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Research Focus

The Pleistocene re-wilding gambit

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Re-wilding parts of North America with exotic Old-World species is an exciting but controversial conservation proposal hijacked by opinions over appropriate conservation baselines and details of implementation. Debate over its worth has become partisan. Here, I summarize the multifaceted issues surrounding Pleistocene re-wilding and edge debate from hazy conceptual arguments to empirical questions that can plug gaps in knowledge and begin to resolve this divisive conservation issue.

What is all the fuss about?

There is a 'brouhaha' in conservation biology. A group of prominent scientists [1,2] have resuscitated a forgotten conservation idea [3] that seeks to combine elements of restoration ecology with *ex situ* conservation. Arguing that ecological landscapes and evolutionary trajectories in North America have changed considerably since the extinction of large megafauna 13 000 years ago, the scientists suggest introducing proxies for these 'ecological engineers' and reinstating past selection pressures that might restore ecological and evolutionary processes. These proxies would be either extant species that are descended from those species that went extinct during the Pleistocene, or morphologically similar species, if no descendants exist. For example, Bactrian camels *Camelus bactrianus*, various Eurasian equids *Equus* sp., African *Loxodonta africana* and Asian *Elephas maximus* elephants, extant cheetahs *Acinonyx jubatus* and lions *Panthera leo* would be released in the USA and Canada as substitutes for their extinct North American counterparts, such as North American camelids *Camelops* spp., equids, mammoths *Mammuthus primigenius* and extinct big cats. The idea is radical because it would involve actively introducing exotic large mammals to huge game parks or to range free in North America and has predictably attracted considerable popular attention [4,5].

The concept is a bold conservation step because it questions the conventional but arbitrary 1492 conservation benchmark (i.e. the date that Caucasians arrived in the New World) to which conservation biologists seek to restore North American communities. The idea provides a loose plan for restoring past ecological and evolutionary processes, something that conservation biologists acknowledge to be important, but to which they have hitherto paid only lip service; the proposal has already injected new interest and discourse [6–9] into what is arguably a flagging conservation mantra of doom and gloom. Furthermore, an attempt to restore a grassland ecosystem in Siberia has been made using these methods [10].

Against this group of scientists are pitted a similarly august group of opponents [11], some from the same university, Cornell, who argue that Pleistocene re-wilding is flawed on three broad fronts: scientific, practical and societal. Both groups are clear in distinguishing re-wilding (the reintroduction of recently extirpated native species into their indigenous habitats) from Pleistocene re-wilding (populating North American big game parks with exotic Old-World species that are descended from extinct Pleistocene ancestral species or that are ecological proxies for such extinct ancestors). The debate centers on the Pleistocene re-wilding.

The science

The ecological debate between the two camps runs as follows (Table 1). Pleistocene re-wilders assume: (i) that we know the species composition and abundance of long-lost ecological communities in North America, providing a target at which conservation practitioners can aim. In certain areas, such as the Great Basin of Nevada, we know about historical communities at a gross scale; however, opponents argue that the details are hazy and provide little more than a moving target at which to fire. Paleontologists could help hone this discussion. (ii) Re-wilders recognize the danger of importing diseases from the Old World to the New, but think that the dangers can be minimized through carefully controlled and monitored small-scale experimental introductions; their adversaries deem it too risky. Ivory tower debates notwithstanding, society recognizes the danger of disease for livestock and US Customs implement strict controls of foodstuffs and animals that might be hard to alter. (iii) There are additional arguments: introductions of proxy species have no guarantee of success judging from documented difficulties of reintroduction attempts of native fauna, and inappropriate food, parasites or disease could scupper the best intentions. (iv) Will it be possible to limit adverse biological consequences of inevitable escapes? These include native fauna facing ontogenetically novel predators, fragile vegetation succumbing to new forms of herbivory, and even hybridization between Old- and New-World mammals. These hypothetical worries are difficult to resolve in the abstract, but past experience and the precautionary principle suggest that none can be dismissed lightly (Table 1).

The evolutionary debate centers on whether novel introductions would really mimic selection pressures that were assumed to be experienced by North American wildlife 13 000 or more years ago. For example, in the face of

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Table 1. The Pleistocene re-wilding gambit

Considerations	Caveat or problem
Scientific (ecological)	
Assumes ecological processes unchanged from 13 000 years ago[a]	Difficult to support or refute as cannot identify Pleistocene endpoint[b]
Importing new diseases to North America with adverse effects on native fauna[a] and livestock	Difficult to assess in advance but precautionary principle speaks against it[b]
Introductions difficult to achieve	Reintroductions have mixed success, with few general rules to emerge; thus introduction success unpredictable[b]
Escapees will not affect native communities or hybridize with native fauna	Likelihood unknown
Scientific (evolutionary)	
Would provide same selection pressures on North American flora and fauna as 13 000 years ago[a]	Difficult to support or refute as based on morphological similarity of predators and herbivores to extinct counterparts[b]
Would increase evolutionary potential of Old-World introductions	Why necessary when selection pressures occur in contemporary Old-World communities?[b]
Practical	
Cost of fencing	Seen as crucial[a] but no attempt to provide costs of fencing reserves (likely to be astronomic)[b]
Salaries for scientists and practitioners to assess small-scale introductions	New-World salaries higher than those in the Old World[b]
Sets precedent for increased wildlife trade[a]	Has similarities to introductions of exotics now deemed a major conservation concern[b]
Conservation funding is not transferable[a]	Little support for this; that Pleistocene re-wilding could invigorate conservation biology implies funds are transferable
Societal	
Public acceptance of living in proximity to large predators is difficult in some parts of North America[a]	Could be an insurmountable problem in certain regions[b]
Reduces number of ecotourists to Africa and Asia[a]	Difficult to assess before re-wilding implemented
Diminishes appreciation of native fauna in favor of charismatic exotics[a]	Difficult to assess before re-wilding implemented[b]
Suggests Old-World conservation efforts are failing compared with those in the New World[a]	No data to support; zoos already provide a back up to *in situ* conservation[b]

[a]Discussed by Donlan *et al.* [1,2].
[b]Discussed by Rubenstein *et al.* [11].

African cheetahs, would American pronghorn *Antilocapra americana* maintain high levels of vigilance and flight speed that were thought to have evolved in response to predation by North American cheetahs [12]? Second, do we need to enhance and diversify selection pressures currently experienced by Old-World mammals by shipping them to the New World? I would argue that a 'megazoo' scenario would relax selection pressures on species that would be no longer subject to Old-World diseases and competition. Resolution of both of these issues might only occur after many years and, in 2007, simply comes down to informed guesswork.

Logistics

Practical considerations center on economics, particularly of fencing large areas of the North American west, and comparatively high salaries for North American managers and scientists. Could conservation agencies afford these? On the positive side, green philanthropists such as the Ted Turner Foundation (http://www.turnerfoundation.org) are interested in Pleistocene re-wilding, but could they really meet the expense of erecting and maintaining hundreds of kilometers of lion- or elephant-proof fences? Carefully calculating the tradeoff between enclosure size, fencing and maintenance costs is a key step in any re-wilding enterprise.

Another practicality is the source of exotic animals. Undoubtedly, these should initially come from captive-bred stock in North America but, if zoos run short, would it open the door to legalizing trade in exotic (and sometimes endangered) species? Finally, given higher costs in the west than in developing countries, might Pleistocene re-wilding, sold under the guise of conservation, siphon funding from more traditional conservation goals of restoring and protecting extant native fauna in Asia and Africa as well as in North America?

The wider canvas

Societal issues hinge on local acceptance by rural communities living next to large, sometimes dangerous, animals, and diverting tourism from developing countries to Canada and the USA. Certainly, US citizens take personal safety seriously (e.g. worries about jogging and camping in wilderness areas) and federally sponsored programmes eradicated large carnivores from many areas of the USA at the end of the 19th century because of livestock losses. Given these reservations, it is likely that barriers might never come down, reconfiguring the Pleistocene re-wilding concept to simply being exotic game parks far larger but akin to Safari World in California. And might Pleistocene re-wilding redirect tourists from African adventures to rocky mountain west safaris? Proponents of Pleistocene re-wilding argue that tourist interest is nontransferable, whereas opponents say that it would undermine tourist-related conservation revenue in developing countries. This is surely subject to empirical investigation using willingness-to-pay questionnaires.

More nebulous but valid concerns are diminishing the public's appreciation of native New-World fauna when it is contrasted with tropical megafauna at home (again, open to investigation before decisions are made); and the implicit idea that large mammals are somehow safer in the USA than in Africa and Asia. This is arguable but open to empirical investigation: how do we balance absence of corruption against government assault on the Endangered

Species Act, the Arctic Wildlife Refuge and federally owned lands in North America with widespread corruption but a range of success stories in the Old-World tropics (e.g. four new national parks have been gazetted in Tanzania alone within the past four years)?

Conclusion

Clearly, there is much to discuss. The re-wilding concept invites conservation practitioners to revisit the ecological and evolutionary targets that they want to shoot at; it calls paleontologists to work with conservationists in understanding stasis and change in Pleistocene ecosystems; it challenges captive-breeding institutions to rethink the conventional wisdom of keeping exotic species in the confinement of standard zoos, now under renewed scrutiny [13]; and it asks conservation biologists to reopen debate on the nature of the historical, geographical, genetic and ecological differences between past (re)introductions of California condors *Gymnogyps californianus* to Big Sur, wolves *Canis lupus* to Yellowstone, peregrine falcons *Falco peregrinus* from many continents to North America, south American cougars *Puma concolor* to the Everglades, wild turkeys *Meleagris gallopavo* to California; Arabian oryx *Oryx leucoryx* to Arizona; and African cheetahs to Texas.

On the other side of the coin, uncertainty about so many Pleistocene re-wilding issues; the understandable difficulties that its proponents have in facing these criticisms head-on using data; and conventional conservation dogma, backed up by pest biology, that novel introductions are hazardous for both ecological communities and agribusiness all argue against Pleistocene re-wilding. There is an air of desperation in the Pleistocene re-wilding idea to which we are all sympathetic. Conservation biology has developed into a science of documenting population declines, species losses and habitat destruction in excruciating detail but sadly doing little about it. Pleistocene re-wilding is a proactive idea that could galvanize the conservation community out of its helplessness and, for that alone, deserves merit.

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A recognition-free mechanism for reliable rejection of brood parasites

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Hosts often discard eggs of avian brood parasites, whereas parasitic chicks are typically accepted. This can be explained theoretically by fitness losses associated with adults learning to recognize parasitic young and mistakenly rejecting their own young. A new experimental study confirms that rejection of parasitic chicks, without relying on memory to discriminate between foreign and own young, is a feasible and potentially cost-free mechanism used by reed warblers to reject common cuckoo chicks. By abandoning broods that are in the nest longer than is typical for their own young, parents can reliably reject parasite nestlings and reduce fitness losses owing to having to care for demanding parasitic young. Discrimination without recognition has important implications for the realized trajectories of host–parasite coevolutionary arms races.

Introduction

Social parasites exploit the foraging and breeding efforts of their hosts. Obligate brood parasitic birds, for instance, lay

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