Oral Presentation Abstracts
Day 1: Causes and impacts of megafaunal loss

Ghosts of lost giants

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A few tens of thousands of years ago, a mere blink of an eye on ecological and geological timescales, every continent except Antarctica carried abundant large herbivores and carnivores. There has been debate on the causes of the disappearance of these creatures, but less focus on understanding the environmental implications of these extinctions. Did Pleistocene megafaunal extinction cause large scale ecological and biogeochemical changes? How does a possible human role in these extinctions alter our perception of the history of human relationships with nature? What echoes do contemporary ecosystems carry of these lost megafauna? What lessons can be learnt in the context of ongoing megafaunal loss in many regions of the world? And what are the potential, the challenges and the ethics of "bringing back" megafauna into the contemporary, rapidly changing world of the Anthropocene? All these themes will be explored in this three-day workshop.

Mammoth extinction, refugia, and the effects of climate and people

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A global database of some 2400 published and new radiocarbon dates on woolly mammoth (*Mammuthus primigenius*) has been audited, using objective criteria, to around 1900 'good' dates. This represents by far the largest number of dates for any extinct megafaunal species, allowing detailed mapping of range changes in the trajectory to extinction, although direct dates for North America outside Alaska/Yukon are few. Mammoths were widespread across northern Eurasia and Beringia for much of Greenland Stadial 3 (GS-3) and the early part of GS-2, but the species vacated western and central Europe entirely for the interval 21.5-19.5 ka, in the middle of GS-2 and corresponding to the maximum extent of the European ice sheet. The range expanded again in late GS-2, but in the Bølling warming (14.6-13.9 ka) both the European and Siberian ranges became restricted and possibly disjunct. Re-dating of key specimens now suggests that with the afforestation of the Allerød (13.9-12.8 ka), Europe and western Siberia were completely vacated by mammoths; this corresponds closely in time with the global extinction of woolly rhino (*Coelodonta antiquitatis*) and cave lion (*Panthera leo*) – see presentation by Stuart. The Younger Dryas (GS-1, 12.8-11.7 ka) saw North American woolly mammoth extinct, and Eurasian populations restricted to northernmost Siberia with a short-lived re-invasion of north-east Europe. By 11 ka (within the earliest Holocene), mammoth was extinct in mainland Eurasia. Terminal island populations in the Beringian region expired on St Paul (Pribilof Islands) around 6.5 ka and Wrangel Island around 4 ka. The major shifts in mammoth range after 40 ka correspond to climatic and vegetational events, suggesting these as the main driving force. Although distributional gaps are hard to deduce from fossil data, the terminal distribution of *M. primigenius* is at least consistent with severe range reduction, and probably fragmentation, prior to extinction. Such reduction to small, refugial populations probably affected many megafaunal species, in a cyclical manner, throughout the climatic oscillations of the Quaternary. In most cases, these populations survived to re-expand on the return of favourable conditions. At each major climatic cycle, however, some species failed to survive the refugial phase, producing the observed 'background' level of extinction. At the last refugial contraction (broadly at the last glacial-interglacial transition but varying in time among species), extinctions substantially exceeded background rate, leading to the suggestion of a critical human contribution to extinction. While this idea is attractive, evidence of mammoth hunting is limited, especially in the far northern 'refugial' areas, and the significance of celebrated mammoth-bone

assemblages such as Yana River and Berelekh is unclear. Thus far there is no evidence for human occupation of either St Paul or Wrangel Island (the terminal mammoth refugia) until after the extinction of their respective mammoth populations.

Ancient DNA reveals past global population dynamics links to climate-driven range dynamics

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Assessing population size and range dynamics during Late Quaternary climate change is critical to understanding extinctions dynamics, their legacy (populations and species) on species' contemporary distributions, as well as identifying species most likely to be at future risk. Improvements in radiocarbon dating methods, advances in recovering ancient DNA (aDNA), and increased spatiotemporal resolution of palaeoclimate data, combined with sophisticated ecological and coalescence models, have improved our understanding of how single species and populations responded to past climate change. However, a global synthesis on past population responses to climate change across species and ecosystems is still lacking. We have compiled a large-scale phylogeographic dataset of modern and ancient DNA for 20 mammal species (4013 mtDNA sequences) to estimate in a comparable analytical framework past trends in population size and other population events (i.e., population splits) over the last 50,000 years. We also use range simulations to explore the mechanisms (i.e., niche lability, dispersal potential) that may explain Late Quaternary population and range size dynamics. Past responses vary across taxa and geographical location, suggesting complex responses to climate change. Our study provides a large scale multi-taxa comparative framework to Late Quaternary population responses under environmental change and lays the foundations to better forecast future extinctions based on genetic parameters.

The case for Clovis overkill in North America

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Although it is fairly clear that Paul Martin's more than 40 year old blitzkrieg model of Pleistocene overkill is not correct, in North America the overkill hypothesis persists in a similar but slightly modified form. In this paper, I review the archaeological evidence for human hunting and the geochronology of human colonization and megafaunal extinction in the terminal Pleistocene of North America. While overkill remains a controversial idea in American archaeology, multiple lines of evidence converge to suggest not only human association with North American megafaunal extinctions, but also that human hunting of extinct taxa is most likely to blame.

Ecological state changes and megafaunal extinctions in southern Patagonia, South America

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South America lost more species of megafauna near the Pleistocene-Holocene transition than any other continent, but the timing of extinctions and possibly also the causes seem to differ depending on ecological setting, with potentially earlier extinction in the tropics, a protracted event during which species dropped out over a few thousand years in the mid-latitudes, and a fairly sudden disappearance of species in southern Patagonia (south of 50°). Here we focus on the sudden event in the Patagonia, comparing vetted radiocarbon dates of the youngest known occurrences of megafauna, archaeological presence, and environmental proxy data to examine the role of threshold and interaction effects in triggering abrupt extinction. We focus on the Ultima Esperanza region of Chile, but also bring in information from other sites in the Southern Cone. In this area, *Mylodon*, *Hippidion saldiasi*, *Lama cf. owenii* and *Vicugna vicugna*, *Smilodon*, *Panthera*, all drop out of the record near 10,000 radiocarbon years ago. Humans entered the region slightly earlier, but by the time of extinction had increased in numbers as judged from frequency of archaeological remains. Contemporaneously, Nothofagus increased relative to grass, and other vegetation changes also occurred, as indicated by pollen from Mylodon dung and peat cores. Fire frequency increased near the same time, glaciers retreated relatively quickly, and temperature warmed in the vicinity. The coincidence of all these events suggests that the rapid extinction of the megafauna resulted from the interaction of multiple drivers, none of which by themselves may have been adequate to cause such an abrupt loss of megafauna, but whose interaction triggered a sudden ecological state change. Comparison of the information now available from southern Patagonia with other regions of South America is expected to further clarify the pattern and causes of extinctions at the continental scale.

Anthropogenic drivers of megafaunal extinction: support from a high resolution, quantitative global analysis

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There is considerable debate over the relative importance of anthropogenic and climatic drivers of the Late Pleistocene megafaunal extinctions. Key to the debate is the extent to which human arrival and climatic change coincided with the extinctions in different parts of the world. To account for the uncertainty in these data we divided the world into 14 regions and we assigned extinctions and arrivals in each to a 4,000 year time period. We then calculated the proportion of megafaunal genera going extinct per region per time period and fitted generalized non-linear models to these data, using human arrival dates and temporally and spatially explicit climate reconstructions as predictors. We used best estimates from archaeological and genetic data for extinction and human arrival dates, but ensured that our models included all plausible dates to ensure they are robust to future advances. We modelled the effects of humans as a non-linear function with the effect peaking soon after arrival and decaying over time, dependent on the size of the region being colonised. Models including human arrival performed best, suggesting that although climate contributed to extinctions, human arrival is likely to have been the decisive factor. To our knowledge this is the first study to quantitatively assess all global megafaunal extinctions of the last 80,000 years in relation to climate change and human migration at such high spatial and temporal resolution.

Global Late Quaternary megafauna extinctions linked to humans, not climate change

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The Late Quaternary megafauna attrition was a severe global-scale extinction event. To date, focus has been on the extinction chronology of individual or small groups of species, specific geographic regions, or macroscale studies at very coarse geographic and taxonomic resolution, limiting the possibility of adequately testing the proposed extinction hypotheses. We present the first global analysis of this extinction based on comprehensive country-level data on the geographic distribution of all 177 large mammal species (≥10 kg) that have gone globally or continentally extinct between the beginning of the last interglacial at 132,000 years BP and the late Holocene 1000 years BP, testing the relative roles played by glacial–interglacial climate change and humans. We show that the severity of extinction is strongly tied to hominin palaeobiogeography, with at most a weak, Eurasia-specific link to climate change. This first species-level macroscale analysis at relatively high geographic resolution provides strong support for modern humans as the primary driver of the worldwide megafauna losses during the Late Quaternary.
In light of this global megafauna attrition we explore how predator-prey communities have been altered. We assess macroscale mammalian predator-prey community structures to: 1) analyse felid resilience to further attrition of prey species richness; 2) determine the extent predation as a process has been altered by the loss of guild members; and 3) identify regions that could be suitable for predation rewilding by comparing current felid ranges with potential felid ranges and prey availability.

Radiocarbon chronology of extinct and surviving megafauna in Northern Eurasia

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Northern Eurasia is an especially fruitful region for the study of Late Quaternary megafaunal extinctions, not only because of the wealth of available archaeological, paleontological, and environmental data, but also because it has by far the largest number of radiocarbon dates made directly on megafaunal remains. Our research over the past 13 years, funded by the UK Natural Environment Research Council, has included amassing a substantial database of radiocarbon dates made directly on megafaunal material by: a) AMS dating more than 700 samples at Oxford (ORAU); b) incorporating AMS dates from recent ancient DNA projects; and c) objectively auditing other dates from the literature. The calibrated dates are used to construct detailed chronologies for the extinct species and also many of the survivors. Plotted as time-sliced maps and as chronological/geographical charts, these reveal distinct patterns for each species.
Extinctions in northern Eurasia were staggered over tens of millennia, and within each species populations disappeared earlier from some regions than from others. For example, cave bear *Ursus spelaeus* was probably extinct by ca. 28.5 ka, close to the onset of Greenland stadial GS-3, whereas cave lion *Panthera spelaea* and woolly rhinoceros *Coelodonta antiquitatis* survived until ca. 14 ka. Others survived in limited areas into the Holocene, e.g. giant deer *Megaloceros giganteus* to at least 7.7 ka in western Siberia and European Russia. Species such as saiga *Saiga tatarica* also underwent severe range reductions during the late Quaternary, but managed to survive until the present day.
Comparing these patterns with environmental proxy data, it is evident that climatic and vegetational changes had major impacts on species' ranges. Moreover, the contrasting chronologies and geographical range contractions are consistent with environmental drivers relating to species' differing ecologies. However, the possible role of humans in this process has still to be satisfactorily explored.

Recalibrating the Anthropocene: humans, megafauna and global biogeochemical cycles

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The thin film of organisms that inhabit the surface of the planet influence their environment in many ways. Studies on extant elephants, for example, demonstrate that browsing influences plant structure and composition, as well as compaction of soils, which can lead to alterations in the water table among other things. Herbivorous mammals are also major producers of methane, a greenhouse gas with a high global warming potential; domestic livestock currently contribute ~15-20% of the annual input. While it is clear that the human-mediated extinction of herbivorous megafauna in the late Pleistocene must have had profound effects on terrestrial community structure and function, less clear are the potential impacts it may have had on atmospheric gas exchange and perhaps even climate.

Here, using allometric relationships between body mass and density, methane production and geographic range, we calculate the annual decrease in the methane source pool resulting from the extinction of 114 large-bodied herbivorous species in the Americas ~13,400-11,500 ybp. Because previous workers have not examined explicitly the allometric relationship between methane production and body mass, we devised a novel way to estimate methane output, which yields significantly better fits to empirical data than the standard IPCC methodologies. Data were compiled from experimental studies for mammals spanning a spectrum of digestive strategies (e.g., hindgut versus foregut herbivores), life stages (e.g., growing, subadult, mature) and body mass (10-4,000 kg) to reflect the normal variation present in wild populations.

Our results suggest the megafauna extinction led to a loss to the global atmospheric pool of at least ~9.6 Tg (upper limit, 25.5 Tg) CH4 annually; sufficient to explain a significant portion (12.5-100%) of the ~200 ppbv decrease in atmospheric methane detected in isotopic analyses of ice-core records from this time. The reduction in methane is also synchronous with the Younger Dryas stadial, an abrupt transition ~12,800 ybp where climate returned to near glacial conditions in the higher latitudes of the Northern Hemisphere. Our analysis suggests human activities measurably influenced global biogeochemical processes and climate long before the development of agriculture, complex civilizations and the industrial age. Finally, we note that current methane inventories underestimate the contribution by wildlife to the global output and also likely overestimate output by small domestic livestock.

Predator–prey dynamics in late Pleistocene North America

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Current efforts to understand the ecological roles of large carnivores within ecosystems are greatly hampered because there are so few extant communities with significant populations of more than one or two large predator species. The limited studies that have been done indicate that prey densities within communities with just two large predator species are much lower than those with a single predator species. This suggests that predator to prey ratio will increase with large predator species richness, resulting in increased interspecific competition among big carnivores. Given that the species richness of large carnivores in late Pleistocene communities was more than double that observed today, it appears likely that predation would have kept ungulates at relatively low densities and competition among large

carnivores would have been intense. Testing this hypothesis is difficult because species abundance is notoriously difficult to ascertain from fossil assemblages due to biases in preservation. However, relative predator-prey densities may be revealed from studies of dental growth rates, wear, and fracture. Among extant large carnivores, rates of tooth wear and fracture increase when prey numbers are low, competition intensifies, and carcasses are more fully utilized. Remarkably, analyses of dental attrition in late Pleistocene North American large carnivores have documented very high levels of tooth fracture that exceed those of most living carnivores. This suggest that at the time of human arrival to North America, ungulate prey were already at low densities due to top-down forcing, making them more vulnerable to the effects of this unusual new predator.

Megafaunal extinction and its impact on mammalian community structure

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What happens to a biota after a size biased extinction? Approximately 10 kya in North and South American and 46 kya in Australia, virtually all of the mammalian megafauna disappeared. This extinction was fundamentally different from previous ones in that it was highly size biased and directly affected only a portion of the available biota. Moreover, unlike earlier events, the pattern and timing of the late Quaternary extinction across the globe suggests that migrating humans played a large role. Using body size, trophic category and species composition as metrics, I evaluated the effects of the late Quaternary extinction on community structure. There was significant turnover in community composition likely related to the extinction and climate change. However, community body size distributions before and after the extinction do not show significant changes in shape. Comparison to current communities indicates that body size distributions show greater changes in shape across latitudes now than we see in the temperate zones before and after the extinction. Within communities, the different trophic groups show significant differences in their body size distributions across all time periods. Regardless of taxonomic identity or time period, different trophic groups occupy different regions of a community body size distribution. Herbivores have a more peaked body size distribution than do carnivores or omnivores. In addition, body size distributions of herbivores and omnivores tend to have a more positive skew than carnivores. Finally, omnivores have lower mean and median body sizes than do either herbivores or carnivores. The similarity in community body size distributions across time, despite changes in taxonomic richness and composition suggest that there are fundamental rules structuring communities and these rules operate consistently during times of major climate change.

Estimated loss in species, phylogenetic and functional diversity in mammals as a consequence of the Late Pleistocene and Holocene range collapses and extinctions

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Several studies have compared geographic patterns in past diversities with geographic patterns in present diversities, but such comparisons are difficult because of different quality and quantity of information in the two datasets. In this study we have tried a different route by estimating potential contemporary natural distributions of all mammal species if no species had become extinct in the Late Pleistocene or Holocene and no species had its range influenced by humans, making more direct comparisons possible.
For this we estimated potential distributions for 725 species accepted by IUCN where we found evidence or at least strong indications for recent human-induced range changes and 258 species that went extinct

before 1600AD, but later than 130,000 years BP, while we assumed that the range of the remaining species were not influenced to any larger extent by humans. Excluding marine species this led to a total change from 1,076,442 to 1,289,403 occurrences in 100 by 100 km cells. For the 725 IUCN species with recent range changes we used available information on historic distributions whenever possible and if this was not the case estimated potential ranges based on the ecological characteristics and the geography of the current range. For the extinct species we generally estimated potential current range based on fossil-co-occurrence patterns, assuming that a given extinct species would also have suitable climatic conditions in the areas currently inhabited by the same species assemblages it co-occurred with in the past.
In this presentation we will compare these potential distributions with the contemporary patterns (i.e. the loss in diversity) for the three different diversity measures both species, phylogenetic, and functional diversity and for all mammals as well as for megafauna only. We will discuss the geographic variation in the extent of loss as well as the potential drivers of this variation.

Megafauna and ecosystem dynamics in the Plio-Pleistocene: insights from the Italian fossil record

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During Ice Age the Italian peninsula supported a broad range of megafauna: saber-cats, mammoths and rhinos were common elements of the prehistoric landscapes. I present multiple lines of evidence that indicate a strong link between changes in the megafauna community structure and ecosystem functioning at both local and regional scale. Palaeoecological reconstructions of biomass fluxes and predator–prey relationships suggest that Late Pliocene/Early Pleistocene (c.ca 2.0 million years ago, Ma) Italian ecosystems were under top down control from the carnivores. Middle and Late Pleistocene (from 1.1 Ma until 0.3 Ma) ecosystems were under bottom up control from the large herbivores, likely because of stronger climatic instability. Indeed, the biomass of herbivorous megafauna shows a strong positive correlation through time with isotopic climatic proxies. This demonstrates how fossil records may be used to obtain insights on the link between ecosystem functioning and climate changes. More data are needed on the extant ecosystems to enhance and refine palaeoecological interpretations and their potential use as a tool for preserving future biodiversity.

Marine megafaunal extinctions and trophic cascades: what really happened to Steller's sea cow?

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The late Pleistocene extinction of so many large-bodied vertebrates has been variously attributed to two main causes: rapid climate change and the impacts of humans as they spread from the Old World to previously uninhabited continents and islands. Many large bodied vertebrates, especially large apex predators, hold their associated ecosystems together through top down forcing processes, especially trophic cascades. Thus, a third possibility for at least some of the Pleistocene extinctions is that they occurred through the shifts in necessary ecosystem characteristic, which disappeared with the loss of one or more keystone species. Here we explore this idea for sea otters and Steller sea cows. Sea cows consumed kelps and perhaps other large, fleshy macroalgae, which are maintained in abundance on coastal reefs across the North Pacific Ocean by way of the sea otter-sea urchin-kelp trophic cascade. When sea otters are lost from a shallow reef system, sea urchins increase to a point where they reduce kelp biomass (and by proxy, net primary production) from fleshy macroalgae by 95 to 99 percent. It is thus possible

that the associated decline of obligate kelp feeders, like the Steller sea cow, caused them to dwindle to extinction via rapid declines in carrying capacity and, ultimately, demographic stochasticity. Although Steller sea cows had become extinct by the time the first European explorers visited most of the North Pacific Ocean, they survived in abundance in the Commander Islands, the one location in their historical range that was never colonized by aboriginal peoples. The shipwrecked Bering Expedition discovered the Commander Islands in 1741. By 1754 the local sea otter population had been hunted to extinction, and sea cows were extinct by 1768. Although this latter extinction event is thought to be a consequence of direct human overkill, we show that it is also an almost inevitable consequence of the loss of sea otters, even if not a single sea cow was killed directly by humans. This example raises the possibility that just a few directly caused extinctions of large vertebrates resulted in the coextinction of numerous other species.

Trophic downgrading before trophic downgrading: the influence of the terminal Pleistocene extinction on the North American carnivore guild

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Trophic downgrading occurs when an ecosystem loses its apex consumers leaving what had been mesoconsumers as the new top of the food chain. The intensity of modern trophic downgrading is unlike anything since the end of the Pleistocene. North America once supported a diverse suite of megafauna and consequently, more complex trophic interactions. These interactions likely changed with the extinction of most megafauna around 13 thousand years ago, including the very largest carnivores. Indeed, our modern perception of tropic downgrading is biased by a world where the "largest" apex consumers within most terrestrial communities are actually mesocarnivores several orders of magnitude smaller than their paleontological precursors, that may not even be ecological equivalents.
To gain a better understanding of the long-term effects of trophic downgrading, we examine the late Pleistocene event. We employ fossil occurrences from the Neotoma paleontological database, modern specimens from the museum collections, and 1,000-year CCSM3 climate simulations for the last 21,000 years to model changes in the realized niches of twenty key North American carnivore species ranging in body mass from 147g to 139kg. To address the question of how broad scale trophic downgrading affects long-term interactions within a guild, we calculated the extent of interspecies niche overlap as well as characterized niche expansions and contractions. We choose 4 time intervals: a) late Pleistocene prior to the megafaunal extinction, b) early to middle Holocene, following the event, c) late Holocene, after the thermal maximum, and d) modern. The niche of a species is defined by the abiotic environment and is influenced by biotic interactions. Therefore, we interpret greater niche partitioning and niche contractions as evidence for greater negative interactions, such as intraguild competition and predation. We find patterns of trophic release following the Pleistocene extinction that are consistent with contemporary community studies.

Day 2: Environmental impacts of megafaunal loss

Ecological impacts of extinction of Australia's Pleistocene megafauna

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Australia is significant to our understanding of the roles of human impact and climate change in causing global extinction of late Quaternary megafauna, because people arrived on this continent in the middle of

the last glacial cycle, during a period of climatic stability and well before the climate upheavals of the Last Glacial Maximum and the Pleistocene/Holocene transition. The Australian case therefore provides a test of whether human impact alone was capable of removing large vertebrates from an entire continental fauna. Recent studies using multiple independent lines of evidence strengthen the conclusion that human arrival did cause rapid and synchronous megafaunal extinction across Australia, with no contribution from climate change. The decoupling of extinction and climate change in Australia also helps us to understand the ecosystem consequences of megafaunal extinction, because in Pleistocene Australia signals of the effects of removal of mega-herbivores are less confounded by environmental shifts driven by climate than they are on other continents. I review studies of environmental change in Australia across the period of megafaunal extinction. This evidence shows that the effects were sometimes large, consisting of changed forest composition, increased fire activity, and increased vegetation density in woodlands and shrublands. However, these impacts varied across the continent, being least in unproductive environments where plant growth was likely to be strongly limited by low temperature or rainfall.

A natural experiment in keystone herbivore removal: Pleistocene extinctions, novel communities, and enhanced fire regimes in North America

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In North America, the last deglaciation (18,000–6,000 BP) was a period of widespread environmental upheaval. The extinction of the North American megafauna and the formation of novel plant associations are well-known features of this interval, but linkages between these phenomena were complicated by the limitations of the fossil record. The dung fungus Sporormiella has provided an opportunity to test the impacts of the megafaunal extinctions on ecosystems, by locally timing the loss of megaherbivores relative to changes in vegetation, fire, or other functions of interest. Across a transect of sites in the Great Lakes region of the United States, the local population collapse of megaherbivores was immediately followed by changes in forest community composition and increased fire activity. The loss of keystone megaherbivores may thus have altered ecosystem structure and function via the release of palatable hardwoods from herbivory, and the accumulation of fuel loads. The response of local vegetation was highly variable both within and between sites, suggesting that local site factors influenced the individualistic response of taxa to the same regional forcing. As a natural experiment of the past, the Pleistocene extinctions reveal clues as to how ecological novelty may emerge in response to the loss of keystone herbivores, particularly when in tandem with climate change.

Temperate mountain grasslands as ghosts of megafauna past

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Mountain grasslands in North America and Europe, supporting rich, shade-intolerant herbaceous plant and animal communities, are known as balds, poloninas, or mountain meadows. Historical records and recent community studies suggest a long history for many. They are declining in areal extent everywhere, due to encroachment by woody plants. These ecosystems have engendered much ecological research and speculation regarding their origins and maintenance, but controversy has led to management inaction for some, and their continued persistence is in doubt. We have proposed a new, unified climate-herbivore hypothesis to explain their origins and persistence. Maximal glacial advances during the Pleistocene likely created lowered climatic tree lines in places like the southern Appalachians, Oregon Coast Range, and East Carpathians. We posit that the resulting grassland - herbaceous communities were subsequently maintained by the grazing, browsing, trampling, and girdling actions of herbivores, beginning with the

diverse megafaunal herds of the Pleistocene. Based on the ecosystem engineering of extant herbivores worldwide, it seems reasonable to infer similar top-down effects on the vegetation structure of Pleistocene North America and Europe. We further infer that some of these systems were subsequently maintained by the seasonal altitude migrations of mid-sized herbivores such as bison (wisent) and elk (red deer) and other species through much of the Holocene, but with significant loss of grassland extent due to decreased herbivore diversity and density. Some of these systems were then maintained inadvertently by the pastoral activities of human settlers. In short, we propose that many of these rare and declining ecosystems are mere remnants of once more open ecosystems, and that a "chain of herbivores" since at least the late Pleistocene best explains their contemporary persistence. Our hypothesis also implies that restoring native herbivores, or close ecological surrogates, may help maintain these threatened ecosystems in some regions.

Nutrient dispersal by megafauna: are nutrient limitations a consequence of the Pleistocene extinctions?

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In the late Pleistocene (~50–10,000 years ago), ninety-seven genera of large animals (>44kg) (megafauna) went extinct. In this talk, I will explore the potential effect of these extinctions on nutrient biogeochemistry, land cover, and even early human development. I will focus on the impact on phosphorus and sodium using a novel mathematical framework that analyses this lateral transport as a diffusion-like process and demonstrates that large animals play a disproportionately large role in the horizontal transfer of nutrients across landscapes. For example, we predict that the extinction of the Amazonian megafauna may have led to a >98% reduction in the lateral transfer flux of the limiting nutrient phosphorus (P) with similar, though less extreme, decreases in all continents outside of Africa. This resulted in strong decreases in phosphorus availability in Eastern Amazonia away from fertile floodplains, a decline which may still be ongoing. The Pleistocene megafaunal extinctions resulted in major and ongoing disruptions to terrestrial biogeochemical cycling at continental scales and increased nutrient heterogeneity globally. This highlights the important ecosystem service of nutrient dispersal that current endangered megafauna may provide in Africa and Asia.

Decline of large herbivores: impact on vegetation in terrestrial and aquatic ecosystems

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Large herbivores are declining or have disappeared in many places globally. The question is what that means for the diversity and functioning of contemporary ecosystems. In grasslands, large herbivores such as bison or introduced cattle have the ability to consume tall, fibrous plants which dominate the vegetation in productive systems. By removing these plants they increase plant diversity by providing light and colonization sites for subordinate forb species. Furthermore, they provide access to the vegetation for smaller herbivores and facilitate their foraging. Large herbivores are able to counteract the effects of enhanced nutrient availability by consuming the extra plant production and maintain high plant diversity and grazing lawns which attract smaller grazers. The direction and magnitude of the impact of large grazers varies with habitat productivity. Whereas these principles are demonstrated for grassland ecosystems, much less is know about the role of large herbivores in aquatic ecosystems. Hippos, manatees and dugongs come to mind when thinking of large aquatic herbivores. In this talk I explore similarities and differences among terrestrial and aquatic habitats considering the role of large grazers in these ecosystems and therewith the potential consequences of their decline.

Pre-extinction interglacial ecosystem structure – the European case and global perspectives

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Paleoecological studies of the Pleistocene interglacials offer a window into near-time warm-period ecosystems before the end-Pleistocene and Holocene megafauna losses. By looking to these periods we can study how megafauna-rich ecosystems function without modern human interference, notably how they are structured, how much diversity they maintain, and which factors and processes are involved.
European interglacial ecosystem structure is a useful study case here due to the rich European paleoecological literature. Considering the most recent Pleistocene interglacials, the flora and fauna is nearly fully composed of extant species of plants, invertebrates, and small vertebrates, but contains a highly expanded large mammal community. There is often high diversity of plant and animal species of varied ecological requirements, ranging from old-growth forest species to species of various open habitats.
A new analysis using fossil and subfossil beetles as indicators of megafauna abundance and vegetation structure provides quantitative insights. Notably, herbivore-dung-associated beetles were much better represented during the Last Interglacial compared to the early Holocene and rather close to the level for the historical cultural landscape. Furthermore, beetle assemblages indicate a greater representation of relatively closed forest in the early Holocene relative to a greater mixture of open vegetation and forest in the Last Interglacial. Hence, abundant large herbivores appear to have been associated with high temperate vegetation structural diversity prior to the megafauna extinctions.
Overall, the paleoecological data points to forest-dominated, but highly heterogeneous interglacial ecosystems in Europe, with the megafauna playing an important role in sustaining structurally diverse vegetation and thereby a rich species diversity. There are indications that these findings generalize to other regions. Importantly, they are in line with recent studies of pollen, fungal spores, and charcoal from localities in North America and Australia, and paleoecological work from other parts of the world also point to the ecological importance of the formerly rich megafauna.

The rapid decline of Asia's megafauna and its consequences for seed dispersal

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We estimate that Asian elephants have lost 95% of their historical range, tapirs 98%, and the three species of Asian rhinos over 99%. This dramatic decline of Asia's megafauna has profound but poorly understood implications for the ecological trajectories and conservation of the region's ecosystems. For example, many tree species – especially those with large fruits and seeds – depend on megafaunal mutualists, the only animals capable of swallowing their seeds and effectively disperse them over long distances in ways that enhance germination and establishment. As elephants, rhinos, and tapirs continue to disappear from Asian forests their role in seed dispersal is lost without replacement. In this presentation I will report our team's ongoing efforts to (a) understand the ecological function of Tropical Asia's megafauna in seed dispersal, (b) quantify their ongoing decline, and (c) make predictions about future forest dynamics in a range of mega-defaunated scenarios. Our work includes the combination of feeding trials and field ecological studies of elephants, tapirs, and sun bears, to understand the way they process different kinds of fruits and seeds and the spatial pattern of seed dispersal they provide; the systematic inspection of megafauna's dung to identify plants they disperse; and the use of camera traps to record interactions of the mammal community with megafaunal-syndrome plants. Besides this, we are quantifying Tropical

Asia's functional impoverishment and using all the previous information to build up a forest dynamics modeling frame-work that will allow us to understand the ultimate consequences of losing the large-bodied dispersers in the region.

Pleistocene megafauna extinctions: functional loss of mutualistic seed dispersal services

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Pleistocene megafauna extinctions affected many different groups of animals, most likely determining the loss of a sizeable number of distinct ecological functions. Yet most analyses to date have emphasized predator-prey interactions, community assembly patterns, and loss of phylogenetic diversity. However, recent evidence points to a central role of many extinct megafauna herbivores as mutualists with plants, with a key role as seed dispersers. An important step in understanding the amazing aspects of this mutualistic interaction of megafauna mammals with angiosperm plants is to discuss the roles and effectiveness of megafauna herbivores as frugivores and seed dispersers. Here we approach this problem by addressing the seed disperser effectiveness (SDE) of extinct Pleistocene mammals as consumers of plant fruits. We review different aspects of frugivory in extant mammal frugivores and build mechanistic models to infer the effectiveness patterns of Pleistocene megafauna. We use current movement data of extant megafauna, anatomic and ecophysiological alometries of digestive systems, and fleshy fruit typologies to infer the mutualistic services likely provided by extinct megafauna. While important knowledge gaps still remain to uncover some important aspects of SDE variation for extinct animals, our exercise highlights salient features of Pleistocene megafauna that help revealing their enormous influence in their habitats and understanding current traits and patterns shown by their plant partners surviving in present-day neotropical environments.

Reconstructing past ecological networks: the reconfiguration of seed-dispersal interactions after megafaunal extinction

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Extant megafauna are central components in modern communities, affecting ecological processes and shaping biological communities. Likewise, megafauna were ecologically important species in Pleistocene communities. The widespread extinction of megafauna probably affected a variety of ecological processes including seed dispersal. The many examples of anachronic plants – extant plant species whose fruits and seeds would have been shaped by interactions with extinct interaction partners – suggest several plant species relied on megafauna for seed dispersal. Seed-dispersal interactions are embedded within interaction networks so that the extinctions may have had not only direct but also indirect effects over plant communities. We combined ecological data, paleontological information and network analysis to investigate how the extinction of large mammals at the end of Pleistocene and two waves of human colonization could have affected the structure of a species-rich seed-dispersal network in Central Brazil. We show that the Pleistocene seed dispersal network would have been rearranged after the extinction of large mammals. The loss of megafauna and the arrival of humans, which most likely acted as seed

dispersers of several plants, would have merged network compartments that were previously loosely connected. After the Colonial Period, livestock would have restored the original organization. However, the megafaunal extinction led to a significant shrinkage, in terms of body-size, in the disperser assemblage of those plants dispersed mainly by large mammals. This reduction in the size of seed dispersers likely affected the recruitment of large-seeded plants, indirectly affecting the recruitment of smaller-seeded species, via processes such as asymmetrical competition. Finally, we show that mammals that we now consider key species in the seed-dispersal network probably had a less distinctive role in the Pleistocene context. The ongoing extinction of key large vertebrates will continue to reshape ecological networks most certainly affecting the fate of plant communities.

Differential impacts of Pleistocene mega-herbivores on nitrogen availability

Elizabeth S. Jeffers

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At the end of the Pleistocene period there were marked changes in nitrogen availability within ecosystems globally. Given the association in time of changing nitrogen availability with the loss of the largest mega-herbivores (e.g. woolly mammoth and the giant deer from Eurasia), an important research question to be addressed is to what extent did the extinction of these species drive the observed changes in nitrogen availability within ecosystems. To address this question, palaeoecological records of change in mega-herbivore density (Sporormiella accumulation rates), nitrogen availability (sedimentary δ15N) and plant biomass (pollen accumulation rates) were analysed from sites across Britain during this period of faunal change. Mechanistic modelling of these data was used to infer the relationships between plant biomass, mega-herbivore density and nitrogen availability through time.
Results show that the impacts of mega-herbivores on nitrogen availability are context-dependent, which is in keeping with findings from modern studies of large herbivores. The fossil bone record at each of the sites shows clear differences in the faunal assemblages and suggests that the differential impacts of the mega-herbivores on nitrogen availability may be attributable to the unique digestive strategies of each faunal community.

Lateral transport of nutrients by herbivores: local impacts and global perspectives

Adam Wolf

Princeton University, USA

Animals translocate nutrients by consuming nutrients at one point and excreting them or dying at another location. Such lateral fluxes may be an important mechanism of nutrient supply in many ecosystems, but lack quantification and a systematic theoretical framework for their evaluation. This paper presents a mathematical framework for quantifying such fluxes in the context of mammalian herbivores. We develop an expression for lateral diffusion of a nutrient, where the diffusivity is a biologically determined parameter depending on the characteristics of mammals occupying the domain, including size-dependent phenomena such as day range, metabolic demand, food passage time, and population size. Three findings stand out: (a) Scaling law-derived estimates of diffusion parameters are comparable to estimates calculated from estimates of each coefficient gathered from primary literature. (b) The diffusion term due to transport of nutrients in dung is orders of magnitude large than the coefficient representing nutrients in bodymass. (c) The scaling coefficients show that large herbivores make a disproportionate contribution to lateral nutrient transfer. We apply the diffusion equation to a case study of Kruger National Park to estimate the conditions under which mammal-driven nutrient transport is comparable in magnitude to other (abiotic) nutrient fluxes (inputs and losses). Finally, a global analysis of mammalian herbivore transport is presented, using a comprehensive database of contemporary animal distributions. We show

that continents vary greatly in terms of the importance of animal-driven nutrient fluxes, and also that perturbations to nutrient cycles are potentially quite large if threatened large herbivores are driven to extinction.

Should we bring back the European megafauna?

George Monbiot
Environmental author and journalist, UK

We still live in an elephant-adapted ecosystem. Deciduous European trees and shrubs show powerful signs of elephant-proofing (and possibly some rhinoceros adaptations). As farming retreats from less fertile ground (one estimate suggests that an area in Europe the size of Poland will be vacated by 2030), re-establishing only the European mesofauna begins to look unambitious. Should we consider rewilding lions, hyaenas and hippopotamus, and proxy species such as Asian elephant and black rhinoceros? Could Europe have its own Serengetis?

Day 3: Megafauna and ecosystem function in the Anthropocene

Differential defaunation and extinction of ecological processes: consequences for ecosystems and humans

Rodolfo Dirzo
Stanford University, USA

Direct and indirect drivers of biodiversity change lead to a contemporary process of selective defaunation, whereby particular groups of animals are being decimated, while others are proliferating. In many tropical sites, the decline of medium- and large-bodied species is accompanied by a pulse of increase in abundance of several species of small mammals leading to a process of differential defaunation. In this presentation I will present results from studies that show that: i) Under conditions of selective defaunation, ecosystems (e.g., tropical rain forests in Southeast Mexico) undergo changes in understory plant-mammal interactions, including the local extinction of mammalian herbivory and exacerbated predation of rodent-preferred small seeds, ultimately affecting plant establishment and, potentially, forest regeneration patterns; ii) Large mammal defaunation and small mammal proliferation associated with context-dependent site productivity, land use change and hunting/poaching (e.g., in East African savannahs), bring about changes in risks of rodent-borne disease in humans. Collectively, these instances and available information indicate that the current pulse of selective defaunation that characterizes the Anthropocene can have cascading effects on biodiversity, ecosystem processes and services, including human health.

Effects of soaring elephant numbers on South African savanna habitats

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Carnegie Institution, USA

Although elephant (Loxodonta) densities are plummeting in parts of central Africa, populations have soared in protected areas of southern Africa over the past two decades. Quantifying the ecological effects of high elephant density is requisite to determining longer-term feedbacks that will lower future elephant populations. However, the effects of large elephant populations on savanna habitats are poorly unknown due to strong environmental covariates with elephant habitat preferences and browsing behavior. Using repeat high-resolution Light Detection and Ranging (LiDAR) measurements of woody plant canopy gains

and losses from 2008 to 2012, we assessed rates of habitat change across regional gradients of climate, soils, and topography in two million hectares of the Kruger National Park, South Africa. Background rates of woody plant loss (herbivore-free turnover) range from 0.1 to 1.2 plants per hectare, depending upon precipitation and topographic position. Against this abiotic template, elephants are responsible for an additional 1–2 orders of magnitude increase in woody canopy loss, with their largest relative effect in low-lying areas near water sources. Losses in canopy height exceed that of canopy gain by up to 300%, with the largest loss-to-gain ratios found in areas with relatively higher rainfall and/or on higher fertility soils. These and other findings strongly suggest that woody canopy habitat loss caused by large elephant populations occurs in a spatially explicit, regionally diverse pattern governed by abiotic factors affecting elephant preferences. Current rates of canopy loss in Kruger suggest that portions of the savanna ecosystem exposed to high elephant densities will collapse in as little as a decade. Rates and patterns of recovery will likely depend on climate and related feedbacks such as fire.

Low tree diversity of Central African forests: artefact of history or product of filtering by megafauna?

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Co-authors: Lisa Davenport, Raoul Niangadouma, Edmund Dimoto, John Claudes Mouandza, Olivia Scholtz and Maria Ruiz Jaen

Africa has been called the "odd man out" because the tree diversity of African equatorial evergreen forests is much lower than that of forests in other parts of the tropics. Low diversity has been attributed to a smaller area of forest and a history of drought, fire and forest contraction. However, despite low alpha diversity, the flora of Gabon is very rich, including some 4,700 documented species in an area of 270,000 km^2. Could it be that the anomalously low alpha diversity of Central African forests is not merely an artifact of history but partly imposed in ecological time by the activities of megafauna?
In comparison with Amazonian forests, Gabonese forests are better stocked with large trees and strikingly deficient in numbers and diversity of small trees (≥10 cm, <20 cm dbh). To investigate why this might be so, we examined several hypotheses representing expected or possible impacts of megafaunal herbivory on tree regeneration processes in Gabonese forests. Density of small saplings and diversity of large saplings were inversely associated with the local density of elephants. In an attempt to control for elephants, we tested the hypothesis that steep slopes might serve as refugia from elephant foraging. Although slopes bore fewer elephant trails than adjacent level sites, we found evidence of elephant foraging on all slopes inclined at <30 degrees. In a comparison of paired level and sloped sites, the diversity of small trees was higher on slopes. Accordingly, the incidence of break scars on saplings (≥2 cm dbh and <6 cm dbh) growing on level ground (105/100 stems) was higher than on slopes (77/100 stems). In conclusion, the low density and diversity of small trees in African equatorial forests appears to result from high mortality of saplings attributable to elephant foraging. More broadly, elephants, along with other large mammals such as gorillas, duikers, red river hogs and rodents, appear to act in concert as powerful filters on the tree recruitment process in African forests that still retain intact megafaunal communities.

Contemporary large vertebrate defaunation modulates tropical forest ecosystem services

Carlos A. Peres
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Here I examine the extent to which contemporary tropical forest dwellers, including semi-subsistence and commercial hunters, deplete large vertebrate populations across the Neotropics. Consequences of present-day overhunting to mammal prey assemblages are then compared to projections of prehistoric

overkill. The spatial extent of game depletion envelopes is then estimated for lowland Amazonia, and illustrated for a few vertebrate species on the basis of a source-sink demographic model that takes into account hunting effort and species sensitivity to hunting. The basin-wide distribution of residual vertebrate biomass in structurally undisturbed forests is then explained in terms of key environmental variables, including forest type, floristic diversity, forest hydrology, rainfall seasonality, soil fertility and degree of hunting pressure. Regional scale estimates of aggregate vertebrate biomass are highly variable and crucially dependent on the interaction between baseline habitat productivity and levels of offtake. Finally, on the basis of a vast network of 2,345 canopy tree plots, I estimate the consequences of persistent overhunting to forest structure and composition, and ultimately the magnitude of forest biomass ecosystem services lost due to seed dispersal limitation induced by the chronic depletion of large-bodied forest frugivores.

30 years of rewilding in the Netherlands: the impact of herbivores on closed canopy forest

Frans Vera
Oostvaardersplasse, The Netherlands

Tens of thousands non-breeding moulting Greylag geese moult during May, June and July, shedding their wing feathers in the Oostvaardersplassen, a nature reserve in a polder in the center of the Netherlands. This polder was reclaimed in 1968. During their moult they graze extensive reed beds in the marshy part, creating in this way a mosaic of shallow water en reed vegetation, which is the biotope of many marsh-inhabiting plant and animals species, among others many bird species. The grazing geese drive the succession and overthrow the paradigm that in natural conditions herbivores follow the succession.
Before and after the moult they congregate in grassland in the dry part of the reserve. These grasslands are created and maintained by indigenous large ungulates wild cattle, horses and red deer. Without them the grasslands would change into a closed canopy. As a consequence, the geese will disappear from the marsh and in their wake the marsh-inhabiting species. In the marsh this cascade of events will result in a mire forest. Therefore the large herbivores overthrow the paradigm that large herbivores follow the succession as well. This paradigm resulted in the closed canopy forest as the commonly accepted baseline for the natural vegetation in the northern temperate hemisphere and made indigenous large herbivores non-exiting ecological entities.
By creating grassland, the large indigenous herbivores create in wood-pastures the conditions for the survival of light demanding tree species such as Pedunculate oak (*Quercus robur*) and Sessile oak (*Q. petraea*) and shrub species such as Hazel (*Corylus avellana*), Blackthorn (*Prunus spinosa*) and Hawthorn (*Crataegus mongyna*). They do so by creating a mosaic of grasslands, shrubs, scrub, trees and groves. These light demanding species disappear in the climax closed canopy forest that develops in their absence, because they cannot regenerate successfully there. They are outcompeted by shade tolerant tree species such as Small and Broad leaved lime (*Tilia cordata* and *T.playphyllos*), Hornbeam (*Carpinus betulus*) and Beech (*Fagus sylvatica*). In wood-pastures all tree species regenerate in grazed open grassland by means of thorny nurse species like Blackthorn and hawthorn that protect the seedlings as nurse species against the large herbivores. This especially favours the light demanding species, whose presence during many thousands of years is confirmed by pollen analysis.

Lessons and future prospects from a Pleistocene rewilding in Siberia

Sergey Zimov
Pacific Institute for Geography, Russia

Over the course of hundreds of millions of years plants in terrestrial ecosystems tended to protect themselves from herbivores with poisons, spikes or tall branches. Decomposition and biological cycling in these ecosystems was low. But 20 millions of years ago have appeared grasses and high productive herbs. These plants are characterized by very high rates of growth, which is possible only on very fertile soils.

These plants were evolving in symbiosis with herbivores. Giving several harvests of leaves during a year grasses and herbs maintained animal biomass of tens of tons per square kilometer. Herbivores in turn provided rapid and weather independent nutrition cycling (animal stomach is +36°C any time). At such a high grazing pressure, slowly growing plants (competitors of grasses) could not sustain on the pastures. This is a very aggressive ecosystem. In the late Pleistocene pasture ecosystems have invaded most parts of the continents. Forest area was an order smaller than today. Analyses of density of bones preserved in the permafrost indicated that even in most severe conditions in the north of Siberia animal density on average was 10 ton per square kilometer. Analyses of atmospheric methane and its isotopes dynamic have showed that biomass of big herbivores on the planet in the late Pleistocene reached 2*109 ton, i.e. was higher than biomass of all species in the modern civilization. Humans as a species have evolved in these pasture ecosystems. Sharp Holocene warming has promoted rapid human expansion to all continents and its chances for survival. Because of the increased hunting pressure animal density in many of the pasture ecosystems had become insufficient to maintain biocycling and pasture ecosystems were replaced by forests or tundra.
In pasture ecosystems grasses very rarely produced mature grains and mostly they were reproducing by vegetative method. Vanishing wild herbivores humans have lost the traditional food source but because of that appeared a way for artificial pasture ecosystems –farmlands and domestic pastures.
Experiments in "Pleistocene Parks" worldwide have indicated the possibility for revival of high productive pasture ecosystems in mid and high latitudes.

The science of science fiction: bringing back the mammoth

Beth Shapiro
University of California Santa Cruz, USA

The recent discoveries of remarkably well-preserved, mummified mammoth remains in Northern Siberia have renewed enthusiasm for bringing these iconic creatures back to life. Motivated both by scientific curiosity and by an insatiable appetite on the part of the popular press for news that straddles science and science fiction, a new discipline, termed de-extinction, has appeared. Among the several de-extinction projects that are actively underway today is to bring back the mammoth. In the past, it was believed that the first step of mammoth de-extinction would be to find an intact mammoth cell that could then be used in nuclear transfer. However, it is now known an intact mammoth cell is an extremely unlikely to be preserved, even in association with the best preserved remains. However, recent advances in paleogenomics and genome editing technologies provide a promising new road to de-extinction and do not require an intact mammoth cell. I will discuss progress to date in the effort to bring the mammoth back to life, highlighting the many technical challenges that have yet to be overcome. I will discuss challenges associated with transforming an elephant cell into a mammoth cell, engineering a baby mammoth, and releasing a baby mammoth into the wild. Finally, I will discuss the environmental and ethical questions that arise when contemplating any de-extinction.

Re-wildling visions and controversy: unsettling the conservation regime

Paul Jepson
University of Oxford, UK

The contemporary nature conservation paradigm in Europe is founded on a small set of dominant framings of nature rooted in cultural traditions: the pastoral, the high forest and the uplands. The desire to conserve benchmark species assemblages that characterize these natural archetypes has given rise to influential institutions that have embedded a compositionalist approach in European conservation policy and practice. This paper will suggest that re-wilding controversies indicate a fundamental tension between this 'compostionalists' institutional architecture and the functionalist approach that re-wilding embodies. It will argue that we need a strategy to deal with these fundamental tensions - one that creates institutional space for re-wilding/functionalism to develop and gain traction without threatening existing conservation

institutions. One possible strategy is to align re-wilding with objectives in the 7th EU Environment Programme and 2020 Biodiversity strategy relating to restoration of ecosystems and natural capital: specifically to position re-wilding as a cost-effective approach for the restoration and reclamation of lands degraded by mining, agriculture and other processes. This could create an experimental approach to conservation in Europe that would complement and interact with the established conservation regime to promote institutional reflexivity. By introducing new natural archetypes into the European landscape such a strategy is likely to i) generate new forms of public engagment with nature, and ii) reinvigorate public debate on the nature-society relationship. This would strengthen the democratic legitimacy of future conservation regimes.

Massive loss of forest elephants in Central Africa

Fiona Maisels

Wildlife Conservation Society

Co-authors: Samantha Strindberg, Wildlife Conservation Society, and Stephen Blake, Max Planck Institute

The forest and savannah elephants of Africa are now thought to have diverged about five million years ago, at about the same time as the divergence of Asian elephants and woolly mammoths. Recent research has demonstrated that, in the absence of forest elephants, the African tropical forest ecosystem alters in structure, diversity, and composition. This is because elephants play a highly important role as "ecosystem engineers" and "forest gardeners" by dispersing the seeds of fruiting trees over large distances, and by creating trails and forest clearings. Surveys across the range of forest elephants in Central Africa have shown that both their numbers and range are diminishing very rapidly due to increased illegal killing – driven by high ivory prices in the Far East – that now reaches into the most remote corners of the continent. The long-term effects of this are likely to result not only in a change in the characteristics of one of Earth's primary carbon sequestering forests, but also in a reduction of food for the rest of the frugivore community, including primates, ungulates, and large frugivorous birds.

Rewilding: nine key challenges

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Rewilding has become one of the most vigorously debated topics in contemporary conservation despite being both poorly defined and applied. Based on a systematic review of the academic literature and self-identified 'rewilding' conservation interventions, we propose that a project should only be regarded as rewilding if it has all the following components: a species reintroduction or proxy species introduction; habitat restoration directly or indirectly caused by the reintroduced species, and; intended and unintended social impacts or outcomes of the reintroduction and/or restoration. Research is needed on all components if the conservation community is to learn from these fascinating socio-ecological experiments. In this context, we identify nine key questions for future rewilding projects: (1) What is the role of humans? (2) How do we deal with "monsters"? (3) Who cares if rewilding is non-analogue? (4) How and why do we justify baselines? (5) Can we rewild with small species? (6) How do we deal with scale? (7) When do we rewild with carnivores? (8) Is there overlap between rewilding and zoos? (9) How do we integrate monitoring and assessment across interdisciplinary boundaries? There are no definitively correct answers to these questions, because answers are specific to the socio-ecological contexts in which each project takes place. However, responding to these challenges is essential to designing path-breaking conservation interventions and opportunities for learning.

The rewilding debate is not based on experiments: a critical look at the rewilding debate and an example of actual rewilding status in Denmark

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Rewilding projects are gradually being planned and implemented throughout Europe. These attempt to reintroduce missing predators and herbivores into ecosystems to protect or restore missing ecological functions. In parallel, rewilding issues are being heavily discussed within and outside the scientific community, as the idea of re-establishing possibly long-extinct populations can be quite controversial. Despite an increasing number of rewilding publications per year and the fact that rewilding is an increasingly hot topic in conservation biology and practical nature management, there is still a critical lack of experimental rewilding studies. Instead, the literature is dominated by essays or opinion pieces. We argue that it is crucial to emphasize evidence in the rewilding debate and emphasize the need for more empirical and, particularly, experimental studies.

Despite ongoing debate in academic circles, rewilding projects are moving ahead in many areas, promoted by nature management agencies and private individuals. These projects are often not well publicized. To understand the extent of rewilding studies within Denmark, we surveyed rewilding projects by contacting all public nature managing entities in the Denmark: 98 municipalities and 22 nature agencies. In parallel, we investigated the attitude towards rewilding as a management tool in nature management among participants at two national biodiversity and nature conferences.

This survey, based on answers from more than 90% of the public nature managing entities, showed that rewilding projects have already been initiated in 20% of the Danish municipalities and an additional 8% of Danish municipalities are planning to execute rewilding projects within the next 5 years.

Results from the questionnaire, based on answers from 167 respondents, revealed that more than 90% of the respondents were familiar with the term "rewilding" and were in favor of implementing rewilding as a nature management tool. The respondents clearly stated that lack of land was the main challenge for implementing rewilding, while pointing towards the Danish National Parks, extensive farm land and NATURA 2000 areas as potential rewilding areas.

As the number of rewilding projects grows rapidly in Europe, there is an increasing need for researchers to evaluate these projects to ensure future successful implementation of rewilding in European nature management.

A role for rewilding in English nature conservation practice?

Keith Kirby
University of Oxford, UK

During the late nineties and early 2000s there was a perception that CAP reforms would lead to significant land coming out of productive agricultural use. This coincided with the publication (in English) of Frans Vera's book *Grazing and Forest History*. These triggered an interest in the concept of rewilding amongst the conservation agencies and NGOs and whether it had a role in British (but particularly English) conservation practice.

Key elements for the conservation sector to emerge from the subsequent debate included:

The uncertainties around the composition of the pre-Neolithic landscape and the role of wild herbivores in it.

Whether even this period could be considered 'natural' in the light of increasing evidence for Mesolithic and earlier human impacts;

The potential to use large herbivores as part of creating future, potentially rich, mosaic landscapes;

Rewilding was best seen as 'direction of travel'– if treated as the 'state' that had to be reached, it ceased to be very useful under British conditions;
Areas subject to 'rewilding' would almost certainly lose species as well as (hopefully) gain new ones because of the cultural nature of British, particularly English, landscapes – the losses were likely to occur early in the process, the gains would be more long-term;
The conservation objectives for rewilding areas would need to change to focus on processes since the habitat/species outcomes were unpredictable and the option of intervening to maintain particular species goes against the rewilding idea;
There are a range of legal and social issues that need to be addressed if 'rewilding' is to move beyond being merely very extensive farming.

Rewilding is therefore a potentially useful approach to conservation, but needs to be pursued alongside more conventional, interventionist approaches. At least for the short to medium term it is likely to remain a minor component of British, particularly English conservation practice.

The politics of rewilding and reintroduction: the lion and the cheetah in India

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Restoring nature from disturbed to less anthropogenic states is a frontline and redeeming feature of 21st century conservation. A central strategy of this project has been the (re)introduction extinct mammals that had substantial impacts on ecosystem function in the past. However, amidst the clamor for ecological reintroductions, social and political dimensions of extinction and reintroduction – critical for enabling interventions – are glossed over. How is the ecological extinction of large mammals underpinned by socio-political processes? Who decides what is lost and what political logics influence species reintroduction? What is to be introduced, and whose authority, knowledge and voices count in the process? We examine these questions through two case studies of lion and cheetah reintroduction in India. We show how the demise of these two species in India were driven partly by the hunting practices of colonial and Indian princely elites, and argue that the project of reintroduction is driven by similar proponents in the postcolonial context. Here, questions about national (and regional) identity and authoritarian modes of conservation practice are at play. We then draw upon current scholarship that contests the nativeness of both the lion and cheetah in India to open up debates on differences between reintroduction and (re)wilding. We argue that decisions behind reintroduction, especially on the choice of proxies, are as much about politics as they are about science. We conclude by discussing the implications of this argument for understanding reintroductions/(re)wilding outside its familiar 'Western' domain.

Rewilding in a crisis discipline

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Biodiversity conservation is increasingly viewed as a discipline in crisis. Over the past decade, new intervention-based and human-centered strategies have been proposed and are gaining support. Some of those approaches are being viewed as incompatible with historical strategies for biodiversity conservation. At one extreme is the view that "wilderness", as we once perceived it, no longer exists and successful conservation strategies will rely heavily on management actions, and will often explicitly integrate human needs. At the other extreme is the view that such approach runs counter to conservation biology, is fundamentally flawed, and is akin to "gardening." I argue that this internal conflict will have relatively little influence outside of those engaged in it because of at least two factors: both mental models widely exist in

the population and are influenced less by science than other information, and the two extreme strategies are not mutually exclusive. As a conservation approach, rewilding is perhaps unique because it is supported (and criticized) from proponents of both "wilderness" and "gardening." Where it falls on this continuum depends on a number of factors, particularly your view of historical ecology. Rewilding projects are becoming increasingly common around the globe, and public support is growing to the point that grassroots efforts are emerging. Prescriptive science, however, is not keeping up with demand. More science is needed for the growing number of rewilding efforts in order to inform decision-makers and practitioners on the potential costs, risks, and benefits of this biodiversity conservation strategy.

Poster Presentation Abstracts

Conserving ecosystem modifiers: a double-edged sword

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The drastic decline of megaherbivores from the world's oceans has contributed to a growing uncertainty of their functional contribution to the dynamics of marine vegetated ecosystems. Conservation efforts have focused on restoring these flagship populations to historically pristine levels, without much understanding of the sometimes-unintended consequences these population increases can have on extant ecosystems. This becomes particularly important given that most megaherbivores are ecosystem engineers. We studied the dominant megaherbivores (the dugong, Dugon dugong, a herbivorous fish, Sarpa salpa and the green turtle, Chelonia mydas) in three seagrass meadow systems in order to understand the functional consequences of their engineering. While the dugong populations we studied were at critically low densities in the Andaman and Nicobar Islands (India), both Sarpa salpa densities in Medes Islands in Catalonia and green turtle populations in the Lakshadweep Archipelago (India) are among the highest recorded, thanks to enhanced protection. At all three locations, we assessed the impacts of these megaherbivores by deploying exclusion cages in seagrass meadows, measuring direct herbivory rates on seagrasses, evaluating seagrass responses to elevated herbivory rates (in terms of production) and assessing the community of seagrass-dwelling fish or invertebrates to test for cascading effects. Our results show that all three herbivorous species are important ecosystem engineers, significantly modifying the density and canopy structure of meadows. Even at critically low present densities, dugongs were able to overgraze meadows in which they fed, and the high density populations of fish and turtles (in the Mediterranean and Lakshadweep respectively) had strong effects on grazed meadows including decreased seagrass shoot biomass and production, shifts in dominant seagrass species and lowered habitat structure. Taken together, this suite of habitat changes had serious cascading implications for the entire ecosystem: with increasing structural loss, these ecosystems showed major declines in communities of invertebrates and fish. In addition, in the Mediterranean, we document that megaherbivore fish can trigger complex indirect interactions, modifying predator-prey dynamics by increasing predation rates on other keystone herbivores. Our work across these systems is highlighting the fact that marine megaherbivores are potentially strong interactors capable of producing a cascade of direct and indirect effects on seagrass ecosystems. This has important implications when setting conservation targets for these flagships since it requires a more holistic understanding of the functional consequences of their conservation on entire ecosystems given their present extent and carrying capacity.

Niche Evolution of Anatomically Modern Humans (AMHs) During the Late Pleistocene

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The spread of *Homo sapiens sapiens*, the most competitive and resource consuming megafauna species, across the planet and their role in the extinction of megafauna species during the late Pleistocene have attracted special interest among researchers. Population genetics and diffusion models have led to new insights about the timing and geographic location of human distribution and migrations routes. However, the modes and drivers of those migrations are still largely unexplored. Did AMHs track specific environmental conditions meanwhile maintaining the same climatic niche or did humans adapted to novel environmental conditions while changing their climatic niche? What is the potential range size dynamics of AMHs during the Late Pleistocene and what is the role of climate forcing and technological developments as drivers of those patterns?

We applied community ecology and macroecological models to paleoclimatic reconstructions and to a database of 5,300 archaeologically associated radiocarbon dated materials to investigate the evolution of climatic niche of central and north Eurasian populations of AMHs between 46 and 11kya. We also mapped their potential distributions to test whether AMHs climatic niche changes are reflected by range size dynamics, and assessed the role of climate and cultural/technological advancements in driving these patterns.

We show that the climatic niche dynamics can be divided into two periods largely coinciding with the Marine Isotope Stages (MIS) 3 and (MIS) 2. The climatic niche of AMHs was highly unstable during the MIS3 punctuated by significant changes while it reached stability during the MIS2. The amount of different climatic conditions inhabited by humans, niche breadth, increased approximately until the LGM, and was punctuated with some periods of niche breadth explosion. Additionally, the temporal dynamics in niche breadth are partly reflected by the temporal dynamics of geographical range size. Overall, our results suggest two different modes of human migration: niche evolution to adapt and colonize habitats with new climatic conditions during MIS3 and niche stasis and tracking suitable environments during MIS2. Finally, both climate forcing and cultural/technological advancements drove partially the evolution of AMHs climatic niche.

Our framework can accurately reconstruct the spatiotemporal climatic niche dynamics of AMHs and can complement population genetic and diffusion model approaches to better understand the mechanisms driving the human expansion across the planet.

Do megafauna diffuse nutrients across landscapes? An empirical study of mineral concentrations in litter and soil in Langoué Bai, Gabon

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The study aimed to provide a first empirical test for the recently proposed hypothesis that mega-herbivores diffuse minerals from nutrient hotspots, as well as for the idea that major elephant pathways act

as 'nutrient arteries' in a forest landscape. Litter and soil samples were collected from transects along a major elephant trail originating at Langoué Bai, Gabon – a natural forest clearing believed to be a hotspot of salts in the landscape. Generalised linear mixed effects models were used to identify effects of distance from the Bai, distance fro the elephant trail, distance from nearest tree, soil moisture, inclination, and soil mineral concentration on the concentrations of Na, K, Mg, and Ca in litter.

Range changes in extant and extinct mammals during the terminal ice age

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The biodiversity crisis is currently underway as a result of climate change, but the scientific understanding on dynamic processes of range contraction and extinction is still at an early stage. Comprehensive studies have been done on the last glacial, focussing on the influence of climate on the geographic distributions of mammals, as well as their community compositions and refugia. However, a comparison between biogeographic ranges of extinct and extant species on the time period 60 to 8ka bp in Europe has yet to be done. This project will address this problem by updating and combining the Stage Three and S2AGES databases that consist of radiocarbon dates with associated archaeology and faunal remains. Spatial and statistical analyses will provide novel insights into the biogeographical range changes of mammalian species over time.

Shadows of mega-faunal seed dispersal mechanisms in western Amazonian forests

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The large post-Pleistocene mass extinction of a large number of large animal species likely had a significant effect on plant populations in terms of their demography, recruitment patterns, and regional distribution. In this study, we first characterized the fruits and seeds of a hyper-diverse Neotropical woody flora and then applied Guimaraes' *et al.* operational definition of megafaunal fruits to determine which of the 1,100 tree species in a large forest plot were likely previously dispersed by megafauna. Second, we contrasted the spatial pattern and recent population structure and dynamics of these groups of species. Finally, we examined how widespread these megafauna-dispersed species are currently throughout South American tropical forests. We use both these local and regional results to infer the impact of megafaunal extinction on woody plant communities and predict the further long-term persistence of populations of these species.

Beavers back in Scotland?

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Eurasian beavers disappeared from Scotland over 400 years ago, and the matter of whether or not they should be returned has been the subject of considerable debate for well over a decade. In 2008, the

Scottish government approved a licence for the Scottish Wildlife Trust and the Royal Zoological Society of Scotland to undertake a 5-year trial reintroduction of beavers to Knapdale Forest, Argyll. This reintroduction could be considered solely on the grounds of putting back something that was carelessly lost, but perhaps more importantly, it delivers a process that was lost to the UK ecosystem. Beavers have a marked influence on their environment and on other wildlife due to their river damming and tree-felling activities. Dam construction creates ponds, and filters sediment from water that seeps through them, creating environmentally-rich wetlands. Beavers may also be an annoyance that flood gardens and drains, fell orchards and deflect streams. Salmon fishermen fear their sport will be damaged. The question is whether the habitat creation and ecological services rendered by returnee beavers will, or will not, outweigh their potential for pestilence.

One of the conditions of the licence for beaver reintroduction was that the trial was independently monitored; the monitoring process is coordinated by SNH, and WildCRU have responsibility for monitoring the ecology of the released beavers (other independent partners monitor a number of other aspects of the release). The final year of the trial will be in 2014. In the meantime, recent surveys have reported a much larger population of immigrant beavers in the Tayside valley (from either escapees or illegal releases). Scottish Government will decide formally on the longer-term future of beavers in Scotland in 2015, but for the time being at least beavers are back and the first steps to rewilding Britain are underway.

We will present an overview of the trial release, including our role in monitoring beaver ecology and some of the challenges in drawing inferences from a trial release of a very small number of animals, as well as preliminary assessments of the presence of beavers, and their impact, in the more human-dominated landscape of the Tayside river catchment.

Both mega- and meso-browsers control African woodland dynamics

Christopher O'Kane

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The role of mesobrowsers in the long-term dynamics of woodlands has been largely ignored in favour of the better known role of the systems megaherbivore, elephant. Such suggestions have clear implications for our understanding of how such ecosystems function over the long-term and, consequently, may be of relevance in designing rewilding projects.

Grazing of free-ranging cattle

Simon Webb

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Extensive grazing of free-ranging cattle is a proxy for natural grazing and associated disturbance within woodland and open fell habitats in the English Uplands. This is progressing away from intensive agricultural grazing towards wilder and more naturalistic systems.

Magnitude and variation of prehistoric bird extinctions in the Pacific

Tim Blackburn

Director of the Institute of Zoology, London

The largest extinction event in the Holocene occurred on Pacific islands, where Late Quaternary fossils reveal the loss of thousands of bird populations following human colonization of the region. However, gaps in the fossil record mean that considerable uncertainty surrounds the magnitude and pattern of these extinctions. We use a Bayesian mark-recapture approach to model gaps in the fossil record and to quantify losses of nonpasserine landbirds on 41 Pacific islands. Two-thirds of the populations on these islands went extinct in the period between first human arrival and European contact, with extinction rates linked to island and species characteristics that increased susceptibility to hunting and habitat destruction: large-bodied, flightless, island endemic birds living on smaller, drier islands were more likely to go extinct. We calculate that human colonization of remote Pacific islands caused the global extinction of close to 1,000 species of nonpasserine landbird alone; nonpasserine seabird and passerine extinctions will add to this total.

Flagships for nature conservation in a defaunated landscape

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The central zone of Chile is characterized by a globally important concentration of endemic species, as well as a highly anthropogenic landscape. This area of Chile is under-represented by protected areas, and nature in central Chile is considered non-existent or degraded by the Chilean public. Due to historical defaunation and land-use changes, central Chile also lacks a megafaunal flagship candidate species which could serve to attract attention to biodiverse habitats of central Chile. We develop spatially explicit approaches to flagship implementation in central Chile. First, we consider the distributions of a set of micro/mesofauna and trees that have previously been identified as a flagship fleet for nature engagement in central Chile. Where flagship fleet distributions overlap, landscapes have potential to attract nature-based tourism and environmental education. Second, we consider how the reintroduction of the guanaco (Lama guanicoe), a regionally extirpated large herbivore, could change perceptions and valuations of the landscape. We conclude that reintroduced guanaco could act as "phoenix flagships" to improve engagement with central Chilean landscapes. Thirdly, we map areas of potential reintroduction for guanacos and other megafauna in central Chile, and consider the implications for positive engagements with nature and the landscape in the future.

Competitive release of small herbivorous mammals after the late Pleistocene megaherbivore extinctions

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Community ecologists have observed that extirpation or exclusion of megaherbivores leads to shifts in trophic interactions due to the competitive release of rodents and other small herbivorous mammals. Did the late Pleistocene megafaunal extinctions also result in competitive release of small herbivores? Increase in population sizes, speciation, increase in body size, and changes in allometry are outcomes of competitive release. Of these phenomena, only increase in body size is testable for small herbivores following late Pleistocene megaherbivore extinctions. We approach this question through two independent predictions derived from the literature on mammal body size distributions. First, we target a

group of small herbivore genera with high body size plasticity, to ask whether their current body sizes are larger as the percent of megafaunal extinctions increases, comparing across continents. Second, we target a small size class whose taxa are likely to have been under strong control by competition. We predict that, independent of smaller and larger body size classes, the number of species in this size class should increase with megaherbivore extinctions across continents. We find strong support for both predictions. Since small herbivores and megaherbivores compete indirectly or feed on different life stages of the same plants, the evidence for widespread competitive release of small herbivores provides a new perspective on predicting structural habitat changes in the Holocene and Anthropocene.

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Thank you for coming