of *Homo sapiens* and pushes the timing of their appearance back to more than 300,000 years ago. Behaviourally modern *Homo sapiens* migrated from Africa at 100 ka (possibly earlier). The upper Palaeolithic Model set the date of the emergence of behavioural modernity (e.g., burial, fishing, figurative arts, blade technology) at around 50 ka (e.g., Klein, 1995). Recent studies pushed this date back to 165 ka in South Africa (Marean *et al.*, 2007) and further (D'Errico, 2003).

[20] For more on these issues, see Boivin *et al.* (2017, ch. 2).

[21] See Bond *et al.* (1999), Hemming (2004), Long and Stoy (2013) and Milner *et al.* (2016) for descriptions of Pleistocene climates.

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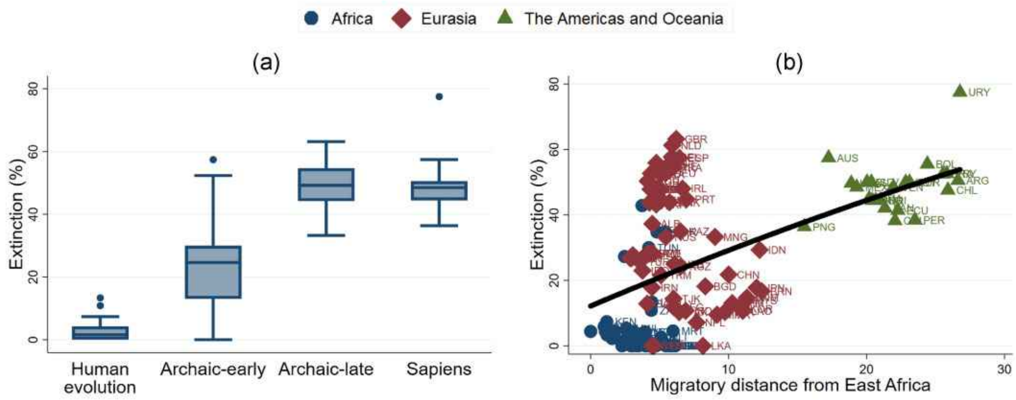

Fig. 3. *The Late Quaternary Extinctions.*

Notes: The figure shows the variation in the severity of the LQE across human paleo-biogeographical regions. Extinction rates are based on fossil records, including extinction events after Homo sapiens' arrival and from 132 ka to around 10 ka (Sandom *et al.*, 2014). In panel (a), the middle line and box represent the median and first to third quartiles. The whiskers extend to the upper and lower adjacent values that are no more than 1.5 times the interquartile range, and the dots indicate outside values. Human evolution includes countries in sub-Saharan Africa. Archaic-early and archaic-late include Eurasian countries below and above the 50th parallel north. North Africa is grouped with the archaic-early region. Sapiens include Oceania and the Americas. In panel (b), the migratory distance from East Africa is the great circle distance from Addis Ababa (Ethiopia) to the country's modern capital city in units of 1,000 km. The fitted line corresponds to an unconditional regression. See Section 2.2 and Online Appendix B for discussions of all variables.

human species, *Homo sapiens* had a larger brain and group sizes (around 150 persons; Gamble, 2013) and had advanced projectile weapons developed for hunting predator-savvy animals of Africa (Shea and Sisk, 2010). They competed fiercely with other large mammals over resources and extensively used fire and other methods for clearing land. These features were potent threats to the survival of other large mammals *everywhere* during *Homo sapiens*' dispersal. However, the severity of these threats varied with animal species' ability to adjust to ecosystems dominated by humans, i.e., regions in which animals and humans co-existed and co-evolved longer lost fewer species on *Homo sapiens*' arrival. For instance, human arrival to the Americas resulted in 'over-kill' (rapid loss of prey species due to overhunting; Martin, 1984) and mass extinctions.

There is an ongoing debate regarding the importance of human activities and climate change in the LQE. A contentious point has been America's extinctions, where human arrival and climate change happened almost simultaneously. However, based on carbon isotope dating of the decline of the large mammals, Surovell *et al.* (2016) found evidence of significant human presence during these extinctions in the Americas. Recent global studies of the LQE have found evidence of the impacts of both humans and climate change, with humans having a more substantial effect on the LQE everywhere except in Europe (Sandom *et al.*, 2014).

2.1.1. *Data and methods*

The following regression equation examines the impact of human dispersals on megafauna extinction:

$$e_i = \alpha h_i + X_i'\gamma + u_i, \tag{1}$$

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where e_i is the country i extinction rates, h_i includes proxies of human arrival, X_i is a vector including a constant term and co-variates of e_i and h_i. u_i is a random error term. The primary interest lies in α. The expectation is for this coefficient to remain a robust determinant of e_i with the inclusion of other variables.

Extinction rates are based on fossil records and include extinction events that occurred *after Homo sapiens*' arrival to different regions from 132 ka to around 1 ka (Sandom *et al.*, 2014). Except on the islands, which are not included in the data, most of these extinctions happened before the Holocene (before 10 ka). Moreover, in many instances where animal species went extinct in the Holocene, extinction started in the Pleistocene (Mann *et al.*, 2019). The sample includes 177 known extinct and extant large mammalian species in each Taxonomic Databases Working Group country.[22] The widely used definition of megafauna is large mammals weighing more than 44 kg. In Sandom *et al.*'s (2014) data, 154 out of 177 species (or 90%) are species weighing more than 44 kg.

The main variables quantifying the patterns of human dispersal are human arrival dummies. These are four binary variables for different human paleo-biogeographical regions discussed in Section 2.1.[23] In the presentation of regressions results, these dummies are referred to as 'Human evolution', 'Archaic-early', 'Archaic-late' and 'Sapiens'.

Apart from human arrival dummies, migratory distance from East Africa (Ashraf and Galor, 2013) and millennia of *Homo sapiens* settlement (Borcan *et al.*, 2021) are used for h_i. Migratory distance from East Africa is the great circle distance (in units of 1,000 km) from Addis Ababa (Ethiopia) to the country's modern capital city along a land-restricted path forced through one or more of five intercontinental waypoints. The millennia of *Homo sapiens* settlement indicate thousands of years since the initial uninterrupted settlement of anatomically modern humans (before 2000 CE) on the territories that now belong to modern-day countries.

Climate change could confound e_i and h_i. To account for this possibility, X_i includes controls for climate change during the Pleistocene–Holocene transition. Sandom *et al.* (2014) provide four measures of climate change for this period: temperature anomaly, precipitation anomaly, temperature velocity and precipitation velocity between the LGM and present-day climate.[24] In general, climate anomaly represents deviations from a reference value, which, in the current case, is the present-day climate. Velocity indicates the speed at which species need to migrate to stay in the same enveloped climatic condition.[25] Sandom *et al.* (2014) use these variables to proxy for the full glacial-interglacial amplitude of climate change magnitude since the LGM and show that they correlate strongly with the climatic fluctuations of the past 100,000 years. These climate variables are highly correlated, and Sandom *et al.* (2014) find that temperature anomaly and precipitation velocity correlate strongly with extinction rates. Thus, baseline specifications include only these

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[22] With some exceptions, TDWG (Taxonomic Databasis Working Group) regional classification corresponds to countries' current borders. The exceptions are large countries such as Russia, China, the United States, Brazil, Australia, India, Argentina, Mexico, South Africa and Chile, for which data are available at the within-country level. Because other controls are available at the country levels, the average extinction rates across TDWG regions are used for these countries. Within-country variation in extinction for large countries is minimal, and averaging at the country level does not affect the main results.

[23] As a reminder, these regions are: sub-Saharan Africa (human evolution), North Africa and areas below the 50th parallel north in Eurasia (archaic-early; countries with central latitude < 45), Eurasian countries above the 50th parallel (archaic-late; countries with central latitude ≥ 45) and Oceania and the Americas (sapiens).

[24] All variables are calculated from the WorldClim data at a resolution of 2.5 arcminutes.

[25] The velocity of climate change is calculated as the temporal trend divided by a spatial gradient in a climate variable such as temperature or precipitation. More specifically, climate velocity $= \Delta$ (climate variable)/year $\div$ Δ (climate variable)/km (Ordonez and Williams, 2013).

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two variables.[26] Both variables are presented in absolute value and are standardised to fall between 0 and 1, with 0 and 1 representing the lowest and the highest climate change magnitudes, respectively.

Biodiversity generally decreases from the tropics to the poles (Willig *et al.*, 2003). Ecologically diverse regions and regions of high tectonic activities had high speciation rates and were humans and other mammals' primary dispersal routes and preferred habitats in the Pleistocene (Diamond, 1997; Gamble, 2013). Larger continents were home to more megafauna species, and Eurasia's east–west axis orientation facilitated species dispersals (Diamond, 1997). Hence, X_i includes absolute latitude, mean elevation, terrain roughness (mountainousness) and ecological diversity (based on Köppen–Geiger climate zones). Other controls are continent size and axis.

Continental differences in human culture could confound the relationship between dispersal and extinction. For example, one possibility is that Eurasians were inherently (culturally or genetically) more capable of collective action aimed at common resources and prevented mass extinction. However, note that in terms of brain and group size, there are no noticeable differences between *Homo sapiens* who dominated Africa and colonised Eurasia and those who later occupied the Americas and Oceania (Gamble, 2013). Archaeological records show that Paleo-Indians domesticated many plant species and developed agriculture, i.e., they could collectively manage resources (Diamond, 1997; Larson *et al.*, 2014). Besides, cultural explanations cannot justify Eurasia's high variation in extinction rates and the absence of extinction in sub-Saharan Africa.

Nevertheless, to account for the broad heterogeneities of human cultures, X_i includes the quadratic form of human genetic diversity. Genetic diversity is an aggregate measure of genetic and biological differences between populations, and the literature uses this variable to proxy for populations' ability to cooperate and innovate (Ashraf and Galor, 2013). Furthermore, the set of controls for geography and climate is correlated with many unobserved demographic and cultural features and guards against the potential omitted variable bias.

Other demographic factors, such as population density, could influence the relationship between h_i and e_i. However, this is unlikely because from 90 ka to 10 ka, human populations were most dense in sub-Saharan Africa (around 25 people per 100 km^2), where extinction was negligible. Outside this region, human density *decreased* along the out-of-Africa dispersal routes and at higher latitudes (Timmerman and Friedrich, 2016). This pattern implies a *negative* relationship between human arrival and extinction, the opposite of what we observe in Figure 3. The Americas and Australia experienced mass extinction despite their low human densities, a testament to the disruptive effect of human niche construction and the importance of human–fauna co-evolution in these extinctions.

Table 1 presents summary statistics for some of the variables discussed above. Online Appendix B shows summary statistics for all variables. Table 1 reports means and standard deviations. Extinction rates (column 2) increase monotonically from sub-Saharan Africa to the Americas (human evolution to sapiens). Column 3 shows that the archaic-late region experienced the most severe climate change (measured by temperature anomaly) among all regions. The magnitude of climate change is comparable in other areas. The LQE was substantial in higher latitudes of Eurasia (column 4). Outside this continent, latitude and extinction do not co-vary. The last column shows that a distinct feature of the archaic-early region is its topological fea-

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[26] Other specifications include the first two principal components of all four variables to use all the available information.

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Table 1. *Descriptive Statistics.*

	(1) Migratory distance	(2) Extinction (%)	(3) Temperature anomaly	(4) Absolute latitude	(5) Terrain roughness
Human evolution	3.6	2.4	0.3	11.8	0.1
(sub-Saharan Africa, $N = 39$)	(1.6)	(3.1)	(0.0)	(7.7)	(0.1)
Archaic-early	6.4	24.7	0.4	30.0	0.3
(Eurasia-early, $N = 46$)	(2.9)	(14.0)	(0.1)	(11.6)	(0.2)
Archaic-late	5.6	49.1	0.6	50.0	0.1
(Eurasia-late, $N = 20$)	(1.1)	(8.5)	(0.1)	(4.0)	(0.1)
Sapiens	16.4	46.9	0.3	16.5	0.2
(Oceania, $N = 2$)	(1.2)	(14.9)	(0.0)	(14.8)	(0.2)
Sapiens	22.5	48.6	0.3	15.9	0.2
(The Americas, $N = 21$)	(2.5)	(8.1)	(0.1)	(10.6)	(0.1)

Notes: Human evolution indicates sub-Saharan Africa. Archaic-early and archaic-late human includes Eurasia's regions below and above the 50th parallel north, respectively. North Africa is grouped with the archaic-early region. Sapiens include Oceania and the Americas.

tures, measured by the terrain roughness index. These regions were biodiversity hotspots and mammals' preferred habitats during the last ice age.

With the standard assumptions on the distribution of u_i, estimating (1) using ordinary least squares (OLS) is appropriate. However, extinction rates are based on fossil records and are aggregated at the country level. Moreover, large mammals are wide-ranging species, and their populations could pass the extinction threshold (the threshold after which the birth rate remains lower than the death rate) in response to regionally shared environmental factors that h_i or X_i do not capture. These could result in spatial error clustering and biased and inconsistent estimates (Anselin, 1988; Kelly, 2019).[27] Therefore, the next section estimates (1) as a Spatial Autoregressive (SAR) model with a spatial error term (SARerr) using generalised spatial two-stage least squares (GS2SLS; Kelejian and Prucha, 2010). Additionally, the paper employs Conley's (1999) method to account for spatial correlations.

Both methods (SARerr and Conley's) are Generalised Methods of Moments (GMM) approaches that allow interactions between unobserved factors in adjacent spatial units. They utilise a spatial weight matrix to define the spatial relationships among the observations. In regression analyses, the spatial weight matrix is an inverse-distance contiguity matrix, allowing stronger spatial dependence among neighbours closer to each other.[28] Conley's method does not assume a specific functional form for spatial correlation. While SARerr models estimate the spatial dependence in the dependent variable, considering both the independent variables and the spatial lag of the dependent variable in a specific regression framework.[29]

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[27] Spatial clustering violates the assumption of independent errors, i.e., $Cov(e_i, e_j) \neq 0$ for $i \neq j$.

[28] In SARerr models, the spatial weight matrix is row-normalised, and the neighbourhood is defined as the second neighbour. Conley's method requires imposing a cut-off distance for spatial correlation. For regressions evaluating outcomes in the pre-colonial era, e.g., in (1), the cut-off distance is set to 5,000 km. This threshold does not allow for spatial interaction between the Old and New World, which is a reasonable assumption for the pre-colonial era (Ashraf and Galor, 2013). For regressions evaluating outcomes in the past 500 years (Section 3), the cut-off distance is set to 10,000 km to allow for spatial dependence between all continents.

[29] These models include an error term that accounts for unexplained spatial dependence after considering the spatial lag and independent variables. More precisely, $u_i = \lambda w_i u_j + \zeta_i$ in (1), where λ is the autocorrelation parameter, $w_i u_j$ represents spatially lagged error terms with spatial weights of w_i, and ζ_i is a random error term. See Darmofal (2015) for a discussion of spatial models and Kelejian and Prucha (2010) for the GS2SLS method.

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Table 2. *Regressions of Equation (1).*

	Dependent Variables: Extinction Rates								
	OLS						GS2SLS		
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Human evolution	-0.22^{***}	-0.20^{***}				-0.21^{***}			-0.21^{***}
	(0.02)	(0.04)				(0.04)			(0.04)
Archaic-late	0.24^{***}	0.16^{***}				0.16^{***}			0.14^{***}
	(0.03)	(0.04)				(0.03)			(0.03)
Sapiens	0.24^{***}	0.22^{***}				0.26^{**}			0.29^{***}
	(0.03)	(0.04)				(0.08)			(0.08)
Migratory distance			15.50^{***}	18.80^{***}			19.42^{***}		
			(1.43)	(1.45)			(1.78)		
Sapiens settlement					-3.42^{***}			-3.40^{***}	
					(0.24)			(0.27)	
Genetic diversity						-11.70			-11.30
						(7.17)			(7.01)
Genetic diversity^2						8.88			8.64
						(4.99)			(4.89)
Temperature anomaly		-0.06		0.06	0.07	-0.09	-0.09	-0.01	-0.12
		(0.12)		(0.13)	(0.13)	(0.11)	(0.12)	(0.12)	(0.10)
Precipitation velocity		-0.04		-0.10	-0.10	-0.03	-0.05	-0.06	-0.01
		(0.06)		(0.06)	(0.05)	(0.05)	(0.06)	(0.05)	(0.05)
Absolute latitude		0.60^{***}		0.92^{***}	0.46^{***}	0.57^{***}	0.94^{***}	0.47^{***}	0.59^{***}
		(0.13)		(0.12)	(0.13)	(0.13)	(0.11)	(0.13)	(0.12)
Mean elevation		-0.08^{***}		-0.09^{***}	-0.09^{***}	-0.08^{***}	-0.06^{**}	-0.06^{**}	-0.06^{***}
		(0.02)		(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)
Terrain roughness		0.29^{**}		0.31^{**}	0.26^{*}	0.27^{**}	0.15	0.15^{*}	0.20^{*}
		(0.09)		(0.10)	(0.10)	(0.10)	(0.08)	(0.08)	(0.08)
Ecological diversity		-0.09		-0.14^{*}	-0.02	-0.08	-0.11^{*}	0.00	-0.07
		(0.06)		(0.06)	(0.05)	(0.06)	(0.05)	(0.04)	(0.05)
Continent size		-0.00		-0.00	-0.00^{*}	-0.00	-0.00	-0.00^{*}	-0.00
		(0.00)		(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
Continent axis		-0.09^{***}		-0.03	-0.09^{***}	-0.06^{*}	-0.00	-0.08^{**}	-0.06^{*}
		(0.02)		(0.02)	(0.02)	(0.03)	(0.03)	(0.03)	(0.03)
N	128	128	128	128	125	128	128	125	128
R^2	0.78	0.88	0.26	0.78	0.83	0.89	0.77	0.83	0.89

Notes: The table presents regressions of (1), with the extinction rates as the dependent variable. Human evolution, archaic-late and sapiens are dummy variables for sub-Saharan Africa, Eurasia-late, and the New World. Archaic-early (Eurasia-early) is omitted. Heteroscedasticity-robust standard errors are reported in parentheses. All regressions have constants. For spatial models, pseudo-R^2s are reported. ***Significant at 1%. **Significant at 5%. *Significant at 10%.

2.1.2. *Results*

Table 2 presents regressions of (1). The sample includes 128 countries for which data on extinction and the independent variables are available. In regressions that use millennia of *Homo sapiens* settlement, the sample size falls to 125 countries. Columns 1–6 show OLS results, and columns 7–9 present spatial models.

In column 1, human arrival dummies are the only explanatory variables, corresponding to Figure 3(a). All three dummies are significant at the 1% level, and they jointly explain 80% of the variation in extinction. These suggest that compared with the archaic-early (the omitted group), the LQE was 20% milder in sub-Saharan Africa (human evolution) and 20% harsher in the Americas and Oceania (sapiens).

Column 2 adds controls for climate change and geography to column 1, which increases the explanatory power of regression by 10% (from 0.8 in column 1 to 0.9 in column 2). Climate change variables are not statistically significant. Latitude, elevation, terrain roughness and continent axis

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are statistically significant, generally at the 1% level. The coefficients of human arrival dummies remain stable and statistically significant at the 1% level.[30]

The remaining columns present additional robustness checks. Since the impacts of climate change and geography remain stable in all models, they are not discussed further to save space.

Columns 3 and 4 use migratory distance from East Africa instead of human arrival dummies. In the unconditional model (column 3), migratory distance explains 30% of the variation in the LQE. With the inclusion of climate change and geography in column 4, the R^2 of the regression rises to 0.8, and the impact of migratory distance becomes *stronger*. The coefficient of 19 for migratory distance in column 4 indicates that a 6,000 km increase in the migratory distance—the distance between Zambia (the centre of sub-Saharan Africa) and Southwest Asia (humans' gateway into Eurasia)—increases the LQE by around 12%, which corresponds to half of the difference in the LQE between human evolution and archaic-early (Table 1). As another example, the distance between Central America and Southwest Asia is 15,000 km, which translates into a 30% increase in extinction, i.e., late human arrival fully explains the extinction gap between archaic-early and sapiens (Table 1).

In Table 2, column 5, millennia of *Homo sapiens* settlement, along with other controls, are included in the model. The coefficient of -3 ($\text{SD} = 0.2$) means that an additional 80,000 years of human settlement—approximately the difference between human evolution and archaic-early—corresponds to a 24% decrease in extinction. Thus, the timing of human arrival fully explains the extinction gap between these two regions (Table 1). Column 6 introduces the quadratic form of human genetic diversity as an additional variable in the regression presented in column 2. However, the analysis reveals that the impact of genetic diversity is statistically insignificant, and its inclusion does not alter the results obtained in column 2.

Columns 7–9 show the spatial regressions estimated using GS2SLS. The results closely resemble those obtained through OLS estimation. This outcome is to be expected, given that human paleo-biogeographical regions were largely isolated from each other during the Pleistocene era, making it unlikely for them to form spatial clusters. Table A4 in the Online Appendix (columns 1–3) uses Conley's (1999) method to incorporate spatial autocorrelation in (1) and confirms Table 2's results.

Table A2 (Online Appendix A) examines climate change interactions with human dispersal. The justification for these models is the simultaneity of climate change with *Homo sapiens* dispersal and that climate change could have guided the dispersal. The impact of all three proxies of human dispersal patterns (human arrival dummies, migratory distance and sapiens settlement) remains highly stable and statistically significant in these models.

Building on Sandom *et al.* (2014), this section's results strongly support theories that, starting with Martin (1984), have attributed these extinctions to human activities. The following section examines the aftermath of these extinctions.

2.2. *Plant and Animal Domestication by* Homo sapiens

Humans lived in mobile bands of hunter-gatherers foraging on wild species for most of their history. Shortly after the Holocene, domestic species appeared independently in isolated locations, and subsistence strategies gradually shifted from foraging to farming. By the mid-Holocene

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[30] Sandom *et al.* (2014) find statistically significant effects of climate change without controlling for geography in their models.

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Table 3. *Extinction, Biogeographical Endowments and Domestication.*

	(1) Extinction rates (%)	(2) Wild progenitors of domesticable megafauna	(3) Large-seeded wild grass	(4) Centres of independent domestication
Sub-Saharan Africa	2	0.2	3.9	8
[Human evolution, $N = 39$]	(3)	(0.4)	(0.6)	
Eurasia	32	4.0	11.0	22
	(17)	(1.4)	(13.7)	
[Archaic-early, $N = 46$]	25	4.0	15.6	17
	(14)	(1.5)	(14.1)	
[Archaic-late, $N = 20$]	49	3.8	0.5	5
	(9)	(1.1)	(0.5)	
Oceania	47	0.0	1.0	1
[Sapiens, $N = 2$]	(15)	(0.0)	(1.4)	
The Americas	49	0.2	3.4	9
[Sapiens, $N = 21$]	(8)	(0.4)	(1.5)	

Notes: The abundance of wild progenitors of megafauna species with traits suitable for domestication is from Larson and Fuller (2014). Figure B2 (Online Appendix B) presents the geographic distribution of these species. Olsson and Hibbs (2005), who used Diamond's table 8.1 (1997, p.135) to construct this variable, is the data source on the distribution of large-seeded wild grass species. Olsson and Hibbs refer to this variable as 'domesticable plants'. However, not all species mentioned in Diamond (1997) were domesticable or domesticated, and non-grass domesticable plant species (e.g., fruits) were not included in Diamond's data. Hence, Table 3 follows Diamond (1997) and labels this variable as 'large-seeded wild grass species'. This variable is available for 96 countries in the current sample. Centres of independent domestication are regions in which native populations independently domesticated their plants or animal species from the early- to mid-Holocene. Figure 4 presents the location of the plant and animal domestication centres. Online Appendix B presents data definitions and sources.

(around 5,000 years ago), sedentism and agricultural economies familiar to today's humans emerged in many places.

Table 3 shows that there was considerable variation in the distribution of domesticable species and the occurrence of domestication. Column 2 shows that, on average, four domesticable megafauna species were endemic in Eurasia, while other regions were not endowed with such species for the most part.[31] This does not mean that there were no *candidate* species (species resembling their domesticated Eurasian counterparts) on other continents. Diamond (1997) argues that sub-Saharan Africa had 51 candidate species, and even after the LQE, there were 24 extant candidate species in the Americas. He argues that, except for the llama and alpaca in the Americas, none of the candidate species of other continents had the traits permitting domestication by humans.

Column 3 shows that Eurasia also had the highest concentration of large-seeded wild grass species (ancestors of species such as wheat, barley, lentil pea, rice, millet and soybean; Diamond, 1997; Larson *et al.*, 2014) that later became humans' most valuable crops, although this is not as dramatic as the differences in domesticable megafauna. The last column of the table shows that centres of independent domestication—regions in which native populations independently domesticated their plant or animal species—are disproportionately located in Eurasia.

An overlooked aspect of these differences is the disparities *within* Eurasia. Large-seeded wild grass species are disproportionately concentrated in the archaic-early region, particularly in its Mediterranean area. Diamond (1997) attributes this to climate and geography. More importantly,

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[31] Of the 'Ancient Fourteen' species (Diamond, 1997), only the llama and alpaca were available in the Americas (in the Andes, specifically). Only the wild progenitors of the donkey, cow and pig were available in Africa (mainly in the Mediterranean regions). The rest (the sheep, goat, horse, Arabian camel, Bactrian camel, reindeer, water buffalo, yak, Bali cattle and gaur) were exclusive to Eurasia.

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despite the availability of domesticable megafauna (species such as the cow, the pig and the horse) in the archaic-late region, most animal domestication occurred in the archaic-early region. This region is the cradle of plant and animal domestication and human civilisations.[32]

Microevolutionary approaches to plant and animal domestication (the MES) maintain that random environmental changes pushed humans towards more intense exploitation of their resources, with natural selection as the ultimate cause of the evolution of domestication. For example, Broad Spectrum Revolution theories maintain that, by causing an imbalance between populations and their subsistence resources, factors such as population pressure and climate change during the Pleistocene–Holocene transition necessitated the broadening of the subsistence base, which resulted in the emergence of agriculture in some cases (Flannery, 1969; Cohen, 1977).

Recent studies point to the insufficiency of such approaches in explaining the empirical evidence of domestication (e.g., Zeder, 2017a; Bowles and Choi, 2019). In many instances, domestication happened without population pressures and generally during the Holocene's warmer and more stable climates. Moreover, long periods of human management preceded the appearance of domestication-related morphological changes. Plant and animal domestication occurred roughly simultaneously, sometimes multiple times in the same species. Independent domestication was more common than previously thought and had a broader geographic scope.

Zeder (2016; 2017a) argues that domestication is a macroevolutionary phenomenon, i.e., it involves long episodes of co-evolutionary interactions between humans, animals and plants, with significant multi-generational ecological and cultural impacts. Hence, microevolutionary processes are insufficient in explaining co-evolutionary aspects of domestication. She shows that the EES framework explains empirical evidence of domestication better than the MES.[33]

The following argument uses Zeder's (2017a,b) description of the evolution of domestication. However, the comparative aspects of the theory—the exploitation of the patterns of human dispersal and megafauna extinction as a source of variation in human incentives for niche construction—are novel. This modification allows the paper to use the EES's structure and explain the geographic patterns of domestication.[34]

2.2.1. *The evolution of domestication*

What explains the concentration of domesticable species and the cases of independent domestication in Eurasia, particularly in its lower latitudes (the archaic-early region)? This section hypothesises the LQE as a catalyst for change in co-evolutionary interactions between humans, animals and plants, and argues that this change underlies the evolution of domestication.

Human species were initially herbivores. By 2.6 ma, their diet shifted towards meat, and there is evidence of persistent carnivory in Africa by 2 ma (Dennell, 2017). After this, megafauna meat became a crucial source of human nutrition, and prey species' movements incentivised human dispersal (Carotenuto *et al.*, 2016). Humans depend heavily on megafauna ecosystem function and trophic values for survival (Mann *et al.*, 2019).[35]

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[32] Fossils and genetics indicate the earliest signs of domestication in Southwest Asian species around 11 ka and around 8 ka in the Chinese Loess Plateau (Larson *et al.*, 2014).

[33] Zeder's works on domestication provides extensive empirical evidence supporting EES.

[34] See Riahi (2020; 2022) for more detailed descriptions of the mechanisms connecting extinction to domestication.

[35] Malhi *et al.* (2016) argue that, apart from their trophic values, megafauna represented resources, power, danger and charisma to humans. They tremendously affected the human psyche and spirituality, as depicted in our ancestors' cave paintings.

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Plant species evolved to depend on megafauna ecosystem functions, attuning their seed dispersal and defence mechanisms to their presence. According to Galetti *et al.* (2018), megafauna was crucial to plant seed dispersal, because they could digest large amounts of seeds and retain them in their guts while travelling long distances. In response, plants developed various defensive strategies, including producing vulnerable tissue only when herbivores were absent, growing in remote habitats, creating spines and thorns and maintaining fitness following herbivore damage.

The LQE, unleashed by *Homo sapiens* dispersal, disrupted these prolonged interdependencies, requiring a replacement for megafauna ecosystem functions. The absence of megafauna, the dominant ecosystem engineers of ice ages, decreased seed germination and disrupted the long-distance dispersal of megafauna-dependent plants (Galetti *et al.*, 2018). Fluctuations in the supply of humans' most important subsistence resource incentivised shifts in strategies towards resource management aimed at restoring stability, pushing humans towards lower-ranked species such as plants and smaller animals (Broad Spectrum theories). As a result, extant plant and animal species had to adjust their strategies to maintain fitness and survive in these new ecologies.

Zeder (2017a) argues that plants and animals gained evolutionary advantages by entering the domestication process with humans. For example, some plants and animals relocated to humanly modified ecosystems to exploit their features. Weedy annual plants, including barley, millet and quinoa, entered domestication by colonising soils disturbed by human activities. Wolves, wild cats, boars and chickens ventured into human settlements to feed off human refuse and smaller prey species. Many perennial plant and tree species, as well as most livestock animals, entered domestication through human common resource management, such as channelling water, landscape burning, building traps and herd management.

Successful domestication requires species with innate capacities to adjust to humanly modified ecosystems (e.g., plasticity and evolvability). Plant domestication requires species adaptable to human manipulations of growing conditions, i.e., plant species may depend on humans (or domesticated animals) for seed dispersal, have lower physical and chemical defence levels and have more predictable germination (Larson *et al.*, 2014). Animal domestication demands species that can tolerate human presence and reproduce under human care. A crucial requirement for domestication in human societies is the incentives for sustained niche-constructing activities over generations, i.e., multi-generational collective actions for common resources.

The variation in the LQE across human paleo-biogeographical regions indicates vast differences in human societies' incentives for, and species' responses to, common resource management in those regions. The traits of African megafauna saved them from extinction and, in turn, subsided the need for resource management by hunter-gatherers. On other continents, there was a need for resource management, with vastly different outcomes. High extinction rates in the Americas and Australia correspond to animal species unfamiliar with human predatory behaviours and plant species that evolved to depend on New World megafauna for survival—evidenced by the concentration of 'megafauna fruits' (large fleshy fruits) with inefficient seed dispersal mechanisms in the Americas and Australia (Galetti *et al.*, 2018).[36]

The archaic-early region's prolonged, but moderate, extinction represents human societies with enduring incentives for resource management, megafauna species under steady pressure to evolve in response to human control, and plant species with the opportunity to exploit human–fauna niche constructions.

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[36] A similar argument applies to the archaic-late region. Apart from the late human arrival (compared with the archaic-early region), the magnitude of climate change (Table 1) and *Homo sapiens*' competition with Neanderthals, who survived in this region until 40,000 years ago, could have contributed to extinction in this region.

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To summarise, there are two preconditions for domestication. First, persistence incentives for change in all species' subsistence and survival strategies towards more mutualistic partnerships. Second, plant and animal species should have the capacity for fast adjustments (in an evolutionary sense) to the new dominant ecosystem engineers of the late Pleistocene (*Homo sapiens*). Both of these conditions existed in the archaic-early region, making this region the most likely candidate for the evolution of domestication. Domestication was *less* likely in other areas because incentives were not strong enough, species were not ready enough, or both.

Thus, extinction rates should have a non-linear effect on the occurrence of domestication, i.e., animal species with traits permitting domestication should be more abundant in regions with intermediate values of extinction, and the likelihood of plant or animal domestication should be higher in those regions. This argument does not mean that megafauna extinction was the sole cause of plant or animal domestication, or that no domestication exists in the absence of extinction. The idea is that the variation in the extinction rates across human paleo-biogeographical regions proxies for differences in species' incentives and abilities for engaging in co-evolutionary interactions relating to domestication. The theory has limited explanatory power for within-region variation in the outcomes.[37]

2.2.2. *Data and methods*

The following model examines the impact of extinction on the distribution of domesticable megafauna:

$$m_i = \beta_1 e_i + \beta_2 e_i^2 + X_i'\gamma + u_i, \tag{2}$$

where m_i denotes domesticable megafauna species (hereafter, megafauna) native to the region i, this variable indicates the number of wild progenitors of megafauna species that were prehistorically native to modern-day countries and had traits suitable for domestication.[38] The previous section's argument requires e_i (the extinction rates) to enter the model quadratically. Other variables are defined as before. The next section estimates (2) as a spatial model.[39]

Let s_i be a continuous variable indicating humans' dominant subsistence strategy in the region i, ranging from foraging to resource management. We do not know whether (or to what extent) humans practised resource management in a region. However, archaeological records provide information on the success of prehistoric populations in domesticating their native species. Figure 4 presents the location of the plant and animal domestication centres based on the latest evidence (Zeder, 2017a). Hence, we can define an indicator $y_i \in \{0, 1\}$, which takes 1 for domestication centres, and 0 otherwise (see Table B1 of Online Appendix B). With s_i as the latent variable, the likelihood of domestication in i is:

$$Pr(y_i = 1|e_i, X_i) = F(\beta_1 e_i + \beta_2 e_i^2 + X_i'\gamma), \tag{3}$$

---

[37] The multi-disciplinary literature on the origins of domestication and agriculture offers many factors that were involved in this process, for example, climates, population pressures, foraging technologies, sedentism, resource abundance, ownership of resources, nutritional requirements, cultural context, opportunity cost, risk reduction and economies of scale. See Weisdorf (2005), Cohen (2009), Zeder and Smith (2009), Price and Bar-Yosef (2011) and Tisdell and Svizzero (2017) for a survey of the current literature. Barker (2006) presents a history of thought on the origins of agriculture.

[38] Online Appendix B presents data definitions and sources. Figure B2 (Online Appendix B) presents the geographic distribution of these species.

[39] In this case, spatial clustering might arise if large mammals native to a region evolved favourable traits for domestication in response to unobserved shared selective pressures (any phenomena that change the fitness of organisms within an environment) not included in the model.

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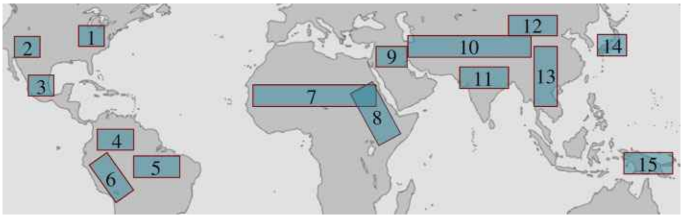

Fig. 4. *Plant and Animal Domestication Centres (Zeder, 2017a).*

where F is a parametric function of the independent variables, and other variables are defined as before. Since most domestication occurred from the Holocene (Larson *et al.*, 2014), X_i also includes mean temperature and precipitation over the 1961–1990 time period as proxies of the Holocene climates. The next section estimates (3) using maximum likelihood complementary log–log, and linearly using GS2SLS and Conley's GMM.[40] The expectation is for β_1 and β_2 to be, respectively, positive and negative in (2) and (3).

The identifying assumption is that the LQE is a source of *exogenous* variation in *Homo sapiens*' incentive for changing their subsistence strategy from foraging to resource management and for plant and animal species' broad responses to human control. This assumption drives its validity from Section 2.1, which showed that differences in the severity of the LQE during *Homo sapiens* dispersal are due to archaic humans dispersal patterns and the extent of human–fauna co-evolution.

Reverse causality and confounding factors could bias the estimates of the effect of extinction on domestication. For example, human herd management might cause extinction, or environmental differences between human paleo-biogeographical regions could affect extinction's severity and domestication's feasibility. However, there is no justification for a permanent shift in subsistence strategies from foraging to management (sustained multi-generational above tribal cooperations and coordination aimed at common resources management) without a persistent threat to common resources. *Intensive* management became traceable in archaeological records at the end of the Pleistocene and generally in the early Holocene (Larson and Fuller, 2014), while the process of extinction started *after Homo sapiens* arrived in different regions when humans were foragers. Besides, Section 2.1 showed that the *regional* variation in the LQE originates from differences in human–fauna co-evolution, even after controlling for confounding factors. Finally, X_i in (2) and (3) include controls for climate change, geography, biogeography and region-fixed effects to guard against omitted variable bias.

Cultural differences between hunter-gatherer societies (their inherent abilities for cooperation) could confound the relationship between extinction and the dependent variables in the above equations. This happens if, for example, Eurasians were culturally or genetically more capable of resource management, prevented extinction (unlike their counterparts in the Americas and Oceania) and domesticated more species (unlike their counterparts in sub-Saharan Africa). However, if humans' ability to prevent extinction was the key to domestication, sub-Saharan Africa, where all mammals survived into the Holocene, should have had the highest concentration of domesticated species, not Eurasia. Moreover, Paleo-Indians successfully domesticated many plant species,

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[40] The cumulative distribution function of complementary log-log model ($C(y_i) = 1 - exp\{-exp(y_i)\}$) is asymmetric around 0 (Cameron and Trivedi, 2009). The justification for the complementary log–log model is the scarcity of domestication.

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and some regions developed plant-based agriculture. Besides, there is considerable variation in extinction and the success of domestication within Eurasia (Table 3), where populations were arguably more culturally homogeneous. And finally, X_i in both equations includes human genetic diversity's quadratic form, human arrival dummies and continent dummies to account for broad cultural differences.

The above empirical strategies borrow from Riahi (2020; 2022). However, he examines the impact of extinction on centres of independent plant domestication and mammal domestication separately. The current paper uses a broader definition of domestication centres, i.e., in (3), $y_i = 1$ if regions i's population independently domesticated *any* plant or animal species from early- to mid-Holocene.[41] Moreover, Online Appendix A examines interactions between climate change, human dispersal and domestication, which Riahi (2020; 2022) should have considered.

2.2.3. *Results*

Table 4 presents regressions of (2) and (3). The dependent variable in columns 1 and 2 is megafauna. Columns 3–7 show the results for the likelihood of domestication. Confirming the previous sections' arguments, all models' estimated optimal extinction (the row below Extinct^2) consistently signals the ideal co-evolutionary foundation for domestication and agriculture in the archaic-early region.

Column 1 is an unconditional spatial regression of megafauna on the quadratic form for extinction (extinct and extinct^2). Column 2 includes climate variables, geography, genetic diversity and continent fixed effects.[42] Since the impact of these variables is not the paper's primary interest, their coefficients are not shown.[43] In both columns, extinct and extinct^2 are significant at the 1% level and suggest an optimal extinction rate of 35% within a standard deviation of archaic-early's mean in Table 3. Table A4 in the Online Appendix (columns 4 and 5) finds similar results using Conley's (1999) method.

Figure 5(a) shows the extinction effects with a 99% confidence band from column 2's regression. Extinction impact is substantial; a 30% deviation from the optimal rate (towards sub-Saharan Africa or the Americas' rates) corresponds to two fewer domesticable species. The LQE explains half of the difference in biogeographical endowments between Eurasia and other regions in the conditional model.

The remaining columns evaluate the impact of extinction on the likelihood of plant or animal domestication in (3). In column 3, extinct and extinct^2 are the only independent variables. These variables are statistically significant at the 1% level and suggest an optimal rate of 27%—the archaic-early's extinction rate in Table 3. Figure 5(b) shows the marginal effect of extinction on the likelihood of domestication from column 3. With a 27% extinction rate, the likelihood of domestication is 0.6, with ±0.2 confidence band. A 25% deviation from the optimal rate (towards sub-Saharan Africa, Eurasia-late, Oceania, or the Americas' rates) reduces the chance of domestication to 0.2, a three-fold reduction.

Columns 4–9 check the robustness of column 3's results. Column 4 includes domesticable megafauna and asks whether the impact of extinction on domestication works exclusively through

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[41] Thus, centres of domestication include 26 and 17 countries, respectively, in Riahi (2020; 2022). In the current paper, 40 countries constitute domestication centres (see Online Appendix B).

[42] The autocorrelation parameter (the row below genetic diversity^2) in column 1 is 0.8 (SD = 0.0), indicating spatial error clustering in this specification. With the addition of the controls in column 2, this parameter falls to 0.2, which is statistically significant only at the 10% level. Thus, spatial clustering does not affect column 2's estimates.

[43] See Riahi (2020; 2022) for detailed discussions of the effect of these variables, particularly climate change and for additional robustness checks.

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Table 4. *Regressions of Equations (2) and (3).*

	Dependent Variables							
	Domesticable megafauna		Likelihoods of plant or animal domestication					
	GS2SLS		ML					GS2SLS
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Extinct	12.28***	10.01***	12.84***	13.05**	20.74***	14.25**	26.73***	2.86**
	(2.07)	(2.44)	(3.38)	(4.32)	(5.72)	(5.45)	(7.30)	(1.05)
Extinct^2	−17.80***	−14.35***	−24.13***	−24.50**	−41.17**	−34.40**	−48.84***	−5.17***
	(3.11)	(3.49)	(6.50)	(7.98)	(13.22)	(10.63)	(14.37)	(1.41)
[Optimal extinction %]	[35]	[35]	[27]	[27]	[25]	[20]	[27]	[27]
Domesticable megafauna				−0.01			0.50	0.06
				(0.10)			(0.34)	(0.04)
Human evolution						−0.01	0.55	0.40
						(0.15)	(0.40)	(0.32)
Archaic-late						0.33*	0.56*	0.41*
						(0.13)	(0.22)	(0.17)
Sapiens						0.45***	0.03	−0.58
						(0.12)	(0.31)	(0.50)
Genetic diversity		−128.21			−81.36		−88.04	−99.83
		(79.48)			(165.76)		(207.88)	(55.09)
Genetic diversity^2		92.30			51.49		39.27	66.79
		(56.70)			(123.80)		(152.01)	(38.71)
Autocorrelation	0.81***	0.23*						−0.13
	(0.04)	(0.11)						(0.14)
Climate change		Yes			Yes		Yes	Yes
Geography		Yes			Yes		Yes	Yes
Holocene climate		Yes			Yes		Yes	Yes
Continent fixed effects		Yes			Yes			
Continent size and axis							Yes	Yes
N	128	128	128	128	128	128	128	128

Notes: The table presents regressions of (2) and (3). Human evolution, archaic-late and sapiens are dummy variables for sub-Saharan Africa, Eurasia (above the 50 parallel) and the New World (the Americas and Oceania). The omitted category is archaic-early (North Africa and Eurasia below the 50 parallel). Columns 6 and 7 report the average marginal effects of human arrival dummies. Controls for climate change are the first two principal components of temperature anomaly, precipitation anomaly, temperature velocity and precipitation velocity between the LGM (15 ka) and present-day climates. Contorts for geography are absolute latitude, mean elevation, terrain roughness, and ecological diversity. Continent fixed effects are dummy variables for Africa, Asia, the Americas and Oceania. Europe is omitted. Holocene climates are the mean temperature and precipitation of the present-day climate. Heteroscedasticity-robust standard errors are reported in parentheses. All regressions have constants. ***Significant at 1%. **Significant at 5%. *Significant at 10%.

domesticable species abundance.[44] Megafauna is insignificant, and its inclusion does not change the extinction coefficients. Column 5 controls genetic diversity, climate variables, geography and continent dummies. Extinction variables remain significant, and their coefficients *increases*. Column 6 controls for human arrival dummies and reports their average marginal effect (AME). Archaic-late and sapiens are significant and positively affect the likelihood of domestication. The extinction coefficients remain significant (at the 5% level) and comparable to column 1's. Thus, conditions (geographical, cultural, climatic or other) of Europe, Oceania or the Americas were even more conducive for domestication than archaic-early; the main barrier to domestication in these regions was the extent of human–fauna co-evolution and the severity of extinction. Column 7 adds megafauna, genetic diversity, climate variables, geography and continent features (size and axis) to column 6 regression. This further *increases* the magnitude of extinction's effect on domestication and makes human arrival dummies insignificant.

[44] This regression does not include large-seeded wild grass species used in Table 3. This variable does not have enough between-region variation; in practice, human arrival and continent dummies absorb its effect. Besides, because it is available for 96 countries in the current sample, its inclusion in regressions results in the loss of valuable information.

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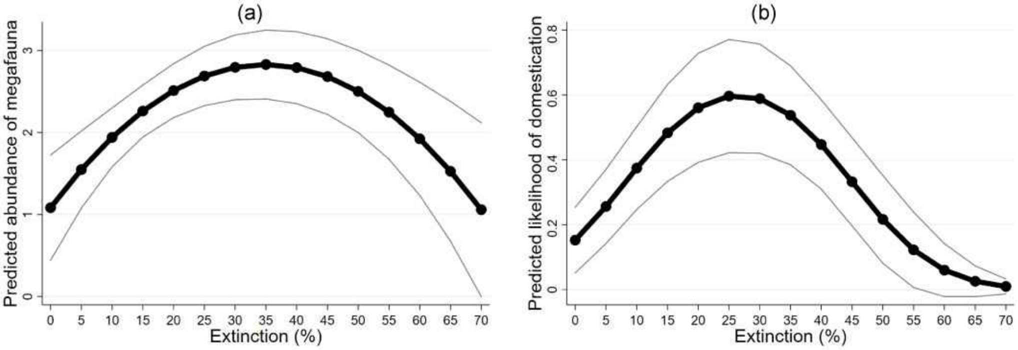

Fig. 5. *The Effects of Extinction on Biogeographical Endowments and Domestication.*
Notes: Panel (a) shows the effect of extinction from the GS2SLS regression of column 2 (Table 4). It shows that a 30% deviation from the optimal rate (35%) corresponds to two fewer domesticable species. Panel (b) shows the marginal effect of extinction on the likelihood of plant or animal domestication from the complementary log–log regression of column 3 (Table 4). With a 27% extinction rate, the likelihood of domestication is 0.6, and a 25% deviation from the optimal rate reduces the chance of domestication to 0.2. The confidence band in both figures is 99%.

Column 8 presents the spatial equivalence of column 7. The autocorrelation parameter is −0.1 (SD = 0.1), indicating the results are not affected by spatial clustering. Table A4 in the Online Appendix (column 6) obtains similar results with Conley's (1999) method. Table A3 in the Online Appendix shows that the impact of extinction on domestication remains highly stable in specifications that allow for richer interactions between climate change variables and human arrival dummies and when climate change variables enter the model quadratically.

3. Extinction and Economic Divergence

Plant and animal domestication are the most important innovation of the Holocene (Diamond, 2002). Agricultural economies proceeded from domestication, bringing radical demographic, cultural and institutional transformations. Hence, the relationships between extinction, biogeographical endowments and domestication (Figure 5) put the LQE events at the centre of the Holocene's continental divergence in economic performance.

Following the emergence of domestic species in the centres of independent domestication and with the warmer Holocene climates, human subsistence strategies gradually transformed into exploiting those species. Fully fledged agricultural economies emerged with a gap of a few millennia (between 8 and 10 ka) in Eurasia's domestication cradles, and the Neolithic way of life diffused from centres of domestication to other regions.

Ancient DNA studies have shown that Southwest Asian farmers and their domesticates migrated to Europe and reached the Iberian Peninsula, Britain and Scandinavia by 6 ka. These farmer populations quickly assimilated local hunter-gatherers, and agricultural economies developed in most of Europe by 6 ka. Agriculture diffused from Southwest Asia to North Africa mainly by cultural exchange and to South and Central Asia via a combination of migration and cultural transmission (Nielsen *et al.*, 2017; Zeder, 2017b). This means that hunter-gatherer populations in Eurasia were culturally and institutionally receptive to farmer populations and their ideas, i.e., they were familiar with resource management practices required for agriculture.

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By contrast, the dispersal of livestock (sheep, goats and cattle) to sub-Saharan Africa was much slower (by around 4 to 5 thousand years compared with North Africa). Mobile foraging populations only adopted some domestic animals (mainly goats) without transforming their economies (Zeder, 2017b). In the Americas, although morphological signs of domestication appear in some plant species around 9 ka (squash, maize, leren in Meso-America and South America; Larson *et al.*, 2014), agricultural economies emerged much later (around 3 ka) and had limited scope.

Several authors argued that the transition from foraging to farming was accompanied by institutional transformations involving well-defined property rights over land, livestock and other resources and more hierarchical social structures (e.g., North and Thomas, 1977; Acemoglu and Robinson, 2012; Bowles and Choi, 2019). The previous section's argument on the evolution of domestication entails the co-evolution of human subsistence strategies and institutions.

A defining characteristic of hunter-gatherer societies is their horizontal conception of the world in which humans and other species exist within the same hierarchical level (Cauvin, 2000; Vigne, 2011). The removal of megafauna and the appearance of domesticated animals enabled humans to control nature and become the dominant niche constructor. Humans are above other animals in these new ecosystems, and horizontal cultures and institutions must change to vertical and hierarchical.

Domestication involves long-term co-evolutionary interactions between humans and targeted species. During this time, human subsistence strategies gradually transform from foraging to management with increasing intensity, and species' traits evolve in conjunction with these transformations. Hence, we can hypothesise the co-evolution of institutions in conjunction with subsistence strategies and species traits and exploit the variation in extinction rates (and human–fauna co-evolution) to present a comparative theory of institutional evolution.

Recall that the threat of extinction—the instability in the supply of hunter-gatherers' most valuable common resource—was an incentive for shifting subsistence strategies from foraging to management. Collective actions for common resources require trust, cooperation and coordination, which could bring institutional change. Ostrom (1990; 2005) argues that the success of such actions and the robustness (adaptability to disturbances) of the institutional arrangements governing the commons depend on the resource's features, which, in the current context, are species' traits. A measurable resource that is less mobile and regenerates quickly is easier to manage.

When the common resource is reasonably manageable (Eurasian species), the most likely outcome is a self-organised system that allows users to achieve optimal depletion rates of resources. The emerging institutions in these situations can be a polycentric system—a complex constellation of independent decision-making units promoting cooperation and coordination among users with a central conflict-resolution mechanism. Those institutions could encourage sedentism and facilitate the emergence of property rights that were prerequisites for agricultural economies (North and Thomas, 1977; Dow and Reed, 2015). However, a common resource that is hard to manage and fluctuates rapidly (species in other regions) makes trust, cooperation and coordination among users more complex and the emerging institutional arrangements less robust.

After the LGM (21 ka), such gradual changes in cultures and social structures are observed in many distant societies, first in Eurasia and later in the New World (Vigne, 2011). Archaeological records of Southwest Asia—the cradle of animal domestication—show a gradual evolution of institutions in conjunction with a change in subsistence strategy from foraging to resource management. The first evidence of sedentism in this region comes from 16 ka in the Middle

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Euphrates Valley in Iraq and South Palestine. These semi-settled communities practised herd management without hierarchical institutions, a social structure resembling polycentric institutions. These societies gradually evolved into larger settlements, more intensive cultivation and advanced hunting technologies (the Pre-Pottery Neolithic A). The early Pre-Pottery Neolithic B (9.6 to 9.5 ka) marks the birth of animal husbandry. Fully hierarchical and exploitative institutions of the Middle East (e.g., Sumerians and Akkadians) appeared almost 5,000 years after the birth of animal husbandry.[45]

The above argument establishes a close association between constructed niches shaping human interactions with nature and constraints governing social interactions: the same factors that provided the archaic-early region with a comparatively ideal co-evolutionary foundation for domestication (Figure 5) contributed to the early emergence and the robustness of its polycentric institutions, which paved the way for hierarchical social structures. Other regions' suboptimal co-evolutionary conditions made such institutional arrangements either absent or less robust.

In his effort to explain the features of Eurasian civilisations and the success of European colonisation, Diamond (1997) attributes the prevalence and productivity of agricultural economies in Eurasia to its biogeography, particularly the abundance of domesticable animals. These animals significantly increased land fertility and crop productivity and enabled Eurasia to support larger and denser populations. For example, introducing the heavy plough—invented in Southwest Asia's centres of domestication and agriculture—to Europe in 1000 CE increased this continent's agricultural productivity by around 15% (Andersen *et al.*, 2016).

Economic literature provides ample evidence supporting Diamond's theory and connecting the past to current inequalities in comparative development (e.g., Olsson and Hibbs, 2005; Putterman, 2008; Ertan *et al.*, 2016; Borcan *et al.*, 2018; Olsson and Paik, 2020; Riahi, 2021). Cultural practices originating from domestication and agriculture also persist and influence current socioeconomic outcomes (Olsson and Paik, 2016; Roland, 2020; Cao *et al.*, 2021).

Figure 6 illustrates the relationships between extinction, agriculture and historical development, and summarises the findings of the literature mentioned above. Figure 6(a) plots the correlation between the abundance of wild ancestors of domesticable megafauna and extinction, corresponding to the regression of column 1 in Table 4. The last section showed that this inverted U-shaped relationship is significant and stable—see Figure 5(a). Figure 6(b) plots the correlation between the abundance of domesticable megafauna and the timing of agricultural transition (see the tables' notes for definitions), and, corresponding to Diamond's (1997) theory, shows where those species were abundant, agricultural economies developed earlier. Figure 6(c) plots the correlation between an index of technology in 1500 CE and domesticable megafauna. It shows that regions with higher prehistoric diversity of domesticable species were considerably more technologically advanced in 1500 CE.

Finally, Figure 6(d) shows that earlier transitions to agriculture are associated with faster economic growth over the past 500 years. The fitted dashed line in Figure 6(d) shows that with the exclusion of Asia's centres of domestication from the sample, the agricultural transition becomes an even stronger predictor of continental differences in growth.[46] This underlines the

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[45] For more on these cultures, see Zeder and Smith (2009) and Vigne (2011).

[46] Olsson and Paik (2020) document a 'reversal of fortune' within the Western agricultural core, i.e., Asia's centres of domestication (the group of countries in the lower right quadrant of the graph) grew slower than European nations that acquired domesticated species from Southwest Asia and transitioned later. They attribute this Eurasian reversal to cultures and institutions.

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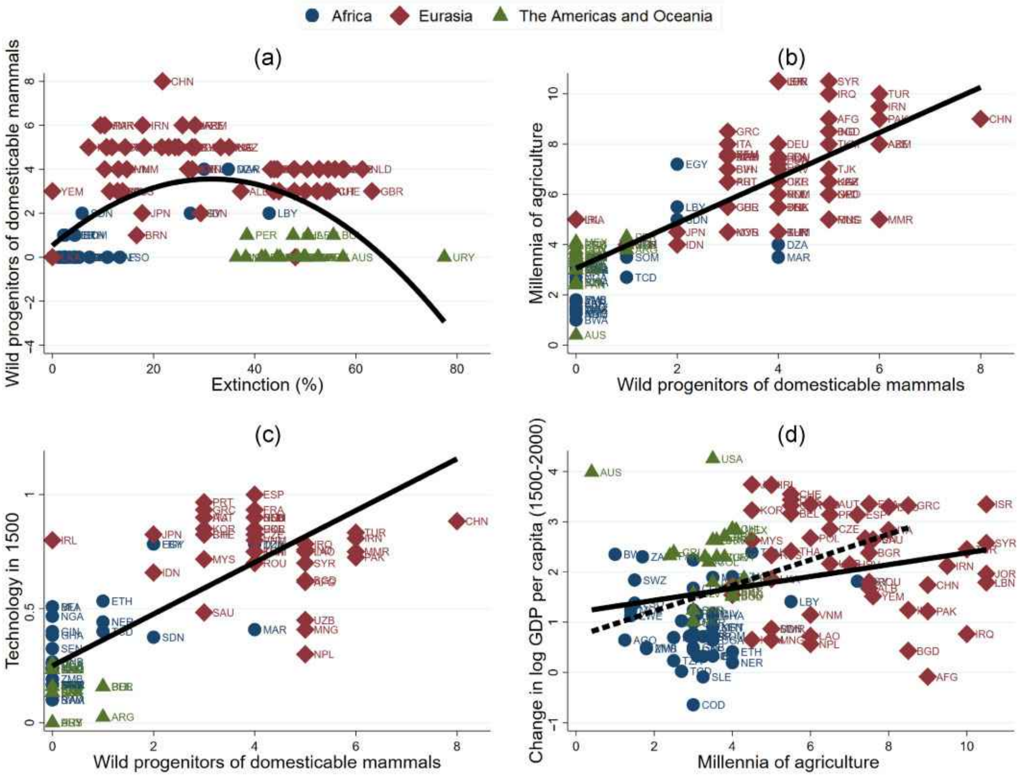

Fig. 6. *Extinction, Agriculture and Development.*

Notes: This figure illustrates the relationship between extinction, biogeographical endowments and measures of pre-colonial development. The fitted lines in all graphs correspond to unconditional regressions. Domesticable megafauna is the abundance of wild progenitors of large mammalian species prehistorically native to modern-day countries and had traits suitable for domestication (Larson and Fuller, 2014). Millennia of agriculture is the number of years that elapsed until the year 2000 CE, since most of the population residing within a country's modern national borders began practising sedentary agriculture as the primary mode of subsistence (Putterman, 2008). Technology in 1500 CE indicates the state-level development in agriculture, transportation, military, industry and communications in 1500 CE. The absence and presence of specific technology are assigned zero and one values, respectively (Comin *et al.*, 2010). The change in the log of real GDP per capita from 1500 CE to 2000 CE (1990 Geary–Khamis dollars) is from Maddison (2003), as reported by Acemoglu *et al.* (2008). The fitted dashed line in panel (d) is obtained from a sample that excludes Asia's centres of domestication (the group of countries in the lower right quadrant of the graph). Online Appendix B presents data definitions and sources.

importance of Eurasia's technological and institutional comparative advantages that originated from domestication and agriculture in the success of European colonisation and the rise of Europe.

Another critical channel connecting the LQE to divergence in development is its direct and indirect impacts on historical disease environments. Its direct impact involves disruptions in mammal-based pathogen dispersal mechanisms (Doughty *et al.*, 2020). The indirect impact is through domestication and agriculture (Crosby, 1986; Diamond, 1997).

Jones *et al.* (2008) find that 60% of 335 emergent infectious diseases in human populations from 1940 to 2004 are zoonotic diseases. Host species richness strongly predicts zoonotic pathogens

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emerging from wildlife populations. Doughty *et al.* (2020) argue that megafauna have an extensive home range and gut length, and ectoparasites (e.g., ticks, fleas, lice) and microbes rely on these animals for transport. They show that, globally, the LQE resulted in an almost seven-fold reduction in the movement of gut-transported microbes and the home ranges of vector-borne pathogens. The highest disruptions in pathogen dispersal occurred in the Americas and northern Eurasia (the archaic-late and sapiens regions), which underwent mass extinction. Pathogen dispersal was least disrupted in sub-Saharan Africa (human evolution region), which hindered the diffusion of Eurasian domesticates into this region (Zeder, 2017b). Doughty *et al.* (2020) provide tentative evidence that the LQE isolated pathogens might have forced some to adapt to humans and domesticated animals in Eurasia.

Eurasia's infectious pathogens, which became Europeans' agents of conquest in the New World (Diamond, 1997), evolved to exploit the proximity and high density of human and domestic animal populations. Smallpox originated from camels or cattle, measles from cattle, and influenza from ducks and pigs. Typhus and bubonic plague were most likely derived from cats and rodents (Wolfe *et al.*, 2007; Spinney, 2020). malaria (falciparum and vivax) and yellow fever originated in Africa from gorillas and African apes (Wolfe *et al.*, 2007; Loy *et al.*, 2017). Other tropical diseases such as AIDS, Chaga's disease and sleeping sickness originated from primates and herbivore mammals (Wolfe *et al.*, 2007).

Hence, continental differences in human niche constructions resulted in divergence in prehistorical and historical disease environments and differences in human populations' immune systems through various forms of natural selection. Cook (2015) shows that the prehistoric abundance of domesticable animals positively affects an index of Human Leukocyte Antigen (HLA) diversity—genes on chromosome 6 tasked to recognise self from non-self and play a vital role in the human immune response to infectious pathogens. More diversity in the HLA system provides more genetic resistance to infectious pathogens. He finds the highest diversity of the HLA system in Eurasian populations, followed by sub-Saharan Africans and the indigenous people of the New World.

These differences had colossal consequences with the start of European expansion after 1500 CE: smallpox, influenza, typhus and bubonic plague eradicated between 50% and 95% of the indigenous peoples of the Americas (Diamond, 1997; Acemoglu *et al.*, 2003), aided Europeans' conquest of the New World and incentivised the Atlantic slave trade. Mass extinctions of megafauna and the absence of animal domestication in the Americas and Oceania, combined with their relatively low human population densities, meant that their disease environments were comparatively hospitable to European settlers. In Africa, malaria and yellow fever were deadly to European colonists and provided a barrier to rapid colonisation of this continent, and also motivated the Atlantic slave trade. All of these factors contributed to the rise of Europe (Crosby, 1986; Diamond, 1997; Acemoglu *et al.*, 2005).

Without a country-wide measure of prehistoric and pre-colonial disease environments, Figure 7 uses well-known proxies of historical disease environments to provide visual examples. Figure 7(a) shows a negative correlation between the log of European settler mortality during colonisation (Acemoglu *et al.*, 2001) and extinction in former European colonies. On average, the disease environments of colonies that underwent mass extinction were more hospitable to Europeans. In Figure 7(b), the share of populations of European descent (Putterman and Weil, 2010) correlates strongly and positively with the extinction rates in a sample that excludes Europe, indicating colonists settled more in regions that lost more megafauna species. Figure 7(c) shows that the LQE is related to historical health outcomes, life expectancy in 1940 (Acemoglu

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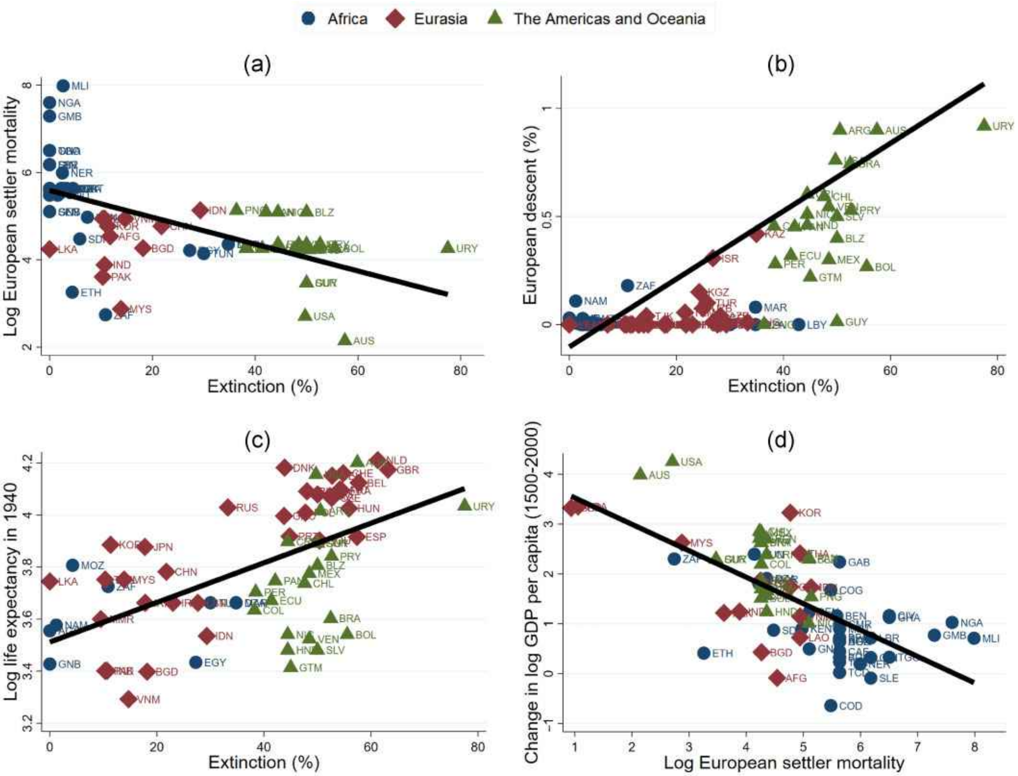

Fig. 7. *Extinction, Historical Disease Environments and Development.*
Notes: This figure illustrates the relationships between extinction and the proxies of historical disease environments. The fitted lines in all graphs correspond to unconditional regressions. European settler mortality is the log of mortality rate faced by European settlers (soldiers, bishops and sailors) stationed in the colonies between the seventeenth and nineteenth centuries (Acemoglu *et al.*, 2001). European descent is the fraction of countries' population that can trace their ancestral origins to Europe due to migrations occurring as early as 1500 CE (Putterman and Weil, 2010). Life expectancy in 1940 is the log of life expectancy at birth in 1940 according to the UN Demographic Yearbooks and League of Nations (Acemoglu and Johnson, 2007). Online Appendix B presents data definitions and sources.

and Johnson, 2007), before the international epidemiological transition and the widespread use of modern medicines, was considerably higher in regions with more severe extinction.

The above arguments tie the LQE indirectly to European colonial policies, i.e., regions with disease environments inhospitable to Europeans experienced the most hurtful colonial policies, with persisting effects on development. For example, Acemoglu *et al.* (2001) find that settler mortality explains a large portion of the contemporary difference in former European colonies' economic performance through its impact on colonial institutions. Nunn (2008) finds significant adverse effects of the Atlantic slave trade on African countries' subsequent development. Figure 7(d) plots the correlation between the log of European settler mortality and the change in the log of GDP per capita from 1500 to 2000 CE. The hostility of disease environments to Europeans adversely affects growth over the past 500 years.

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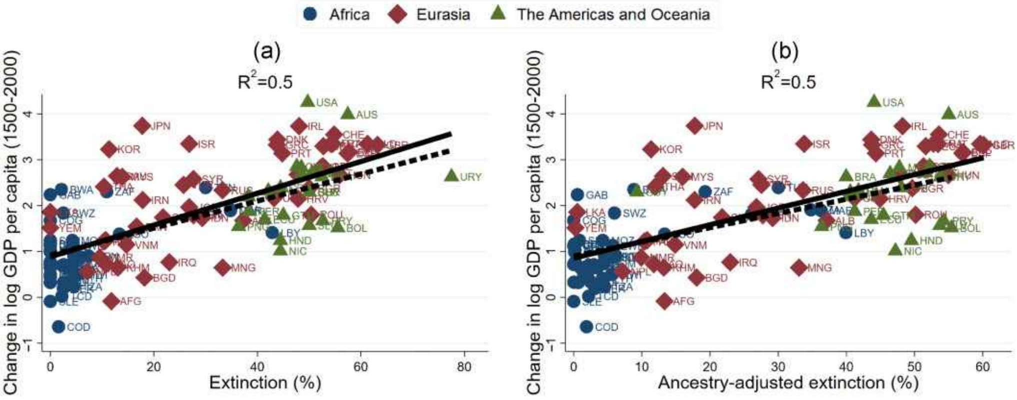

Fig. 8. *Extinction and Economic Growth.*

Notes: This figure illustrates the relationship between extinction and economic growth over the past 500 years. The fitted lines in all graphs correspond to unconditional regressions. Figures 7 and 8 propose historical processes responsible for this relationship. The change in the log of real GDP per capita (1990 Geary–Khamis dollars) is from Maddison (2003), as reported by Acemoglu *et al.* (2008). Panels (a) and (b) use unadjusted and ancestry-adjusted values of extinction rates, respectively. The ancestry-adjusted values account for mass movements of populations during the European expansion and the Atlantic slave trade after 1500 CE using Putterman and Weil's (2010) World Migration Matrix. The fitted dashed lines in both graphs are obtained from samples that exclude Europe. Table 6 examines the robustness of these statistical associations. Online Appendix B presents data definitions and sources.

Overall, the LQE events are fundamental to broad historical processes that the literature recognises as the roots of divergence in the long-run economic performance: Eurasia's technological, institutional and cultural features, and the patterns of European colonisation after 1500 CE.[47]

Figure 8 shows the association between extinction and growth, condensing the impact of the historical processes originating from the LQE on long-run development. Figure 8(a) shows the correlation between extinction rates and growth over the past 500 years. Figure 8(b) uses the ancestry-adjusted values of extinction, accounting for mass movements of populations during the European expansion and the Atlantic slave trade after 1500. Both figures show considerably faster economic growth in regions with higher extinction during *Homo sapiens*' dispersal.[48]

3.1. *Data and Methods*

The following regression equation examines the robustness of Figure 8's correlations:

$$y_i = \beta e_i + X_i'\gamma + u_i, \tag{4}$$

where y_i is the change in the log of real GDP per capita from 1500 CE to 2000 CE (1990 Geary–Khamis dollars) from Maddison (2003), as reported by Acemoglu *et al.* (2008). Some regressions use the log of GDP per capita in 2000 CE from Penn World Tables for robustness check.

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[47] The proposed mechanisms connecting the LQE to inequalities in economic development are broad and not exclusive, i.e., there may be other plausible channels that this paper does not consider. For example, the LQE changed the planet's physical structures, trophic structures, ecosystem biochemistry and regional climates (Malhi *et al.*, 2016; Mann *et al.*, 2019) and can affect various aspects of development directly or indirectly through those.

[48] The fitted dashed lines in both graphs are obtained from samples that exclude Europe. Thus, European countries, a group of fast-growing nations with high extinction rates, do not drive these relationships.

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Table 5. *Descriptive Statistics.*

	Extinction rates (%)	Change in log GDP per capita (1500–2000)	Log GDP per capita (2000)
Human evolution	2	0.8	6.9
(sub-Saharan Africa, $N = 39$)	(3)	(0.6)	(0.9)
Archaic-early	25	1.9	8.4
(Eurasia-early, $N = 46$)	(14)	(0.9)	(1.1)
Archaic-late	49	2.8	9.6
(Eurasia-late, $N = 20$)	(9)	(0.8)	(0.9)
Sapiens	47	2.8	9.1
(Oceania, $N = 2$)	(15)	(1.7)	(1.9)
Sapiens	49	2.2	8.7
(The Americas, $N = 21$)	(8)	(0.7)	(0.6)

Table 5 presents descriptive statistics for the dependent variables. Other variables are defined as before.

The objective of (4) is to establish extinction as a deep historical process affecting continental divergence in economic performance, not that extinction directly causes growth, which is implausible and incompatible with the paper's argument. Hence, X_i includes correlates of e_i and other deep determinants of long-run economic development, i.e., climate change, geography, biogeography, Holocene climate, continent fixed effects, region dummies and human genetic diversity. All variables are justified based on Section 2's arguments. Some specifications include religion (fractions of Protestants, Catholics and Muslims in populations).

3.2. *Results*

Table 6 reports OLS regressions of (4) and Table A5 in the Online Appendix shows the spatial regressions. Since the spatial models agree with the OLS results, they are not discussed further to save space.[49]

The dependent variables in columns 1–7 are the change in the log of GDP per capita from 1500 to 2000 (henceforth, growth). The sample includes 115 countries where data on all variables are simultaneously available.

Column 1 shows an unconditional regression of growth on extinction, corresponding to Figure 8(a). Extinction is associated with 50% of the variation in growth in this sample. The extinction coefficient of 3 (SD = 0.3) suggests that a 50% increase in extinction—the difference between human evolution and archaic-late or sapiens—translates into a 1.5-point increase in growth. Table 5 shows that sub-Saharan Africa's growth is 1 log point lower than the Americas' and 2 log points lower than archaic-late and Oceania's. Thus, extinction explains the entire growth gap between sub-Saharan Africa and the Americas and 90% of the gap between sub-Saharan Africa and Eurasia's archaic-late in this model.

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[49] Reviewing the literature on the historical roots of development, Kelly (2019) finds that spatial clustering could result in large t statistics, driving one to conclude that the unit's past features explain modern outcomes in a spatial unit. This issue is less of a concern here because (4) *primarily* exploits the between-region variation in extinction to explain the continental divergence in development. These regions were isolated from each other in the late Pleistocene, and most of the Holocene, and it is unlikely they formed spatial clusters. Moreover, unlike the global studies Kelly (2019) evaluates, the current paper does not have a direct causal claim, i.e., extinction is not the cause of divergence in development; it is a historical event related to economic development, most likely through other historical processes discussed in previous sections. Section 4 discusses this issue more clearly.

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Table 6. *OLS Regressions of Equation (4).*

	Dependent Variables								
	Change in log GDP per capita (1500–2000 CE)							Log GDP per capita (2000 CE)	
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Extinction	3.47***		3.32***	3.69***	3.12***	4.04***	2.81***	4.92***	3.49**
	(0.30)		(0.68)	(0.66)	(0.67)	(0.82)	(0.73)	(0.37)	(1.30)
Human evolution		−1.06***	−0.36	−0.17					
		(0.19)	(0.25)	(0.27)					
Archaic-late		0.90***	0.01	−0.07					
		(0.24)	(0.27)	(0.28)					
Sapiens		0.36	−0.47*	−0.38					
		(0.22)	(0.22)	(0.62)					
Africa					−0.49	−0.61	−0.31		−0.55
					(0.35)	(0.38)	(0.58)		(0.51)
Asia					−0.21	0.25	0.64		0.43
					(0.34)	(0.41)	(0.49)		(0.44)
Oceania					−0.17	−0.57	−0.75		−1.39
					(0.79)	(0.76)	(0.77)		(0.71)
The Americas					−0.65	−0.97	−0.86		−1.70*
					(0.82)	(0.83)	(0.76)		(0.83)
Genetic diversity				69.07	38.25	37.88	49.08		138.93
				(51.91)	(58.17)	(61.32)	(54.11)		(139.29)
Genetic diversity^2				−50.69	−28.84	−27.26	−38.32		−101.38
				(37.39)	(41.15)	(43.16)	(39.67)		(96.52)
Domesticable megafauna						−0.17**	−0.22***		−0.53
						(0.06)	(0.06)		(0.30)
Climate change							Yes		Yes
Holocene climate							Yes		Yes
Geography							Yes		Yes
Religion							Yes		Yes
N	115	115	115	115	115	115	115	125	125
R^2	0.51	0.45	0.54	0.55	0.56	0.59	0.70	0.57	0.73

Notes: The table presents OLS regressions of (4). In columns 8 and 9, the ancestry-adjusted values of extinction rates, genetic diversity and megafauna are used in regressions. Human evolution, archaic-late and sapiens are dummy variables for sub-Saharan Africa, Eurasia (above the 50 parallel) and the New World (the Americas and Oceania). Archaic-early (North Africa and Eurasia below the 50 parallel) is the omitted category. Controls for climate change are the first two principal components of temperature anomaly, precipitation anomaly, temperature velocity and precipitation velocity between the LGM (15 ka) and present-day climates. Holocene climates are the mean temperature and precipitation of the present-day climate. Contorts for geography are absolute latitude, mean elevation, terrain roughness and ecological diversity. Religion is the percent of population in 1980 which is Catholic, Protestant, or Muslim. Heteroscedasticity-robust standard errors are reported in parentheses. All regressions have constants. ***Significant at 1%. **Significant at 5%.

Column 2 presents a regression of growth on human arrival dummies. These dummies jointly explain 50% of the variation in growth. Human evolution and archaic-late have significant effects, suggesting that growth in archaic-late is 2 points higher than human evolution's growth, and 1 point higher than archaic-early (the omitted group) because of fixed differences between these regions. Column 3 includes extinction and human arrival dummies, column 4 adds the quadratic form for genetic diversity to column 3's model and column 5 includes genetic diversity along with continent dummies. The extinction coefficient remains remarkably stable and statistically significant in all three columns at the 1% level. Human arrival dummies, genetic diversity, and continent dummies are insignificant.

The relationship between extinction and growth may result solely from differences in populations' biogeographical endowments. To examine this, column 6 adds megafauna to the column 5 model. This variable is significant, and its inclusion in the regression *increases* the extinction co-

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efficient, from 3 in column 5 to 4 (SD = 0.8) in column 6. Other variables remain insignificant.[50] Column 7 adds geography, climate variables and major religion shares to column 6 regressions. The explanatory power of the regression increases from 0.6 in column 6 to 0.7 in column 7. Still, column 6's results do not change, i.e., the effect of extinction is quantitatively and statistically significant, and genetic diversity and continent dummies are insignificant.

Columns 8 and 9 use the log of GDP per capita in 2000 as the dependent variable and the ancestry-adjusted extinction values. The sample includes 125 countries for which data on all variables is available. In column 8, extinction is the only independent variable, which is highly significant and explains 60% of the variation in per capita income ($R^2 = 0.6$). Column 9 includes the entire set of controls from column 7. The regression's R^2 only slightly increases (from 0.6 to 0.7), and the extinction coefficient lightly decreases and remains significant. The coefficient of 3.5 (SD = 1.3) suggests that a 50% increase in extinction raises per capita income by around 1.7 log points, which is around 60% of the current income gap between sub-Saharan Africa and Eurasia's archaic-late (3 log points), and 85% of the gap between sub-Saharan Africa and the Americas (2 log points). Genetic diversity and continent dummies are insignificant in column 9.

Overall, Table 6 supports the paper's central argument that continental divergence in economic performance originates from deep ecological differences resulting from human niche construction, i.e., niche construction is the formative evolutionary process of economic divergence.

4. Factors Underlying the Broadest Pattern of History

Previous sections show that historical and evolutionary processes involved in economic divergence are highly intertwined; they instigate one another cyclically and reciprocally and shape human populations along with their cultures, institutions and ecologies. The evolutionary process of niche construction powered human dispersal; dispersal changed humans genetically through microevolutionary processes of genetic drift and natural selection and transformed animal and plant species by co-evolution. Random environmental changes or critical junctures such as climate change function as push and pull forces, sometimes acting as a catalyst and other times as a barrier during these processes.

Acemoglu and Robinson (2012) argue that critical junctures are exogenous events (e.g., climate change, discovering new resources and diseases) affecting multiple nations simultaneously. How societies exploit these critical junctures varies with their institutions; societies experience different historical processes resulting in institutional drift. The authors provide numerous examples of divergences resulting from the interplay of critical junctures and institutional drift and argue that, once societies experience a critical juncture, even minor institutional differences can produce very different outcomes.[51] The critical juncture framework is particularly appealing because it agrees with the EES on the causes of divergence, i.e., in both theories, evolutionary change results from reciprocal interactions between random (historical or evolutionary) processes and environmental changes.

In the current context, the core historical processes are human dispersals and megafauna extinction (Figure 9, panel A); the critical junctures are the end of the last ice age and the

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[50] Interestingly, the megafauna coefficient is negative, while the dummy for Asia becomes positive (from columns 5 to 6). These indicate a 'resource curse' in Asia's centres of domestication (e.g., Olsson and Paik, 2020).

[51] For example, they show that small institutional differences in England, France and Spain—countries with many similarities in their historical experiences—resulted in fundamentally different development paths once exposed to the Atlantic trade economic opportunities.

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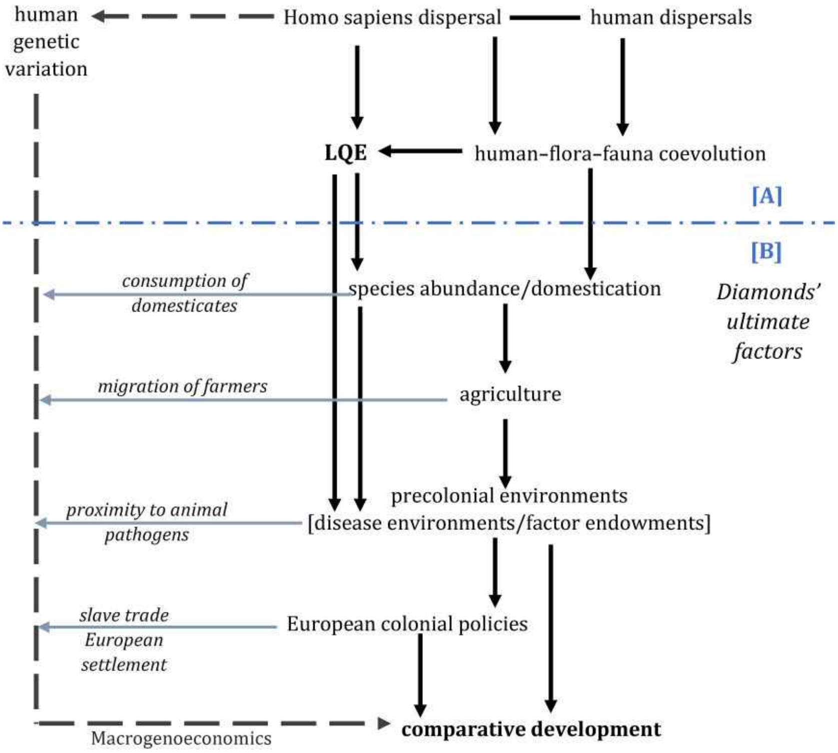

Fig. 9. *Factors Underlying the Broadest Pattern of History.*

Holocene's warmer climates, with niche construction as the formative evolutionary process. Human dispersal produced human paleo-biogeographical regions through co-evolution. With *Homo sapiens* dispersal and climatic upheaval of the late Pleistocene, these co-evolutionary histories became crucial to the survival of megafauna populations in different areas, which, in turn, provided varying incentives for cooperation and coordination among hunter-gatherers. The outcomes (the severity of extinction and the emerging cultures and institutions) were contingent on co-evolutionary histories (the adaptability of plant and animal species to humanly modified ecosystems). The warming-up of the climate in the Holocene was another critical juncture, and the outcomes (the feasibility of domestication and agriculture) varied with rather significant differences in institutions and biogeographical endowments.

The compounding effect of these factors—the interactions between historical events, evolutionary processes and critical junctures—constitutes the deep determinants of development. A close interconnection exists between humanly modified ecosystems shaping human interactions with nature (constructed niches) and humanly devised constraints regulating social interactions (institutions). Divergence results from historical accidents, i.e., each event is random yet alters the likelihood of future events. Economic development becomes a path-dependent process because human populations' institutional and ecological inheritance influence their capacities for exploiting each other and the opportunities arising from critical junctures.

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Following the tradition of the MES in distinguishing between ultimate and proximate causes of evolution (Mayr, 1961), Diamond (1997) attributes the ultimate advantages of Eurasia to its abundance of domesticable species (which he attributes to chance) and continental geography, particularly axis orientation (see Figure A2 of the Online Appendix A).[52] This paper provides an opportunity to revise his 'Factors Underlying The Broadest Pattern of History'.

The ultimate advantage of Eurasia is its position along humans' out-of-Africa migratory path. It provided comparatively optimal co-evolutionary foundations for domestication and agriculture and paved the way for the evolution of the Old World's infectious pathogens. Sub-Saharan Africa remained ecologically stable, and the Americas and Australia became extremely unstable on *Homo sapiens*' arrival, which, in both cases, delayed domestication and agriculture. Broadly speaking, Diamond reached a similar conclusion: 'History followed different courses for different peoples because of differences among people's environments, not because of biological differences among peoples themselves' (1997, p.25).

Macrogenoeconomics (Ashraf and Galor, 2013; 2018) provide a different interpretation of divergence in development. It argues that *Homo sapiens*' out-of-Africa migration impacts long-run development by causing genetic differences between populations and maintains that Eurasians' level of genetic diversity was optimal for development. By contrast, the genetic diversity of Africans and the indigenous peoples of the New World made them less capable of Eurasian-type cooperation and innovations.[53] The dashed arrows in Figure 9 correspond to these theories' causal chain.[54] The remainder of this section re-evaluates these theories in light of this paper's evidence and argument.

Human dispersal from Africa influences human genetic variation because of the serial founder effect. The founder effect occurs when a new colony is established by a few members of the original population, resulting in the loss of genetic variation in the new colony. The serial founder effect happens in long-distance migration and the repeated occurrence of founder effects. Hence, most genetic differences between human populations are caused by the evolutionary process of genetic drift, with natural selection playing a secondary role.

Homo sapiens' out-of-Africa migration includes three major founder events (Henn *et al.*, 2012): the dispersal from Africa into the Near East, the dispersal from South Asia into Oceania, and the dispersal from North Asia into the Americas. Because of these founder events, sub-Saharan populations are the most genetically diverse and the least genealogically related to other people. Outside Africa, genetic diversity decreases along out-of-Africa migratory paths.

Because all human migrations were out-of-Africa migrations with similar geographic patterns (Section 2.1), these major founder events correspond to human paleo-biogeographical regions. Hence, human genetic variation strongly correlates with the environmental differences between

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[52] He argues that Eurasia had the highest endowments of domesticable megafauna (71 species) because of its features, such as size and axis. Eurasia is the world's largest landmass in the east-west direction, facilitating species spread. It is ecologically diverse, with extensive temperate forests, tropical rainforests, deserts and tundra habitats. Other continents are smaller than Eurasia, and Africa is ecologically less diverse. However, he attributes the *domesticability* of Eurasian species and the peculiar absence of those traits on other continents to chance. Riahi (2022) elucidates the source of Eurasian species' traits.

[53] These claims stem from seemingly robust statistical associations between genetic diversity and economic performance, showing Eurasians' genetic diversity predicts higher population densities in 1500 CE and per capita income in 2000 CE.

[54] Following Ashraf and Galor (2013), a growing body of empirical research has attributed multiple aspects of disparities in comparative development to genetic differences between populations. See Ang (2013; 2019), Hansen (2013), Desmet *et al.* (2017), Gorodnichenko and Roland (2017), Bove and Gokmen (2018), Arbatli *et al.* (2020) and Depetris-Chauvin and Özak (2020).

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these regions, most notably with the extent of human–fauna co-evolution and the severity of megafauna extinction. These challenge macrogenoeconomics theories because they assume that *Homo sapiens*' out-of-Africa only impacts human genetic diversity and has no other consequences.[55] This paper shows that human dispersal has colossal ecological impacts that are consequential to development.

Moreover, differences in human environments resulting from the fundamental historical processes induce further endogeneity in genetic diversity (Figure 9, panel B). Laland *et al.* (2010) and Conley (2016) provide many examples of gene–culture interactions and cultural selection pressures. Human consumption of domestic species resulted in genetic changes associated with alcohol metabolism, lactose tolerance, sickle-cell anaemia and starch-metabolising enzymes. Human proximity to animal pathogens resulted in genetic changes in human immune systems. Other human migrations further exacerbate the endogeneity of genetic diversity, for example, the migration of farmers from Southwest Asia to Europe and from the Iranian plateau to South and Central Asia.

Finally, macrogenoeconomics does not examine the impact of genetic diversity on domestication or agriculture and instead uses outcome variables that were undoubtedly the outcome of agricultural transition and biogeographical endowments (e.g., population densities). Table 4 shows that genetic diversity has insignificant U-shaped relationships with domestication, which is the opposite of Ashraf and Galor's (2013) prediction. Riahi (2020) and Olsson and Paik (2020) also find insignificant U-shaped relationships between genetic diversity and the timing of the agricultural transition. Consequently, Table 6 shows that genetic diversity does not explain growth over the past 500 years. Macrogenoeconomics' documented correlations between genetic diversity and economic outcomes capture the impact of human dispersal on development through the historical processes that Figure 9 presents. Riahi (2017; 2021) shows that valid proxies for these processes remove the statistical associations between genetic variation and economic performance.

Overall, the EES shows that microevolutionary processes such as genetic drift or natural selection are insufficient in explaining macroevolutionary patterns of dispersal and domestication. This paper provides an important empirical application of the EES and shows that Eurasians' genetic composition did not make them capable of collective actions for domestication and agriculture; Eurasian animals made those innovations possible. Figure 9's framework guides researchers in empirical evaluations of the impact of deep-rooted genetic (or cultural) variables on socioeconomic outcomes. Hopefully, it will prevent harmful conclusions such as 'European colonisation significantly altered the genetic diversity [of former colonies] ... toward the optimal level for development' (Ashraf and Galor, 2013, p.43).

5. Conclusions and Further Research

Since the beginning of the Industrial Era in the eighteenth century, human activities have resulted in a substantial rise in atmospheric CO_2, an increase in surface temperature, a considerable decrease in the land ice sheets and a continuous rise in sea levels and ocean warming.[56] Accompanying these is the global loss of biodiversity in an ongoing wave of human-driven extinction known as the Sixth Extinction. A recent study finds that with the current levels of global heating,

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[55] For example, Ashraf and Galor's (2013) identifying assumption is that 'distances along prehistoric human migration routes from Africa have no direct effect on economic development during the Common Era' (p.15).

[56] See https://climate.nasa.gov/.

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we are dangerously close to crossing six climate tipping points, after which the breakdown of global ecologies is self-sustaining and will continue even with no further warming (Armstrong McKay *et al.*, 2022).[57]

The propelling forces of these global ecological instabilities are our thirst for resources and ability to manipulate environments to increase our fitness. These forces have been the most potent source of co-evolutionary ecosystem changes since our species' appearance in Africa and dispersal from this continent. Such is the power of human niche construction, an evolutionary process more fundamental than Darwinian natural selection. This process is at the heart of the Extended Evolutionary Synthesis, calling for revising Neo-Darwinian theories to include broader evolutionary processes and inheritance mechanisms.

This paper presents the first adaptation of the Extended Synthesis for studying deep determinants of long-run economic development. It uses these theories to evaluate the impact of human dispersal from Africa and the resulting extinction of large mammals on macro-level development outcomes. Empirical analyses exploit the variation in extinction as a source of exogenous pressure on hunter-gatherers to practice resource management and suggest that this change in subsistence strategy provides the impetus for cultural and institutional change among hunter-gatherers. Some areas of Eurasia had the ideal co-evolutionary foundation for human domination over other species and made Eurasians institutionally more capable of exploiting the Holocene climatic stability. Variation in extinction rates is related to continental differences in technologies, institutions, disease environments and economic performance. The evolutionary process of niche construction and the historical processes of dispersal and extinction fundamentally affect continental divergence in economic development.

The economic impact of human dispersal from Africa needs to be studied more in economic literature. Although this paper focused on dispersal across continents, many other minor dispersals occurred within continents, and high-resolution data on those are becoming increasingly available. Examining the ecological and economic impacts of those dispersals with the help of this paper's framework will improve our understanding of deep determinants of development. The paper proposes broad mechanisms connecting dispersal and extinction to biogeography, disease environments and institutions. Evaluating these mechanisms with microdata is an exciting area of research and can help researchers design novel instruments informed by historical and evolutionary processes. Recent years have witnessed a multi-disciplinary rise in interest in studying the evolution of preferences, cultures and social norms. Applying the Extended Synthesis to this literature is inevitable and promising.

Exploring the deep determinants of development provides valuable guidelines for the challenges arising from the global ecological instabilities we face today. The root causes of these instabilities are intense competition and overexploitation of shared resources, with the climate tipping point resembling the extinction threshold of megafauna species. Economic theory tells us that the nature of the challenge (resources and users' features) dictates the direction of the required institutional transformations. When the number of users is limited, users know each other's reputations, and when the resource is measurable and stationary, attaining optimal solutions without strongly hierarchical institutions is feasible. Many of these factors exist today. Our current institutions are the biggest obstacle. Our economic and political institutions—by-products

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[57] These tipping points are the Greenland Ice Sheet collapse, the West Antarctic Ice Sheet collapse, the collapse of ocean circulation in the polar region of the North Atlantic, coral reef die-off in the low latitudes, sudden thawing of permafrost in the northern regions, and abrupt sea ice loss in the Barents Sea.

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of the interplay between past historical processes and critical junctures—evolved to respond to national and regional priorities and need to be revised for global common resource management.

The polycentric institutions that evolved in response to the Pleistocene–Holocene ecological instabilities enabled human populations to manage their subsistence resources, take advantage of the Holocene warming climates, domesticate many species and develop agriculture. Those institutions are examples of human niche construction with profound evolutionary and economic consequences, i.e., they resulted in the Anthropocene—a geological era characterised by human dominance over the biosphere (Zeder and Smith, 2013). The next institutional revolution should curb and coordinate our pursuit of self-interest.

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Additional Supporting Information may be found in the online version of this article:

Online Appendix
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