Journal
Frontiers of Biogeography, 8(3)

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Publication Date
2016

DOI
10.21425/F58328431

opinion

An argument supporting de-extinction and a call for field research

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Abstract. With recent advances in biotechnology, the resurrection of recently extinct species has become a possibility, provoking a debate about the wisdom of what has become known as de-extinction. Regardless of the current feasibility and ethical controversies over de-extinction, ongoing technological advancement is likely to result in resurrected species in the near future. In our opinion, de-extinction will be followed by proposals for reintroduction into the wild. We argue that this development could be valuable for the advancement of ecological understanding and conservation. However, the current conversations are happening in a vacuum. We therefore call for the initiation of field experiments using physiological and ecological surrogates. This type of research could shed light on the potential impacts of resurrected animals on modern ecosystems. While this research would have challenges, it could provide valuable information on the ecology of the past and better prepare scientists and wildlife managers for de-extinction.

Keywords. Conservation, de-extinction, field experiments, re-wilding, reintroduction

Introduction to de-extinction and framing the issues

During the late Quaternary (<50,000 BP) and extending into the present, numerous species have gone extinct across the globe (Koch and Barnosky 2006, Julien et al. 2007, Faith and Surovell 2009). These extinction events have undoubtedly modified ecological functioning of many ecosystems. For example, the extinction of Pleistocene megafauna from the Americas and Eurasia appears to have changed the structure, diversity, and composition of temperate, tropical, and boreal ecosystems (Zimov 2005, Gill et al. 2009, Zimov et al. 2012, Doughty et al. 2013). For instance, grasslands are some of the most threatened ecosystems, in part because of the encroachment of woody vegetation, perhaps due to the reduction of megafauna browsers and increases in herbivorous grazing animals (Van Auken 2000, however see Ratajczak et al. 2012 for the complexity of woody plant encroachment). Considering the role of extant large mammals in African and Asian grasslands and savannas (Dirzo et al. 2014), including their major influence on distribution and abundance of woody plants and in ecosystem processes (McNaughton 1985, Van Auken 2000, van Langevelde et al. 2003, Sandom et al. 2014), it is reasonable to infer that many extinct megafauna were important in past ecological processes (Johnson 2009, Gill 2014). In addition to Pleistocene megafaunal extinctions, species loss has continued into historical times, with the current extinction process affecting almost all taxa, including species of all sizes. For example, the passenger pigeon (*Ectopistes migratorius* L.) with its immense populations probably would have had major impacts on forest structure in eastern North American and initiated cascading effects throughout the food web (Ellsworth and McComb 2003). Similarly, the recent loss of multiple frog species throughout the world is likely having major consequences for ecosystems (Verburg et al. 2007).

While extinction has typically been considered permanent, recent technological advances in genetic engineering and cloning have made the return of extinct species a possibility, a process referred to as de-extinction (Sherkow and Greely 2013, Shapiro 2015). For example, CRISPR (clustered regularly interspaced short palindromic repeats) technology can be used to modify the genome of extant species to match the genome of closely related extinct species (Campbell and Hofreiter 2015). Simpler cloning technology might also be used to resurrect more recently extinct species in which intact genomes survive in tissue samples. Some near successes of de-extinction include the Pyrenean ibex (*Capra pyrenaica pyreciaca* Schinz, which ultimately died, but was the first animal of an extinct subspecies resurrected, Folch et al. 2009) and the gastric brooding frog (*Rheobatrachus* spp. Liem) which survived through the early larval stages (White 2013). It seems likely that further improvements in technology will make de-extinction a reality (Donlan 2014).

De-extinction is distinctive from existing conservation ideas, such as reintroduction and rewilding, and has the potential to change conservation strategies dramatically. Reintroduction has been a commonly used conservation tool to restore ecological functioning (Gibbs et al 2008, Ripple and Beschta 2012). Rewilding landscapes over a large scale with extant species is a loftier goal (Samson et al. 2004). De-extinction is an even more radical idea that would bring back extinct species, which could then be added to existing or re-wilded ecosystems. Indeed, if de-extinction becomes a reality, we believe that the next logical argument among some scientists would be reintroduction of these resurrected species into the wild (Shapiro 2015).

Potential benefits, risks, and challenges

Benefits

De-extinction is likely to happen, assuming technological challenges can be overcome. While not all scientists advocating de-extinction are also in favor of reintroduction, this process is of particular interest to ecologists and conservation biologists (Donlan 2014). Reintroduction—especially if the extinct species represent unique ecological niches not represented by extant species—could be of particular ecological value. For example, the deciduous forests of North America are missing a large number of recently extinct and ecologically unique species that appear to have been important in structuring this community. The loss of important seed predators, such as the passenger pigeon and Carolina parakeet (*Conuropsis carolinensis* L.), may have had cascading effects through this system, including drastic alteration of plant communities (Ellsworth and McComb 2003).

De-extinction could also re-establish more ancient evolutionary relationships, benefiting numerous organisms. Evidence from living animals suggest that de-extinction could substantially alter ecosystem functioning, perhaps in ways that enhance biodiversity. Extant megafauna, such as elephants (Asner et al. 2009), ungulates (Asner et al. 2009), large cats (Jorge et al. 2013), canines (Ripple and Beschta 2012), and giant tortoises (Hansen et al. 2010) have profound influences on modern habitats. Historical reintroductions (e.g., wolves in Yellowstone, bison in the Great Plains) have demonstrated the impact that the reintroduction of large animals can have on ecosystems (Knapp et al. 1999, Hill et al. 2008, Ripple and Beschta 2012). While the interaction of large mammals in Pleistocene ecosystems were bound to have been complex, we hypothesize that they would be similar to living species.

Extinct animals may have been important seed dispersers for many plants and may be responsible for living anachronistic plants (Janzen and Martin 1982). Elephants consume large quantities of fruit and disperse the seeds over long distances (Dudley 2000, Campos-Arceiz and Blake 2011) in South Asia and Africa. Some plant species rely upon large grazers to remove competitively dominant plant species (Olff and Ritchie 1998). It seems probable that extinct megafauna had similar ecosystem-wide effects. Therefore, it is possible that de-extinction would provide additional ecosystem services that current biological communities cannot.

Ironically, resurrecting extinct animals could also improve the chances of preserving the genetic legacy of extant animals. For example, a cloned mammoth would presumably be created by altering the genetic code of the Asian elephant (*Elephas maximus* L.) to create a cold-adapted organism (Shapiro 2015). If these animals were then re-introduced to an environment where they can be well-protected, the Asian elephant genome would also be partially preserved, an important goal considering the plight of extant elephants in their native range (Wittemyer et al. 2014).

Risks

Risks of de-extinction include invasiveness, disease transmission, and unforeseen species interactions (Donlan et al. 2006, Sherkow and Greely 2013, Donlan 2014). These risks are evident with modern introductions (Pejchar and Mooney 2009), so caution and pre-emptive protocols would be prudent to mitigate risk. In case of unforeseen problems, response plans also need to be developed. However, it is not clear how these risks from resurrected species would be different from traditional reintroduction programs, even though these are widely supported by the scientific community and the public (Donlan 2014). We support the argument that de-extinction, if accompanied by introduction to the wild, is comparable to reintroductions of extirpated populations (Jørgensen 2013, Jones 2014, Seddon et al. 2014). Reintroduction of extirpated populations, with varying levels of success, have included mammals (e.g., wolves; Ripple and Beshta 2012), reptiles (e.g., Galapagos tortoises; Gibbs et al 2008), plants (Godefroid et al. 2011), and arthropods (Shepherd and Debinski 2005). These reintroductions also involved intense human activity such as captive breeding, efforts to maintain genetic variation, and intense monitoring after release. These activities often succeeded in the goal of reestablishment of ecological interactions, often with substantial environmental benefit. Perhaps the most noteworthy was wolf reintroductions in the Yellowstone Ecosystem, which appear to have had wide-ranging and profound ecological effects, many beneficial to biodiversity (Ripple and Beschta 2012). Noteworthy is that most reintroduced populations in the U.S. are designated "experimental" for management purposes and can be removed if necessary (e.g., red wolves in the Great Smokey Mountains; Henry 1998). We fully expect and recommend that any reintroduction of a resurrected species be treated the same way, which would presumably lessen environmental risk. Since conservation laws vary by country, international cooperation is likely necessary in advance of actual de-extinction, such as working under the International Union for Conservation of Nature (IUCN) guidelines or other cooperative agreements.

The social aspects of de-extinction are also varied and important. These include concerns that it will misallocate conservation funds (Mark 2013) and will relax public sentiment for conservation (Donlan 2014). Several authors have argued that conservation funds will be transferred from traditional conservation programs to riskier de-extinction programs (Ryder 2002, Redford et al. 2013). Others have argued that de-extinction efforts will bring in new sources of money, in particular from biotechnology companies (Jones 2014). For instance, the Ark Corporation was developed specifically for de-extinction efforts with money that was unlikely to be utilized for traditional conservation work (Regalado 2013). If extinction was viewed as reversible, would de-extinction reduce public interest in conservation? While possibly an issue, conservation support is already in decline, and by all evidence inadequate to arrest species extinction (Kareiva and Marvier 2012). It is also possible that resurrection of extinct species could increase public awareness and excitement for conservation.

Challenges

Feasibility is a major challenge to de-extinction and effective reintroduction (Jones 2014). Some authors have suggested that cloning or genetic engineering will never produce a population large enough and with enough genetic diversity to be viable (Ehrlich 2014), a problem for many small populations, illustrated by the ongoing genetic hurdles with the Florida panther (*Puma concolor coryi* Bangs; Johnson et al. 2010). An additional issue is that many species have locally adapted populations (Grady et al. 2011), genetic diversity that would almost certainly be impossible to recreate from the limited samples available from the Pleistocene remains of extinct animals. However, many conservation success stories have shown that small populations with little genetic diversity can give rise to large and biologically viable populations if allowed to expand sufficiently (e.g.,

Table 1. Basic ecological questions about Pleistocene ecology that could be studied, methods of study, and selected examples.

Questions?	Research Method	Feasible Example
Are current plant communities novel because of Pleistocene Extinction?	Controlled introduction of analog species to habitat	Study effect of Asian or African elephants on North American vegetation with semi-wild animals and replicated exclosures
How did extinct animals interact with surviving species?	Controlled introduction of analog species to habitat where living species persist	Replicated large plots with horses with bison together, separate, or both absent (2X2 factorial design)
How did the extinction of Pleistocene animals affect ecosystem function?	Controlled introduction of analog species to habitat	Study carbon and nitrogen cycles on habitats with analog species compared to replicated exclosures
Effect of high diversity grazing community of the Pleistocene compared to the lower diversity community of the present	Introduction of analog species and extant native species in appropriate habitat	Re-creation of Pleistocene grazing/browsing community in the Great Plains of U.S. with all living megafauna plus elephants, horses, camels, and tapirs as analogs. Compare to replicated exclosures
How did Pleistocene extinction affect seed dispersal?	Laboratory feeding trials with analog species	Feeding of fruits to captive elephants (and other analogs); retrieve seeds from dung and test for survival and growth

northern elephant seal; *Mirounga angustirostris* Gill; Bonnell and Selander 1974). It has also been argued that there is no remaining habitat for extinct species (Pimm 2013). While habitat loss has reduced many habitats to non-viable ecosystems, many areas still remain. Temperate North America, where large areas of relatively intact habitat remain and many native species survive, would be a good candidate for reintroduction of resurrected species. The High Plains in particular (especially parts of eastern New Mexico, Colorado, and Wyoming) contain many large ranches with unplowed, native grasslands, several of which contain a nearly full complement of modern flora and fauna—even healthy numbers of large animals such as elk, pronghorn, and mountain lion (Wilkenson and Turner 2013). While small animals would be difficult to contain, if de-extinction and reintroduction includes large mammals, some of these areas could conceivably be fenced similar to some African parks (e.g., Lake Nakuru National Park; Mwangi and Western 1997) to prevent damage to surrounding private lands and communities.

There will also undoubtedly be cultural limitations to de-extinction, including substantial concern from government agencies and the general public (Shapiro 2015). Therefore, as de-extinction efforts progress, a realistic educational system must be enacted to accompany it. Educational programs in schools and outreach by public and private conservation organizations, similar to what is done with traditional conservation efforts, would need to be implemented.

Preparing for the future

Current research on several species, including mammoths (Shapiro 2015), the passenger pigeon (Hung et al. 2013), and the gastric brooding frog (White 2013), is increasing the likelihood of at least some resurrected species in the near future, and that arguments for reintroduction will follow. Since we predict that de-extinction will become a reality, we wish to make a call to action to perform field research. We hope that this type of research will pre-emptively answer questions, such as potential species interactions of resurrected species, the nature of old evolutionary relationships, and past and future ecosystem functioning (Table 1). This type of research could also mitigate potential risks.

It has been hypothesized that many current ecosystems are novel, because of the extinction of megafauna (Gill et al. 2009). Several paleoecologists have suggested that the extinction of Pleistocene megafauna changed North America from a grazer/browser dominated ecosystem to one controlled by fire, which may have had important consequences for plant species diversity (Johnson 2009). For example, grazing can reduce the frequency and intensity of fire, allowing woody plants to become established, which then influences the abundance of browsing animals ultimately controlling woody plant encroachment (van Langevelde et al. 2003, Sankaran et al. 2008). Although studying the effects of de-extinction is seemingly paradoxical—since we do not have any formerly extinct animals to study—there are reasonable alternatives. The most obvious solution would be the use of extant ecological and evolutionary analogs (Donlan 2005, Donlan et al. 2006).

Recent preliminary experiments from our laboratory have shown that some North American plant species survive and grow better after passing through the digestive system of elephants, compared to native seed dispersers (Boone et al. 2015). This study suggests that important ecological relationships could be re-established through de-extinction. Living elephants are considered physiologically and ecologically similar to extinct elephants from Eurasia and the Americas (Kalb et al. 1996, Dudley 2000; but see Green et al. 2005), and these could be utilized to perform additional more complex field experiments. Captive elephants could be introduced into field sites to study grazing, browsing, trophic cascades, and disturbance impacts on plant and animal communities, similar to research that has been performed by the reintroduction of other large mammals, such as bison (Knapp et al. 1999, Moran 2014) and wolves (Ripple and Beschta 2012).

Reintroduction of large mammal analogs has been initiated by scientists in Asia with the establishment of the "Pleistocene Park" along the Kolyma River in northeastern Siberia (Zimov 2005). They have reintroduced Yakutian horses (*Equus ferus caballus* L.), Muskox (*Ovibos moschatus* Zimmermann), and Wisent (*Bison bonasus* L.). Acquiring animals for the project has been challenging and not without set-backs, so results are preliminary. However, the researchers have already shown substantial changes in plant communities, including an increase in grasses and declines in mosses and shrubs. Also interesting was an apparent change in ecosystem processes that models indicate could modify greenhouse gas emissions by reducing methane release (Zimov et al. 2012). A similar park, Askania-Nova in the Ukraine, has a mixture of native and introduced surrogates living in a natural environment, but a literature review finds very little research, with the exception of studies on Przewalski's horse behavior (*Equus ferus przewalskii* Poliakov; Zharkikh et al. 2009). The current conflict in the area, however, makes ecological research difficult. Performing similar experiments in other locations (with more political stability) and habitats where extinctions occurred would expand our knowledge of potential effects of de-extinction.

Such experiments, although logistically challenging would be reasonably practical. One field experiment we propose is the interaction of bison, pronghorn, horses, and elephants on the Great Plains of the United States. Bison (*Bison bison* L.) and pronghorn (*Antilocarpa Americana* Ord) are native, while the horse (*Equus ferus caballus*) and elephants (*Loxodonta* or *Elephas*) would be appropriate analogs for the extinct North American horses (*Equus* spp.) and Mastodons (*Mammut* spp. Blumenbach), respectively. Fossil evidence suggests that bison, pronghorn, horses, and elephants were some of the most abundant mammals during the Pleistocene (Guthrie 1968, Spencer et al. 2003). This quartet is ecologically similar to the Serengeti-Mara group consisting of zebra, wildebeest, gazelle (two species), and African elephant. This combination of grazers (zebra: low-quality grass, wildebeest: high-quality grass), browsers (gazelles), and ecosystem engineer-browsers (elephant) has a profound effect on ecosystem functioning (McNaughton 1985). Bison, pronghorn, and horses are widely available in the western U.S. For example, the National Bison Association organizes the trading of bison among ranchers, and conservation groups often sell excess animals (Robert Hamilton, Tallgrass Prairie Preserve Director, personal communication). There is also a surprisingly large number of captive elephants in zoos, circuses, and sanctuaries in North America (several hundred animals; Mason et al. 2009). With the increasing concern for elephant welfare in captivity, returning them to a wild or semi-wild environment could find public support. Although not directly related to conservation, the ethics of keeping highly intelligent and social animals, such as elephants, in captivity is very suspect. Providing a place in the wild for them to live more natural lives, especially if they cannot be returned to a true wild state in their native range, would be more ethically defensible than the current model of captivity.

There would no doubt be difficulties in introducing elephants to wild habitats. Modern Asian and African elephants are tropical animals, not tolerant of cold weather, and they have complex social structure not easy to replicate in captive populations. Therefore, they would most likely have to be introduced in a semi-wild condition where they have access to shelter during the colder months of the year, but would be able to interact with the native ecosystem the rest of time. Unbeknownst to many ecologists, there are two facilities in the United States that house elephants in this way: The Elephant Sanctuary in Tennessee and the Performing Animal Welfare Society in California. Both of these facilities allow elephants to roam over relatively large areas of natural and semi-natural habitats, while the facilities provide shelter when necessary. Experiments using this type of partially wild situation would be an excellent prelude to resurrected animals that would be physiologically adapted to the North American climate.

Experimental reintroductions would not have to be limited to the four species described above. Another formerly common Pleistocene mammal group in North America was the camelids. Extant species of camels from South America or Asia could be experimentally introduced to North American habitats as an additional browser (Donlan et al. 2006). Other examples of potential surrogate species include modern tapirs, peccaries, and a variety of predators.

De-extinction efforts could be paired with conservation organizations such as zoos to propel conservation forward to save species that still survive. Currently, it is unclear how effective zoo educational efforts are at promoting positive action for conservation, with evidence suggesting that the zoo experience does little to improve knowledge or motivate people to act on behalf of conservation (Kellert and Dunlap 1989, Mazur and Clark 2001, Kuhar et al. 2010). Thus, it has been hypothesized that a more *in situ* approach to conservation focusing on ecological processes and realistic human-animal relationships would be more effective in conservation (Hutchins and Conway 1995, Mazur and Clark 2001). Engaging in breeding and introducing resurrected species could be an advancement for the future of zoos. For example, the Northern white rhinoceros (*Ceratotherium simum cottoni* Lydekker) is almost certain to go extinct soon since natural reproduction of the remaining individuals is unlikely (Swaisgood et al. 2006). Technology developed through de-extinction studies could be applied to this living species which currently exists only in captivity.

While the above experiments would help elucidate some possible effects of de-extinction, there are several caveats. Unlike large mammals, it is much more difficult to design experiments to determine the effects of small species reintroduction, because their analogs would presumably be more mobile and more difficult to contain in a controlled study (but see Heske et al. 1994 for an example of small rodent exclosures). Apex predators present other unique challenges, including large habitat area requirements, low fecundity, and high risk of human conflict. Furthermore, the population regulation of analog species would have to be performed by humans, unless all species interactions could be established within the study system.

Conclusion

Our basic argument therefore is to do the field research. Debates about the morality and ethics of de-extinction are of great importance, and it is imperative that we proceed with caution, but de-extinction is likely to occur in the near future regardless, assuming technological obstacles are overcome (Donlan 2014). Once extinct animals are resurrected, proposals for reintroduction are likely to follow. If this proposal occurs, then the important goals are to assure that we get the most ecological and scientific benefits from the process, while minimizing risk. Debates about the ecological impacts are currently being undertaken without enough data, yet the research that would answer these questions is possible, despite being logistically challenging. By bringing together ecologists, social scientists, and conservation minded organizations, it might be possible to address these ecological questions and proceed with de-extinction using good science. Not only will this research guide us toward responsible de-extinction actions, it will also provide exciting information on past ecological and evolutionary history of our planet.

Acknowledgments

Thanks to R. Dirzo, H. Mooney, D. Gordon, and P. Seddon who provided valuable comments to an earlier draft of this manuscript. Several anonymous reviewers provided valuable comments and greatly improved the paper. This work was supported in part by the J. Keith Sutton Research Award to C. N. Davis.

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Submitted: 14 August 2015
First decision: 13 April 2016
Accepted: 25 October 2016
Edited by Matthew Heard