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The Biogeographic Roots of World Inequality: Animals, Disease, and Human Settlement Patterns in Africa and the Americas Before 1492

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Summary. — Building on recent insights from archeology, genetics, and linguistics I challenge Jared Diamond's grand narrative of the biogeographic roots of world inequality. I argue that this narrative pays insufficient attention to contrasting patterns of human settlement in Africa and the Americas. I develop alternative hypotheses concerning the role of domesticated animals in shaping human disease environments and processes of state formation prior to the Columbian exchange. My overarching objective is to enhance the debate on the deep roots of world inequality by tackling Eurocentric conceptions of world development and exploring the potential of new comparative and multi-disciplinary research perspectives.

Key words — world inequality, biogeography, animals, disease, Africa, America

1. INTRODUCTION

Columbus' crossing of the Atlantic heralded an era of European conquest and colonization at an unprecedented scale. In the centuries following 1492, Europeans established and extended global trade networks and exported their languages, values and norms to distant corners of the world. The scientific and industrial revolutions of the 18th century unleashed a second wave of imperial expansion in the long 19th century. During the 20th century Europe's hegemonic power started to evaporate. Not only had a former British colony, i.e., the US, overtaken Europe in terms of technological leadership, the global diffusion of industrial technologies also spurred economic growth in former 'developing' regions. At the start of the third millennium it seemed that the era of major economic divergence had given away to a new era of economic convergence.

The historical roots of Europe's path to world dominance have been intensively debated by scholars from the humanities, social sciences and natural sciences (Allen, 2011; Diamond, 1997; Jones, 1981; Landes, 1998; Lal, 1998; Mokyr, 1990; North & Thomas, 1973; Tilly, 1990; Turchin & Nefedov, 2009; Welzel, 2014; Wittfogel, 1957). This debate has stimulated the search for new historical sources and empirical insights, but failed to reach a conclusive stage. Asia's economic 'renaissance' during the second half of the 20th century has provoked fundamental re-interpretations of the historical meaning of European or Western 'dominance'. Some scholars have even argued that, viewed from the wider scheme of human history, European expansion was not much more than a temporary aberration of the standard historical pattern in which Asia, rather than Europe, rules the world (Frank, 1998; Morris, 2010). This has clear repercussions for the way history is written.

Most historians now acknowledge that *Eurocentric* explanations of world inequality have impeded a deeper understanding of what was essentially a global, rather than an exclusively European phenomenon. In the debate on the nature and timing of the *Great Divergence* between Western Europe and China the problem of Eurocentrism has been explicitly brought to the fore (Bin Wong & Rosenthal, 2011; Pomeranz, 2000). The critiques reside in a broader current of discontent, especially voiced by world historians, regarding the use of Western economic and political concepts in the study of non-Western historical developments; the use of biased historical sources and one-sided benchmarks in global comparisons; and the lack of attention being given to non-European perspectives on world development (Austin, 2007; Carney & Rosomoff, 2011; Ringmar, 2011; Said, 1979; Wolf, 1982).

This study aims to break new ground in the debate on the deep roots of world inequality, by exploring the potential of unconventional comparative and multi-disciplinary research perspectives. I develop my argument by scrutinizing a famous popular account of Europe's ascendancy, that is Jared Diamond's thought-provoking study of the biogeographic roots of world inequality. His central argument is that Eurasia had a clear biogeographic advantage in the evolution of peasant-based states over other world regions, and that current global inequalities in wealth and power can be traced back to these environmental conditions. In his widely praised *Guns, Germs and Steel* (1997), Diamond argues that complex social orders emerged predominantly in Eurasia because of favorable biogeographic conditions for the development of stratified societies, centralized states and advanced military and naval technology. The diffusion of sedentary agriculture in Eurasia was facilitated by a (much) larger pool of domesticable plants and animals than in Africa or the Americas, which could spread along a horizontal continental axis with limited variation in climate zones. In addition, longstanding proximity to

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domesticated animals gave Eurasians a comparative advantage in disease resilience, which created a highly unequal playing-field in the confrontation between Europeans and native American peoples after 1492.

Since Diamond's thesis is largely based on insights from evolutionary biology, he claims that his account avoids the pitfalls of Eurocentrism. According to Diamond, Europe derived its technological and military supremacy from an environmental comparative advantage, and not from innate racial, intellectual, or cultural superiority (1997, pp. 18–22). Moreover, by sidestepping the question why Europe, and not Asia, heralded the industrial revolution, Diamond reserved space for historical contingency: no matter where path-breaking technological innovations were made first (Europe, China, India, or Japan), they were just more likely to occur in Eurasia than elsewhere.

A closer inspection of Diamond's thesis reveals problems of reciprocal comparison that are typical for such one-dimensional narratives of world development. Since the central tenet is to explain why Eurasia was *exceptional*, the two vertical-axis continents, Africa and the Americas, are predominantly analyzed and discussed *in comparison to* Eurasia, but not in comparison to one another.[1] Diamond argues that Africa and the Americas both disposed of a smaller pool of domesticable plants and animals than Eurasia; that they both enjoyed less favorable conditions for the diffusion of high-productive species because of their vertical axes; that in both regions this resulted in less diverse agricultural systems and lower rates of population density; and that in both continents this yielded less favorable conditions for the development of sophisticated military technology, fiscal capacity, and centralized states. In other words, the biogeographic roots of world inequality are primarily understood in terms of Eurasian unicity.

Does Diamond's explanatory framework keep up when shifting the comparative lens toward the vertical-axis continents? Building on recent insights from archeology, genetics, and linguistics I argue that the Africa–America comparison confronts Diamond's meta-narrative with three fundamental problems. First, Africa and the Americas were lowly populated regions around 1500 AD, but they were lowly populated for different reasons. Africa, the cradle of humankind, was lowly populated because of specific environmental constraints to agricultural productivity growth, comparatively favorable conditions for nomadic pastoralism and an exceptional human disease environment. However, these three conditions cannot explain why the Americas were lowly populated. In fact, being the last region to be settled by humans in the global migration chain, the Americas may have been lowly populated because of late human presence, rather than specific biogeographic constraints to sedentary agriculture. This argument will be developed in Section 3.

Second, Diamond's account of the role of domesticated animals in shaping comparative disease environments requires revision. Diamond argues that the intimate contact of European farmers with livestock produced hotbeds for new human diseases and that European resilience against these diseases gave rise to a highly unequal Atlantic exchange of 'germs' after 1492. That native Americans died in large numbers from diseases introduced by Europeans is beyond doubt, even though the arrival of African slaves played a major role as well (Mann, 2011; McNeill, 2011). However, I will argue in Section 4 that new insights from genetic research emphasize the importance of wild animals in the evolution of human pathogens and point to Africa as the source region of smallpox, the biggest killer disease introduced in the Americas. Genome sequence studies of other disease vectors call for a rethinking of the environmental conditions that gave rise to Old World epidemics.

Third, Diamond argues that the availability of domesticated animals – especially the 'big five' of horse, cattle, sheep, goat, pig – created conditions for mixed farming that supported the rise of powerful peasant-based states capable of large-scale imperial conquest. These domesticated animals contributed to the agricultural surpluses that formed a precondition for the evolution of 'large, dense, sedentary, and stratified societies' (1997, p. 87). In Section 5 I will argue that contrasting trajectories of state formation in Africa and the Americas do not fit the casual argumentation very well, especially if one considers the role of domesticated animals in the development of state taxation. I will argue that the *absence* of livestock may have supported the rise of strong central states in Mesoamerica, while the *presence* of livestock in the African savannah areas may have severely complicated state centralization. Agro-pastoralism in the African savannah served to mediate subsistence risks in climatologically instable environments, but gave rulers hard times in mobilizing resources to centralize power. Without reaching firm conclusions, I argue that the role of domesticated animals has been much more variegated than Diamond's account leads us to believe. But most important, I contend that there is enormous scope for Africa-America comparisons in gaining a deeper understanding of diverging regional development trajectories.

2. GUNS, GERMS, AND STEEL

According to Diamond, Eurasia enjoyed three advantages for the development and diffusion of sedentary agriculture. First, Eurasia is the largest continent of the world, covering ca. 36% of total land mass, thus raising the odds. Second, Eurasia has been blessed with an exceptionally large pool of wild plant and animal species suitable for domestication, including the most productive species. Third, the horizontal orientation of the continental axis facilitates the diffusion of domesticated plants and animals in comparatively homogenous eco-zones. Compared to Eurasia, Africa and the Americas are smaller sized continents with smaller pools of plants and animals suitable for domestication, whose diffusion has been hampered by the vertical orientation of their continental axes. The American axis stretches all the way from Alaska to Cape Horn, with enormous varieties in climate zones and a tight bottleneck in Central America. In Africa, the Sahara desert and the rainforest belt were additional barriers to the continental diffusion of plant and animal species (1997, pp. 186–189).

Village-based agriculture evolved in the *fertile crescent* around 11.000–10.000 BC with the domestication of starch wheat (emmer), protein-rich chickpeas, oil-rich olives, goats, and sheep. Diamond argues that it is no coincidence that the Neolithic revolution originated in Southwest Asia and spread from there across Eurasia and the Mediterranean shores of North Africa, but not further south. The Mediterranean disposed of excellent climatological and ecological conditions for the evolution of annual grasses, with large varieties in altitudes and season-bound temperatures (1997, pp. 135–142). The diffusion of domesticated plants and animals in Eurasia was enhanced by an independent agricultural revolution in East Asia (China), where early agricultural societies emerged on the basis of domesticated rice, millet, pigs, and silkworms (1997, p. 100; Barker, 2006; Smith, 1995).

Independent domestication of plants and animals also occurred in sub-Saharan Africa and the Americas, but these had smaller productive potential. West Africa and the Sahel experienced the domestication of African rice, pearl millet, sorghum, yam, the palm-oil tree and the guinea fowl. Coffee and teff were domesticated in Ethiopia. Mesoamerica was the cradle of maize, beans, pumpkins, and turkeys, while agriculture in the Andean highlands developed on the basis of potatoes, manioc, and llamas/alpacas. Using data from Blumler (1992) Diamond shows that out of the 56 wild grasses with a seed weight 10 times above average, 39 were found in Eurasia (including North Africa), compared to only 4 in sub-Saharan Africa, 11 in the Americas, and 2 in Australia (1997, p. 140). Moreover, the wild ancestor of maize (*teosinte*), which became the most important American staple crop, required a lengthy evolution to produce the high-yielding kernels of present-day variants.

Of the 148 wild mammals weighing over 50 kg, 72 were found in Eurasia, 51 in sub-Saharan Africa, 24 in the Americas, and only 1 in Australia. From this reservoir of large mammals 13 were successfully domesticated in Eurasia, including the ‘big five’ (1997, p. 162). Although sub-Saharan Africa was home to vast numbers of large game, including zebras, elephants, antelopes, and buffalos, none of these large mammals were ever domesticated. The llama/alpaca was domesticated in the Andean highlands, where it was used as a packing animal and a source of meat, but it proved useless as a source of agricultural or proto-industrial draft power.[2] Mesoamerican farmers had to make do with dogs and turkeys, but they had no access to animal traction power prior to the arrival of the Spaniards.

Europe played no role in the invention of agriculture. European agriculture emerged on the basis of *imported* domesticated plant and animal species. Diamond’s explanation for European hegemony thus rests crucially on his argument that the conditions for the *diffusion* of plant and animal species were much better along the Eurasian horizontal axis, than along the vertical axes of Africa and the Americas. Europe was a ’latecomer’, but it was blessed with biogeographic conditions that enhanced agricultural diversification and the creation of food surpluses, which, in turn, stimulated population growth. Larger population densities enhanced commerce, city growth, and created conditions for the centralization of state power through tax systems, bureaucratic technology (calendars, scripture) and investments in military capacity such as guns, steel swords, and ocean-going vessels (1997, p. 87).

Diamond argues that domesticated animals were crucial in the long-term evolution of powerful peasant-based states. They enhanced proto-industrial technological development by providing traction power for ploughs, mills, and transportation. They raised agricultural productivity by supplying fertilizer and complemented people’s diets with dairy products and animal protein. Moreover, the intimate contact between humans and livestock created hotbeds for human pathogens such as measles, flue, smallpox, pertussis, malaria, and tuberculosis, since disease-causing parasites evolved in animal hosts and subsequently mutated into human-borne variants. Intensive contact between growing populations of livestock and humans created a transmission ecology that simultaneously raised mortality rates and partial resistance against major ‘civilization diseases’ (1997, pp. 206–214; McNeill, 1976; Pearce-Duvet, 2006; Tanabe, 2001). Since people outside Eurasia failed to develop resistance against these germs, Europeans had an enormous advantage in the conquest of the New World (Crosby, 2003 [1972]; Flynn & Giraldez, 2004; Mann, 2011).

Diamond’s thesis has received empirical support from Olsson and Hibbs (2005), who have demonstrated in a cross-country regression framework that biogeographic conditions such as absolute latitude, climate suitability to agriculture and the number of annual or perennial wild grasses and domesticable big mammals can explain a considerable part of present-day variation in per capita income. Spolaore and Wacziarg (2013) support this view by showing the impact of long-term intergenerational transmission of biological and cultural traits on economic development. Putterman and Weil (2010) and Easterly and Levine (2012) have shown that people originating from areas with early centralized states are richer today and have transferred new technologies and knowledge to areas with low levels of ‘state antiquity’. All these empirical studies emphasize how particular evolutionary advantages have bolstered trajectories of economic divergence in the very long run.

3. HUMAN MIGRATION AND THE DEVELOPMENT OF AGRICULTURE

The population density estimates presented in Table 1 confirm Diamond’s observation that Africa and the Americas were considerably less densely populated than Eurasia around 1500, and this remained the case far into the 20th century (1997, p. 263). These population estimates are open to discussion because the estimates for Africa and the Americas are not much more than educated guesses. However, even with a margin of error of 100%, the overall picture would not really change: Eurasia was on average more densely populated and the density levels of substantial territories at the outer ends

Table 1. *Average population densities per world region c. 1500 AD*

	Population (millions)	Land area (millions km^2)	Density (people/km^2)
Africa total (incl. Sahara desert)	50–100	29.5	1.7–3.4
Sub-Saharan Africa (excl. Sahara desert)	40–80	20.7	1.9–3.8
Central & South America	15–70	19.2	0.8–3.6
North America	5–30	24.7	0.2–1.2
Eurasia total	350	53.0	6.6
India	110	3.0	36.7
China	100	9.3	10.8
Japan	15	0.4	37.5
Western Europe	57	3.5	16.3
Eastern Europe	14	1.1	12.7
Average of three continents	716–846	164	4.4–5.1

Sources: Baseline Eurasian and African population estimates are from Maddison (2010), own mark-ups added; American population estimates based on Denevan (1992), taking the extremes of 20–100 million for the region as a whole into account. See Mann (2005, chap. 4) for a discussion; Land surface data are from FAOSTAT.

of its vast landmass far exceeded the joint average of the three continents.

In this section I will develop the argument that Africa and the Americas indeed had relatively low density levels in 1500, but for *distinctively different* reasons. African population growth was limited by biogeographic constraints to agricultural intensification, in line with Diamond's view. Yet, the evidence for the Americas is much less convincing. Given the late date of human migration into the Americas and the relative abundance of resources for hunters and gatherers, it is not clear that the development of farming was jeopardized by a lack of suitable species for domestication. In many areas there may simply have been very little incentives to start farming in the first place, and in those places where sedentary agriculture did gain ground (e.g., Central Mexico, Andean highlands), population densities were not considerably lower than in India, China, or Western Europe. In other words, there is a need to analyze contrasting patterns of human settlement in a greater depth.

The *Out-of-Africa* thesis holds that today's world population derives from a single origin in sub-Saharan Africa several million years ago. In the 1940s to 1970s this thesis was based on archeological excavations of hominid fossils in South and East Africa (Lewin, 2005, p. 15), but it received a more solid foundation by genetic research since the late 1980s. Genome sequencing studies have demonstrated that African populations are genetically more diverse than non-African populations, indicating that the first splits in the human genetic tree must have occurred in Africa (Cann, Stoneking, & Wilson, 1987; Li *et al*., 2008). Recent studies of mitochondrial DNA (mtDNA) suggest that *Homo sapiens* appeared about 200,000 BP, but did not leave Africa before 100,000 BP, probably via the Arabian Peninsula (Tishkoff *et al*., 2009). Migration into Eurasia was accompanied by a sharp reduction in the genetic variation of the immigrants, a so-called population bottleneck. It is currently held that non-African peoples can be retraced to ca. 600 effective founding females and ca. 400 effective founding males (Campbell & Tishkoff, 2008, pp. 404–405; Liu, Prugnolle, Manica, & Balloux, 2006).[3]

Migration *into the Americas* occurred much later, but it involved a similar population bottleneck. Evidence from mitochondrial DNA obtained from people with native American roots and ancient DNA retrieved from pre-Columbian human remains suggests that the Americas became populated by a comparatively homogenous group of people with common ancestors from Eastern Siberia (Eshleman, Malhi, & Smith, 2003; Greenberg, Turner, & Zegura, 1986). One study even suggests that the entire pre-Columbian American population may have derived from as few as 80 founding individuals (Fagundes *et al*., 2008, p. 584). Although most scholars believe that the continental migration went exclusively via Beringia and not via the Polynesian islands into South America, it is unclear whether this happened by foot or by boat. Archeological remains of the Clovis culture reveal that human presence in the Americas dates back to at least 12,500 BP, which coincides with a relatively brief period of an ice-free corridor in the Bering Strait, opening up a land route between Siberia and Alaska. Yet, the possible remains of a pre-Clovis culture in south-central Chile suggest an earlier date of human settlement. In this case it is more likely that the first migrants sailed down the coast from Alaska along the Western shores of North America, to then push further South over land (Blench, 2008; Eshleman *et al*., 2003, p. 12; Mann, 2005). Most genetic studies maintain that the in-migration occurred in a narrow time-window, with a majority of studies suggesting dates from 13,000 to 23,000 BP (Blench, 2008).

Linguists debate whether these early immigrants spoke a similar language, or that consecutive waves of migrants were responsible for the introduction of different language families in the Americas, which then further split into a broad range of small and isolated phyla characterized by large phonological and syntactical diversity (Campbell, 1997, p. 98). One of the big puzzles of American demographic history is that genome sequencing studies consistently point to the homogeneity of the early American population, while linguists point to the high diversity of Amerindian languages. In his grand survey, Campbell (1997, p. 170) observes that out of the c. 400–450 language families in the world, 118 are found in Southern America, 58 in North America, and another 18 in Mesoamerica (a total of 194). In South America alone, there were ca. 1,500 individual languages at the time of first contact with Europeans, which is comparable to Africa with an estimated 2,146 living languages at present (Lewis, Simons, & Fennig, 2013).[4] The large number of isolates and small phyla in the linguistic landscape of pre-Columbian America testifies to a large degree of fragmentation and isolated linguistic development (Adelaar & Muysken, 2004; Campbell & Grondona, 2012). Blench (2008, p. 8) argues that if human settlement would have occurred as late as 12,000 BP, the rate of linguistic diversification must have been extraordinarily high. Languages, like genes, take time to diverge.[5]

Despite the lack of conclusive evidence on the nature and timing of the *out-of-Africa* and *into-America* migratory waves, the temporal order of human settlement offers an interesting paradox. Table 2 presents the evolutionary growth rates based on the available estimates of the earliest date of human presence and population size around 1500 AD. The evolutionary growth rates in Eurasia were considerably higher than in Africa, but much lower than in the Americas. The American evolutionary growth rate is roughly a factor 8 of Africa's and a factor 3 of Eurasia's. These calculations are largely insensitive to changes in the population estimates of 1500 AD and the size of the early settler population. Even if we assume as much as 10,000 founding individuals in the Americas, its long-term rate would still be 6 times the African and 2.5 times the Eurasian rate.

These differences in evolutionary growth rates tell us something about the biogeographic conditions for human reproduction, although we do not know exactly what. A first possible explanation is that evolutionary growth rates among hunter–gatherer populations were more or less equal across the globe because the checks on population growth operated

Table 2. *Dates of first human settlement and evolutionary growth rates up to 1500 AD*

	200.000 BP	100.000 BP	25.000 BP	(millions)	min	max
Africa*	1,000			50–100	0.005	0.006
Eurasia	0	1,000		350–450	0.013	0.013
Americas	0	0	1,000	20–100	0.040	0.046

Sources: Timing of first modern human presence in Africa and Eurasia from Tishkoff *et al*. (2009, p. 1035); for America Eshleman *et al*. (2003, p. 12); Lower-bound population estimates 1500 AD from Maddison (2010); upper-bound estimates for Africa and Eurasia my own mark-up; For America Denevan (1992) and Mann (2005, chap. 4). *Note:* *Africa includes North Africa.

via low fertility rates. Nomadic peoples tend to raise fewer children because of the physical efforts imposed on women and the need to restrict the size of nomadic bands to remain mobile. Covering considerable distances by foot each day eats into energy reserves, reduces fecundity, and raises the rate of miscarriages. Infanticide and sexual restraint were widely practiced to contain group size. Fertility rates rose with the onset of sedentary agriculture, as sedentary lifestyles reduced the risk of miscarriage, decreased the burden of tending small children, and raised the value of child labor. If this scenario is true, the higher evolutionary growth rates in the Americas can be explained by the fact that the period of nomadic reproduction regimes was much shorter than in Africa and Eurasia, as the switch to sedentary reproduction regimes followed relatively soon after human migration into the New World.

An alternative explanation is that rates of population growth had been higher in the Americas already *before* the development of sedentary agriculture. This possibility draws on Darwin's *invasive species theory*: species that enter into a new territory without close relatives multiply faster because of a lack of natural enemies. If human pathogens had several million years to evolve, mutate, and diffuse in Africa, then the first migrant populations in Eurasia may have experienced a formidable head-start as they pushed into comparatively pristine disease environments (McNeill, 1976, p. 25; Reader, 1998, pp. 239–248). Given the late settlement of the Americas, and the fact that migration into the New World was accompanied by a population bottleneck, the demographic 'bonus' of a disease-free environment may thus have operated from the early days of human settlement in the New World as well. Moreover, rather than controlling group size, nomadic bands and tribes may have opted more often for splitting apart. That is, patterns of mobility and reproduction may have evolved differently in an 'empty' continent than in settled areas.

This second scenario, which cannot be dismissed right away, has two important implications for the transition to sedentary agriculture which Diamond fails to consider. First, if the incentives for foragers to change their strategies of reproduction were different in the Americas, the biological fact that the *opportunities* for domestication were larger in Eurasia may not have been decisive. Diamond mentions, almost in passing, that resource depletion has been the most likely factor in changing the reproduction strategies of foragers, but he does not situate these changes carefully in time and place. If resources for hunting and gathering remained abundant in the Americas, than what should have forced native American foragers to adopt farming in the first place?

Second, and related to the question posed above, in those places where sedentary agriculture emerged quite early and gave rise to the evolution of powerful centralized states (e.g., Central Mexico, Andean highlands), there is no evidence that population densities were significantly lower than in any of the 'older' Eurasian civilizations. The population of Tenochtitlan, the Aztec capital, has been estimated in the order of 150,000–200,000 people, which was comparable to the largest European cities (Paris, London, Naples) around 1500 AD (Bairoch, 1988, pp. 135–141). Teotihuacan, located some 70 km to the North, was inhabited by more than 100,000 people around 500 AD.

Perhaps more important than city size, the central valley of Mexico, the homeland of the Aztec (14th–5th C.), Toltec (8th–0th C.) and Teotihuacan (1st–5th C.), supported a dense *network* of cities. In the early 16th century, there were over 20 cities within a radius of 50 km along the shores of *lake Texcoco*, and several more a little further inland. Conservative estimates of 0.5 million people for the Mexican basin alone, yield a population density level exceeding 150 pp/km^2. The total land area of the Aztec empire at its largest extent under the reign of Moctezuma II (1502–1520) has been estimated at ca. 200,000 square kilometers. A lower bound total population estimate of 5 million gives an average density of 25 pp/km^2, which is comparable to density levels in the eastern part of China or the western part of Europe at that time (Maddison, 2010). The population estimate of 25.2 million by Borah and Cook (1963, p. 88) even implies a density of ca. 125 pp/km^2. Density levels in the Inca empire, which at its peak covered ca. 0.9 million km^2 (McEwan, 2006, p. 3), were certainly lower. With conservative population estimates of 4 million and more widely cited figures of 10–16 million, they ranged between 4 and 18 pp/km^2 (McEwan, 2006, pp. 93–96). Indeed, around 1500 more than half of the total pre-Columbian American population may have been living in one of these two focal areas of Spanish conquest (Denevan, 1992).

As far as the archeological evidence goes, there were no polities with comparable degrees of population concentration in sub-Saharan Africa (Coquery-Vidrovitch, 2005). It is possible that the Sokoto Caliphate in present-day Northern Nigeria reached 10 pp/km^2 in the course of the 19th century, when it incorporated over 5 million people on a surface of ca. 500,000 km^2 (Lovejoy, 2005, p. 8). But that would still be less than half of the lower bound estimate for the Aztec empire. In Ethiopia, one of the most stable areas of human settlement in sub-Saharan Africa, density levels did not reach the threshold of 10 pp/km^2 before the 20th century. The largest concentrations of people before 1500 AD may have been in the rainforest belt west of present-day Ghana, around the Yoruba cities of Ile-Ife and Benin-city (Southwestern Nigeria), but there is little evidence for intensive agricultural systems underpinning large concentrations of people (Ogundiran, 2013, p. 860).

The African–American contrast in the spatial distribution of population is yet another sign that the biogeographic roots of human settlement patterns were quite different in both continents. This is a relevant observation in view of the 'diversity debit' hypothesis, the idea that ethnic, religious, linguistic, or racial fractionalization impairs long-term economic or human development (Gerring, Thacker, Lu, & Huang, 2015). High degrees of ethnic fractionalization in sub-Saharan Africa have been an oft-cited barrier to long-term economic or human development (Alesina & La Ferrara, 2005; Casey & Owen, 2014; Easterly & Levine, 1997), but the deep roots of this 'fractionalization' are not well understood. To which extent were large parts of the native American population part of multi-dimensional networks of political, economic, or cultural integration? This question goes far beyond the scope of this paper, but it underlines the relevance of the Africa–America comparison in studies of world development.

In this discussion the differential role of human epidemics should also be considered. It is possible that a significantly lower incidence of human epidemics supported the development of population centers around highly productive agricultural systems in the Americas up to a point that cities such as Tenochtitlan did not depend on structural replenishments from the countryside in order to grow. Large concentrations of people in Africa, on the other hand, may have been prone to a much higher incidence of crowd diseases and therefore be less sustainable. I will further elaborate on the role of human diseases in contrasting African–American human settlement patterns in Section 4.

The bottom line of this section is that the evolution of African and native American populations has taken place *in distinctively different ecological environments* before the Columbian reconnection enhanced the Atlantic exchange of germs, plants, and animals (Crosby, 2003 [1972]). These ecological differences, combined with the late presence of *Homo sapiens* in the Americas, give reason to believe that demographic regimes were operating under different mechanisms in the vertical axis continents. Hence, it cannot be a priori assumed that higher *average* population densities in Eurasia testify to more favorable conditions for agricultural development. Lower *average* densities in the new World may also reflect a later date of human presence combined with a greater abundance of resources for foragers, which produced weak incentives for changing prevalent strategies of reproduction. The high population densities in Central Mexico and the Peruvian Andes demonstrate that some environments in the New World were certainly conducive to agricultural intensification, but that does not demonstrate that these were the only suitable areas.

4. AFRICA: THE CRADLE OF ‘OLD WORLD’ DISEASES?

Diamond’s claim that domesticated animals played a crucial role in shaping an *exceptional* Eurasian disease environment requires rethinking on three grounds. First, recent genetic research suggests that the origins of most of the major communicable diseases can be traced back to a wild-animal source, and that some of these human pathogens existed long before the first domesticated animals appeared on the scene. Second, recent genetic research has indicated that Africa is the most likely source region of smallpox, the biggest killer disease that Europeans introduced in the New World. Third, if domesticated animals have created a decisive European advantage in imperial conquest, then it was a partial advantage at best. Europeans were killed in large numbers by African diseases, also in areas where Africans kept no livestock at all (i.e., the tsetse-ridden forest belt). The wider argument I will develop in this section is that Africa’s disease environment should be considered as the real exception from the global pattern, and that this has little to do with intimate relations to domesticated animals, but rather with the evolutionary history of hominid species in Africa and subsequent patterns of human migration.

Genetic research has challenged many conventions. Epidemic diseases that were once thought to derive from domesticated animals, are now thought to have evolved from wild animals. For this study, smallpox and measles are the most important examples, because these two diseases are held responsible for the lionshare of excess mortality in the Americas during the 16th and first half of the 17th centuries (Borah & Cook, 1963; Crosby, 2003 [1972], p. 42; Mann, 2005). Diamond (1997, p. 207) claims that both smallpox and measles evolved in Eurasia from intensive farmer’s contact with their livestock. The argument is that the viruses causing small pox and measles stem from the same families as the viruses causing cowpox and rinderpest, respectively. However, recent studies of the DNA genome of the *variola virus* (VARV), the etiologic agent of smallpox, indicate that the disease has African roots (Li *et al*., 2007). Out of a broad geographically distributed sample of 47 VARV isolates, Li *et al.* were able to derive two primary VARV clades, one severe and one milder variant. The severe variant probably stems from an ancestral African rodent-borne variola-like virus about 16,000–68,000 BP. The milder variant has likely diverged from an ancestral VARV in West Africa about 1400–6300 BP (2007, p. 15787). Europeans thus introduced an *African disease* in the Americas; a disease which had been around long before the first mammals were domesticated.

Measles offer a similar story. Since *Paramyxoviridae Morbilli* are from the same family as the virus that causes rinderpest, it has long been assumed that the human variant had evolved from cattle. However, genome sequencing studies point out that the *Morbilli* genus is more closely associated to the *Paramyxoviridae* found in rodents, bats, and snakes. Although it remains unclear when and where the Morbilli split from a shared wild-animal ancestor virus, there is no genetic evidence for a connection to domesticated animals (McCarthy & Goodman, 2010).

Malaria, still responsible for high rates of child mortality in sub-Saharan Africa, also became a major killer disease in the New World after 1492. Diamond suggests that *Plasmodium falciparum*, the parasite that causes *malaria tropica* – the most aggressive and lethal variant – evolved from domesticated birds like chicken and ducks (1997, p. 207, Table 11.1). However, a close variant to *P. falciparum*, has been retrieved in African gorilla populations and genome sequence analysis of both, the human and gorilla parasites, suggest that the disease has been transmitted from gorillas to humans in Africa (Liu *et al*., 2010). Some scholars have argued that it may have happened when the first hominids split from Gorilla’s and chimpanzees millions of years ago, others have pointed to much more recent dates around 3200 and 7700 BP (Pearce-Duvet, 2006, pp. 376–377; Rich, Licht, Hudson, & Ayala, 1998; Volkman *et al*., 2001).[6]

The prevalence of aggressive strains of malaria and yellow fever, along with other tropical disease unique to Africa (e.g., sleeping sickness, ebola, river blindness) go a long way in explaining why Europeans restrained from conquering the interior of Africa until the late 19th century and, instead, confined themselves to forts and factories along the coast (Curtin, 1989). When European slave ships transmitted malaria and yellow fever to the New World, these African diseases had a huge impact on the subsequent demographic reconfiguration of the Americas. Since Africans had acquired partial resistance, they were better equipped to survive in the tropical disease environments of the Atlantic plantation economies. Hence, the transmission of African diseases affected subsequent cost–benefit calculations underpinning the Atlantic slave trade (Mann, 2011; McNeill, 2011).

Table 3 presents a list of ten of the most severe Old World diseases that have been transmitted to the New World after 1492. The table shows that only in the case of influenza the role of domesticated animals is uncontested. Influenza differs from many other epidemic diseases because it is caused by viruses which ‘rejuvenate’ every year. Influenza viruses have multiple origins, and tend to evolve among others in birds (wild and domesticated), pigs, and humans.[7] The other nine epidemic diseases have most likely evolved from wild animals. This does not disprove that dense animal and human populations are hotbeds of diseases, but it redirects attention to the more fundamental question of why Africa and the Americas had such different disease environments before 1500 AD.

If we think of the evolution of a new epidemic disease in terms of a probability function, $p(E_x) = \mathrm{t}(h, a, \mathrm{te})$, that estimates the probability (p) of the evolution of a human pathogen (E) at a given point in time (x), there are at least four interrelated variables to be considered: the density of human populations (h), the density of animal populations (a), the variety of eco-systems that may have functioned as suitable transmission ecologies (te), and all of these three variables interact with the time (t) that microbes are granted to jump from animal to human hosts (the reverse also occurs, but is of lesser interest here).

There is no evidence that wild animals in Africa were living in smaller concentrations than livestock herds in Eurasia. And

Table 3. *Origins of ten of the most severe Old World diseases according to recent genetic studies*

	Epidemic	Pathogen	Vector	Genetic mutation into human disease variant			Sources
				Source region	Source animal	Date	
1	Smallpox	*Variola major; variola minor*	Humans; airborne, direct contact	sub-Saharan Africa	Rodent-borne variola-like virus (V. major). V. minor unknown	16,000–68,000 BP (V. major) 1,400–6,300 BP (V. minor)	Li *et al.* (2007)
2	Influenza	*Influenzavirus A, B, C*	Humans, mammals, birds	Multiple. Most avian and pig-borne types from South and East Asia	Multiple: birds, pigs, humans	Multiple	Bouvier and Palese (2008)
3	Tuberculosis	*Mycobacterium tuberculosis*	Humans; airborne, direct contact; non-pasteurized cow milk	Multiple types from sub-Saharan Africa and Eurasia	Bison or humans; not cattle	At least 17,000 BP	Rothschild *et al.* (2001)
4	Bubonic plague	*Yersinia pestis*	Rat fleas	East Asia	Rodents	At least since first millennium AD	Morelli *et al.* (2010)
5	Malaria	*Plasmodium falciparum; plasmodium vivax*	Mosquitos (Anopheles)	sub-Saharan Africa	Gorillas	Unknown	Liu *et al.* (2010)
6	Yellow fever & Dengue fever	*Flavivirus*	Mosquitos (*Aedes aegypti*)	sub-Saharan Africa	Bats, rodents?	Unknown	Cook and Holmes (2006)
7	Measles	*Paramyxoviridae Morbilli*	Humans; airborne, direct contact	Unknown	Rodents, snakes, bats, salmon? Not cattle as previously thought	At least since first millennium AD	McCarthy and Goodman (2010)
8	Typhus	*Rickettsia typhi; rickettsia prowasekii*	Rat fleas; lice on humans	Unknown	Humans?	Before 1500 AD	McLeod *et al.* (2004), Raoult, Woodward, and Dumler (2004)
9	Cholera	*Vibrio cholerae*	Contaminated water, food; seafood; mainly tropical areas	India	Shellfish, zooplankton?	At least since first millennium AD	Sack, Sack, Balakrish, and Siddique (2004)
10	Leprosy	*Mycobacterium leprae*	Humans; probably airborne	Middle East, India?	Humans or other primates	2000–5000 BP	Schuenemann *et al.* (2013)

Sources listed in last column of the table.

if many of the more severe human pathogens originally derive from wild animals like bats, birds, or rodents, it is not evident that domesticated animals are the dominant factor in this probability function. If ecological diversity and evolutionary time are important for the evolution of human microbes, it is far more likely that Africa's vertical axis, tropical conditions and early hominid presence have offered a combination of factors enhancing $p(E_x)$. If this is the case, than it is the relatively 'brief' period of human presence, rather than a lack of domesticated animals, that explains the low incidence of major killer diseases in pre-Columbian America. And this contrast is brought to light much better in comparison with Africa than in comparison with Eurasia.

5. DOMESTICATED ANIMALS AND PRE-COLUMBIAN STATE FORMATION

Extending the discussion to pre-Columbian state formation opens up yet another vastly underexplored area for the Africa–America comparison. For reasons of space, I will confine the discussion in this section to one specific, but crucial aspect of comparative state development: the evolution of fiscal systems. Fiscal systems constitute the backbone of state formation processes, because states require revenues to broadcast power. At the same time, states have to invest in military and administrative capacity to incentivize tax-payers to comply with state tax regulations and to defend the collective polity against external threats.

In Diamond's conception of world development the relationship between domesticated animals and state formation boils down to the idea that farm animals enhance agricultural productivity and thus create taxable economic surpluses. These surpluses enhance economic specialization and give rise to social classes that are exempt from subsistence activities (e.g., rulers, bureaucrats, merchants, priests). Social stratification is accompanied by (military) technological innovations, more complex political organizations, and literate bureaucracies that employ scripture for administrative purposes (1997, p. 87). In addition, domesticated animals, such as horses, can contribute to the military power of states.

The Africa–America comparison casts a different light on the role of domesticated animals in shaping processes of state formation and the design of tax systems in particular. First, the absence of farm animals did not prevent the rise of powerful empires in Central Mexico (e.g., the Aztec empire) and the Peruvian highlands (e.g., the Inca empire), begging the question how important domesticated animals were after all. But second and more important, in Sub-Saharan Africa domesticated animals such as cows, goats, and camels were primarily used as *mobile* economic assets. This aspect of animal mobility affected the opportunities and constraints to African state taxation in several respects.

In a seminal article on the origins of the state Carneiro (1970) developed the theory of environmental circumscription. Comparing pre-Columbian states in the New World (e.g., Mexico and Peru) with the Old World states in the Nile, Indus, and Tigris-Euphrates valleys, he pointed out that the ecological conditions in these ancient states (e.g., climate, soil type, altitude, drainage patterns, available food crops, animals etc.) differed enormously. Ancient states thus emerged in places with highly varying conditions for agriculture, but they shared one thing in common: they were all located in areas of *circumscribed* agricultural land, that is, mountains, deserts, or seas sharply delimited the area of cultivation (1970, p. 734). These environmental barriers prevented the migration of farmers outside the state orbit and facilitated the development of a collective polity (see also Herbst, 2000).

The widespread practice of nomadic pastoralism in Sub-Saharan African adds an important aspect to Carneiro's theory. The option of animal herding turned 'closed' agricultural land frontiers around major rivers or mountain areas into permeable livelihood frontiers. Cattle spread south of the Sahara as early as 7000 BP and became a central object of worship in the early kingdoms along the middle Nile (i.e., Kerma and Nubia) (Welsby, 2013). Cattle spread to the Niger basin around 4500 BP (Gifford-Gonzalez & Hanotte, 2011). The states in Southern Africa that culminated into Great Zimbabwe (c. 1000–1500 AD) were also organized around agro-pastoral subsistence production in combination with long-distance trade to the Indian Ocean (Pikirayi, 2013). Especially in the African savannah areas outside the tsetse-ridden forest zones, cattle, horses, goats, and camels were kept in considerable numbers. Livestock served as a storage of wealth and as a source of risk-mediation in ecologically fragile and climatologically instable environments. Cattle were also a vital source of animal fat, protein and raw materials for handicrafts (leather, horn, bone etc.).

Contrary to African rock paintings of cattle herds, in Mesoamerica wild animals such as the jaguar, the feathered bird, and the serpent featured as objects of worship and artistic expression. Mesoamerican farmers disposed of dogs and turkeys, but neither of these animals were critical to the development of agriculture, nor useful as draft animals. The ecological advantages of the Mexican basin consisted of a combination of volcanic soils, fresh water sources, and the possibility to mediate subsistence risks by using the variation in altitudes to diversify food production. Maize, beans, squash, cocoa, and a variety of fruits offered a combination of protein, vitamins, and calories that could support a growing population. The presence of llama/alpaca in the Andean mountains created limited opportunities to cross land frontiers, since their mobility was restricted to elevated terrains (McEwan, 2006).

Collective action theory places the evolution of fiscal systems at the center of the Hobbesian dilemma: why do people engage in complex forms of cooperation given their selfish nature? Following key studies on collective action theory by Olson (1965), Levi (1988) and Lichbach (1996), Blanton and Fargher (2008) have explored the cooperative features of fiscal systems in a broad comparative analysis of pre-modern states across the world. Following Levi (1988) they conceptualize state formation as the outcome of a bargaining process between 'rulers' and 'tax-payers', departing from the notion that individual interests and collective interests do not necessarily align, that all stakeholders have agency – i.e., they can influence the rules and practices of resource distribution -, and that rulers make informed choices regarding tax regulations and tax-payers regarding their compliance. Rulers seek revenue to co-opt political allies, to keep the military aligned, and to provide public goods (defense, infrastructure, law and order). If they do well, they maintain tax compliance, but if they set their demands too high or engage in obsessive resource squandering, rulers risk erosion of the tax base or outright revolt. Tax payers, on the other hand, can vote with their feet against predation or communicate their preferences on the allocation of collective resources via direct political engagement.

According to Blanton and Fargher (2008) local resource endowments structure this bargaining process by determining the options of revenue extraction. The authors distinguish between internal and external sources of revenue to predict the nature of the ‘social contract’ that will emerge. Internal revenues stem directly from a broad population of tax-payers and require a more intensive social contract between rulers and tax-payers, whereas external revenues “*originate from specific, highly productive point sources, allowing tax administration to be carried out by a comparatively small, and, presumably, highly motivated work force and administrative staff rewarded with high social standing and a share of the state's wealth*” (2008, p. 112). In the coding of revenue sources Blanton and Fargher confirm the idea that historical African polities have relied to a larger degree on external revenues than the Aztec and Inca empires in the New World (2008, p. 116 and 135). African rulers relied in particular on the control of mineral resources, long-distance trade or trade monopolies to cement their power (Fortes & Evans-Pritchard, 1940; Hopkins, 1973).

Figure 1 presents a framework that integrates the role of domesticated animals in this collective action perspective on state taxation. In this framework taxes are considered to be a function of (a) the military reach of rulers that seek to enforce tax-payer's compliance and (b) the relative mobility of tax-payers that enables them to evade taxation. The presence of ‘military animals’ enlarges the power of rulers to enforce taxation by extending the geographical control of resource flows. The presence of herding animals enlarges the mobility of tax-payers to escape taxation. The former condition raises the bargaining power of the rulers, the latter condition the bargaining power of tax-payers. In addition, herding animals may lower the perceived value of public goods such as military protection, since these collective arrangements are difficult to uphold in vast pastoral hinterlands.

The bottom-right quadrant describes the conditions that underpinned the rise of the major West African savannah empires, such as the empires of the Middle Niger (Ghana, Mali, Songhai). Rulers had limited options to tax local agricultural surpluses, because sedentary cultivation practices were often combined with pastoral activities. Herding animals enabled potential tax-payers to escape fiscal control. Of course, it was not impossible to tax nomadic pastoralists, but the costs of taxation easily outweighed the marginal revenues. Marchetti and Ausubel (2012) have argued that the costs of fiscal control will particularly increase beyond distances of 5–10 km, that is, beyond distances that can be covered by traveling back and forth in one day without overnight stays or additional logistic provisions.

If tax-payer mobility is large, rulers may focus on either securing a highly productive point source (upper-right quadrant), or, in case they can cover long distances, try to secure major trade arteries and commercial centers. The West African states disposed of a relatively large military reach because of their recourse to camel and horse-back soldiers. The primary task of these soldiers was to guarantee the safety of the trans-Saharan trading caravans and reduce the number of price-raising middlemen. The armies were composed of elite-warriors because they required considerable investments in equipment (horses, weapons, armour). These investments were recovered by the rents extracted from the Trans-Saharan trade (gold, salt, cloth, slaves), which by itself also depended on camels (Goody, 1971).

The major challenge of the ruling elite was to keep these militia aligned and preventing splits into opposing factions (Reid, 2012). McIntosh describes the urban landscape of the middle Niger basin as one of ‘cities without citadels’ (2000; 2005, p. 10). The major hubs of the Trans-Saharan trade Gao, Timbuktu, and Djenne-Djenno, lacked signatures of centralized power: palaces, tombs, temples, pyramids, towers, stèles, squares, forts, or giant sculptures. They evolved as a chain of scattered villages without a marked centre and did not sustain high levels of permanent settlement. Hopkins has suggested that these ‘urban’ populations may have fluctuated between 15,000 and 80,000 inhabitants, depending on the trading seasons (1973, p. 19). The Mali and Songhai rulers managed to build an empire on controlling long-distance trade, but they did not seem to care much about investments in exquisite urban architecture symbolizing a strong ‘social contract’ between state and citizens.

The upper-left quadrant describes the conditions in the Central Mexican valley. Indeed, the capacity of Aztec rulers to enforce tax-payer compliance and supply public goods was of a different order. The Aztec state invested in the regulation of water supplies to enhance agricultural productivity and to accommodate the need for central coordination with expanding farming populations (Blanton, 2012). These investments were paid from mandatory labor services for construction projects and agricultural work on elite estates. These resources were complemented by tributes in kind consisting of agricultural and non-agricultural commodities (Berdan, 2012; Wohlgemuth, 1991). Military capacity was not based on the ability to cover large distances – this actually proved a problem for keeping the Aztec empire together -, but rather on the mobilization of large numbers of foot soldiers that could

	Tax-payer mobility	
State tax enforcement power	Low (*absence of herding animals*)	High (*presence of herding animals*)
Low (*absence of military animals*)	State revenues from local labour andagrarian surpluses	State revenues from high productive point source
High (*presence of military animals*)	State revenues from local economic surplus and long-distance trade	State revenues from high productive point sourceand/or long-distance trade

Figure 1. *Relationship between domesticated animals and state taxation.*

exert sufficient credible threat to keep potentially disloyal states committed to the central political body. The huge expenses of the Aztec rulers on ceremonial architecture and state symbols testified to an intensively negotiated collective identity (Conrad & Demarest, 1984).

In the Inca empire, investments in sedentary agriculture were also seen as the key to maintain a stable state-regulated resource flow. Contrary to the Aztec empire, however, the Inca rulers based their taxes on an elaborate system of census-taking, including detailed population counts and land surveys. State taxes further consisted of mandatory labor services (i.e., *mita*) and tributes in kind, part of which were invested into the construction of a large network of highways (40,000 km of paved roads and bridges) and an army of foot soldiers. The Inca brought distant peoples into the realms of the state, which they controlled via a highly effective communication and food storage infrastructure. The emanation of a state-centred religion was essential to cement these power structures. Both empires were thus built on a more intensively developed system of collective resource pooling, where broad populations of tax-payers complied to the fiscal demands of the state in return for a more varied range of 'public goods', than those observed in the West African states of the Middle Niger.

Of course, these are distinctions of degree and they do not translate unconditionally to other parts of the vertical-axis continents. In fact, one could argue that the Ethiopian state had more in common with the Inca empire than with any other African state. The Ethiopian state used its own language, its own system of record keeping and adopted a successful strategy of tying the power of the ruling dynasty to a shared Christian identity and history (McCann, 1995). Variations in altitude were exploited to diversify food production and harvest water for field irrigation. It was also the only place south of the Sahara where cattle were used in a system of mixed farming, supplying draft power for plough-based cultivation. But the case of Ethiopia underlines my central point that the role of domesticated animals in the evolution of pre-Columbian states is much more differentiated than Diamond suggests. Indeed, to explore the big questions of pre-modern state formation the use of reciprocal regional comparisons is indispensable.

6. CONCLUSION

Building on recent insights from archeology, genetics, and linguistics this study has challenged Diamond's grand narrative of the biogeographic roots of world inequality. By shifting attention away explaining European exceptionalism – or Eurasian exceptionalism for that matter – and focussing attention on the vertical-axis continents of Africa and the Americas, I have tried to explore new ground for a multi-disciplinary research agenda.

The critique I have developed on Diamond's meta-narrative can be briefly summarized in three points. First, Africa and the Americas were lowly populated regions around 1500 AD, but there is no reason to belief that they were so for similar reasons. There is no evidence that the environmental constraints to agricultural productivity growth in Sub-Saharan Africa prevailed in the Americas. The Americas may have been lowly populated because of late human presence, rather than specific biogeographic constraints to sedentary agriculture. Second, there is no reason to belief that human disease environments in Eurasia were 'exceptional'. If anything, Africa seems to be the cradle of the most lethal old world diseases that were transmitted to the New World after 1492. Third, the role of domesticated animals in shaping the conditions for the development of stratified societies and centralized states is much more variegated than a Eurasian-based account leads one to belief.

This study has called for new research that helps to better understand the African–American differences in human settlement patterns. Especially for the American case it is crucial to connect genetic with linguistic research in order to obtain a more coherent account of the dispersal of early immigrants across the continent. Why and when did resources for foragers become scarce in different parts of the New World? There is also a pressing need to better understand the ecological constraints to African population growth. This requires a more systematic reflection on the question why Africa has been the source region of many severe human pathogens. Is there a link with human evolution? In what ways did human interactions with wild and domesticated animals contribute to the evolution and spread of human pathogens?

The Africa–America comparison also calls for a more contextualized study of the role of domesticated animals in varying processes of early state formation. How could Mesoamerican states reach high population densities without domesticated animals? What was the role of horses and camels in the military operations of West African states? And how did nomadic pastoralism effect the design of tax systems? All these questions require a multi-disciplinary research approach. But more importantly, they require a widespread acknowledgment that our knowledge of the deep roots of diverging regional development paths can benefit from the adoption of unconventional comparative perspectives.

NOTES

1. For sake of brevity 'Africa' refers to 'sub-Saharan Africa' henceforth, unless otherwise indicated.

2. In the Americas, a number of mammals had gone extinct just before the arrival of modern humans or under pressure of early human expansion. The causes of this wave of mammal extinction are subject to a larger debate about the dating of first human settlement in the Americas. See Mann (2005, chap. 5) for an overview.

3. The small size of the founding population does not necessarily imply that there was just one migratory event. The group itself must have been larger as it also included 'non-founding' people, the probable census size is about 3,000 individuals (Campbell & Tishkoff, 2008, p. 405). Another study estimates the size of this founding population at 1,500 persons (Garrigan & Hammer, 2006).

4. The total number of living languages in the Americas is nowadays much lower, 1,060 according to the *Ethnologue* atlas, because many pre-Columbian languages have gone extinct or are critically endangered.

5. There is a growing literature arguing that ethno-linguistic and genetic diversity correlate. Tishkoff *et al.* (2009) have identified 14 African ancestral gene clusters in populations that correlate with self-described ethnicity and a shared cultural-linguistic background (cf Campbell & Tishkoff, 2008). Ashraf and Galor (2013) found a positive correlation between genetic diversity and various contemporary measures of ethno-linguistic fractionalization. Michalopoulos (2012) has shown that linguistic variation is positively associated with ecological biodiversity, in particular regional variation in land quality and elevation.

6. Liu *et al*. (2010, p. 424) show no evidence for the idea that malaria developed among early hominids during the split from apes some 5–9 million years ago, but find it impossible on the basis of their evidence to propose an alternative date.

7. It is theoretically possible that typhus has evolved in the New World, but it is not likely (Raoult, Woodward, & Dumler, 2004).

REFERENCES

Adelaar, W. F. H., & Muysken, P. (2004). *The languages of the Andes*. Cambridge: Cambridge University Press.

Alesina, A., & La Ferrara, E. (2005). Ethnic diversity and economic performance. *Journal of Economic Literature, 43*(03).

Allen, R. C. (2011). *Global economic history: A very short introduction*. Oxford: Oxford University Press.

Ashraf, Q., & Galor, O. (2013). Genetic diversity and the origins of cultural fragmentation. *American Economic Review: Papers & Proceedings, 103*(3), 528–533.

Austin, G. (2007). Reciprocal comparison and African history: Tackling conceptual eurocentrism in the study of Africa's economic past. *African Studies Review, 50*(3), 1–28.

Bairoch, P. (1988). *Cities and economic development: From the dawn of history to the present*. Chicago: University of Chicago Press.

Barker, G. (2006). *The agricultural revolution in prehistory: Why did foragers become farmers?* Oxford: Oxford University Press.

Berdan, F. F. (2012). Central Mexican states and imperial tribute systems. In D. Nichols, & C. A. Pool (Eds.), *The Oxford handbook of Mesoamerican archaeology* (pp. 653–659). New York: Oxford University Press.

Bin Wong, R., & Rosenthal, J. L. (2011). *Before and beyond divergence: The politics of economic change in China and Europe*. Cambridge: Harvard University Press.

Blanton, R. E., & Fargher, L. (2008). *Collective action in the formation of pre-modern states*. New York: Springer.

Blanton, R. E. (2012). Cities and urbanism in prehispanic Mesoamerica. In D. L. Nichols, & C. A. Pool (Eds.), *The Oxford handbook of Mesoamerican archaeology* (pp. 708–725). Oxford: Oxford University Press.

Blench, R. (2008). *Accounting for the diversity of Amerindian languages: Modelling the Settlement of the new world*. Conference paper presented at the Archaeology Research Seminar, RSPAS, November 21. Canberra.

Blumler, M. A. (1992). *Seed weight and environment in Mediterranean-type grasslands in California and Israel* (Ph.D. thesis). University of California, Berkeley.

Borah, W. W., & Cook, S. F. (1963). *The aboriginal population of central Mexico on the eve of the Spanish conquest*. Berkeley, CA: University of California Press.

Bouvier, N. M., & Palese, P. (2008). The biology of influenza viruses. *Vaccine, 26*(Supplement 4), D49–D53.

Campbell, L. (1997). *American Indian languages: The historical linguistics of Native America*. New York: Oxford University Press.

Campbell, L., & Grondona, V. M. (2012). *The indigenous languages of South America: A comprehensive guide*. Berlin: Mouton de Gruyter.

Campbell, M. C., & Tishkoff, S. A. (2008). African genetic diversity: Implications for human demographic history, modern human origins, and complex disease mapping. *Annual Review of Genomics and Human Genetics, 9*, 403–433.

Cann, R. L., Stoneking, M., & Wilson, A. C. (1987). Mitochondrial DNA and human evolution. *Nature, 325*(6099), 31–36.

Carneiro, R. L. (1970). A Theory of the Origin of the State. *Science, 169*(3947), 733–738.

Carney, J. A., & Rosomoff, R. N. (2011). *In the shadow of slavery. Africa's botanical legacy in the Atlantic world*. Berkeley, CA: University of California Press.

Casey, G. P., & Owen, A. L. (2014). Inequality and fractionalization. *World Development, 56*, 32–50.

Conrad, G. W., & Demarest, A. A. (1984). *Religion and empire: The dynamics of Aztec and Inca expansionism*. Cambridge: Cambridge University Press.

Cook, S., & Holmes, E. C. (2006). A multigene analysis of the phylogenetic relationships among the flaviviruses (Family: Flaviviridae) and the evolution of vector transmission. *Archives of Virology, 151*(2), 309–325.

Coquery-Vidrovitch, C. (2005). *The history of African cities south of the Sahara: From the origins to colonization*. Princeton: Markus Wiener Publishers.

Crosby, A. W. (2003 [1972]). *The Columbian exchange: Biological and cultural consequences of 1492*. Westport, Conn.: Praeger.

Curtin, P. D. (1989). *Death by migration. Europe's encounter with the tropical world in the nineteenth century*. Cambridge: Cambridge University Press.

Denevan, W. M. (1992). *The native population of the Americas in 1492*. Madison, Wisc.: University of Wisconsin Press.

Diamond, J. (1997). *Guns, germs and steel. The fates of human societies*. New York: W.W. Norton & Company.

Easterly, W., & Levine, R. (2012). The European origins of economic development. *National Bureau of Economic Research working paper 18162*.

Easterly, W., & Levine, R. (1997). Africa's growth tragedy: Politics and ethnic divisions. *Quarterly Journal of Economics, 112*(4), 1203–1250.

Eshleman, J. A., Malhi, R. S., & Smith, D. G. (2003). Mitochondrial DNA studies of native Americans: Conceptions and misconceptions of the population prehistory of the Americas. *Evolutionary Anthropology: Issues, News, and Reviews, 12*(1), 7–18.

Fagundes, N. J. R., Kanitz, R., Eckert, R., Valls, A. C. S., Bogo, M. R., Salzano, F. M., *et al.* (2008). Mitochondrial population genomics supports a single pre-clovis origin with a coastal route for the peopling of the Americas. *The American Journal of Human Genetics, 82*(3), 583–592.

Flynn, D. O., & Giraldez, A. (2004). Path dependence, time lags and the birth of globalisation: A critique of O'Rourke and Williamson. *European Review of Economic History, 8*(1), 81–108.

Fortes, M., & Evans-Pritchard, E. E. (1940). *African political systems*. London: Oxford University Press.

Frank, A. G. (1998). *ReOrient. Global economy in the Asian age*. Berkeley, CA: University of California Press.

Garrigan, D., & Hammer, M. F. (2006). Reconstructing human origins in the genomic era. *Nature Reviews Genetics, 7*(9), 669–680.

Gerring, J., Thacker, S. C., Lu, Y., & Huang, W. (2015). Does diversity impair human development? A multi-level test of the diversity debit hypothesis. *World Development, 66*, 166–188.

Gifford-Gonzalez, D., & Hanotte, O. (2011). Domesticating animals in Africa: Implications of genetic and archaeological findings. *Journal of World Prehistory, 24*(1), 1–23.

Goody, J. (1971). *Technology, tradition, and the state in Africa*. London: Oxford University Press.

Greenberg, J. H., Turner, C. G., & Zegura, S. L. (1986). The settlement of the Americas: A comparison of the linguistic, dental, and genetic evidence. *Current Anthropology, 27*(5), 477–497.

Herbst, J. (2000). *States and power in Africa. Comparative lessons in authority and control*. Princeton, NJ: Princeton University Press.

Hopkins, A. G. (1973). *An economic history of West Africa*. London: Longman.

Jones, E. L. (1981). *The European miracle: Environments, economies, and geopolitics in the history of Europe and Asia*. Cambridge: Cambridge University Press.

Lal, D. (1998). *Unintended consequences. The impact of factor endowments, culture, and politics on long run economic performance*. Cambridge: MIT Press.

Landes, D. S. (1998). *The wealth and poverty of nations: Why are some so rich and others so poor?* New York: W.W. Norton.

Levi, M. (1988). *Of rule and revenue*. Berkeley, CA: University of California Press.

Lewin, R. (2005). *Human evolution: An illustrated introduction*. Malden, MA: Blackwell.

Lewis, P. M., Simons, G. F., & Fennig, C. D. (2013). *Ethnologue: Languages of the world* (17th ed.). Dallas, Texas: SIL International.

Li, J. Z., Absher, D. M., Tang, H., Southwick, A. M., Casto, A. M., Ramachandran, S., *et al.* (2008). Worldwide human relationships inferred from genome-wide patterns of variation. *Science, 319*(5866), 1100–1104.

Li, Y., Carroll, D. S., Gardner, S. N., Walsh, M. C., Vitalis, E. A., & Damon, I. K. (2007). On the Origin of smallpox: Correlating variola phylogenics with historical smallpox records. *Proceedings of the National Academy of Sciences of the United States of America, 104*(40), 15787–15792.

Lichbach, M. I. (1996). *The cooperator's dilemma*. Ann Arbor: University of Michigan Press.

Liu, W., Li, Y., Learn, G. H., Rudicell, R. S., Robertson, J. D., Keele, B. F., *et al.* (2010). Origin of the human malaria parasite *Plasmodium falciparum* in Gorillas. *Nature, 467*(7314), 420–425.

Liu, H., Prugnolle, F., Manica, A., & Balloux, F. (2006). A geographically explicit genetic model of worldwide human-settlement history. *American Journal of Human Genetics, 79*(2), 230–237.

Lovejoy, P. E. (2005). *Slavery, commerce and production in the Sokoto caliphate of West Africa*. Trenton, NJ: Africa World Press.

Maddison, A. (2010). *Historical statistics on world population, GDP and Per Capita GDP, 1-2008 AD*, <http://www.ggdc.net/maddison/>.

Mann, C. C. (2005). *1491: New revelations of the Americas before Columbus*. New York: Knopf.

Mann, C. C. (2011). *1493. Uncovering the new world Columbus created*. New York: Knopf.

Marchetti, C., & Ausubel, J. (2012). Quantitative dynamics of human empires. *International Journal of Anthropology, 27*(1–2), 1–62.

McCann, J. (1995). *People of the plow. An agricultural history of Ethiopia, 1800–1990*. Madison, Wisc.: University of Wisconsin Press.

McCarthy, A. J., & Goodman, S. J. (2010). Reassessing conflicting evolutionary histories of the Paramyxoviridae and the origins of respiroviruses with Bayesian multigene phylogenies. *Infection, Genetics and Evolution, 10*(1), 97–107.

McEwan, G. F. (2006). *The Incas: New perspectives*. Santa Barbara, CA: ABC-CLIO.

McIntosh, R. J. (2005). *Ancient middle Niger: Urbanism and the self-organizing landscape*. Cambridge: Cambridge University Press.

McIntosh, R. J. (2000). Clustered cities of the middle Niger: Alternative routes to authority in prehistory. In D. Anderson, & R. Rathbone (Eds.), *Africa's urban past* (pp. 19–35). Portsmouth, NH: Heinemann.

McLeod, M. P., Qin, X., Karpathy, S. E., Gioia, J., Highlander, S. K., Fox, G. E., *et al.* (2004). Complete genome sequence of *Rickettsia typhi* and comparison with sequences of other rickettsiae. *Journal of Bacteriology, 186*(17), 5842–5855.

McNeill, W. H. (1976). *Plagues and peoples*. Garden City, N.Y.: Anchor Press.

McNeill, J. R. (2011). *Mosquito empires. Ecology and war in the greater Caribbean, 1620–1914*. New York: Cambridge University Press.

Michalopoulos, S. (2012). The origins of ethnolinguistic diversity. *American Economic Review, 102*(4), 1508–1539.

Mokyr, J. (1990). *The lever of riches: Technological creativity and economic progress*. New York: Oxford University Press.

Morelli, G., Song, Y., Mazzoni, C. J., Eppinger, M., Roumagnac, P., Wagner, D. M., *et al.* (2010). Yersinia pestis genome sequencing identifies patterns of global phylogenetic diversity. *Nature Genetics, 42*(12), 1140–1143.

Morris, I. (2010). *Why the west rules – For now. The patterns of history, and what they reveal about the future*. London: Profile Books.

North, D. C., & Thomas, R. P. (1973). *The rise of the western world: A new economic history*. Cambridge: Cambridge University Press.

Ogundiran, A. (2013). Towns and states of the West African forest belt. In P. Mitchell, & P. Lane (Eds.), *The Oxford handbook of African archaeology* (pp. 859–873). Oxford: Oxford University Press.

Olson, M. (1965). *The logic of collective action: Public goods and the theory of groups*. Cambridge: Harvard University Press.

Olsson, O., & Hibbs, D. A. (2005). Biogeography and long-run economic development. *European Economic Review, 49*(4), 909–938.

Pearce-Duvet, J. M. C. (2006). The origin of human pathogens: Evaluating the role of agriculture and domestic animals in the evolution of human disease. *Biological Reviews, 81*(3), 369–382.

Pikirayi, I. (2013). The Zimbabwe culture and its neighbours: Origins, development, and consequences of social complexity in southern Africa. In P. Mitchell, & P. Lane (Eds.), *The Oxford handbook of African archaeology* (pp. 915–928). Oxford: Oxford University Press.

Pomeranz, K. L. (2000). *The great divergence. China, Europe and the making of the modern world*. Princeton: Princeton University Press.

Putterman, L., & Weil, D. N. (2010). Post-1500 population flows and the long run determinants of economic growth and inequality. *Quarterly Journal of Economics, 125*(4), 1627–1682.

Raoult, D., Woodward, T., & Dumler, J. S. (2004). The history of epidemic typhus. *Infectious Disease Clinics of North America, 18*(1), 127–140.

Reader, J. (1998). *Africa: A biography of the continent*. New York: A.A. Knopf.

Reid, R. J. (2012). *Warfare in African history*. Cambridge: Cambridge University Press.

Rich, S. M., Licht, M. C., Hudson, R. R., & Ayala, F. J. (1998). Malaria's eve: Evidence of a recent population bottleneck throughout the world populations of *Plasmodium falciparum*. *Proceedings of the National Academy of Sciences of the United States of America, 95*(8), 4425–4430.

Ringmar, E. (2011). Malice in wonderland: Dreams of the orient and the destruction of the palace of the emperor of China. *Journal of World History, 22*(2), 273–298.

Rothschild, B. M., Martin, L. D., Lev, G., Bercovier, H., Bar-Gal, G. K., Greenblatt, C., *et al.* (2001). *Mycobacterium tuberculosis* complex DNA from an extinct bison dated 17,000 years before the present. *Clinical Infectious Diseases, 33*(3), 305–311.

Sack, D. A., Sack, R. B., Balakrish, N., & Siddique, A. K. (2004). Cholera. *The Lancet, 9404*, 223–233.

Said, E. W. (1979). *Orientalism*. New York: Vintage Books.

Schuenemann, V. J., Singh, P., Mendum, T. A., Krause-Kyora, B., Jäger, G., Bos, K. I., *et al.* (2013). Genome-wide comparison of medieval and modern *Mycobacterium leprae*. *Science, 341*(6142), 179–183.

Smith, B. D. (1995). *The emergence of agriculture*. New York: Scientific American Library.

Spolaore, E., & Wacziarg, R. (2013). How deep are the roots of economic development? *Journal of Economic Literature, 51*(2), 1–45.

Tanabe, Y. (2001). The roles of domesticated animals in the cultural history of the humans. *Asian Australasian Journal of Animal Sciences, 14*(SPI), 13–18.

Tilly, C. (1990). *Coercion, capital, and European states, A.D. 990–1992*. Cambridge MA: Blackwell.

Tishkoff, S. A., Reed, F. A., Friedlaender, F. R., Ehret, C., Ranciaro, A., Froment, A., *et al.* (2009). The genetic structure and history of Africans and African Americans. *Science, 324*(5930), 1035–1044.

Turchin, P., & Nefedov, S. A. (2009). *Secular cycles*. Princeton, NJ: Princeton University Press.

Volkman, S. K., Barry, A. E., Lyons, E. J., Nielsen, K. M., Thomas, S. M., Choi, M., *et al.* (2001). Recent origin of *Plasmodium falciparum* from a single progenitor. *Science, 293*(5529), 482–484.

Welsby, D. (2013). Kerma and Kush and their neighbours. In P. Mitchell, & P. Lane (Eds.), *The Oxford handbook of African archaeology* (pp. 751–764). Oxford: Oxford University Press.

Welzel, C. (2014). Evolution, empowerment, and emancipation: How societies climb the freedom ladder. *World Development, 64*, 33–51.

Wittfogel, K. A. (1957). *Oriental despotism: A comparative study of total power*. New Haven: Yale University Press.

Wohlgemuth, N. H. M. (1991). *Intensification of agriculture within the basin of Mexico during the Aztec period* (Ph.D. thesis). University of California, Berkeley.

Wolf, E. R. (1982). *Europe and the people without history*. Berkeley, CA: University of California Press.