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Journal

Biological Reviews, 94(1)

ISSN

1464-7931

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Publication Date

2019-02-01

DOI

10.1111/brv.12456

Peer reviewed

Climate-driven ecological stability as a globally shared cause of Late Quaternary megafaunal extinctions: the Plaids and Stripes Hypothesis

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ABSTRACT

Controversy persists about why so many large-bodied mammal species went extinct around the end of the last ice age. Resolving this is important for understanding extinction processes in general, for assessing the ecological roles of humans, and for conserving remaining megafaunal species, many of which are endangered today. Here we explore an integrative hypothesis that asserts that an underlying cause of Late Quaternary megafaunal extinctions was a fundamental shift in the spatio-temporal fabric of ecosystems worldwide. This shift was triggered by the loss of the millennial-scale climate fluctuations that were characteristic of the ice age but ceased approximately 11700 years ago on most continents. Under ice-age conditions, which prevailed for much of the preceding 2.6 Ma, these radical and rapid climate changes prevented many ecosystems from fully equilibrating with their contemporary climates. Instead of today's 'striped' world in which species' ranges have equilibrated with gradients of temperature, moisture, and seasonality, the ice-age world was a disequilibrium 'plaid' in which species' ranges shifted rapidly and repeatedly over time and space, rarely catching up with contemporary climate. In the transient ecosystems that resulted, certain physiological, anatomical, and ecological attributes shared by megafaunal species pre-adapted them for success. These traits included greater metabolic and locomotory efficiency, increased resistance to starvation, longer life spans, greater sensory ranges, and the ability to be nomadic or migratory. When the plaid world of the ice age ended, many of the advantages of being large were either lost or became disadvantages. For instance in a striped world, the low population densities and slow reproductive rates associated with large body size reduced the resiliency of megafaunal species to population bottlenecks. As the ice age ended, the downsides of being large in striped environments lowered the extinction thresholds of megafauna worldwide, which then increased the vulnerability of individual species to a variety of proximate threats they had previously tolerated, such as human predation, competition with other species, and habitat loss. For many megafaunal species, the plaid-to-stripes transition may have been near the base of a hierarchy of extinction causes whose relative importances varied geographically, temporally, and taxonomically.

Key words: extinction, Late Quaternary, megafauna, climate change, terrestrial mammals, ecological disequilibrium, allometry.

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I. INTRODUCTION

A global wave of extinctions selectively removed many species of terrestrial megafauna (mammals weighing > 45 kg) around the end of the last ice age, and we are still not sure why. Although not as drastic as the End-Cretaceous or End-Permian extinctions, these Late Quaternary extinctions fundamentally changed the composition of mammalian faunas on continents other than Africa (Wallace, 1876; Romer, 1933; Barnosky *et al.*, 2004b) and in some cases altered the functioning of entire ecosystems (Owen-Smith, 1987; Gill *et al.*, 2012; Johnson *et al.*, 2016; Malhi *et al.*, 2016; Galetti *et al.*, 2017). What caused the Late Quaternary extinctions of megafauna, and what roles did humans play? Was there some shared factor that elevated the risk of extinction for megafauna everywhere? Answering these questions could help to manage the wave of human-caused extinctions that is now underway (Barnosky & Lindsey, 2010; Barnosky *et al.*, 2017).

Numerous explanations have been proposed for megafaunal extinctions during the Late Quaternary, roughly the last 100000 years of Earth’s history (Stuart, 2015). These range from overkill by humans (Sandom *et al.*, 2014; Miller *et al.*, 2016; Surovell *et al.*, 2016), to epidemic diseases (MacPhee & Marx, 1997), to cosmic collisions (Hagstrum *et al.*, 2017), to some aspect of climate change (Cooper *et al.*, 2015; Rabanus-Wallace *et al.*, 2017). Despite long-running debate, numerous hypotheses, and a burgeoning literature, there is still no consensus within the scientific community about the cause of Late Quaternary megafaunal extinctions (Price *et al.*, 2018).

Extinctions result from conspiracies of causes arranged in hierarchies according to their relative importances for the species concerned (Caughley, 1994; Barnosky *et al.*, 2004a). Some of these synergistic causes are shared by multiple species (Caughley, 1994; Burney *et al.*, 2004; Cardillo *et al.*, 2005; Brook, Sodhi, & Bradshaw, 2008). The fact that so many megafaunal extinctions occurred during the Late

Quaternary strongly suggests that one or more causes were widely shared.

Here we hypothesize that one of the most important of these underlying, shared causes of Late Quaternary extinctions was a fundamental shift in the spatio-temporal 'fabric' of ecosystems that occurred during the ice age/Holocene transition. Rapidly changing climate during the ice age created widespread transient ecosystems in which the eco-physiological traits associated with large body size endowed megafaunal species with special advantages. But these and other traits associated with being large became disadvantages within the more stable climate regime of the Holocene and thus lowered the extinction thresholds for many megafaunal species. Once these thresholds were lowered, individual species fell victim to a variety of proximate extinction causes, whether overkill by humans, disease, habitat loss, or disrupted trophic cascades.

II. BACKGROUND

(1) Temporal and geographic patterns of megafaunal extinctions

The present interglacial, the Holocene, which began 11700 calendar years before present (BP; hereafter 11.7 ka) is impoverished in megafauna compared to the preceding 50+ Ma of Earth's history (Alroy, 2000). This impoverishment is the result of some 64% of megafaunal genera worldwide going extinct sometime over the last roughly 100 ka (Koch & Barnosky, 2006). Although the fossil record is admittedly incomplete, so far there is no definitive evidence for comparable bouts of megafaunal extinction earlier in the Cenozoic (the last 66 Ma) (Alroy, 2000), nor is there evidence for comparable bouts of megafaunal extinctions during previous glacial–interglacial transitions (Stuart, 2015).

The magnitude of megafaunal extinction varied geographically. North America lost approximately 72% of its megafaunal genera (Barnosky *et al.*, 2004b), while South America lost 83% (Barnosky & Lindsey, 2010). Northern Eurasia lost fewer genera, around 29% (Stuart, 2015), while Australia lost some 88% (Barnosky *et al.*, 2004b), and the mega-islands Madagascar and New Zealand both lost 100% (Burney *et al.*, 2004; Perry *et al.*, 2014). Africa alone has retained most of its megafauna; losses there ranged from 5 to 18% (Klein, 1984; Barnosky *et al.*, 2004b). All four mega-herbivore (>1000 kg) genera present in Africa during the Pleistocene survive today (Stuart, 1991).

Late Quaternary megafaunal extinctions occurred in a time-transgressive manner across the planet and occupied varying time intervals. In Australia, they began approximately 400 ka and continued episodically until about 40 ka (Wroe *et al.*, 2013). In Europe, most of the extinctions occurred between approximately 45 and 10 ka (Stuart, 2015), while in North America they seem to have been concentrated within several millennia each side of

the Pleistocene–Holocene transition (Barnosky *et al.*, 2004b; Grayson, 2016). South America's extinction window may have been wider, perhaps between about 15 and 8 ka (Turvey, 2009; Barnosky & Lindsey, 2010, pp. 24–26). Megafauna on islands worldwide experienced waves of extinction during Holocene times (Rick *et al.*, 2013).

(2) Correlations with climate change

Correlations between the timing of megafaunal extinctions and climate changes are problematic. North America's extinctions and at least some of South America's and Europe's coincided with rapid climate changes during the Pleistocene–Holocene transition (Stuart, 1991; Barnosky *et al.*, 2004b; Barnosky & Lindsey, 2010). By contrast, in Madagascar and New Zealand, peak extinction did not coincide with rapid climate changes (Burney *et al.*, 2004; Duncan, Boyer, & Blackburn, 2013; Holdaway *et al.*, 2014). In semi-arid Australia, where bone preservation is often poor, palaeoenvironmental records fragmentary, and the extinctions occurred longer ago, heated debate continues over correlations between extinctions and climate change (Wroe *et al.*, 2013; Cohen *et al.*, 2015; Miller *et al.*, 2016; Saltr e *et al.*, 2016; Price *et al.*, 2018).

(3) Human roles

The evolution and global dispersal of hominins was relatively recent and rapid. Predatory, fire-using hominins inhabited Africa and Eurasia roughly a million years before anatomically modern humans evolved and then dispersed out of Africa approximately 200 ka (Bae, Douka, & Petraglia, 2017; Hershkovitz *et al.*, 2018). *Homo sapiens* reached Australia 50–45 ka (Wroe *et al.*, 2013), colonized northern Eurasia after 45 ka (Bae *et al.*, 2017), crossed from Siberia into North America 20–15 ka (Moreno-Mayar *et al.*, 2018), and spread across North and South America before 12 ka (Meltzer, 2015). The precise timing of human arrival on any continent will probably never be determined within 10^3 – 10^4 years because of the low probability of finding traces of the first colonists. The timing of human arrival on islands is more secure because the search area is smaller and in many cases the arrival was more recent. People reached Madagascar approximately 2.3 ka (Burney *et al.*, 2004) and New Zealand about 0.7 ka (Wilmshurst *et al.*, 2008). Small islands in the Caribbean and Oceania were settled at varying times in the middle and late Holocene (Turvey, 2009).

On many islands, the Holocene arrival of humans correlates closely with the timing of megafaunal extinctions. For instance, the Polynesian settlers in New Zealand exterminated nine species of ratite moa within several centuries of their arrival (Holdaway *et al.*, 2014; Perry *et al.*, 2014). In Madagascar, extinctions also commenced upon human arrival, but then took roughly 2 ka to conclude (Burney *et al.*, 2004; Dewar *et al.*, 2013).

On the continents, correlations between megafaunal extinctions and the timing of *Homo sapiens* arrival are less clear. In Africa, expansion of early hominins into

scavenger/predator niches during the Pliocene may have triggered extinctions among competing carnivores (Werdelin & Lewis, 2013). On the other hand, the initial expansion of early hominins into Europe does not seem to have triggered widespread extinctions there. Instead, most megafaunal extinctions occurred some million years later and possibly accompanied the replacement of *H. neanderthalensis* by anatomically modern humans (Stuart, 1991). Depending on how Australia's records are interpreted, extinctions there were either distinctly out-of-phase with human arrival (Wroe *et al.*, 2013), or lagged them by some 13 ka (Saltré *et al.*, 2016). Human arrival coincided broadly with megafaunal extinctions in lower latitude North America (Stuart, 1991; Barnosky *et al.*, 2004b); however, 'broadly' is the key word here because over half of the extinct fauna there are either not dated at all or have no dates younger than about 20 ka (Meltzer, 2015). In South America, it is possible some megafauna, including *Smilodon*, *Doedicurus*, *Hippidion*, several species of ground sloth, and possibly even gomphotheres, survived until 8 ka, which was at least 6–7 ka after human arrival (Hubbe, Hubbe, & Neves, 2007; Turvey, 2009; Barnosky & Lindsey, 2010, pp. 24–26). In summary, although human arrival is closely correlated with the timing of extinctions on islands during the Holocene, on the continents the correlation remains problematic because of compounding uncertainties about when people first arrived and when megafauna actually went extinct. Some of the causes for uncertainty about the timing of extinction are explored in Section II.4.

The roles played by humans in megafaunal extinctions varied geographically. Undoubtedly, people caused extinctions on many islands (Holdaway & Jacomb, 2000; Burney *et al.*, 2004), but on continents their roles varied widely. Megafaunal extinctions occurred in continental ecosystems ranging from tropical rainforests to Arctic tundra and, in some cases, during periods when people were rare or absent. In Alaska, the extinctions of horse, bison, and mammoth probably occurred without human involvement (Guthrie, 2006; Mann *et al.*, 2013). Similarly, Nikolskiy, Sulerzhitsky, & Pitulko (2011) argue that human hunting of mammoth was rare in Siberia, and at most was the *coup de grâce* for a species already in serious extinction debt (Kuussaari *et al.*, 2009) caused by environmental changes. Even at lower latitudes in the western USA where people were more abundant than in the Arctic, archaeological evidence connecting megafaunal extinctions to hunting remains problematic (Grayson, 2001; Grayson & Meltzer, 2003; Meltzer, 2015). Archaeological evidence for overkill by humans is similarly ambiguous in Australia (Wroe *et al.*, 2013; Jankowski *et al.*, 2016). That said, it is unclear what convincing archaeological evidence for human overkill of megafauna would actually look like (Grayson, 2001), and whether archaeology is even capable of providing evidence for less direct, but nonetheless lethal impacts of humans (Burney *et al.*, 2004): impacts like changes to fire regimes and disruption of food webs. Although extinction processes on islands and continents have been repeatedly conflated (Martin, 1984; Steadman & Martin, 2003; Johnson

et al., 2016), the two settings are in fact biogeographically distinct (Grayson, 2001; Whittaker, Triantis, & Ladle, 2008; Wood *et al.*, 2017), which means basic differences should be expected in the identities and scales of their extinction processes.

In historic times, humans have driven other species to extinction in a depressingly large number of ways (Wood *et al.*, 2017), and only a handful of extinctions are known to have occurred without human involvement (Soulé, 1983; Caughley, 1994). In descending order of subtlety but not necessarily of effectiveness, humans are known to have caused extinctions by overkill (Perry *et al.*, 2014), by habitat alteration (McWethy *et al.*, 2014; Miller *et al.*, 2016), and by trophic disruptions involving multiple processes (Diamond, 1984; Caughley, 1994; Atkinson, 1996; Burney *et al.*, 2004; Brook *et al.*, 2008; Ripple & Van Valkenburgh, 2010).

Humans excel at trophic disruption, in part because of our ability to tap into food chains at multiple levels. In ecosystems where herbivore populations are limited from the top-down by predators rather than from the bottom-up by food availability, human hunters can trigger sequential collapse of both predator and herbivore populations (Janzen, 1983; Ripple & Van Valkenburgh, 2010; Estes, 2016). Unlike most other species, humans can then sidestep the impacts of these extinctions by switching to other food sources (Grayson, 2001). Clearly, no discussion of megafaunal extinctions can ignore the possible roles of humans; however, these roles differed widely in space and time, were often indirect, and have rarely left clear traces in palaeoecological records.

(4) When did Late Quaternary megafaunal extinctions actually occur?

The Signor–Lipps effect, the decreasing probability of discovering the remains of individual organisms as the overall population of their taxon declines (Signor & Lipps, 1982), haunts all discussions of late-Quaternary extinctions (Collen & Turvey, 2009). Because it is impossible to know when the last individual of a species died, estimates of extinction times are necessarily fuzzy. This temporal fuzziness is pertinent to the hypothesis we propose here because, while the ice age's distinctive climate regime did not end until the Holocene began, in some places at least, megafaunal extinctions appear to have occurred before the ice age ended.

How can a hypothesis that blames extinctions on climate changes that occurred during the last glacial–interglacial transition be valid if those extinctions actually occurred before the environmental plaidness of the ice age ended? The answer is, we think, that the extinction dates of many species are underestimated and that many Late Quaternary extinctions actually occurred in the early Holocene.

Numerous factors make it difficult to pinpoint when a prehistoric extinction actually occurred (Collen & Turvey, 2009). Fossil records fade rapidly into the past (Stuart, 1991; Alroy, 2000), and the accuracy and precision of dating are often poor, especially near the upper limit of the ^{14}C technique (Zazula *et al.*, 2014, 2017). Taphonomic processes can change over time, confounding assumptions

about random sampling and the trajectories of population decline (Mann *et al.*, 2013). As a result, the last-appearance dates of most Late Quaternary megafaunal taxa tell us only when the animals were last abundant on the local landscape, not when they became globally extinct (Barnosky & Lindsey, 2010).

If you cannot track a species' descent into extinction, an alternative is to model the decline using probabilistic trends based on sighting records. This has become something of a cottage industry among mathematically minded palaeontologists (Solow, 1993, 2003; McInerney *et al.*, 2006; Buck & Bard, 2007; Collen & Turvey, 2009; Rivadeneira, Hunt, & Roy, 2009; Bradshaw *et al.*, 2012; Alroy, 2014; Saltré *et al.*, 2016). Unfortunately, sighting records are inherently complex because extinction causes are diverse, collaborative, and can change through time. As the Signor–Lipps effect implies, sighting records become increasingly tenuous as populations retract into cryptic refugia (Bennett, Tzedakis, & Willis, 1991; Lister & Stuart, 2008; Kuzmin, 2010; Stewart *et al.*, 2010), yet a population too small to be noticed by palaeontologists is still capable of giving rise to abundant descendants. Invasive species provide startling examples of the demographic resilience of small populations. For example, the 100–160 starlings (*Sturnus vulgaris*) Eugene Schieffelin released in New York City in 1890 and 1891 have increased to >200 million and populated much of North America.

Invasive species are not the only exemplars of demographic resilience. Lazarus taxa once thought to be extinct because of an absence of sightings include the coelocanth (*Latimeria* spp.), the dawn redwood (*Metasequoia glyptostroboides*), and the New Zealand Takahe (*Porphyrio hochstetteri*). Several ice-age megafaunal species are now known to be Lazarus taxa. Irish elk (*Megaloceros giganteus*) were thought to have gone extinct in the terminal Pleistocene, but more recent discoveries reveal they persisted in the Ural Mountains until at least 7.6 ka (Stuart *et al.*, 2004). Even more surprising is the late survival of woolly mammoth (*Mammuthus primigenius*). Prior to 1995, the last mammoth was thought to have died before 10 ka. Since then two, mid-Holocene mammoth refugia have been discovered: one on Wrangel Island in northeastern Siberia (Vartanyan *et al.*, 1995, 2008; Rogers & Slatkin, 2017), the other on Saint Paul Island in the Bering Sea (Guthrie, 2004; Graham *et al.*, 2016). It turns out that mammoth extinction was a spatially complex phenomenon occupying some 10000 years spanning the Pleistocene–Holocene transition (Kuzmin, 2010), which is sobering given that proboscideans leave some of the most obvious fossil records of all megafauna.

Demographic resilience, undiscovered refugia, the Signor–Lipps effect, and the existence of Lazarus taxa imply that species' temporal persistence is routinely underestimated by their last dated fossils and therefore the extinctions of many megafaunal species occurred thousands of years after their youngest ¹⁴C-dated remains. This means the global extinctions of many of these species actually occurred during the Holocene rather than the Pleistocene. This inference is guaranteed to raise the hackles of some palaeontologists

and obviously warrants testing. Sadly, it also blunts the use of chronological correlation as a tool for testing hypotheses about extinction causes (Meltzer, 2015; Grayson, 2016).

III. THE PLAIDS AND STRIPES HYPOTHESIS

(1) Spatio-temporal fabrics, the productivity paradox, and the mammoth steppe

The fabric analogy we employ here originates in Guthrie's (1984) attempt to dismiss the productivity paradox concerning the mammoth steppe, the now-vanished biome that at various times during the ice age extended from Western Europe to the Yukon (Zimov *et al.*, 2012). The productivity paradox arose from the apparent contradiction between palynological data that depicted full-glacial, Arctic landscapes supporting only unproductive tundra vegetation, and the palaeontological data that depicted diverse communities of megafauna inhabiting these same landscapes. This mismatch triggered a long-running controversy about the nature of the mammoth steppe (Ritchie & Cwynar, 1982; Guthrie, 2001; Zazula *et al.*, 2006; Hofreiter & Stewart, 2009; Huntley *et al.*, 2013; Mann *et al.*, 2015).

Guthrie's (1984, 2001) solution to the paradox was twofold. First, he hypothesized that high-latitude ecosystems in unglaciated regions possessed a different 'ecological fabric' during the ice age than in the Holocene as the result of ice-age growing seasons being longer. Longer ice-age summers accommodated a greater diversity of plant species with more complex phenologies, which then provided a greater variety of food resources for megafaunal herbivores. Guthrie then explained away the productivity paradox by asserting that the ice age's phenological 'plaidness' is largely invisible to the methods used to reconstruct ice-age vegetation. It is invisible because the typical pollen record comes from a sediment core from a single lake (restricted spatial resolution), and this core is typically sampled for pollen at intervals corresponding to centuries to millennia (restricted temporal resolution). Compounding the dating-resolution problem, many pre-2010 studies of Arctic palynology relied on the ¹⁴C dating of bulk lake sediment, which often contains an admixture of ancient carbon derived from thawing permafrost in the surrounding watershed (Gaglioti *et al.*, 2014). Further detracting from palynology's resolution is the fact that some of the most speciose plant taxa growing in the Arctic cannot be distinguished from one another based on their pollen (restricted taxonomic and ecological resolution). Guthrie's hypothesis has never been tested explicitly, but studies using precisely dated plant macrofossils rather than pollen to reconstruct vegetation are consistent with Guthrie's (1984) vision of diverse ice-age plant communities (Goetcheus & Birks, 2001; Zazula *et al.*, 2006, 2007).

Having disposed of the productivity paradox, Guthrie (1984, 1990) went on to blame late-Quaternary extinctions on the mammoth steppe on a shift in growing-season phenology. Megafaunal species became extinct because

‘... the Pleistocene-Holocene change was an unparalleled jolt across a threshold toward more constricted growth seasons which sharply reduced resources available for ungulate growth.’ (Guthrie, 1984, p. 262). This occurred, he speculated, because shorter, less-variable growing seasons during the Holocene caused an increase in competition between plant species, which caused a decrease in species diversity. The remaining plant species tended to be *K*-strategists with large investments in anatomy and chemistry that discouraged herbivory. These changes reduced herbivore diversity by restricting forage availability and reducing its protein content. Especially hard hit were caecalid–monogastric ungulates like mammoth, rhinoceros, and equids, which required diverse diets of high-fibre/low-protein plants relatively low in chemical defences. Guthrie (1984) suggested that by reducing the diversity of plant species, the Holocene’s shorter growing seasons converted the mammoth steppe into the relatively unproductive and species-poor ecosystems that occupy boreal regions today. Again, this hypothesis has never been directly tested, perhaps because of the difficulty of documenting prehistoric shifts in growing-season length, plant phenology, and the physiological responses of ungulates.

In a brief contribution that caught the spirit if not the specifics of Guthrie’s (1984) original idea, Lister & Sher (1995, p. 23) expanded the timescale of Guthrie’s hypothesis by suggesting:

‘... constant fluctuations of climate in the Late Pleistocene were partly responsible for maintaining a mosaic of plant communities, by a constant ‘stirring’, favoring a pioneering character of vegetation which supports grazing megafauna.’

Here we take Guthrie’s ecological fabric analogy of seasonal plant phenology, expand it to the millennial scales that Lister & Sher (1995) had in mind, and then enlarge it even further to encompass not just vegetation but other aspects of environmental change (e.g. climate, geomorphology, soil development) that are relevant to the size-dependent eco-physiological attributes of ice-age megafauna.

(2) The new Plaids and Stripes Hypothesis

We use the term ‘Plaids and Stripes hypothesis’ because it is shorter than ‘Temporal Simplification of Spatio-temporal Dynamics Hypothesis’, but note that our version of Plaids and Stripes differs from Guthrie’s (1984) by involving multiple time scales and more environmental variables than just summer climate and plant phenology. The expanded Plaids and Stripes Hypothesis states that during the last ice age (*ca.* 60–15 ka), short-term climate fluctuations added a dimension of temporal complexity that is now missing from many modern ecosystems (Fig. 1). The ice age’s spatio-temporal fabric was fundamentally different from the Holocene’s because it was created by large-magnitude shifts in climate at decadal, centennial, and millennial time scales (Fig. 2). These climate changes were superimposed on the

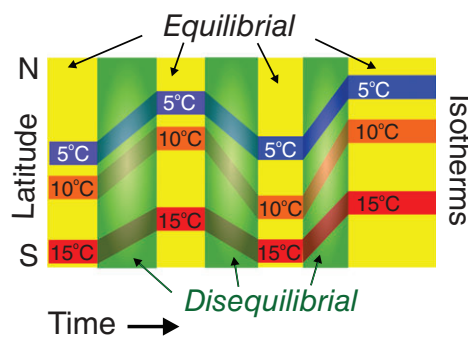


Fig. 1. The expanded Plaids and Stripes Hypothesis. Imagine a landscape where species in three ecological communities (blue, orange, and red) live in equilibrium with a latitudinal gradient in temperature. This landscape is ‘striped’ in the sense that species’ distributions parallel isotherms. Then a series of rapid (decades to millennia) climate changes occur. In response, species must disperse hundreds to thousands of kilometers to catch up with their new range limits, and ecological succession needs to occur before the new equilibria are reached. These processes involve time lags, which cause disequibrial communities to occupy large areas over long periods. Together, these equilibrial and disequibrial states create a spatio-temporal fabric that is now ‘plaid’ rather than ‘striped’.

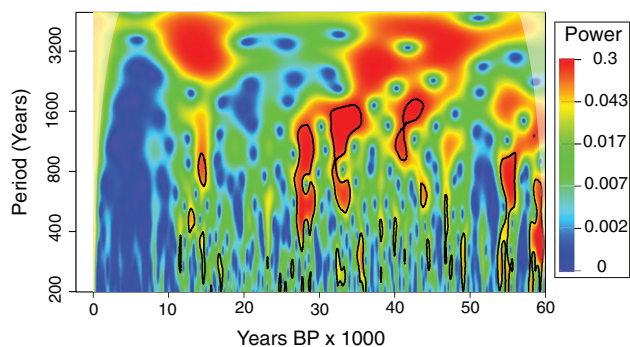


Fig. 2. Holocene climate has been more complacent than that of the ice age. Morelet wavelet analysis (Torrence & Compo, 1998) of the NGRIP $\delta^{18}\text{O}$ record interpolated at 50-year intervals (Rasmussen *et al.*, 2014). Blue indicates periods with little to no power in climate cycles of various wavelengths (*y* axis). Red indicates occurrence of pronounced climate cycles. Black lines outline zones falling outside ($P < 0.05$) the 95% range of 1000 Monte Carlo simulations of red-noise time series using the same autoregressive model as for the NGRIP (AR1) data. White shading on the top corners is the ‘cone of influence’ where cycles become suspect due to edge effects.

same geographic gradients arising from topography and latitude that are familiar to us in today’s world.

The ice age’s large and frequent climatic fluctuations (Fig. 2) kept ecosystems out of balance as plant and animal species struggled to keep up with repeated shifts in their environments. As a result of these lags, the ecological fabrics of ice-age landscapes were more complex than most Holocene ones are. As detailed below, certain eco-physiological attributes shared by megafaunal species

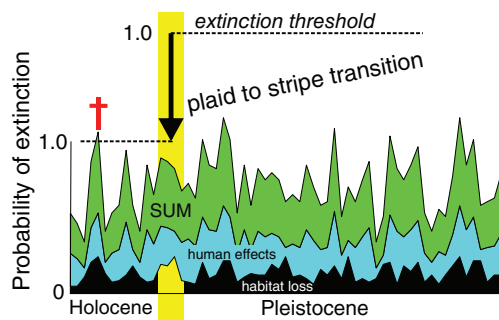


Fig. 3. Extinction risks are hierarchical: they conspire to determine the risk of extinction for individual species. The transition from the mostly plaid ecosystems accompanying the tumultuous climatic regime of the ice age to the striped ecosystems of the climatically stable Holocene may have lowered the extinction thresholds for many megafaunal species because their life forms and life-history strategies were no longer as adaptive as they had been during the ice age. Once these thresholds were lowered, individual species became more vulnerable to a variety of proximate threats, many of which had been only minor threats before.

including greater mobility, lower cost of locomotion, greater dietary breadth, and higher metabolic efficiency allowed them to flourish in these disequilibrium 'plaid' settings.

The plaid world of the ice age ended when millennial-scale instabilities in climate largely ceased in most regions of the world approximately 11.7 ka as the Holocene began. Since then many regions of the planet have settled into new, 'striped' modes of ecology and biogeography, in which ecological fabrics are dominated by environmental gradients established by topography and latitude and that remain relatively stable over multiple millennia. Within this striped regime, the eco-physiological traits of megafauna no longer give them as many advantages; in fact, certain attributes of being large pose distinct disadvantages. As detailed below, these disadvantages include megafaunal species' relatively low population densities (which can translate into small population sizes in striped landscapes), slow rates of reproduction, and the need for large daily food intakes. As a result, the shift from temporally complex, disequilibrium (plaid) ecologies to temporally simpler, equilibrium (striped) ones lowered the threshold for extinction for many terrestrial, megafaunal species (Fig. 3) and increased their vulnerabilities to a variety of species-specific threats. On many landscapes worldwide, the small and the meek inherited the Holocene because climate stability favoured them.

(3) What do plaid and striped landscapes actually look like?

Striped landscapes occur today where plant communities are arranged along climatic gradients (Fig. 4). As long as climate is stable, the locations of these communities remain largely stationary because the ecophysiological requirements of their biota have equilibrated with average environmental conditions.

By contrast, a plaid landscape is one where a large portion of the biota is out of equilibrium with contemporary climate. The novel communities resulting from transient combinations of species add an additional dimension to the ecological fabric – hence the image of plaids *versus* stripes. Reconstructions of shifting biomes during the Pleistocene–Holocene transition provide a glimpse of what ice-age plaid landscapes looked like (Fig. 5). We suggest below that megafaunal herbivores are particularly well-suited for exploiting transient ecosystems and thus were a favoured life form at times like the last ice age when plaid landscapes were widespread.

(4) Requirements of a useful hypothesis

A useful hypothesis about a shared cause of Late Quaternary megafaunal extinctions has at least six requirements. First, it must be explicitly hierarchical and thus compatible both with extinction causes that act synergistically and with proximate causes of extinctions that vary among species. Second, it must invoke a special relationship between body size and some aspect of the ice-age world that made being large more adaptive than it has been during the Holocene, at least on continents other than Africa. Requirements three, four, and five involve the hypothesis being consistent with the spatial and temporal patterns surrounding megafaunal extinctions. These patterns include lack of evidence for extinction bouts during previous glacial–interglacial transitions, early and staggered extinctions in Australia, and the African exception. The sixth requirement is that the hypothesis suggest new and interesting directions of research.

IV. TESTING THE HYPOTHESIS

(1) Large body size was more adaptive during the ice age

According to the Plaids and Stripes Hypothesis, large body size was more adaptive during the ice age because certain eco-physiological traits associated with being large meshed favourably with the unique mode and tempo of the ice-age climate. To develop this argument, we first describe the differences between the climates of the ice age and the Holocene, and then review the eco-physiological implications of large body size in terrestrial mammals.

(a) A fundamentally different ice-age climate

Ice-age climate fluctuated dramatically in response to two different millennial-scale drivers: Dansgaard–Oeschger (D-O) and Heinrich events (Wolff *et al.*, 2010) (Fig. 6). Between ~60 and 11.7 ka, six Heinrich events occurred with a periodicity of about 7000 years (Hemming, 2004), and some 17 D-O events occurred with periodicities of 1500–2000 years (Long & Stoy, 2013). Individual Heinrich events began over the space of several years to a decade and varied in duration from 200 to 2300 years (Hemming, 2004). In Greenland,

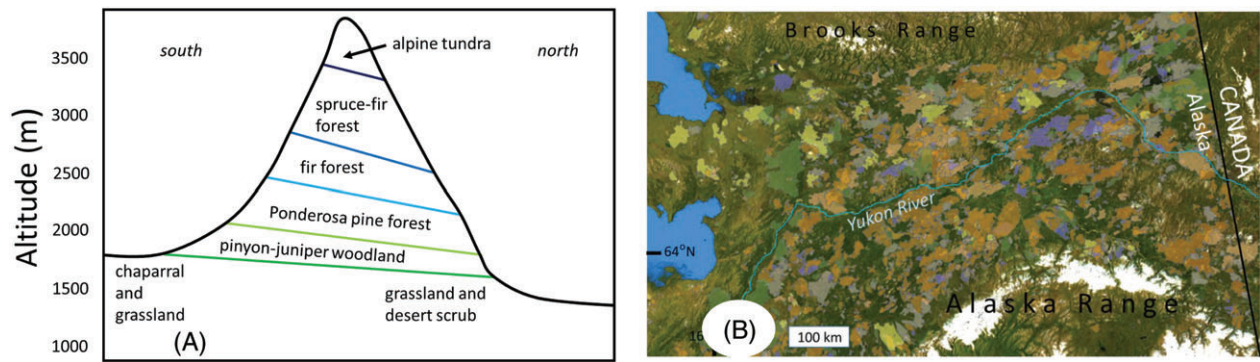


Fig. 4. Modern examples of striped and plaid landscapes. (A) Striped: Altitudinal distribution of plant communities on San Francisco Peaks, Arizona (after Merriam, 1890). These communities have equilibrated with the Holocene’s prolonged equable climate. (B) Plaid: Perimeters of wildland fires since AD 1940 in the boreal forest of Interior Alaska. Different colours depict fires occurring in different decades (<https://afsmaps.blm.gov/imf/imf.jsp?site=firehistory>). In this region, fire-return intervals are 40–150 years (Gaglioti *et al.*, 2016). Today, megafaunal herbivores (moose, *Alces alces*, and caribou, *Rangifer tarandus*) exploit vegetation growing during particular successional stages within these old burns (MacCracken & Viereck, 1990; Rupp *et al.*, 2006).

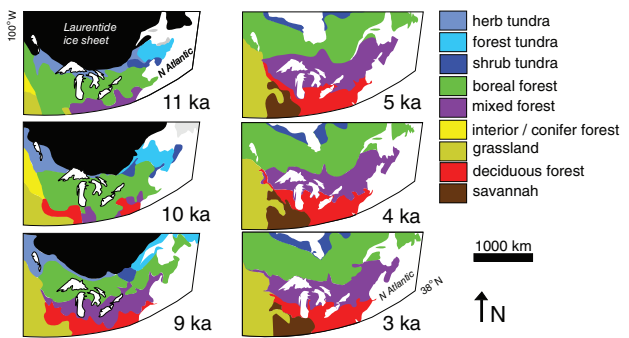


Fig. 5. Ancient examples of plaid (left) and striped (right) landscapes based on the postglacial distribution of biomes in northeastern North America reconstructed from palaeobotanical records (redrawn from Dyke, 2005). Prior to 9 ka, rapid changes in the locations and extents of biomes occurred, at times with little regard for latitudinal climatic gradients. Palynological records suggest that between 11 and 5 ka the northern limits of a number of tree species in northeastern North America lagged behind their physiological range limits by as much as 1500 years because of dispersal lags (Prentice, Bartlein, & Webb, 1991). After approximately 5 ka, biome positions have remained relatively stable. Note that these biomes are defined by vegetation structure – not by the presence of certain indicator species.

D-O events began with rapid warming lasting several decades (Capron *et al.*, 2010; Rasmussen, Thomsen, & Moros, 2016). After several decades to several centuries of maximum warmth, gradual cooling then set in, concluding with a rapid return to full glacial conditions (Wolff *et al.*, 2010; Rasmussen *et al.*, 2014). Increasingly precise palaeo-environmental chronologies have also identified sub-millennial climate fluctuations occurring between and during D-O events (Capron *et al.*, 2010; Milner *et al.*, 2013, 2016).

Because so much palaeoclimatic research has been concentrated at middle and high latitudes, particularly in the North Atlantic region, the most detailed information we

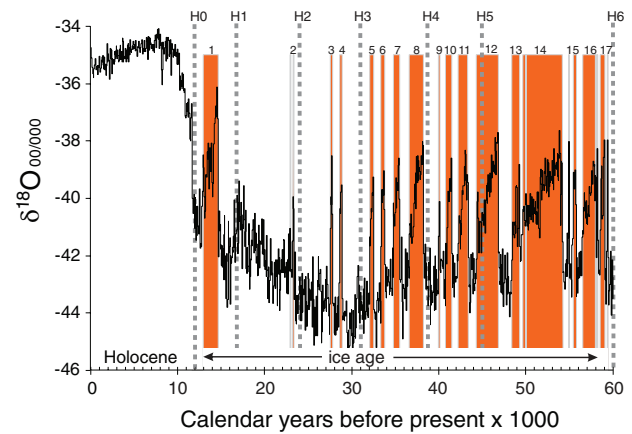


Fig. 6. Changing $\delta^{18}\text{O}$ concentrations in the NGRIP ice core are a proxy for air temperature over Greenland. Up is warmer in the graph, down is colder. The full amplitude of the change in mean annual air temperature between the ice age and the Holocene was about 20°C in Greenland. Since ice-core records like this were first reconstructed (Dansgaard *et al.*, 1993), it has been clear that the ice-age climate had a fundamentally different mode and tempo than the Holocene. The x axis is in b2k-calendar years (years before AD 2000). The $\delta^{18}\text{O}$ data are from Rasmussen *et al.* (2014) and Seierstad *et al.* (2014). Timing of Dansgaard–Oeschger (D-O) events (orange bars) is from Rasmussen *et al.* (2014); timing of Heinrich events (dashed lines) is from Hemming (2004).

have about millennial climate changes comes from there. Nonetheless, the climatic impacts of D-O and Heinrich events affected climate systems globally, in many cases with magnitudes comparable to those observed in the North Atlantic region (Wang *et al.*, 2001; Grimm *et al.*, 2006; Kanner *et al.*, 2012; Denniston *et al.*, 2013).

During Heinrich and D-O events, mean annual temperatures in Greenland fluctuated by 5–17°C (Huber *et al.*, 2006; Kindler *et al.*, 2014), which was approximately

half of the temperature difference between full glacial and full interglacial climate. Reconstructions of mean annual temperature based on the remains of beetles living in northwest Europe during D-O events suggest similar temperature changes there (Atkinson, Briffa, & Coope, 1987; Walker, Coope, & Lowe, 1993; Ponek *et al.*, 2005). Sea surface temperature (SST) in the North Atlantic varied by 3–8°C (Martrat *et al.*, 2007; Maslin *et al.*, 2014). In Norway and Switzerland, cooling in summer during the Younger Dryas, the last of the millennial-scale cold events, was 3–4°C (Birks & Ammann, 2000). In southern France, Ampel *et al.* (2010) inferred only 0.5–2°C changes in July temperature between the warm and cold parts of D-O events; however, in southern Italy D-O events may have triggered changes of 20°C in winter (Allen *et al.*, 1999). Though less well-constrained than temperature, moisture availability also changed radically in many parts of the world during D-O and Heinrich events (Wang *et al.*, 2001; Benson *et al.*, 2003; Shakun *et al.*, 2007; Wang *et al.*, 2007; Tierney *et al.*, 2008; Ayliffe *et al.*, 2013; Deplazes *et al.*, 2013; Stockhecke *et al.*, 2016). Compared to the late Pleistocene, Holocene climate changes across much of the planet have been markedly less frequent and less extreme, except in places like the drylands of Africa (Gasse, 2000).

(b) *Ecological implications of ice-age climate instability*

The only constant feature of the ice-age environment in many parts of the world, including low latitudes, was rapid and repeated change (Roy *et al.*, 1996) (Fig. 6). Through their effects on precipitation, D-O events altered wildland fire regimes in Iberia (Daniau *et al.*, 2007) and North America (Fischer *et al.*, 2015). In both southern Europe and Florida, D-O and Heinrich events caused rapid (<240 year) alternation between forest and non-forest vegetation (Allen *et al.*, 1999; Grimm *et al.*, 2006; Wohlfarth *et al.*, 2008). In unglaciated regions of the Arctic, millennial-scale climate changes were accompanied by population bottlenecks among megafaunal species (Mann *et al.*, 2015). Records of vegetation history during post-glacial times demonstrate that temperature changes with magnitudes similar to D-O and Heinrich events caused biogeographical reorganization across much of North America (Williams *et al.*, 2004; Fischer *et al.*, 2015).

When climate changes rapidly, some species cannot keep up, resulting in ecological communities whose species compositions are not in equilibrium with climate (Davis, 1986; Huntley *et al.*, 2013; Svenning & Sandel, 2013; Blonder *et al.*, 2015; Svenning *et al.*, 2015). These disequilibrium communities can result from slow rates of dispersal and/or delays in primary succession. Slow rates of soil development can delay primary succession by decades to centuries (Matthews, 1982). For instance, near the Klutlan Glacier in the Yukon, soil development was still proceeding apace 250 years after deglaciation (Jacobson & Birks, 1980), and in Arctic Alaska, the development of a steady state, organic soil horizon requires over 500 years (Baughman *et al.*, 2015). Even in temperate rainforests, soil development

continues more than 5000 years after deglaciation (Klaar *et al.*, 2015). Given these lags involving soil development, primary succession is unlikely to have reached its end point in many landscapes during the millennial-scale climate fluctuations of the ice age (Svenning *et al.*, 2015).

Lags in the dispersal of plant species add to delays in community assembly entailed by primary succession, and rapid climate changes during the ice age often exceeded the ability of tree species to keep up (Bennett *et al.*, 1991). In post-glacial times, the establishment lags of different plants have varied from a few decades (Tinner & Kaltenrieder, 2005) to several millennia (Ammann *et al.*, 2013). In post-glacial times, the dispersal rates of most temperate-zone tree species have been < 250 m year⁻¹ (Feurdean *et al.*, 2013) and in some cases < 100 m year⁻¹ (Svenning & Skov, 2007; Bradshaw, Kito, & Giesecke, 2010). As a result of these slow dispersal rates, even within the Holocene's 11700 years span of comparatively stable climate, numerous plant species have lagged several millennia or longer behind their climatic range limits in regions formerly buried by ice sheets (Johnstone & Chapin, 2003; Fang & Lechowicz, 2006; Tollefson *et al.*, 2008; Gavin, 2009; Bradshaw *et al.*, 2010; Elias, 2013; Svenning & Sandel, 2013). The key point here is that during the ice age few plant communities had sufficient time to assemble into equilibrium states before the climate changed again (Huntley *et al.*, 2013).

Ice-age animal communities also were frequently out of equilibrium (Graham & Lundelius, 1984). A reduced degree of latitudinal zonation during the ice age compared to the Holocene suggests that disequilibrium communities were widespread in Europe (Hofreiter *et al.*, 2004). Similarly, boom and bust cycles of megafauna in Arctic Alaska imply disequilibria on the mammoth steppe (Mann *et al.*, 2015), as do the frequent range shifts and population bottlenecks that ancient DNA (aDNA) documents for a number of mammal taxa (Shapiro *et al.*, 2004; Enk *et al.*, 2016; Chang *et al.*, 2017; Froese *et al.*, 2017).

Certain types of disequilibrium ecosystems may have favoured megafaunal herbivores precisely because they were transient. Early successional plant communities dominated by forbs and graminoids are capable of supporting dense populations of megafaunal herbivores (Owen-Smith, 1988; Guthrie, 1990). One reason for this is that immature soils tend to be more fertile than older, more highly weathered ones (Huston, 2012). For example, soils in the drier, short-grass region of the Serengeti have developed on recent volcanic deposits. They have higher fertility than the soils in surrounding wetter regions, whose soils are older and more weathered (Dobson, 2009). Today much of our grazing-based agriculture takes advantage of the high productivity of recently disturbed plant communities and poorly developed soils.

Another reason why early successional communities dominated by forbs and graminoids can be highly productive for megafaunal grazers is because these communities are dominated by ruderal plant species. Weed species are often geographically widespread, complacent to climatic

gradients, and masters of dispersal (Radosevich, Holt, & Ghersa, 1997). Many of them are minimally invested in anti-herbivore defences, relying instead on fertile soils, transience, and wide geographic ranges to assure their persistence. These characteristics enabled them to thrive in the disequilibrium communities widespread during the ice age.

Frequent and large-scale climate changes were not the only disturbances responsible for the plaid ecosystems of the ice age. Geomorphic disturbances associated with fluctuations of the cryosphere disrupted ice-age soils and vegetation. At the peak of the last glacial maximum approximately 21–18 ka, glaciers covered roughly 1/4 of the northern hemisphere (Ehlers, Hughes, & Gibbard, 2016) and repeatedly fluctuated in extent (Dyke, 2005). Around ice-sheet margins, broad regions were affected by shifting outwash streams, sand sheets, sand dunes, and rapidly accumulating loess. Low-latitude regions of Africa, South America, southern Eurasia, and Australia also experienced repeated episodes of geomorphic disturbance caused by shifts in precipitation and temperature. Transfers of water between oceans and glaciers, coupled with isostatic adjustments of the crust beneath ice sheets, caused changes in relative sea level (RSL) (Grant *et al.*, 2014), which alternately exposed and flooded millions of square kilometers of the continental shelves.

An idea of the magnitude of the impacts that ice age climate changes had on the global biota is gained by superimposing ice-age temperature changes onto ordinations of modern biomes and climate (Fig. 7). We can also roughly estimate the distances organisms would have had to disperse in order to keep up with ice-age climate. Today, mean annual temperature varies by approximately 1 °C per degree latitude in the northern hemisphere. Since a degree of latitude corresponds roughly to 100 km, a 5–10 °C warming over the

first few decades of a D-O cycle would cause isotherms to shift 500–1000 km poleward in a region of low topographic relief. Then the cold phase of the cycle would push the isotherms equatorward across a similar distance. Because of the slow rates of tree migration (Svenning *et al.*, 2015), many of the plant species that determined vegetation structure, and hence the identity of biomes, may have had difficulty keeping up.

(c) *The eco-physiological correlates of body size: big is best in plaid*

The ice ages' unique climate regimes created adaptive milieux that in many places were very different from those existing during the Holocene (Lister, 2004). In what ways might unstable climate and ecological disequilibrium favour megafaunal species? Numerous physiological, ecological, behavioural, and life-history traits scale with body mass (Schmidt-Nielsen, 1984) according to allometric relationships in the form $Y = aM^b$, where Y is some biological variable such as metabolic rate or population density, M is body mass, a is an empirically derived constant, and b is the scaling exponent (Brown *et al.*, 2004). Being large puts species at the extremes of several eco-physiological niche axes (Fig. 8), and certain of these allometric extremes may be highly adaptive within plaid landscapes.

(i) *Greater metabolic efficiency.* Larger animals are metabolically more efficient than smaller ones in terms of energy use per unit body mass (White & Seymour, 2005). Kleiber's Law states that basal metabolic rate (q_0) scales as $q_0 \sim M^{0.75}$, although the exact value of the scaling exponent and its physical basis are still debated (West, Brown, & Enquist, 1999; Glazier, 2005). Food intake also scales as $M^{0.75}$ (Clauss *et al.*, 2007). Hence instead of being 1000 times larger, the food requirements of a 5000 kg elephant (*Loxodonta africana*) are only 180 times larger than those of a 5 kg dikdik (*Madoqua kirkii*). Daily metabolic expenditure, which includes

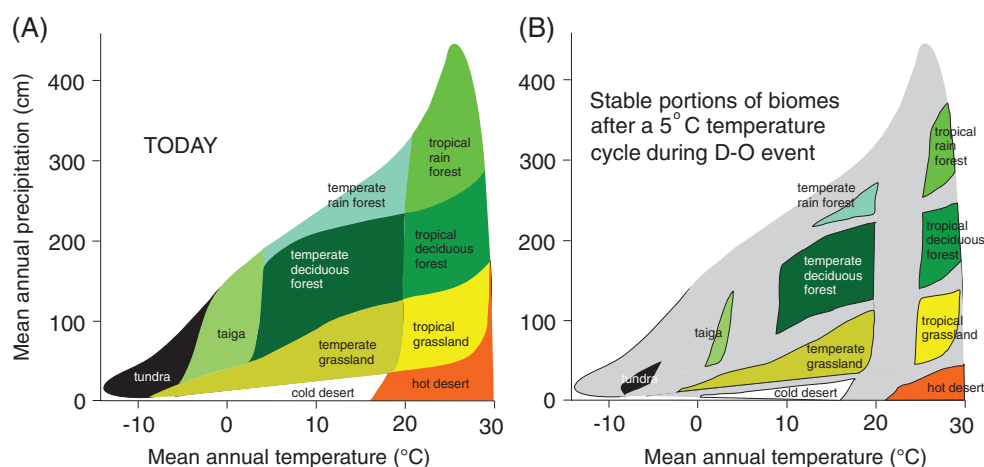


Fig. 7. von Humboldt's nightmare: Only the core areas of biomes familiar to us during the Holocene (A) would have remained stable during the ice age (B) when millennial and sub-millennial climate changes generated widespread 'weed zones' in which plant communities may never have had time to equilibrate with climate. We hypothesize that megafaunal species specialized in exploiting the transient, but often highly productive, weedy plant communities flourishing in the grey zones. D-O is a Dansgaard–Oeschger event. Biome diagram redrawn from Whittaker (1970).

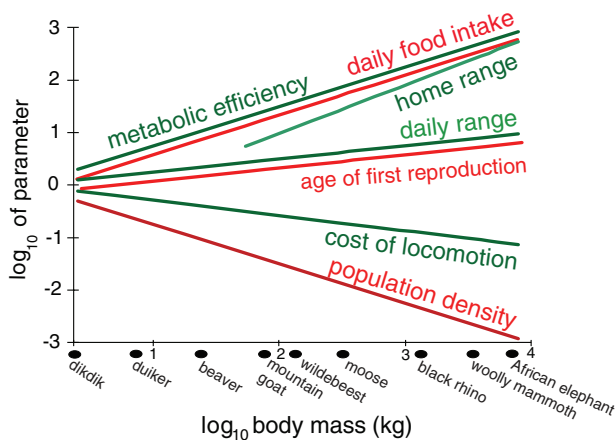


Fig. 8. Allometric trends in ecophysiological traits associated with body mass among terrestrial mammals. Extreme differences exist in these traits between large and small species. For example, the African elephant and dikdik, a diminutive African antelope, differ by 1000-fold in some traits. Because megafaunal species have greater locomotory efficiency, greater metabolic efficiency, increased resistance to starvation, longer life spans, and greater sensory ranges, they are able to exploit transient resource bonanzas widely scattered in space. These advantages come with trade-offs including smaller population sizes, slower reproduction rates, and commitment to the life strategy of coping with local food shortages by dispersing to greener pastures.

the cost of physical activity, also scales (although with a different normalization constant, a) as $M^{0.75}$ (Owen-Smith, 1988), as do daily requirements for nitrogen and minerals (Müller *et al.*, 2013). Thus, assuming no food limitations, the larger the mammalian herbivore, the more efficient it is at converting plants into animal tissue.

(ii) *Broader diets, more-diverse habitats, greater resiliency.* Enhanced metabolic efficiency gives megafaunal herbivores several advantages over smaller species. Because their profit margin is higher, they can subsist on less nutritious forage (Müller *et al.*, 2013). For instance, African elephants can subsist on a wider range of foods than the diminutive dikdik, including fruits, dry leaves, grass stems, bark, and roots (Dobson, 2009). Their size-derived metabolic advantage may be why, in the African savanna, the population metabolisms (mean population density \times mean body mass \times mass-specific metabolic rate) of large herbivores like white rhinoceros (*Ceratotherium simum*) and elephant scale with body mass as $M^{0.45}$, but scale as $M^{0.65}$ among small herbivores like Thompson's gazelle (*Eudorcas thomsonii*) (du Toit & Owen-Smith, 1989). As a result, effective food density can be higher for large herbivores than small ones living in the same landscape. This in turn implies that the habitats of megafaunal species may be more continuously distributed, with fewer unsuitable lacunae (Owen-Smith, 1988). The tendency for larger species to exploit a wider range of resources holds for carnivores as well (Sinclair *et al.*, 2007). Higher effective food density and broader habitats translate into greater resiliency of megafaunal populations to environmental challenges like droughts (Owen-Smith,

1988). Overall, the greater metabolic efficiency of megafauna translates into a wider dietary breadth, a wider range of habitats, and possibly a heightened resiliency in the face of environmental change.

(iii) *Large body size increases fasting endurance.* The amount of stored fat increases with increasing body size in mammals as $M^{1.2}$, while survival time under starvation scales as $M^{0.44}$ (Lindstedt & Boyce, 1985). Overall, the maximum time between necessary refueling is about 200 times longer for an elephant than a mouse (*Mus musculus*), and this scaling of fasting endurance becomes even more pronounced at colder temperatures in accordance with Bergmann's Rule (Meiri & Dayan, 2003). Thus, larger mammals can persist better than smaller ones through extreme weather events that might limit feeding. They also can travel longer distances without food while seeking greener pastures.

(iv) *Larger species have larger home ranges.* Among mammals, home range size (km^2) scales roughly with body mass (kg) as a 1:1 relationship (Jetz *et al.*, 2004). Using only the body masses of mammals weighing > 0.1 kg, Burness, Diamond, & Flannery (2001) found that mass scales as $673 \times \text{home range}^{0.50}$. The body-mass/home-range relationship is complicated by the fact that ranges expand where/when primary productivity is low and contract where/when food is more plentiful (Owen-Smith, 1988). The functional importance of the body-size/home-range relationship is poignantly illustrated by the decline of large mammal populations as African preserves are progressively isolated by human activities (Newmark, 2008).

(v) *Bigger species are often most mobile.* Given their large home ranges, it is no surprise that megafaunal species are the most mobile of non-volant land animals (Sutherland *et al.*, 2000). Species with larger body masses move about their home ranges more quickly than smaller species (Swihart, Slade, & Bergstrom, 1988). The day range, the distance an animal typically moves in the course of its daily activities, scales with body mass as $M^{0.25}$ (Carbone *et al.*, 2004). Species with the largest home ranges also engage in the longest dispersals (Bowman, Jaeger, & Fahrig, 2002), and megafauna tend to walk faster than microfauna while engaged in day-to-day activities.

(vi) *Bigger animals move more efficiently but at a higher net cost.*

The energetic cost of running in terrestrial animals scales as $M^{-0.28}$ (Peters, 1986). Thus a 30 g rodent uses roughly 13 times the energy to move each gram of its weight as a 100 kg pony does over the same distance (Taylor & Heglund, 1982). Interestingly, once mammalian body mass exceeds ~ 10 kg, the metabolic cost of running locomotion is about the same as the most efficient flight in birds. The energy savings achieved by larger mammals occur because the cost of transport scales as limb length $^{-0.77}$ (Pontzer, 2007). On the other hand, the absolute cost of moving a larger body increases steadily as mass increases (Halsey, 2016), so the benefit of the enhanced efficiency of movement for megafauna is only accrued if food is not limiting.

(vii) *Larger animals live longer, but reproduce later and more slowly.*

Both generation length and age of first reproduction scale

as $M^{0.25}$ (Owen-Smith, 1988; Brook & Bowman, 2005; Healy *et al.*, 2014). While generation time and age of first reproduction increase with body mass, maximum rates of population increase decline according to $M^{-0.25}$ (Fenchel, 1974; Fagan, Lynch, & Noon, 2010). These diverging trends have serious implications for the largest species in an ecological community that is suddenly exposed to a new source of mortality; large-bodied species will probably have lower demographic resilience (Brook & Bowman, 2005), and in fact, low reproductive rates are correlated with increased probability of extinction during the Late Quaternary (Johnson, 2002).

(viii) *Big animals are often rare with fewer subpopulations.* Their larger home ranges imply that larger species living on continents have lower population densities. The general relationship between population density (D) and body mass (M) among large terrestrial mammals is $D \propto M^{-0.75}$ (Brown *et al.*, 2004). This amounts to a 5–6-fold decrease in population density for every tenfold increase in body mass. While statistically significant, the relationship between population density and body mass contains considerable noise (Currie & Fritz, 1993). Where it has been studied among birds, the number of subpopulations scales to total population size (N) as $N^{0.75}$ (Keitt *et al.*, 2002), suggesting that metapopulations of large-bodied species contain fewer subpopulations.

(ix) *Larger, rarer species are more prone to population fluctuations.*

As described by Taylor's Law, the rarer a species is, the more its population size varies through time (Keitt *et al.*, 2002). This power law takes the form $S^2 = a\mu^b$ where a is a sampling parameter, b is an index of the aggregation characteristics of the species, s^2 is the variance in population size, and μ is the mean. Empirical studies show the value of b varies between 1 and 2 (Taylor & Heglund, 1982).

(x) *Adult megafauna often escape predation.* The larger you are, the fewer predators you have. On the Serengeti, ungulate species weighing < 150 kg are vulnerable to more predator species than are larger ungulates (Sinclair *et al.*, 2007). As a result, in many ecosystems, large-bodied ungulates tend to be controlled from the bottom-up by food supply rather than from the top-down by predation (Mduma, Sinclair, & Hilborn, 1999; although see Ripple & Van Valkenburgh, 2010). In some situations, the vulnerability of young animals to large predators negates this trend (Grange *et al.*, 2004).

(xi) *Long-distance movements are frequent among megafauna.* In ecosystems where the quantity and quality of forage varies widely through time, some species move long distances tracking food supply (Fryxell, Greever, & Sinclair, 1988; Singh *et al.*, 2010). These movements fall into two overlapping categories: nomadic behaviour and migration (Mueller *et al.*, 2011). Migration is the seasonal, round-trip movement of animals between discrete areas, while nomadism involves opportunistic and unpredictable wandering.

Most migratory and nomadic mammal species are large-bodied ungulates. In today's world, 24 terrestrial mammal species weighing > 20 kg are migratory, all of whom are ungulates, of which 14 live in Africa (Harris *et al.*,

2009). Globally, 17 of the 24 migratory species recognized by Harris *et al.* (2009) track seasonal shifts in the location of nutritious forage. In the Serengeti, millions of wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchellii*) move into the drier, short-grass area of the plains during the rainy season to exploit a flush of grass with high nitrogen content (Holdo, Holt, & Fryxell, 2009). As the dry season develops, they migrate to areas where green foliage persists year-round, albeit at lower nutrient levels (McNaughton, 1990; Dobson, 2009). In Africa, family groups of elephants engage in episodic long-distance movements in response to droughts and overgrazing (van Aarde & Jackson, 2007). Prior to their near-extinction, many buffalo (*Bison bison*) led nomadic lives following greener pastures across the Great Plains of North America (Hart, 2001).

Today the movements of migratory and nomadic ungulates are increasingly constrained by people, but in recent times some of these movements were extensive. Saiga (*Saiga tartarica*) once migrated some 2000 km between the Volga River and Macedonia (Harris *et al.*, 2009), and goitered gazelles (*Gazella subgutturosa*) once roamed 500–700 km year⁻¹ across western Eurasia. Grevy's zebra (*Equus grevyi*) still move hundreds of km year⁻¹ in response to droughts in northern Kenya (Harris *et al.*, 2009). Some caribou (*Rangifer tarandus*) and Mongolian gazelle (*Procapra gutturosa*) routinely travel 1000 km year⁻¹ during their migrations (Mueller *et al.*, 2011).

(xii) *Larger animals often have larger sensory ranges.* To be successful at large spatial scales within a milieu of environmental change, successful herbivores need the high mobility afforded by large body size along with the ability to sense, learn, and remember complex landscapes (Owen-Smith, Fryxell, & Merrill, 2010). In grazing ecosystems, the amount and nutritional quality of forage change continually through space and time. Because green flushes of young vegetation provide the highest nutrition, grazing species track these greener pastures, and they do so with an uncanny ability (McNaughton, 1985). For instance, wildebeest in the Serengeti seem to be able to compare grazing opportunities across distances of >80 km (Holdo *et al.*, 2009).

(xiii) *Being big could make you more responsive to climate change.*

Among mammals, body size is a strong predictor of responsiveness to climate change (McCain & King, 2014). There are multiple reasons for this, including the fact that climate grain size, mobility, and rarity all scale with body size. A positive correlation between extinction probability and body mass exists for late-Quaternary extinctions (Lyons, Smith, & Brown, 2004; Lyons *et al.*, 2016). Polishchuk (2010) found that the probability of extinction among terrestrial mammals scales with population density as $D^{0.75}$, which in turn scales with body mass as $M^{0.75}$.

In summary, megafaunal species tend to have higher metabolic and locomotory efficiencies, larger home ranges, greater resistance to starvation, longer lives, an ability to exploit a wider range of habitats and food types, and greater sensory ranges. Because of their mobility

and various efficiencies, the vast majority of terrestrial animals engaging in long-distance migration or nomadism in today's biologically impoverished world are megafaunal ungulates. Larger body volume, heightened metabolic efficiency, and tolerance for poorer forage give megafaunal species additional advantages in cold habitats where seasonal food shortages occur (Meiri & Dayan, 2003). These eco-physiological traits associated with large bodies may have preadapted megafaunal species for efficiently tracking habitats that were continually shifting in response to the rapid environmental changes of the ice age.

In a striped environment, many of the advantages of being megafaunal disappear. Because ecotones are more stable, long-distance tracking of shifting patches of suitable habitat is no longer needed. Where food resources are limited, the need for large amounts of food tends to negate metabolic efficiency. The ability to travel fast and efficiently become irrelevant when home ranges shrink, as does the ability to be nomadic or migratory. Being able to remember and learn is moot if environmental changes are few and the landscape remains in a stable, striped configuration. Simultaneously, the relatively small population sizes, low population densities, and slow reproductive rates associated with large body mass can reduce resilience in response to population bottlenecks. The probability of extinction varies inversely with population density, so the threat of extinction increases as ranges shrink when plaid landscapes shift into striped ones. By contrast, small-bodied species are comparatively adept at coping with minor shifts in climate by tracking favoured microclimates over short distances while maintaining sizable populations within small areas (Ehrlich & Stenseth, 2001). We suggest that the shift from widespread plaid landscapes to widespread striped ones at the end of the ice age lowered the extinction thresholds for many megafaunal species, making them more vulnerable to a myriad of proximate extinction causes (Fig. 3).

(2) Megafaunal extinctions during previous glacial–interglacial transitions

If the transition between two climate regimes possessing different modes and tempos of environmental change was a widely shared cause of Late Quaternary megafaunal extinctions, why didn't similar bouts of extinctions occur at the outsides of previous interglacials? After all, glacial and interglacials have alternated over the last 2.6 Ma, yet no clear evidence exists for bouts of megafaunal extinction during earlier interglacials in either Eurasia or North America (Stuart, 1991).

We suspect the apparent absence of megafaunal extinctions during earlier glacial–interglacial transitions has three causes. The first relates to the Plaids and Stripes Hypothesis, namely that the climate of the early Holocene may have been more 'stripe conducive' than it was during the opening millennia of previous interglacials. The second concerns the fossil record, namely that limited temporal and taxonomic resolution make it difficult to quantify extinction rates during ancient interglacials. The third cause involves the presence/absence of humans, namely that people were

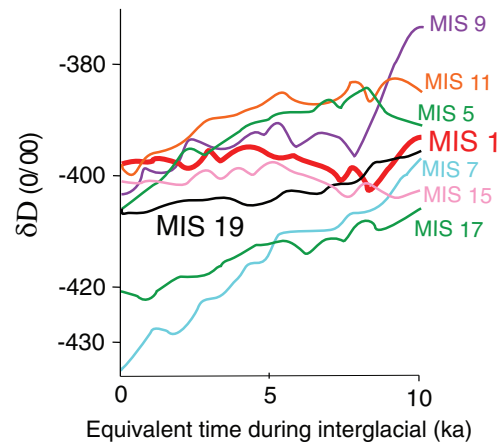


Fig. 9. δD (deuterium/hydrogen) ratio records of air temperatures over Antarctica (Jouzel *et al.*, 2003). δD levels have remained more constant during the Holocene (MIS 1) than during most other interglacial periods. Orbital forcing during MIS 19 (*ca.* 790–760 ka) was the most similar to the Holocene's, and MIS 15 (*ca.* 620–560 ka) has the most similar pattern of deuterium concentration, so it would be of interest to know what was happening to megafaunal species during these two interglacials (redrawn from Ruddiman *et al.*, 2016).

absent from Australia, North America, and South America (the three continents where late Quaternary extinctions were most numerous) during all previous interglacials, but were present when the Holocene began. As detailed below, it is unlikely that any one of these explanations is sufficient on its own, but together they may explain the absence of evidence for megafaunal extinctions during earlier glacial–interglacial transitions.

Taken on its own, the Plaids and Stripes Hypothesis would suggest that more megafaunal extinctions occurred during the early Holocene than previous interglacials because the Holocene had an unusually stripe-conducive climate. We currently lack the detailed chronological control and palaeoecological data from older glacial–interglacial transitions to definitively test this prediction. However, we do know that the climates of past interglacials varied widely (Tzedakis *et al.*, 2009; Herold *et al.*, 2012), mainly because their Milankovitch orbital drivers differed (Shakun *et al.*, 2015; Yin & Berger, 2015), which caused markedly different trajectories of climate change (Fig. 9). The time intervals traditionally considered 'interglacials' often had complex temporal structures that in some cases included multiple 'glacial' interludes (Lang & Wolff, 2011). There have been numerous interglacials, but none possessed a climate regime exactly like the Holocene's.

An interesting illustration of the diversity of interglacial climates is provided by comparing the Holocene with the last interglacial, MIS 5e, the interglacial we know the most about because it is closest to us in time (Fig. 10). During MIS 5e, peak warmth occurred over a 5000-year interval when global mean temperature was warmer than the Holocene's. Besides lasting a shorter time, MIS 5e differed from the Holocene in the mode and tempo of its climate changes.

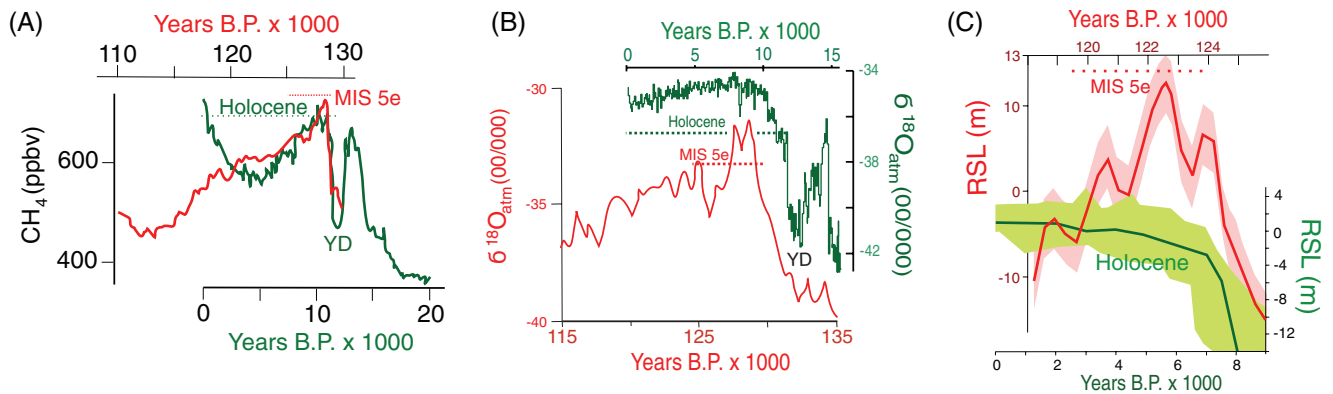


Fig. 10. The mode and tempo of climate change during the last interglacial period, MIS 5e, (dashed horizontal red lines) was more like the ice age than the Holocene (dashed horizontal green lines). (A) Atmospheric methane concentration from the EDC ice core from Dome C in East Antarctica on the EDC3 timescale. YD is the Younger Dryas. Redrawn from Tzedakis (2010). (B) Holocene and last interglacial $\delta^{18}\text{O}$ records from Greenland ice cores. The Holocene data are from the NGRIP core plotted on the GICC05 time scale (Rasmussen *et al.*, 2014). The last interglacial time series is the Greenland synthetic record whose timescale is based on alignment with Chinese speleothem records (Barker *et al.*, 2011). Redrawn from Tzedakis *et al.* (2012). (C) Relative sea level (RSL; red line) in the Red Sea during the warmest part of the last interglacial. The pink error envelope is ± 6 m. The Holocene RSL curve (green line) is redrawn from a compilation by R.A. Rohde based on Fleming *et al.* (1998) and Milne, Long, & Bassett (2005). The error envelope joins the extremes of estimated errors.

Atmospheric methane (CH_4) concentrations declined after a peak lasting < 2000 years, and air temperatures cooled after < 1000 years (Barker *et al.*, 2011). By contrast, CH_4 concentrations during the Holocene have followed a complicated trajectory involving multiple peaks that together have spanned > 10000 years. These comparisons illustrate the climatic diversity of interglacials by showing that in many regions of the world climate was more variable during MIS 5e than during the Holocene (Milner *et al.*, 2013; Hansen *et al.*, 2015).

Records of RSL tell a similar story of millennial-scale instability of climate during MIS 5e (Rohling *et al.*, 2008; Thompson *et al.*, 2011). At sites distant from ice sheets, changes in RSL record fluctuations in the volumes of terrestrial ice sheets (Hearty *et al.*, 2007), which in turn are controlled by climate. During the Holocene, rising RSL stabilized approximately 7 ka (Fig. 10C) and since then has risen slowly by 3–5 m in regions distant from former ice sheets (Peltier & Fairbanks, 2006). By contrast, RSL fluctuated by 6 m within one millennium or less during MIS 5e. Like the brief peaks of CH_4 and $\delta^{18}\text{O}$ during MIS 5e, RSL maintained its highest level for < 2000 years during MIS 5e (Rohling *et al.*, 2008; NEEM, 2013; Hansen *et al.*, 2015). Together, these data suggest the climate of the last interglacial was more plaid-conducive than the Holocene's climate has been.

In addition to differences in Milankovitch forcing, the Holocene climate may be unusual because of anthropogenic effects that have imbued it with anomalous stability beginning in the early Holocene (Ruddiman, 2003, 2007, 2014). Human impacts on greenhouse processes may also have prolonged the present interglacial by several thousand years (Ruddiman *et al.*, 2016), thus delaying the onset of ice-sheet growth (Vavrus, Ruddiman, & Kutzbach, 2008; Vavrus

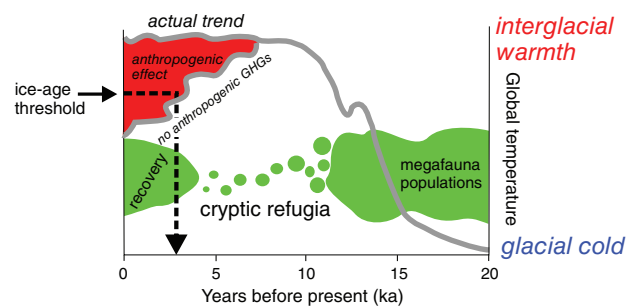


Fig. 11. The trajectory of Holocene climate with and without human influences. Orbital changes triggered deglaciation starting approximately 20 ka and determined when the present interglacial began, but human agriculture and land clearance began to modify global climate in the early Holocene (Ruddiman, 2014). Without these anthropogenic greenhouse effects, the Holocene climate might already be cooling into the next ice age (Ruddiman *et al.*, 2016). Shown in green are hypothetical responses of megafauna to a Holocene climate in the absence of anthropogenic greenhouse gases (GHGs). Like the woolly mammoth, many megafaunal species retracted into cryptic refugia as climate warmed, stabilized, and caused landscapes to shift from ice-age plaids into striped configurations. If the Holocene had ended on schedule, some megafauna – possibly including woolly mammoth – might have re-expanded from their refugia when the plaid world was reinstated by the return of ice-age climate. Climate trends redrawn from Ruddiman *et al.* (2016).

et al., 2011) and the resumption of millennial-scale climate fluctuations. It is possible that without the anthropogenic delaying of the next ice age, perhaps the woolly mammoths surviving on Wrangel Island until 4 ka would have had time to repopulate the boreal region (Fig. 11).

A second reason for the lack of evidence for bouts of megafaunal extinction during previous glacial–interglacial transitions may be the limited temporal and geographical resolution of fossil records from older interglacials compared to the Holocene. For instance, there are <40 fossil vertebrate sites in North America pre-dating the last ice age (>80 ka), compared to thousands from postglacial times (<15 ka) (Bell *et al.*, 2004; Barnosky *et al.*, 2004a). A similar disparity exists in Europe (Stuart, 1991; Schreve, 2001; Markova & Vislobokova, 2016), and it is even more pronounced in regions like Siberia and Alaska where Late Quaternary mammal fossil localities are legion, but only a handful of mid- and early Pleistocene ones are known.

An additional challenge when assessing extinction rates during previous glacial–interglacial transitions is the fact that chronological precision is often much less than ± 10000 years in fossil deposits older than the upper limit of ^{14}C dating (*ca.* 45 ka) (Bell *et al.*, 2004). This makes it difficult to identify glacial–interglacial transitions precisely and to correlate megafaunal remains with the marine and ice-core records that the glacial–interglacial chronology is based upon (Price *et al.*, 2018). Fossil records from ancient interglacials like MIS 19 (790–760 ka), the interglacial whose orbital forcing and isotopic records most closely resemble the Holocene's (Yin & Berger, 2015), are too sparse and imprecisely dated to reject the possibility that population bottlenecks and heightened rates of megafaunal extinctions also occurred then.

Lack of taxonomic resolution in the fossil record adds to the difficulty of detecting bouts of megafaunal extinction in the deep past. Late Quaternary extinctions are usually quantified in terms of genera rather than species because of uncertainties in the species-level taxonomy of many specimens (Stuart, 1991; Grayson, 2016). We suggest that the limited temporal, geographical, and taxonomic resolution in the fossil record make it impossible to say for certain that rates of megafaunal extinction did not increase during previous glacial–interglacial transitions compared to extinction rates during intervening glacial periods. That said, even if rates of megafaunal extinction did increase at the outsides of certain older interglacials, they certainly failed to reach the intensity of the Late Quaternary extinctions in the New World when entire higher taxa (e.g. proboscideans, equids, ground sloths) became extinct. Quantifying extinction rates during ancient glacial–interglacial transitions – perhaps by using DNA extracted from lake sediment – would be a major contribution to the megafaunal extinction debate.

A third contributing reason why more megafaunal extinctions occurred during the Pleistocene–Holocene transition than during earlier glacial–interglacial transitions may relate to the timing of human dispersal across the planet. On the three continents where late Quaternary megafaunal extinctions were most numerous (Australia, South America, and North America), people were absent during all previous interglacials except the last one. On these three continents, human impacts during a time of plaid to stripe transition may have been a key contributor to megafaunal extinctions.

In summary, we suspect three factors jointly explain the apparent lack of megafaunal extinctions during earlier interglacials. The first relates to the Plaids and Stripes Hypothesis in that the tempo and magnitude of climate change varied widely between different interglacials, and some interglacials were probably more conducive to plaid-ness and hence to megafaunal survival than the Holocene has been. This possibility remains to be tested. The fading of the fossil record into the past may also have contributed, in particular the increasing scarcity of fossils and the declining precision of dating control beyond the limit of the ^{14}C method. Another contributing factor may have been the absence of humans during earlier interglacials on the three continents where megafaunal extinctions were most frequent in Late Quaternary times.

(3) Australia's staggered extinctions

Unlike the Americas, where megafaunal extinctions were seemingly concentrated at the end of the last ice age, in Australia they began earlier in the Pleistocene and continued intermittently until approximately 40 ka (Wroe & Field, 2006; Wroe *et al.*, 2013). This staggered schedule of extinctions is consistent with the Plaids & Stripes Hypothesis in that the adaptive advantages of megafauna within plaid environments are negated if aridification drives primary productivity too low. If there are no greener pastures anywhere on the continent, even the most wide-ranging megafauna suffer.

Australia's physical geography has unique characteristics that make megafauna's ice-age advantages susceptible to being trumped by aridity. Australia is the smallest, lowest, oldest, and tectonically most inactive continent, and as a result many of its soils are relatively infertile (Raupach *et al.*, 2001; Owen-Smith, 2013). Because of its low altitude, subdued topography, and location in the subtropical high-pressure zone, Australia has a relatively simple climatic geography. Despite their similar surface areas, today Australia contains only 12 Köppen climate types, while the conterminous USA contains 21 (Peel, Finlayson, & McMahon, 2007).

A unique climate history has accentuated Australia's geographic features as related to megafaunal extinctions. Australia has experienced increasing aridification over the past 20 Ma as continental drift carried it northward into the subtropical high pressure zone (Wroe & Field, 2006; Byrne *et al.*, 2008). This drying trend sped up after approximately 700 ka and has been particularly pronounced over the last 400 000 years (Nanson *et al.*, 2008; Wroe *et al.*, 2013; Miller *et al.*, 2016). Today, 80% of Australia's land area has a mean annual precipitation (MAP) < 600 mm, and 50% has a MAP < 300 mm. During the ice age, the climate was even drier, resulting in deserts covering much of the continent's interior (Williams, 2001). Even while locked in ice-age aridity, Australia experienced the millennial-scale fluctuations that characterized ice-age climates globally (Kershaw, Bretherton, & van der Kaars, 2007; Moss & Kershaw, 2007; Ayliffe *et al.*, 2013; Denniston *et al.*, 2013).

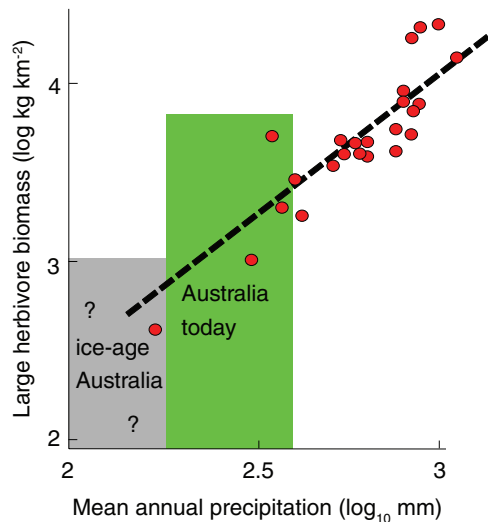


Fig. 12. Relationship between rainfall and biomass of mammalian herbivores in wildlife reserves in eastern and southern Africa (redrawn from Coe *et al.*, 1976). Megafaunal herbivores need large amounts of food, and primary productivity by plants depends strongly on precipitation. Soil fertility also plays a role, permitting higher carrying capacities in areas of higher fertility (Fritz & Duncan, 1994). Mean annual rainfall in interior regions of Australia today is shown in green. Much of the Australian continent became hyperarid during the coldest times of ice ages (grey).

How did long-term desertification affect Australia's megafauna? First, Australia's subdued topography and small size could have resulted in less ice-age plaidness than in comparably sized areas of North America or Africa. Second, reduced primary productivity during times of ice-age aridity may have negated the ecophysiological advantages of being large bodied. In dryland regions of Africa today, herbivore biomass correlates with above-ground primary productivity (Fig. 12) (McNaughton, 1990; Hempson, Archibald, & Bond, 2015), which in turn is controlled by a combination of precipitation (Coe, Cumming, & Phillipson, 1976) and soil fertility (Fritz & Duncan, 1994). In Africa today, the number of ungulate species declines as mean annual precipitation decreases (Faith, 2013). Similarly in Australia today, a significant positive correlation exists between the number of mammal taxa living in an area and the mean annual precipitation there (Faith *et al.*, 2017). Australia is exceptional because during the ice age it experienced aridity bottlenecks that reduced its overall carrying capacity for megafauna to low levels. During these bottlenecks, Australia's biogeographic simplicity - accentuated by its generally infertile soils - may have failed to provide sufficient refugia for megafauna to survive.

(4) The African exception

Another test for the Plaids and Stripes Hypothesis is whether it can help explain why only Africa retains a terrestrial megafaunal assemblage comparable to its ice-age

one (Faurby & Svenning, 2015; Hempson *et al.*, 2015). Undoubtedly there are multiple reasons. Perhaps same set of factors that made Africa a uniquely prolific evolutionary crucible over the last 66 Ma (Werdelin & Sanders, 2010) is somehow responsible for the persistence of megafauna there. A more specific possibility is that because African megafauna underwent lengthy coevolution with hominins, they have been better able to cope with human impacts than have species living on continents only recently colonized by people (Owen-Smith, 1988). This implies that some megafaunal species in Africa were driven to extinction by early hominins, and those surviving have been evolutionarily and/or ecologically sorted for hominin resistance. Such sorting would have been a prolonged and subtle process, because early hominin population densities were low and their hunting technologies simple. Nonetheless, hominins' ability to exploit food chains at multiple levels was probably established early, and this possibly triggered a variety of trophic disruptions (Ripple & Van Valkenburgh, 2010; see also Estes, Burdin, & Doak, 2016). Unfortunately, evidence for such domino effects is subtle (Estes, 2016), and the fossil record of early hominin interactions with African megafauna is sparse. The study of Werdelin & Lewis (2013) comparing the timing of extinctions with the chronology of human evolution is a start at deciphering the long-term sorting effects of hominins on the African fauna.

An additional explanation for the African exception is that Africa has preserved more of its ice-age 'plaid' character than other continents. This is the case because Africa contains extensive low-latitude, semi-arid landscapes, and these dryland ecosystems are particularly susceptible to millennial-scale boom-and-bust cycles in primary productivity (Marchant *et al.*, 2009). These cycles result from a uniquely African hydrological regime that has persisted in being unstable at millennial and sub-millennial time scales throughout the Holocene (Gasse, 2000).

Africa's persistent, ecological plaidness during the Holocene ultimately relates to its physical geography. It is the second largest continent and today has the largest area of arid (Köppen-type B) climate of any continent crossed by the Equator (Peel *et al.*, 2007). Unlike the extensive dryland regions of Australia, active tectonism and volcanism endow Africa with relatively fertile soils (Owen-Smith, 2013). Dryland regions at low latitudes are particularly sensitive to changes in moisture availability because of the existence of particularly strong feedbacks between vegetation and climate (Brovkin, 2002; Hawkins *et al.*, 2003; Good & Caylor, 2011). Large changes in primary productivity and hence in carrying capacity for megafauna are possible in the drylands of Africa following slight changes in effective precipitation (Huang *et al.*, 2016; Wu *et al.*, 2016). As a result, Africa's extensive savannas and deserts are prone to relatively large shifts in vegetation cover triggered by relatively minor climate changes. Droughts and pluvials have occurred on other continents during the Holocene, but seldom at the scale and frequency as in Africa's drylands (Gasse, 2000).

The climatic causes of Holocene plaidness in Africa's dryland regions relate to the dynamics of the Intertropical Convergence Zone (ITCZ), which controls African monsoon systems (Gasse *et al.*, 2008; Maslin *et al.*, 2014). The ITCZ is unstable at multiple time scales including millennial ones, and this was true both during the ice age and the Holocene (Tierney *et al.*, 2008; Tierney, 2013; Willis *et al.*, 2013). Throughout prehistory, the ITCZ has been strongly affected by the 23000-year precession cycle. A peak in irradiance during the early and middle Holocene caused monsoonal rains to penetrate further poleward and intensify, greening the Sahara between 11 and 5 ka (Tierney, 2013). This was followed by a dry interval, and then another greening interval along the Sahara's southern margin between 4 and 3 ka (Willis *et al.*, 2013). These greening episodes were accompanied by northward shifts in plant and animal ranges of >500 km (Watrín, Lézine, & Hély, 2009; Drake *et al.*, 2011). Interestingly, some of the millennial-scale shifts in African precipitation regimes may be caused by Milankovitch drivers unique to equatorial regions (Berger, Loutre, & Mélice, 2006).

If Africa retained its plaidness during the Holocene, why not South America? It too has sizable equatorial and dryland regions. The answer probably lies in differences in the physical geographies of the two continents. South America is significantly smaller, and a larger proportion of its surface area lies at higher latitudes (Fig. 13). The biggest difference is the greater extent of drylands in Africa: about four times the total present in South America today. Presumably, similar differences existed during the ice age as well. In contrast to the plaid-prone drylands that predominate in Africa, tropical and temperate forests cover most of South America today. Testing this explanation for the differences in megafaunal extinctions between Africa and South America will require detailed, continent-wide comparisons of hydrological changes and biome shifts between the two continents throughout the Holocene. A hint that megafauna in South America and Africa responded in similar ways to at least the beginning of the Holocene could be the survival of South American megafauna into the early Holocene (Hubbe *et al.*, 2007; Turvey, 2009; Barnosky & Lindsey, 2010, p. 24–26). Perhaps South America's megafauna lingered because plaidness persisted in its low-latitude savannahs.

V. PREDICTIONS OF THE PLAIDS AND STRIPES HYPOTHESIS

(1) Opposite bottlenecks

While megafauna coped with the ice age's tumultuous climate by tracking shifting habitats across continents, microfauna – for instance, rodents with limited dispersal abilities – would have been forced to either adapt to changing conditions *in situ* or be extirpated. It follows that megafauna and microfauna experienced population bottlenecks at different times during the Late Quaternary

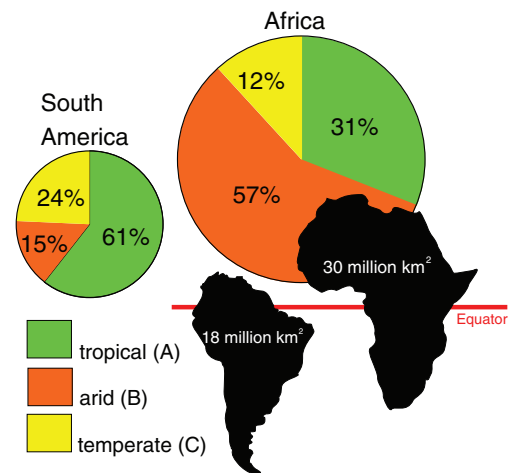


Fig. 13. Africa and South America have very different physical geographies, which may have contributed to their different histories of megafaunal extinction. Africa is unique in having extensive dryland regions lying on both sides of the Equator, which are sensitive to major, episodic shifts in vegetation caused by repeated, millennial-scale climate changes that have maintained extensive plaid landscapes during the Holocene. By contrast, South America is only 60% the size of Africa, lacks arid zones of comparable size, and has a large fraction of its total area lying at higher latitudes. Compilations of Köppen–Geiger climate zones by Peel *et al.* (2007).

(Fig. 14). Megafauna are predicted to have flourished during times of rapid change and conditions of maximum plaidness. Their population sizes and degree of genetic panmixis would have peaked during these times. Population bottlenecks accompanied by lineage turnover would have occurred among megafauna during periods of stable climate when their size-related advantage was less. Microfauna like small rodents should have experienced the opposite trends, with population bottlenecks and lineage turnovers occurring when the climate was changing rapidly. This prediction could be tested using aDNA analyses of precisely dated series of ancient bones belonging to megafauna and microfauna that lived in the same area during the same time interval.

(2) Few megafaunal extinctions on islands without people

We have asserted that the adaptive value of being large changes according to how the eco-physiological implications of body size mesh with temporal stability and spatial scale. Does this mean that megafauna living on islands always experienced striped landscapes – even during ice ages – and so evolved to conform with such settings? If so, this predicts that, in the absence of humans, megafaunal extinction rates did not increase on islands at the end of the ice age. Interestingly, no wave of late Quaternary megafaunal extinctions has been reported from either New Zealand (Wood *et al.*, 2017) or Madagascar (Burney *et al.*, 2004).

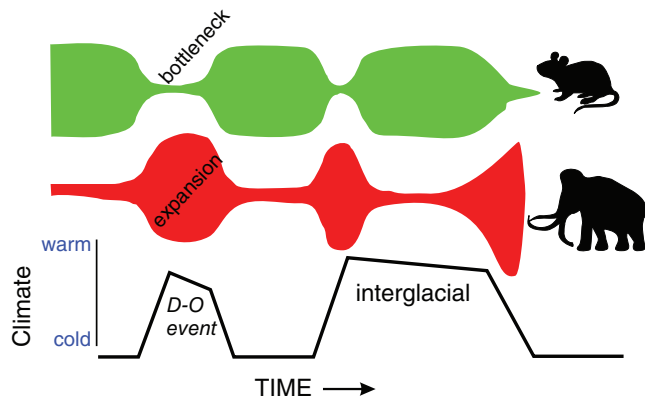


Fig. 14. Opposite bottlenecks? The Plaids and Stripes Hypothesis predicts that megafauna flourished during times of rapid climate change, with coincident peaks in their population sizes and the degree of genetic panmixis (indicated by width of coloured lines). Microfauna that were unable to disperse fast enough to keep up with the changing climate would have experienced the opposite trends.

(3) Eternal plaidness for winged beetles?

A landscape that is alternately striped and plaid for a mammoth may always be plaid from the perspective of a dispersal-prone beetle. In addition to possessing exoskeletons frequently preserved in the fossil record, many Coleoptera species have a high capacity for flight dispersal. Based on his interpretation of the fossil record of beetles, Coope (2004) remarked on the evolutionary stability of beetles compared to other organisms and suggested this resulted from their ability to track favoured habitats across great distances. By virtue of their out-sized dispersal abilities, dispersal-prone beetles should see the world as eternally plaid. If this is true, no late Quaternary wave of extinction should have occurred among beetles, a conclusion implicit in Coope's (2004) observations.

VI. SYNTHESIS

We are especially ill-equipped to think hierarchically, and to juggle simultaneous influences from several nested levels upon the foci of our interests...I seriously wonder if some of the difficulties might not arise from limitations in the common mental machinery of Homo sapiens. Gould (2002, p. 598)

The Plaids and Stripes Hypothesis asserts that a temporal simplification of ecological dynamics accompanying the shift from unstable climates during the ice age to more equable ones during the Holocene contributed to the extinction of many megafaunal species. This happened because ice-age ecosystems often existed in disequilibrium states as the result of plant and animal species being unable to reach their physiological range limits before the climate changed again. Because ecotones were continually shifting, the ice-age world was azonal and ecologically plaid. By contrast, Holocene conditions in many regions have tended to be more zonal and ecologically striped.

Size-related ecological, physiological, and life-history traits made large-bodied herbivores particularly well suited for coping with the ice age's transient habitats.

The ice-age advantages of megafauna included greater locomotory and metabolic efficiency, wider sensory ranges, the ability to migrate long distances, increased resistance to starvation, and longer life spans. Because of these traits, ice-age megafauna may have been well-suited to exploit transient resource bonanzas widely scattered in space. When the Holocene began, many of these advantages were lost. Where food resources are limited, the daily need for large amounts of food can negate metabolic efficiency. The ability to travel fast and efficiently becomes irrelevant when home ranges shrink, as does the ability to be nomadic or migratory. Other attributes of large body size may have posed disadvantages during the Holocene's striped conditions. As ranges shrank and settled into striped configurations, the low population densities and slow reproductive rates associated with large body size may have caused megafaunal populations to decline. Together these disadvantages would then have lowered the extinction thresholds of many megafaunal species in the striped world of the Holocene. This allowed a variety of proximate causes including overkill by humans, disease, competition with other species, and habitat loss to drive megafaunal species to extinction (Fig. 15).

By being explicitly hierarchical, the Plaids and Stripes Hypothesis helps integrate divergent facets of the long-running debate about the causes of Late Quaternary extinctions. Like many recent extinctions, megafaunal extinctions at the end of the last ice age resulted from conspiracies of causes whose relative importances varied across time, space, and taxa. Unfortunately, as the quote from S.J. Gould at the beginning of this section emphasizes, we have difficulty thinking hierarchically and find it easier to pursue singular explanations (e.g. human overkill, global drought, epidemic, or cosmic impact). The plaids to stripes transition may have been basal within the extinction-cause hierarchies of many megafaunal species during the last glacial-interglacial transition (Fig. 15). Depending on location and time, additional causes included a variety of other climate-related phenomena and, in some cases, a variety of human impacts on ecosystem structure and function, the magnitude of which were probably modified by duration of prior exposure of the megafauna to hominins (Owen-Smith, 1987).

The Plaids and Stripes Hypothesis may help explain two anomalies within the overall phenomenon of Late Quaternary extinctions: Australia's staggered extinctions and the persistence of Africa's megafauna to the present. Australia's staggered schedule of extinctions was probably related to its long-term, progressive aridification. Lowered primary productivity during the driest intervals of the ice-age plaid, combined with that continent's biogeographic simplicity (which made refugia hard to find) and infertile soils (which restricted primary productivity) negated the advantages the ice-age plaid would have otherwise afforded megafauna.

One cause of the African exception may have been the retention of plaidness in its extensive drylands during

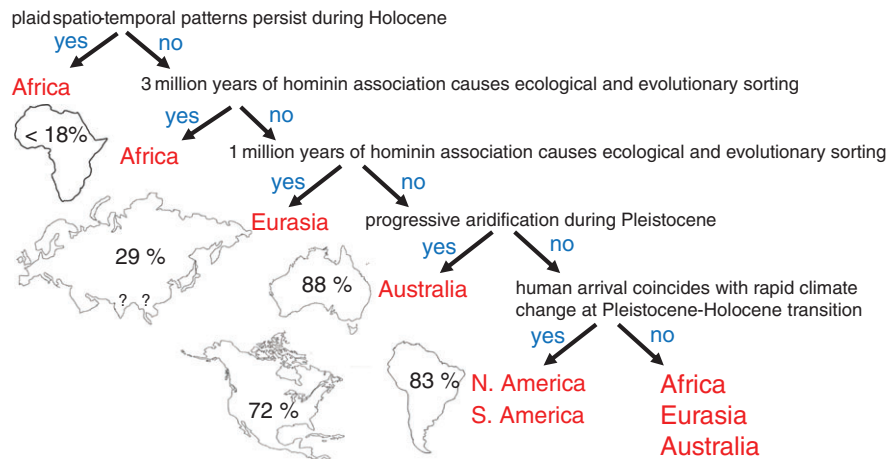


Fig. 15. Late Quaternary extinctions on the continents resulted from conspiring processes whose roles varied according to geography and time. Percentages of megafaunal genera going extinct are shown within each continent's outline. On many continents, the transition from plaid to striped landscapes may have been basal within a hierarchy of extinction causes that included other kinds of climate-change impacts and the impacts of human activities. The fewest extinctions occurred in the drylands of Africa because the spatio-temporal fabric remained largely plaid throughout the Holocene, and possibly because its megafaunal ecosystems had lengthy prior exposure to hominins. Progressive aridification in Australia may have trumped the favourable effects of the ice-age plaid for megafauna, causing extinctions there to be early and – after human arrival – to be severe. Multiple extinction drivers intersected in the Americas when initial human impacts coincided with the conversion from plaid to striped landscapes.

Holocene times. Another may have been the large amount of ecological/ and evolutionary sorting that occurred over the long history of hominin evolution on that continent. Interestingly, Eurasia, which had the second lowest percentage of megafaunal extinctions during the Late Quaternary, also experienced the second-longest history of hominin-megafauna association (Fig. 15).

The Plaids and Stripes Hypothesis may be a part of the explanation for why bouts of megafaunal extinctions do not seem to have occurred during earlier glacial–interglacial transitions. Recent advances in reconstructing the palaeoclimates and palaeoenvironments of previous interglacials reveal they differed widely in their climate histories, and that some interglacials may have been more conducive to plaidness (and hence the retention of megafauna) than the Holocene has been. Another part of the explanation may be the increasing scarcity of fossils and the declining precision of dating control beyond the limit of the ^{14}C method. A third cause for the apparent lack of megafaunal extinctions during earlier glacial–interglacial transitions may have been the absence of humans during earlier interglacials on the three continents (Australia, North America, South America) where megafaunal extinctions were most frequent in Late Quaternary times.

VII. CONCLUSIONS

(1) We suggest that a widely shared cause for Late Quaternary megafaunal extinctions was a fundamental shift in the spatio-temporal fabric of many ecosystems triggered by

the loss of the millennial-scale climate fluctuations that were characteristic of the ice age but that ceased approximately 11700 ka on most continents.

(2) Under ice-age conditions, radical and rapid climate changes prevented many ecosystems from equilibrating with their contemporary climates. Instead of today's 'striped' world where species' ranges have equilibrated with gradients of temperature, moisture, and seasonality, the ice-age world was a disequilibrium 'plaid' where species' ranges shifted rapidly and repeatedly, rarely catching up with their contemporary climate.

(3) Certain physiological, anatomical, and ecological attributes of megafauna pre-adapted them for success in the ice age's transient ecosystems. These traits included greater metabolic and locomotory efficiency, increased resistance to starvation, longer life spans, greater sensory ranges, and the ability to be nomadic or migratory.

(4) When the ice age's plaid world ended, many of the advantages of being large were either lost or became disadvantages. For instance, in the striped world, the low population densities and slow reproductive rates associated with large body size limited the resiliency of megafauna to population bottlenecks.

(5) Disadvantages of being large in striped environments lowered the extinction thresholds for megafauna living on continents worldwide, which then increased the vulnerability of individual species to a wide range of proximate threats including human predation, competition with other species, and habitat loss.

(6) For many megafaunal species living on the continents at the end of the last ice age, the plaid to stripes transition may have been positioned at the base of a hierarchy of extinction causes that included other climate-change-related

effects as well as human impacts. The relative importance of these separate yet conspiring causes varied geographically, temporally, and taxonomically.

VIII. ACKNOWLEDGEMENTS

This work was supported by grants from the Bureau of Land Management and the National Science Foundation (PLR 1417611/1417036). We thank R. Reanier, D. Meltzer, G. Streveler, J. Olnes, R. Ruess, M. Kunz, K. Kielland, G. Zazula, and D. Froese for interesting discussions about the ideas presented here.

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(Received 11 August 2017; revised 14 July 2018; accepted 19 July 2018; published online 22 August 2018)