COMMENTARY

Re-wilding North America

A plan to restore animals that disappeared 13,000 years ago from Pleistocene North America offers an alternative conservation strategy for the twenty-first century, argue **Josh Donlan** and colleagues.

North America lost most of its large vertebrate species — its megafauna some 13,000 years ago at the end of the Pleistocene. And now Africa's large mammals are dying, stranded on a continent where wars are waging over scarce resources. However much we would wish otherwise, humans will continue to cause extinctions, change ecosystems and alter the course of evolution. Here, we outline a bold plan for preserving some of our global megafaunal heritage — one that aims to restore some of the evolutionary and ecological potential that was lost 13,000 years ago, and which offers an alternative vision for twenty-first century conservation biology.

Our vision begins immediately, spans the coming century, and is justified on ecological, evolutionary, economic, aesthetic and ethical grounds. The idea is to actively promote the restoration of large wild vertebrates into North America in preference to the 'pests and weeds' (rats and dandelions) that will otherwise come to dominate the landscape. This 'Pleistocene re-wilding' would be achieved through a series of carefully managed ecosystem manipulations using closely related species as proxies for extinct large vertebrates, and would change the underlying premise of conservation biology from managing extinction to actively restoring natural processes.

Historic vision

Our proposal is based on several observations. First, Earth is nowhere pristine; our economics, politics, demographics and technology pervade every ecosystem. Such human influences are unprecedented and show alarming signs of worsening. Second, environmentalists are easily caricatured as purveyors of doom and gloom, to the detriment of conservation. Third, although human land-use patterns are dynamic and uncertain, in some areas, such as parts of the Great Plains in the United States, human populations are declining¹ — which may offer future conservation opportunities. Fourth, humans were probably at least partly responsible for the Late Pleistocene extinctions in North America, and our subsequent activities have curtailed the evolutionary potential of most remaining large vertebrates. We therefore bear an ethical responsibility to redress these problems.

North American conservationists routinely turn to the arrival of Columbus in 1492 as a

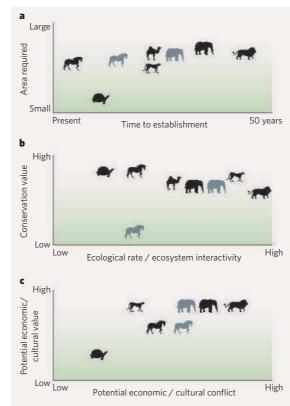


Figure 1 | Pleistocene re-wilding in North America. Symbols represent horses (*Equus caballus* and *E. asinus* in black; *E. przewalskii* and *E. hemionus* in grey), Bolson tortoises, camelids, cheetahs, Asian (grey) and African (black) elephants, and lions. **a**, The likely timescale and area required to restore proxies for extinct large vertebrates. **b**, Conservation value and ecological role (interactivity with other species) on the landscape. **c**, Potential economic/cultural value versus potential conflict.

restoration benchmark. But the arrival of the first Americans from Eurasia roughly 13,000 years ago constitutes a less arbitrary baseline. Mammal body-size distributions were similar across all continents before the Late Pleistocene, but subsequent extinction of most large species drastically altered those distributions in favour of smaller species.

In the Americas, where large-vertebrate losses were greatest, the subsequent changes were undoubtedly ecologically and evolutionarily significant. Large carnivores and herbivores often play important roles in the maintenance of biodiversity, and thus many extinct mammals must have shaped the evolution of the species we know today². For example, the pronghorn (*Antilocapra americana*) evolved over four million years in North American grasslands that changed abruptly in the Late Pleistocene; the now-extinct American cheetah (*Acinonyx trumani*), a key predator, almost certainly shaped the pronghorn's astonishing speed³.

Beasts of old

Although historical perspectives have influenced modern conservation planning, existing programmes do not adequately address the evolutionary potential and long-term processes involved in restoring large-mammal diversity. Africa and parts of Asia are now the only places where megafauna are relatively intact, and the loss of many of these species within this century seems likely. Given this risk of further extinction, re-wilding of North American sites carries global conservation implications.

Moreover, humans have emotional relationships with large vertebrates that reflect our own Pleistocene heritage. More than 1.5 million people annually visit San Diego's Wild Animal Park to catch a glimpse of large mammals more than the number of visitors to most US National Parks. So an understanding of ecological and evolutionary history, inspired by visits to private or public reserves

containing free-roaming megafauna, could strengthen support for conservation. Pleistocene re-wilding would probably increase the appeal and economic value of both private and public reserves, as evidenced by the restoration of wolves to Yellowstone National Park⁴.

We foresee several phases to Pleistocene rewilding, some of which are already under way. The 50-kg Bolson tortoise (*Gopherus flavomarginatus*) was widely distributed across the Chihuahuan desert until the Late Pleistocene. Today it survives only in a small part of northern Mexico and is critically endangered. A number of appropriate sites exist for reintroduction, including Big Bend National Park, Texas. And repatriation of captive Bolson tortoises to a private ranch in New Mexico is currently under study. Restoring North America's largest surviving temperate terrestrial reptile to its prehistoric range could bring ecological, evolutionary, economic and cultural benefits, with no apparent costs (Fig. 1).

Likewise, horses and camels originated in North America, and many species were present in the Late Pleistocene. Feral horses (*Equus caballus*) and asses (*E. asinus*), widely viewed as pests in the United States, are plausible proxies for extinct American species. Also, given that most of the surviving Eurasian and African species are now critically endangered, establishing Asian asses (*E. hemionus*) and Przewalski's horse (*E. przewalskii*) in North America might help prevent the extinction of these endangered species and would restore equid species to their evolutionary homeland.

Similarly, Bactrian camels (*Camelus bactrianus*) in North America could provide a modern proxy for *Camelops*, a late Pleistocene camelid. Wild Bactrian camels are on the verge of extinction, cur-

rently restricted to the Gobi desert. Domesticated or captive camels might benefit arid North American ecosystems by browsing on woody plants that today often dominate southwestern US landscapes. With proper management, camels could provide economic benefits as well⁵. The overall benefits and disadvantages of horses and camels as proxies will depend on local contexts, and possibly on the presence of appropriate predators.

Free to roam

The second, more controversial phase of Pleistocene re-wilding could also begin immediately, with the maintenance of small numbers of African cheetahs (*Acinonyx jubatus*), Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants, and lions (*Panthera leo*) on private property. Many of these animals are already in captivity in the United States, and the primary challenge will be to provide them with naturalistic settings, including large protected areas of appropriate habitat and, in the case of carnivores, live prey.

The African cheetah, a close relative of the American cheetah, has only a modest chance of persisting in the wild in the next century. Breeding programmes are not self-sustaining, but some of the 1,000 captive animals could be used in re-wilding. Free-roaming, managed cheetahs in the southwestern United States could save the fastest carnivore from extinction, restore what must have been strong interactions with pronghorn, and facilitate ecotourism as an economic alternative for ranchers (Fig. 1).

Managed elephant populations could similarly benefit ranchers through grassland maintenance and ecotourism (Fig. 1). Five species of proboscidians (mammoths, mastadons and gomphotheres) once roamed North America in the Late Pleistocene; today many of the remaining African and Asian elephants are in grave danger. Elephants inhibit woodland regeneration and promote grasslands, as Pleistocene proboscidians probably once did. With appropriate resources, captive US stock and some of the 16,000 domesticated elephants in Asia could be introduced to North America, where they might suppress the woody plants that threaten western grasslands. Fencing, which can be effective in reducing human–elephant conflict in Africa, would be the main economic cost.

Lions, which play a pivotal ecological role in the Serengeti, represent the ultimate in Pleistocene re-wilding for North America. They are increasingly threatened, with populations in Asia and some parts of Africa critically endangered. Replacing the extinct American lion (*Panthera leo atrox*), although challenging, has

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clear aesthetic and economic benefits (Fig. 1).

Among the objections to Pleistocene re-wilding is that the proposed proxies are not genetically identical to the animals that formerly existed

in North America. And our vision might strike some as 'playing God'. Existing lions and cheetahs are somewhat smaller than their extinct counterparts, for example, and *Camelus* is different from *Camelops*. 'Same' is relative, however, as illustrated by the highly successful reintroduction of peregrine falcons (*Falco peregrinus*) in North America. Captive-bred birds from seven subspecies on four continents were used, yet there were no differences among the birds in subsequent breeding success⁶, and the subspecies now serve as a collective proxy for the extinct midwestern peregrine falcon.

More challenging objections to Pleistocene re-wilding include the possibility of disease transmission, the fact that habitats have not remained static over millennia, and the likelihood of unexpected ecological and social consequences of reintroductions. These issues must be addressed by sound research, prescient management plans and unbiased public discourse on a case-by-case and locality-by-locality basis. Well-designed, hypothesis-driven experiments will be needed to assess the impacts of potential introductions before releases take place. Large tracts of private land probably hold the best immediate potential for such studies, with the fossil record and research providing guideposts and safeguards. For example, 77,000 large mammals (most of them Asian and African ungulates, but also cheetahs, camels and kangaroos) roam free on Texas ranches⁷, although their significance for conservation remains largely unevaluated.

The third stage in our vision for Pleistocene re-wilding would entail one or more 'ecological history parks', covering vast areas of economically depressed parts of the Great Plains. As is the case today in Africa, perimeter fencing would limit the movements of otherwise freeliving ungulates, elephants and large carnivores, while surrounding towns would benefit economically from management and tourismrelated jobs. A system of similar reserves across several continents offers the best hope for longterm survival of large mammals.

Meeting the challenge

In the coming century, by default or design, we will constrain the breadth and future evolutionary complexity of life on Earth. The default scenario will surely include ever more pest-and-weed dominated landscapes, the extinction of most, if not all, large vertebrates, and a continuing struggle to slow the loss of biodiversity.

Pleistocene re-wilding is an optimistic alternative. We ask of those who find the objections compelling, are you content with the negative slant of current conservation philosophy? Will you settle for an American wilderness emptier than it was just 100 centuries ago? Will you risk the extinction of the world's megafauna should economic, political and climate change prove catastrophic for those populations remaining in Asia and Africa? The obstacles are substantial and the risks are not trivial, but we can no longer accept a hands-off approach to wilderness preservation. Instead, we want to reinvigorate wild places, as widely and rapidly as is prudently possible.

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