



Megafauna in the Earth system

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Understanding the complex role of large-bodied mammals in contemporary ecosystems and the likely consequences of their continued decline is essential for effective management of the remaining wild areas on Earth. The very largest animals are in particular peril owing to a disastrous combination of continued hunting or poaching, habitat alterations, and loss of habitat. Because these threats are ongoing, conservation biologists may not be able to wait for the results of long-term studies before proposing potential mitigation strategies. A recent conference on 'Megafauna and ecosystem function: from the Pleistocene to the Anthropocene' at Oxford Univ. brought together paleontologists, conservation and environmental scientists and others who share an interest in characterizing the influence of large animals on ecosystems. Integrating historical perspectives of Late Pleistocene ecosystems when large-bodied animals were still widespread, with modern studies of areas with varying levels of intact megafauna, the aim was to develop a more holistic understanding of the consequences of the ongoing decline of large-bodied animals around the Earth. The conference resulted in the development of two special features – one in the Proceedings of the National Academy of Science, USA and one in *Ecography* synthesizing the state of our knowledge about the environmental legacies of the terminal Pleistocene megafauna extinction, the complex role of modern large-bodied animals and what the ongoing loss of their ecological interactions might mean in terms of ecosystem function. Here, we briefly review the main themes developed during the conference and outline promising future research directions.

Winston Churchill famously once said 'The nation that forgets its past has no future'. This phrase could just as well be applied to modern science. As we struggle with understanding the consequences of pressing environmental issues such as climate change, habitat fragmentation, and declining biodiversity, a consideration of how animals coped with similar events in the recent past can provide valuable insights into the adaptive limits of animals and the resilience (or lack thereof) of communities and ecosystems. Although such distant events may have had different causal drivers, virtually all species today successfully coped with these earlier challenges. For example, the terminus of the Younger Dryas at ~ 11.5 ka is generally considered a good proxy for anthropogenic warming because the ~ 10°C (18°F) abrupt increase in temperature at high latitudes occurred in perhaps as little as a decade (<www.ncdc.noaa.gov/paleo/abrupt/data4.html>). Indeed, unraveling the effects of anthropogenic environmental change on ecosystems without employing a historic perspective is likely to be too difficult to accomplish for effective mitigation strategies to be enacted in a timely fashion.

One of the more pressing contemporary issues is the decline of megafauna and the loss of their ecological interactions within ecosystems (Table 1). Across the Earth today,

large animals are in peril, particularly predators (Cardillo et al. 2005, Schipper et al. 2008, Barnosky et al. 2011, Estes et al. 2011, Hoffmann et al. 2011, Dirzo et al. 2014). With almost a quarter of species at risk (Table 1), it is clear that without strong and immediate conservation efforts, the future status of many is dire. Yet, aside from aesthetic considerations, we lack a basic understanding of what the decline and ultimate extinction of large-bodied animals means in terms of lost ecosystem function (Terborgh and Estes 2010, Estes et al. 2011). Continued trophic downgrading may lead to any number of unanticipated effects, including changes in the transmission or frequency of disease, alterations in biogeochemical cycling and carbon sequestration and changes in vegetation structure and composition (Estes et al. 2011, Dirzo et al. 2014). Predicting the effects of the loss of ecological interactions is difficult. Nor do we have a synoptic understanding of the thresholds that might lead to the 'unraveling' of ecosystems.

Only recently have we begun to appreciate just how drastically the Earth has been modified by human activities and for how long (Martin 1967, Thieme 1997, Alroy 2001, Barnosky et al. 2004, Lyons et al. 2004, Burney and Flannery 2005, Koch and Barnosky 2006, Smith et al. 2010,

Table 1. Changes in the body mass of mammals over the late Quaternary.

	Late Pleistocene (100 ka)						End Pleistocene (20 ka)						Historic (500 yr)						Modern					
	All species			Extinct species			All species			Extinct species			All species			Extinct species			All species			Extinct species		
	Mean mass (kg)	n	Maximum mass (kg)	Mean mass (kg)	n	%	Mean mass (kg)	n	Maximum mass (kg)	Mean mass (kg)	n	%	Mean mass (kg)	n	Maximum mass (kg)	Mean mass (kg)	n	%	Mean mass (kg)	n	Maximum mass (kg)	Mean mass (kg)	n	%
Africa	63.5	846	6500	651.5	5	0.6	58.9	841	6500	957.9	15	1.8	38.8	827	3940	278.4	5	0.6	36.5	822	3940	68.2	197	24.0
Australia	40.7	259	1500	186.4	24	10.2	4.6	235	420	NA	NA	NA	4.6	213	420	2.9	23	12.0	4.8	191	420	1.0	45	23.6
Eurasia	84.6	849	6500	1118.2	19	0.7	55.3	830	5500	1269	13	1.6	33.2	818	2720	105.1	4	0.5	32.8	814	2720	112.2	168	20.6
North America	111.1	598	10000	913.6	3	0.5	106.8	595	10 000	806.3	71	13.5	9.7	525	825	NA	NA	NA	9.7	525	825	8.2	55	10.5
South America	105.7	791	7580	742.2	5	0.6	101.7	786	7580	910.3	86	12.3	4.5	701	480	NA	NA	NA	4.5	701	480	11.9	105	15.0
Oceans	5569	118	180000	0	0	0	5569	118	180 000	NA	NA	NA	5615	118	180 000	2500	1	0.9	8218	77	180 000	173.7	9	7.7

Mean mass in each time bin is before the event. All marine mammals are included in 'Oceans' and not with continents; we also exclude all volant mammals. Species lists and body mass from MOM ver. 5.0 (updated from Smith et al. 2003). We define Late Pleistocene as ~ 46 ka for Australia, but ~ 100 ka for all other continents. Mean mass for the historic is after LP extinctions, but prior to human-mediated introductions or historic extinctions. Under threat defined as belonging to IUCN categories EX, EW, CR, EN, or VU. Data deficient (DD) animals are not included as vulnerable; thus the % of species under threat is underrepresented. Australia has had a high number of intentional and unintentional successful 'naturalizations' of introduced mammals; these are excluded here. Note the highly skewed body mass of extinct and extant species for each period; not until the modern era is the body size of threatened species largely indistinguishable from the average for species.

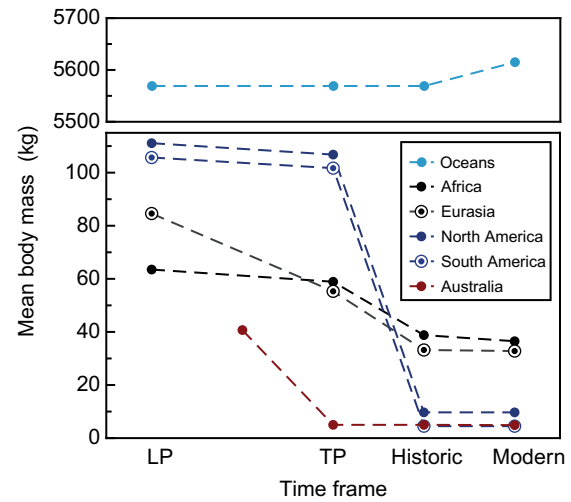


Figure 1. Mean body size of mammals on the continents during the modern, historic (~ last 500 yr), terminal Pleistocene (~ 15 ka) and Late Pleistocene (~ 100 ka). Size changes were driven by extinction events. Note the close correspondence between North and South America, and the precipitous drop of approximately an order of magnitude from the Late Pleistocene to historic period. While body size also dropped in EA and AF, much of the decrease occurred earlier in the Pleistocene and took place over a longer time frame not entirely captured in this figure. Data derived from an updated version of MOM ver. 5.0 (Smith et al. 2003); we ignore originations, which may slightly influence the overall pattern, but should not do so differentially.

Doughty 2013, Sandom et al. 2014, Faurby and Svenning 2015). Starting in the Pleistocene, large-bodied mammals have been systematically extirpated from much of the Earth's surface where they once roamed in abundance (Table 1, Fig. 1; Martin and Klein 1984, Thieme 1997, Martin and Steadman 1999). As recently as the terminal Pleistocene (~ 14 ka), for example, the mammal fauna of the Americas was more diverse than that of present-day Africa (Lyons et al. 2004, Faurby and Svenning 2015). Today, only a handful of large-bodied species remain (Smith et al. 2003). As humans migrated across the globe, from continent to continent, and from continents to islands, extinctions of animals – especially large-bodied forms – followed (Martin and Klein 1984, Martin and Steadman 1999). Indeed, the average body mass of mammals on the continents has dropped precipitously with the spread of humans around the world (Fig. 1). These changes occurred earlier and over a longer time frame in Africa and Eurasia (Fig. 1) because of the longer human presence. The pace of these extinctions increased over time as human populations increased and expanded. Trophic downgrading and the concomitant loss of large-bodied animals, while ongoing for millennia, was particularly acute at the terminal Pleistocene, when the entry of humans into the New World led to the subsequent loss of all mammals over 600 kg (Lyons et al. 2004) in a relatively brief span of time (Fig. 1; Faith and Surovell 2009). The size bias of the terminal Pleistocene megafauna extinction was unprecedented in the mammal fossil record (Alroy 1999, Lyons et al. 2004). The additional mortality imposed on animal populations by human hunting, even if not explicitly size selective, was sufficient to produce a size-biased

extinction because of the allometric scaling of life history features (Zuo et al. 2013).

For decades, a spirited debate has raged about the causal mechanisms underlying the terminal Pleistocene megafauna extinction (Martin 1967, 1984, Grayson 1984, Martin and Klein 1984, Graham and Grimm 1990, Stuart 1991, MacPhee and Marx 1997, Flannery and Roberts 1999, Martin and Steadman 1999, Stuart 1999, Alroy 2001, Barnosky et al. 2004). With the onset of large databases and geospatial analytical tools, it became possible to conduct careful quantitative studies, which have mostly resolved this issue; most scientists now concede that humans played a crucial role through some combination of hunting and habitat alteration (Alroy 2001, Lyons et al. 2004, Koch and Barnosky 2006, Zuo et al. 2013, Sandom et al. 2014, Bartlett et al. 2015). Largely overlooked until recently, however, were the consequences on terrestrial ecosystems and the environmental legacies of the loss of tens of millions of large-bodied animals (but see Zimov et al. 1995, Johnson 2009, Smith et al. 2010, Gill 2014). The Late Pleistocene megafauna extinction is the earliest known example of trophic downgrading (Pardi and Smith 2015), for example, most modern apex predators were mesocarnivores in the terminal Pleistocene. Thus, the Late Pleistocene may be the best analog we have for understanding how the loss of large-bodied animals influences ecosystem function. While there have been a number of recent papers yielding new insights into the impacts of megafauna and their extinction, there has been as yet, no global synthesis. Recent studies linking the perilous status of large-bodied animals with the unraveling of ecosystems (Cardillo et al. 2005, Schipper et al. 2008, Barnosky et al. 2011, Estes et al. 2011, Hoffmann

et al. 2011, Dirzo et al. 2014) has led to renewed efforts to integrate past history into conservation biology.

Following the Late Pleistocene megafauna extinction, there was an abrupt decrease in the biomass on Earth represented by megaherbivores (Barnosky 2008). While the biomass of large-bodied animals eventually ‘recovered’ to levels analogous to those present prior to the extinctions, there was a fundamental shift from a world dominated by wild animals to one largely composed of humans and their livestock (Barnosky 2008, Smith et al. 2015a; Fig. 2). These changes have continued to accelerate over the 19th and 20th centuries, leading to a current global population of well over 4.5 billion domesticated animals, many subsidized with domestic crops (Smith et al. 2015a). Indeed, the overall biomass of domestic animals is now much larger than the estimated mammal biomass at the terminal Pleistocene (Barnosky 2008, Smith et al. 2015a) and probably exceeds the number that could be supported on natural primary production alone. This transition of the biosphere has a number of important implications in terms of ecosystem function.

Operationally, a cow is not a mammoth. First, the much smaller body mass leads to different interactions with vegetation (Owen-Smith 1988). Studies demonstrate that remaining megafauna (e.g. elephants, giraffes and rhinos) are ecosystem engineers (Bakker et al. 2006, Asner et al. 2015, Bakker et al. 2015a, b); their larger extinct cousins probably also had this function (Zimov et al. 1995, Johnson 2009). The extremely large body size of megaherbivores allows them to have a unique impact on forest structure by breaking and knocking down trees; these functions are not replicated by smaller domestic animals (Asner and Levick 2012). Indeed, the transition from the vast ‘mammoth steppe’ of the

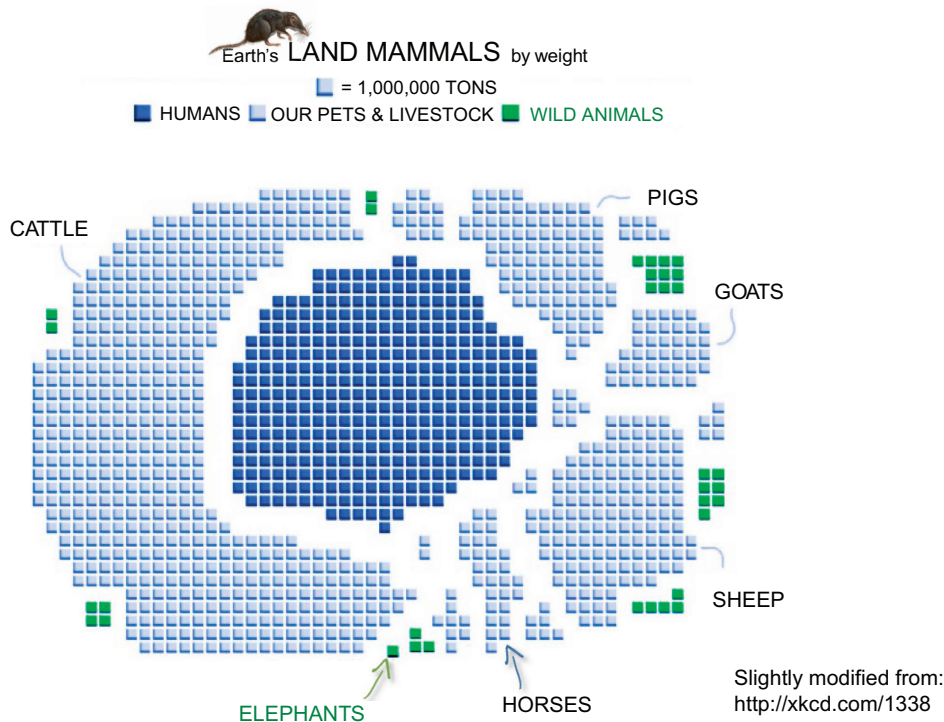


Figure 2. The current biomass of Earth’s land mammals. Modified with permission from: xkcd.com (<http://imgs.xkcd.com/comics/land_mammals.png>). This work is licensed under a Creative Commons Attribution-NonCommercial 2.5 License.

Pleistocene to the more waterlogged habitats of the Holocene may be at least partially owing to the absence of grazing by megaherbivores (Zimov et al. 1995, Johnson 2009). Other studies indicate modern elephants inhibit woodland regeneration and promote the formation of savannah grasslands; equids play a significant role in the dispersal of large-seeded plants (Whyte et al. 2003, Western and Maitumo 2004). Second, the replacement of most wildlife with domestic livestock has led to changes in the ecological functions of these herbivores in ecosystems. For example, domestic animals are unlikely to have taken over the nutrient dispersal roles of the now extinct megafauna because today most are confined in enclosed managed pastures or other settings, often even being housed indoors (Doughty et al. 2015b). The constriction of movement leads to a concentration of nutrients in one area, effectively stopping the diffusion of nutrients through-out ecosystems. These considerations and others lead to the question: are most of the planet's ecosystems in a disequilibrium state as a result of the terminal Pleistocene loss and ongoing decline of giant ecosystem engineers?

In March 2014, a three-day international conference was convened at St John's College at Univ. of Oxford (<<http://oxfordmegafauna.weebly.com>>) to examine these issues. Organized by Yadvinder Malhi, Chris Doughty, and Felisa Smith, the 'Megafauna and ecosystem function: from the Pleistocene to the Anthropocene' workshop pulled together experts from a variety of fields including conservation biology, molecular biology, biogeochemistry/ nutrient recycling, rewilding, and paleontology to examine the ecological interactions of large-bodied animals and their influence on the Earth over various temporal, spatial and hierarchical scales (Fig. 3). The Oxford meeting was unique in combining insights from Pleistocene ecosystems with contemporary studies of megafaunal depletion and its impacts, and folding this into a spirited discussion about megafaunal rewilding. The conference culminated in a wonderfully evocative and passionate talk by British writer George Monbiot, making the case for the megafauna rewilding of Europe. Moreover, the lively scientific interactions at the conference led to the simultaneous development of two special features; one in the Proceedings of the National Academy of Sciences USA, and the present one in *Ecography*. Here, we briefly review the major themes developed during this meeting and highlight some potentially fruitful future directions for continued research (Fig. 4).

Habitat and ecosystem structure

The two special issues include a number of papers that explore the influence of megafauna on habitat and ecosystem structure, which is often the most immediately visible effect of their presence (Fig. 4). In a natural state of megafaunal abundance, many ecosystems experience top-down control where megaherbivores break open what would otherwise be closed-canopy vegetation. Elephants in particular have a pronounced impact through the direct breakage and destruction of woody vegetation. For example, Asner et al. (2015) conduct a uniquely extensive survey of more than 10.35 million woody plant canopies throughout Kruger National

Park in South Africa for 6 yr using advanced airborne remote sensing techniques. Their results clearly demonstrate extensive opening of woody vegetation by elephants. Indeed, elephants were up to twice as important as fire frequency in determining tree fall. Similarly, Bakker et al. provide extensive review of the impacts of megafauna on vegetation structure in terrestrial (2015a) and aquatic systems (2015b). They report that browsers tend to have an inhibiting effect on woody vegetation. In contrast, although grazers can have negative effects on woody cover (through trampling and destruction of seedlings), they may also have positive effects through reduction of grass competition and decrease of fuel load, thereby reducing the frequency and intensity of fire. Moreover, they find that semi-aquatic mammals such as hippopotamuses and beavers are important geomorphological engineers, who can change land, vegetation composition and hydrology at landscape scales. Megafauna can have even have influence on the structure of closed canopy vegetation, Terborgh et al. (2015a, b) note that the forests of Gabon are lacking in small trees when compared to the Amazon, and suggest this is because of the presence of an 'elephant trap', where elephant damage that severely restricts tree recruitment and thereby shapes the structure of the adult tree community. Because tree species diversity is concentrated in the smaller tree size classes, the structural differences result in much reduced alpha diversity in African forests.

The Late Pleistocene extinctions can provide insights into how megafaunal decline leads to shifts in ecosystem structure, and show that ecosystem responses can be contingent on climate, and on the exact nature of the megafauna present. In a study of the impacts of megafaunal decline on ecosystem structure at four sites in the Americas, Barnosky et al. (2015) reported increases in woody cover following megafaunal collapse on two sites. The third site exhibited little ecosystem shift after megafaunal loss because woody vegetation cover was limited by low rainfall. At the fourth site, the lack of proboscideans limited megafaunal control on ecosystem structure. Similarly, following megafaunal collapse in Australia, Johnson et al. (2015) report that at a relatively warm and dry site there was an increase in fuel load and an ecosystem shift away from rainforest vegetation to fire-adapted sclerophyllous vegetation, whereas at a cool high elevation site there was little response to megafaunal loss, presumably because of temperature limitation on woody vegetation. Thus, the magnitude of response to the absence of large-bodied animals likely varied with geography and regional climate. Such an appreciation of megafaunal control on vegetation structure can yield new insights into the artificial, post-megafaunal nature of many contemporary ecosystems. For example, Doughty et al. (2015a) present an analysis that suggests that the woody savannas of South America would have been considerably more open and grassy in the presence of the megafauna (especially enormous proboscideans and ground sloths), which were once abundant. Megafauna also influence forest community composition through seed dispersal, with many large-fruited trees specifically adapted for dispersal via the guts of elephants and other megafauna. Often these large-fruited trees have higher stature and wood density, meaning that range restrictions and population reduction of these tree species can lead to biomass decline. Doughty et al. (2015d) present a case study analysis of the Amazon forest,



Figure 3. A poster ('visual minutes') drawn by artists Rowan Warts and Cécile Girardin during the 2014 Oxford megafauna conference. These artists attended the conference and drew the poster in real time based on ongoing presentations and ensuing discussions.



Figure 4. Contributions to the special feature in both Ecology and the Proceedings of the National Academy of Science USA organized by general scientific 'theme'. Many of these papers straddle multiple areas. Background image reprinted with permission from Karen Carr (< www.karencarr.com >).

providing strong evidence that megafauna extinction led to a long-term and potentially ongoing decline in forest biomass. The effects have been spread out over centuries or millennia because of the slow demographics of large forest trees.

Biogeochemical cycling

A number of papers explore the potential role of the now extinct megafauna on global biogeochemical cycles (Fig. 4). This is a difficult issue to address because we know little about these extinct animals beyond their body sizes and ranges (Smith et al. 2003, Faurby and Svenning 2015). However, much animal behavior and physiology scales with body size. Thus, using allometric relationships we can make predictions about how megafauna likely impacted biogeochemical cycling. For example, Doughty et al. (2015c) explore the interaction between animals and sodium, both now and prior to the megafauna extinctions. Sodium is unique in biogeochemistry because it is an element essential for animals but toxic to plants in excess. Nevertheless, animals get a majority of their sodium by eating plants. Today, much of the Amazon basin is non-halophytic; such plants are less productive with increased sodium concentrations. Using a simple model, they find a difference in the spatial distribution of sodium after the megafauna extinction; today concentrations are greater on the coast than inland, which has implications for both plants and animals. In another paper, Doughty et al. (2015b) quantified global fertility in the oceans, on land, rivers and air. They hypothesized that an efficient system of recycling phosphorus against entropy from the ocean depths to the continental interiors existed in the past but currently is much reduced with the widespread decline of megaherbivores. These authors went on to calculate that globally the ability of animals to transport nutrients away from a point source has decreased to 6% of its former capacity. Overall, these papers predict that large abundant free roaming animals lead to a more fertile planet.

The megafauna extinctions may also have impacted atmospheric composition of gases and perhaps even climate. For example, Smith et al. (2015a) demonstrate that methane production by herbivores scales allometrically with body mass and that the loss of hundreds of millions of megaherbivores across the globe likely resulted in significant decreases in the global methane budget. Intriguingly, the terminal Pleistocene megafauna extinctions occurred just prior to the onset of the Younger Dryas cold interval, which leads to the question of whether the loss of hundreds of millions of large-bodied animal contributed to this event. A unique and precipitous drop in atmospheric methane concentrations is recorded in the ice core record for the terminal Pleistocene, as well as a shift in the primary sourcing of methane isotopes from megaherbivores to wetlands. The authors suggest that other megafauna declines over human history associated with disease or warfare may also have led to changes in the contribution of herbivores to the global methane budget (Smith et al. 2015a).

Atmospheric compositions of CO₂ may also have been affected by megafauna extinctions in several ways. Along with changes in animal respiration, which have not yet been quantified, the structure of vegetation influences carbon

flux. For example, as demonstrated by Bakker et al. (2015a) and Doughty et al. (2015d) megafauna negatively impact savanna tree cover. Since woody biomass often contains more carbon than the grasslands it replaces, woody encroachment can lead to a corresponding drawdown in atmospheric CO₂ concentration. Further, the lost role of megafauna as seed dispersers may be important; numerous New World tree species are dependent on megafauna as seed dispersers (Janzen and Martin 1982). Interestingly, Doughty et al. (2015d) found range reductions in tree species with fruit that were likely distributed by megafauna (Guimarães et al. 2008); their calculations suggest a reduction in the geographic range of tree species results from decreased seed dispersal distance following the loss of large-bodied animal dispersers. Since large-seeded fruit trees tend to have less dense wood, this study also suggests there were fundamental changes in carbon composition in forests, and moreover, that the total carbon content in Amazon rain forests has been reduced by ~1.5% due to the terminal Pleistocene extinctions.

Community assembly and/or species interactions

A core insight emerging from recent work is the strong top-down control that megafauna exert on ecosystem structure (Terborgh et al. 1999, Terborgh and Estes 2010, Estes et al. 2011). The loss of large herbivores and carnivores can cascade through other trophic levels of an ecosystem, shifting the species composition and abundance of other animals, and often leading to a release of pressure on mesocarnivores and mesopredators (Estes et al. 2011). Pardi and Smith (2015) examined such 'trophic downgrading' in the terminal Pleistocene by examining the influence of the loss of apex carnivores on surviving lineages of canids in North America. Using species distribution modeling, they found that surviving canids increasingly partitioned their climatic niche, and contrary to expectations, did not expand into the abiotic niche space vacated by the extinction of apex predators. Instead, the addition of a novel predator, man, into the continent may have outweighed the advantages of reduced intra-guild competition. Thus, the negative pressure of competition with humans and accompanying domestic dogs outweighed the positive effects of trophic release, resulting in little range expansion in the Holocene.

Large carnivores exert a strong control on prey both through direct predation, as well as by the generation of 'landscapes of fear', where prey alter behavior and avoid parts of the landscape where they are most vulnerable to predation (Laundré et al. 2001). This can result in a reduction of herbivore pressure on vegetation. In the Pleistocene, large-bodied carnivores were particularly abundant. The terminal Pleistocene extinction led to the loss of 12 top carnivores in North America alone, including the scimitar cat *Homotherium serum*, the American lion *Panthera leo atrox*, the saber-tooth cat *Smilodon fatalis* and the short-faced bear *Arctodus simus*. These species were all larger than the modern African lion, with the short-faced bear approaching 800 kg (Smith et al. 2003). Work by Van Valkenburgh et al. (2015) suggests that the Pleistocene community richness of large carnivores exerted intense predation pressure and control on the herbivore community, leading to a landscape of fear.

Even the very largest megaherbivores (>5–10 tons), often thought to be immune to predation, were likely affected. Because the Pleistocene carnivore guild was more diverse and composed of larger taxa, numerous species specialized on megafauna. Using historic and modern predator/prey body mass ratios, the authors hypothesize apex carnivores of the Pleistocene likely had the capacity to exert ‘top down’ control on populations by preying on juveniles. This may help explain the co-existence of many large-bodied herbivores.

Megafauna most likely also influenced indirect interactions within communities. Smith et al. (2015b) present an analysis of community assembly following megafaunal collapse at a site in Texas. They demonstrate significant shifts in alpha and beta diversity related both to earlier climate changes as glaciers retreated and to the terminal Pleistocene megafauna extinction. Moreover, they show that the catastrophic loss of 80% of the large-bodied grazers in the community led to an encroachment of woody vegetation and a dramatic increase in the relative diversity of frugivores and browsers. Further, there was a decrease in the number, type and intensity of species associations after the extinction, suggesting that post-megafaunal communities are simpler in structure and possibly less resilient to environmental change. Similarly, Estes et al. (2015) suggests that the extinction of sea cows in the Commander Islands after their discovery by Europeans in 1741 resulted from multiple factors – not just from direct human overkill for the Pacific maritime fur trade. Rather, a major contributing factor was the concomitant hunting and precipitous decline of sea otters. Sea otters are a keystone species in nearshore marine communities, maintaining kelp forest ecosystems by foraging on urchins and other invertebrates (Estes and Palmisano 1974). While humans hunted sea cows, they also exploited sea otters to near extinction (Estes et al. 2015). Thus, the authors demonstrate that the direct extinction of a few large vertebrates in the late Pleistocene can result in a cascading series of co-extinction of other species.

Rewilding

Two of the special issue papers (Fig. 4) focus on ‘rewilding’ (Martin 1999, 2005, Martin and Burney 1999, Donlan et al. 2005, 2006), a recent, often megafauna-oriented approach to nature conservation. The concept of rewilding is rapidly gaining interest among land managers, environmentalists and scientists alike, while at same time also remaining controversial (Oliveira-Santos and Fernandez 2010, Jørgensen 2015). Reflecting its young age and intuitive appeal, the concept of rewilding has evolved and diversified into varied meanings. The first special issue paper on rewilding by Svenning et al. (2015) provides a distinct term ‘trophic rewilding’ and a clear, theory-based definition: ecological restoration strategy that uses species introductions to restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems. It provides a synthesis of the current scientific basis for trophic rewilding, with top-down ecosystem control and trophic cascades as the core conceptual framework and the formerly ubiquitously rich megafauna as a key empirical backdrop. The second rewilding paper by Jepson (2015) provides an important

complementary political and cultural perspective on rewilding within a specific European context. As a core idea, Jepson proposes that a system of experimental sites, which should be close to urban centers to engage the public and to be close to where policy is formed. He argues that a key objective for them should be to experiment with the interplay of ecological restoration with society and economy to help build rewilding’s potential to reinvigorate nature conservation at the broad societal level. Both papers highlight the urgent need for more empirical work; the current empirical studies on rewilding remain too scarce to allow generalization of the ecological effects and potential unintended consequences.

Megafauna extinctions

Not surprisingly given the general interest in the event, several of the papers in the special feature focus on the megafauna extinction itself. For example, Bartlett et al. 2015 employ high-resolution climatic reconstructions of the late Quaternary, megafauna last occurrence dates, and patterns of human colonization to examine the terminal Pleistocene megafauna extinction within an explicitly geospatial context. They find that human colonization patterns were the main driver across the globe, explaining about 60% of the variation in extinction patterns. Climate was also a contributing factor, although it explained no more than ~ 25% of the variation. The study did not assess whether climate directly impacted fauna or if it acted by shifting the distribution of humans (as discussed in Sandom et al. 2014). There are some interesting differences in the ability of their model to characterize extinction patterns; notably it overestimated extinctions in Asia. Both Surovell et al. (2015) and Villavicencio et al. (2015) are concerned with the chronology of extinction, but they come to somewhat different conclusions about causal mechanisms. Using a series of radiocarbon dates on extinct taxa from South America, Villavicencio et al. (2015) report co-existence of humans and megafauna for several hundred to as long as several thousand years. Based on this overlap, they conclude that humans were not the main drivers behind the extinction, but rather that climate changes resulted in the reduction of open habitats that made megafauna susceptible to extinction. Surovell et al. (2015) compiled an extensive list of direct radiocarbon dates on extinct genera from North and South America and examined the timing of the extinctions to test the ‘wave like’ pattern postulated by Paul Martin. Their expectation was that the initial decline of megafauna should correspond with the earliest evidence for human colonization, and that the progression of dates should occur first in eastern Beringia, then in the continental United States, and lastly in South America. They find support for this time transgressive pattern, with extinctions occurring in Beringia ~ 14.5 to 15 ka, in the continental US at around 13.4 ka, and ~ 12.8 ka in South America.

Conclusions

The papers in these special features demonstrate several salient points. First, relative to most of Earth history, we live in a depauperate world, and one that is quickly

becoming more so (Table 1, Fig. 1). The dominant animals on Earth today are humans and our domestic livestock (Fig. 2); remaining wildlife and natural habitats are in decline. Second, given the undeniably important role that large-bodied animals play in ecosystems, there is an urgent need to understand in a holistic way just how ecosystems may 'unravel' with their decline or extinction. Continued trophic downgrading may lead to unanticipated effects that influence virtually all aspects of ecosystems (Estes et al. 2011, Dirzo et al. 2014). As the papers in this special feature demonstrate, the effects of the loss of ecological function can fruitfully be examined using late Pleistocene ecosystems as an ecological proxy. Third, maintaining intact assemblages of large-bodied animals and their ecological interactions will likely take active, rather than passive, management of our remaining wild areas. Both the Jepson (2015) and Svenning et al. (2015) papers highlight the need to develop a much larger, systematic research program exploring the potential for rewilding. This includes the need for understanding the importance of landscape constraints such as available habitat and the interplay with ongoing anthropogenic climate change. Moreover, there is a need for the development of effective management tools for rewilding to succeed, both in terms of ecological dynamics and outcomes and to address societal and political constraints (Svenning et al. 2015). Here too a temporal perspective can yield valuable insights. Indeed, unraveling the complicated and cascading effects of anthropogenic-induced environmental changes and continued biodiversity loss on Earth ecosystems requires long-term experiments to properly characterize both direct and indirect effects that play out over various time scales. Given the rapid decline in natural systems over recent decades (Cardillo et al. 2005, Schipper et al. 2008, Barnosky et al. 2011, Estes et al. 2011, Hoffmann et al. 2011, Dirzo et al. 2014), it is unlikely that wildlife managers have the time to conduct such studies before attempting mitigation measures. Thus, as Winston Churchill posited, past history may hold the key to the future.

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