

## Prospects for rewilding with camelids



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### ABSTRACT

The wild camelids wild Bactrian camel (*Camelus ferus*), guanaco (*Lama guanicoe*), and vicuña (*Vicugna vicugna*) as well as their domestic relatives llama (*Lama glama*), alpaca (*Vicugna pacos*), dromedary (*Camelus dromedarius*) and domestic Bactrian camel (*Camelus bactrianus*) may be good candidates for rewilding, either as proxy species for extinct camelids or other herbivores, or as reintroductions to their former ranges. Camels were among the first species recommended for Pleistocene rewilding. Camelids have been abundant and widely distributed since the mid-Cenozoic and were among the first species recommended for Pleistocene rewilding. They show a range of adaptations to dry and marginal habitats, and have been found in deserts, grasslands and savannas throughout paleohistory. Camelids have also developed close relationships with pastoralist and farming cultures wherever they occur. We review the evolutionary and paleoecological history of extinct and extant camelids, and then discuss their potential ecological roles within rewilding projects for deserts, grasslands and savannas. The functional ecosystem ecology of camelids has not been well researched, and we highlight functions that camelids are likely to have, but which require further study. We also discuss alternative rewilding-inspired land-use models given the close relationships between humans and some camelid species.

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## 1. Introduction

Camelids were among the first species recommended for Pleistocene rewilding in North America (Donlan et al., 2005, 2006). Trophic rewilding is an emerging conservation paradigm that has recently been defined as “species introductions to restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems” (Svenning et al., 2015; see also Naundrup and Svenning, 2015; Sandom et al., 2012; Donlan et al., 2005). In many cases such (re-)introductions are associated with passive conservation management, an emphasis on large protected areas, and a cultural mythology of wilderness (Lorimer et al., 2015). Here, we examine how camelids could be used in both proxy and non-proxy trophic rewilding.

There are currently three wild camelid species and four domestic ones. Of the wild species, vicuñas *Vicugna vicugna* and guanacos *Lama guanicoe* can be found in the Andes and southern cone of South America. Both vicuñas and guanacos are listed as Least Concern by the IUCN Red List (accessed 2015). Vicuñas is

protected by vicuñas Convention in Peru, Bolivia, Chile and Argentina. Both species are listed in CITES and are subject to conservation protections in Chile, Argentina, Peru (where guanacos is considered Endangered) and Bolivia (where guanacos is considered Critically Endangered) (IUCN Red List accessed 2015; Iriarte, 2000; Nugent et al., 2006; Grimberg Pardo, 2010). After many decades of poaching vicuña conservation can be considered a success story (Arzamendia et al., 2006; Bonacic et al., 2002). *Camelus ferus*, the wild Bactrian camel, by contrast is listed as Critically Endangered (IUCN Red List accessed 2015) due to its small and declining population, estimated at around 350–500 in 1997 (Hare, 1997), 1000 in 1999 (Reading et al., 1999) and 950 in 2004 (IUCN Red List accessed 2015). *Camelus ferus* is found in the Gobi desert in China and Mongolia (Kaczensky et al., 2013). The four domestic species, llamas *Lama glama*, alpacas *Vicugna pacos*, dromedaries *Camelus dromedarius* and Bactrian camels *Camelus bactrianus*, as a group can be found on every continent except Antarctica, with a large feral population of dromedary in Australia. The ancestral wild form of dromedary is extinct (Churcher et al., 1999; Lövei, 2007), whereas the probable ancestors of the other three are extant.

All extant camelids share adaptations to marginal habitats. The cameline (subfamily Camelinae: *Camelus* spp.) species are notably adapted to arid desert conditions: they can survive for many days

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without access to water by maintaining hyperglycaemia, allowing for a very low metabolic rate, maintaining a high level of salt in their blood by eating salty plants and drinking brackish water, and raising their body temperature (Soliman, 2015; Wu et al., 2015). They also have morphological adaptations for preventing damage from dust, for walking on sand, for cooling the brain, and for extracting a maximum amount of water from ingested food (Soliman, 2015). Domestic camels predominantly browse woody, including spiny, plants, but it must be noted that they also graze (Sato, 1980; Migongo-Bake and Hansen, 1987). Both cameline and lamine (subfamily Lamelinae: *Lama* and *Vicugna* spp.) species are both grazers and browsers, and have lower metabolic rates than other large grazers and browsers, an adaptation that can be advantageous in arid and semi-arid environments with sparse and low quality forage (Dittmann et al., 2014). Vicuña specialize in high altitudes and predominantly graze (Lucherini, 1996; Wursten et al., 2014). Guanacos by contrast are able to survive in isolated populations in marginal and stressful habitats due to generalist feeding strategies (browsing and grazing), flexible social structure and timing of birth to coincide with rainfall (González et al., 2014; Belardi and Rindel, 2008; Wursten et al., 2014).

Rewilding is most likely to be successful when large fauna can be reintroduced onto large, continuous tracts of land with low likelihood of human-wildlife conflict (Navarro and Pereira, 2012), although it can also be applied to densely populated landscapes (Jepson, 2015). Such wild, abandoned or marginal lands in the Americas, Eurasia and North Africa, East Africa and the Sahel are, in general, likely to have once had at least one camelid species sometime between the Miocene and the present. Australian drylands, although not native habitat for camelids (since they evolved in what became North America after the split between Laurasia and Gondwana), have lost most of their marsupial large herbivores, and thus could be assessed for proxy rewilding (cf. Bowman, 2012). Although the Pleistocene occurrence patterns is usually taken as the earliest reasonable baseline for rewilding, we emphasize that camelids are generalists and their pre-Quaternary as well as Pleistocene and Holocene niches might point to ways in which they can serve as proxy (or ecological analogue) species. The biota in different regions are a product of evolution over millions of years, and shaped by biotic interactions across these time frames and not just between extant species, with large mammal species most having had large continental-to hemisphere-scale range dynamics. Hence, there is no strong biological reason to focus solely on extant species that have occurred in the focal region within the last few hundreds of years.

### 1.1. Camelids from the Miocene to the Holocene

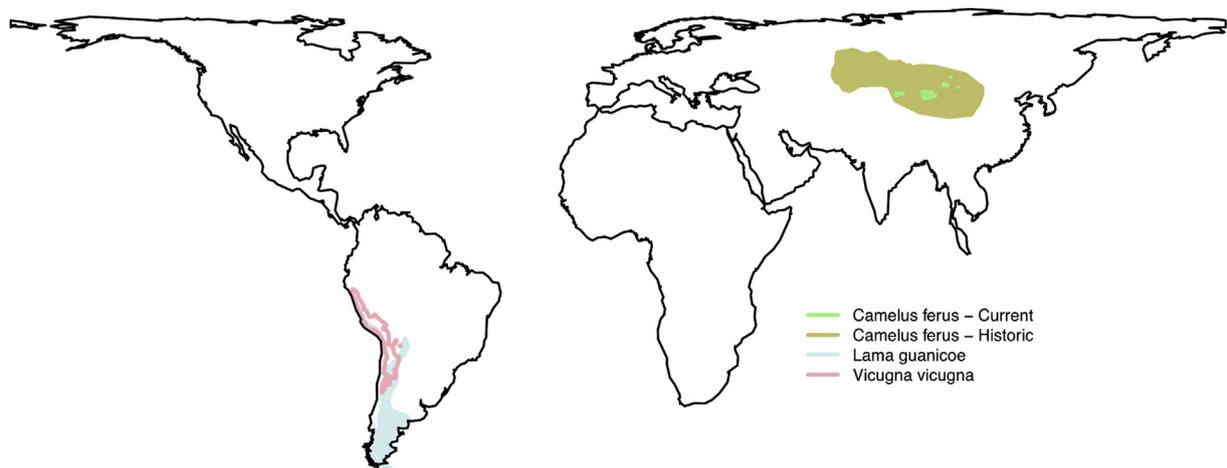
Camelids emerged in the Oligocene (around 34–23 Ma) in North America, with three main branches including the *Poebrotherium*, *Stenomylus* and *Pseudorabis* (McKenna, 1966). They were small, such as *Stenomylus hitchcocki* at just 30 kg around 30 Ma (Mendoza et al., 2006), but later during the Miocene, Pliocene and Pleistocene the camelids radiated into large forms, even megaherbivores ( $\geq 1000$  kg, Owen-Smith, 1988), such as *Gigantocamelus* spp. During the Miocene camelids such as *Gigantocamelus spatulus*, *Megatylopus* spp., *Megacamelus merriami*, *Camelops* spp., *Aepycamelus* spp., *Procamelus* spp., *Paramiolabis* spp., *Protolabis* spp., *Miolabis* spp., *Michenia* spp., *Hemiauchenia* spp., and *Pliauchenia* spp., coexisted with a high diversity of other browsers and grazers, such as rhinoceros, proboscideans, horses, and numerous genera of ruminants, in the savanna woodlands of North America (Janis et al., 2004). These camelids were predominantly browsers and mixed browsers (Dompierre and Churcher, 1996; Feranec, 2003; Semperebón and Rivals, 2010; Kita et al., 2014).

North America had already broken away from Gondwana as part of Laurasia around 175 Ma. Gondwana then broke into South America, Antarctica, and Australia (184–40 Ma). A number of land-bridges sporadically connected Eurasia and North America, all before the emergence of camelids (Brikatis, 2014). This accounts for the lack of early camelids outside North America. Continental drift then allowed this large diversity of camelids to spread beyond North America. However, the formation of the Isthmus of Panama allowed the Great American Biotic Interchange of species, peaking around 3 Ma, towards the end of the Pliocene (Bacon et al., 2015). Among the species from North America that extended their ranges into South America were camelids. The camelids that were present or evolved in South America by the Pleistocene include *Hemiauchenia* spp., and the lamine camelids, *Paleolama* spp., *Lama* spp., *Provicugna* spp. and *Vicugna* spp., which coexisted throughout South America with large grazers and browsers such as the locally evolved toxodonts, *Macrauchenia*, capybaras, and giant sloths as well as other immigrant herbivores such as gomphotheres, horses, deer, tapirs, and peccaries (MacFadden and Shockey, 1997; Hubbe et al., 2013). *Paleolama*, for example, was a browser of the Brazilian tropical dry forests, which are likely to have been much more extensive during the Pleistocene (Pennington et al., 2000), and further south inhabited more open habitats (de Melo França et al., 2015). Other lamine species were primarily grazers (MacFadden and Shockey, 1997). While the rise of the Andes had contributed to increased aridity on the west coast of South America around 14 Ma (Le Roux, 2012), cooling and/or increased aridity are associated with the Ice Age (beginning 10.5–7 Ma) in South America (Pennington et al., 2000). These conditions would have favored camelids.

Meanwhile, a land bridge formed across the Bering Strait linking Eurasia to North America in the late Miocene, allowing faunal interchange throughout the late Miocene until its opening around 5.5 Ma (Rybczynski et al., 2013). The Camelini tribe diverged from the Lamini camelids earlier, around 17 Ma (cited in Rybczynski et al., 2013), 8 Ma (cited in Cui et al., 2007) or 25 Ma (Cui et al., 2007). Notably, dromedaries and guanacos are able to form hybrids despite what is referred to as 11 Ma of reproductive isolation by Skidmore et al. (1999). Either a so-called High Arctic giant camel (*Paracamelus* spp.) and/or *Camelops hesternus* are thought to be the ancestor of Eurasian camels (Zazula et al., 2011; Rybczynski et al., 2013). *Paracamelus* has been found in Spain and China by 6 Ma (late Miocene) and in Eastern Europe, the Levant and North Africa between the late Miocene and early Pliocene (Payne and Garrard, 1983; Titov and Logvynenko, 2006; Gautier et al., 2012; Rybczynski et al., 2013). Geraads (2014) suggests that dromedaries and Bactrian camels are more closely related to one other than to either *Camelus thomasi*, *Camelus grattardi*, or any other African Pliocene and Pleistocene camelid species, based on archaeological morphological evidence. Further, confusing the evidence, the split between the Bactrian and dromedary species is dated at around 8 Ma, apparently while still in North America, by Cui et al. (2007) based on mtDNA analysis. According to population size estimates by Wu et al. (2015), Bactrian camels are present from the end of the Miocene and dromedaries since the end of the Pliocene. On the whole, the evolution and paleoecology of the Eurasian camelines has been studied far less than that of the South American lamines, and appears to be somewhat unresolved.

The modern camelid species are many fewer than their ancestors (Fig. 1). Humans crossed the Bering Strait land bridge from Asia, and have been implicated in the late Pleistocene/early Holocene megafaunal extinctions in the Americas (Sandom et al., 2014). However, evidence that they hunted camelid species in North and South America more than sporadically is lacking (Frison et al., 1978; Haynes and Stanford, 1984; Frison, 1998; Prado et al., 2015; Waters

## Range of extant camelids



## Natural range of extinct camelids

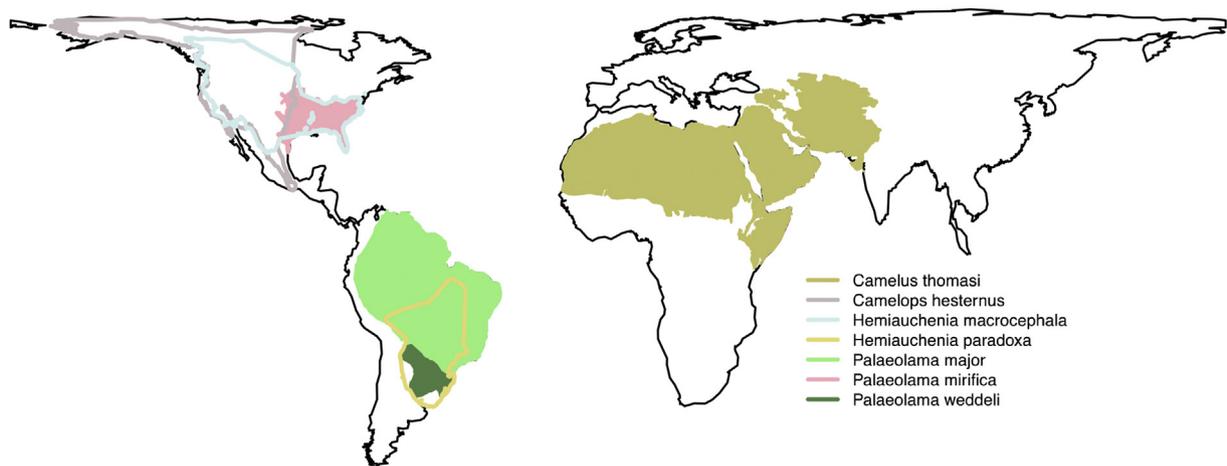


Fig. 1. Top, the current and historical ranges of extant wild camelid species. Domestic species are not shown. Bottom, potential ranges under current climate of seven camelid species that have gone globally extinct in the Late Pleistocene or Holocene (or now only survive in domesticated form). Data from [Faurby and Svenning \(2015\)](#).

et al., 2015). This may be because camelids require water less than other large herbivores, and are thus found more often in marginal habitats and less often at waterholes where they may be surrounded by hunters ([Frison et al., 1978](#)). However, a more likely explanation is that the absence of evidence of extensive human hunting of camelids is due to taphonomic bias ([Surovell and Grund, 2012](#)). During this period, North American camelids were mainly mixed browsers and grazers ([Kohn et al., 2005](#); [Semperebon and Rivals, 2010](#)). At the Pleistocene–Holocene transition in the Pampas, guanaco and *Palaolama* spp. coexisted with among others, *Macrauchenia*, horses (*Equus ferus*), *Toxodon*, and a range of ground sloths such as *Megatherium*, *Eutatus*, and *Glossotherium* as well as large armadillos and their glyptodont relatives, e.g., *Glyptodon*, and there is evidence that both horses and guanaco were hunted by humans ([Borrero et al., 1998](#)). With the onset of a more humid environment in the Pampas around 10,500 ya, the responses of humans are unclear, but their low population has been hypothesized to have impeded overhunting of camelids ([Borrero et al., 1998](#)). This argument, however, is unlikely to be valid ([Alroy, 2001](#)). One hypothesis for the megafaunal extinctions in the Pampas is that increased cooling 14,000 ya followed by warming at

the beginning of Holocene may have favored generalists, including the surviving guanaco and vicuña ([Prado et al., 2015](#)). One unsatisfactory thing about such local explanations is that they ignore that the megafaunal extinction constitute a global-scale event that is unique for the Cenozoic in its size-selective nature. In addition, humans are the only novel feature in the environment differentiating that climate change from previous ones, and must have played a major role in extinction despite lack of direct evidence for extensive hunting ([Surovell and Grund, 2012](#); [Sandom et al., 2014](#)). Further, other species that went extinct throughout South America were as generalist as the surviving camelids, demonstrating that generalist diets alone do not convey extinction survivalship ([Dantas et al., 2013](#); [Franca et al., 2015](#)). *Vicugna vicugna* is proposed to be a surviving subpopulation of *Lama gracilis* ([Weinstock et al., 2009](#)). In any case, all camelid species in North America went extinct by the Holocene, leaving only the currently extant camelines and lamines in Eurasia and South America, respectively.

As in all pastoralist systems, human hunting of camelids is thought to have evolved into domestication and a pastoralist system, often involving transhumance to track environmental variability along altitudinal and other gradients ([Alvard and Kuznar,](#)

2001; FAO, 2001). The process of domestication has been studied extensively in South America and almost entirely ignored in Eurasia. In the Andes and Pampas, wild guanacos and vicuñas were hunted or exploited for their fiber (wool) continuously alongside the domestication of several species or breeds in addition to alpacas and llamas (Gasco and Marsh, 2013; Belardi and Rindel, 2008; Westreicher et al., 2007; Jackson et al., 2005; Yacobaccio, 2004; Lynch, 1983). Camelids were the only domestic large herbivore species of South America. Andean cultures relied in multiple ways on llama breeds, collecting their feces to fertilize staple potato crops, using their fiber for cloth and rope, and transporting trade goods across empires on their backs (Lynch, 1983). Interestingly, unlike in Eurasia and Africa, in South American cultures the milk of camelids has apparently never been a food resource. With the arrival of European colonists and their livestock, several varieties of domestic camelid went extinct, including for example the chili-hueque, a somewhat mysterious domestic guanaco or llama breed from central Chile (Miller, 1980). Overhunting of guanaco starting in the colonial period led to the disappearance of guanacos from parts of their range, including the heavily colonized central zone of Chile (Miller, 1980; Westreicher et al., 2007).

In Eurasia, domestic camel pastoralist cultures are found continuously from Mongolia to the Sahel. The wild Bactrian camel (*Camelus ferus*) may be the ancestor of the domestic Bactrian camel, which is found in northern Asia (Tulgat and Schaller, 1992; Potts, 2004) or a congener (Ji et al., 2009). Bactrian camels are thought to have been domesticated in China, Mongolia or Kazakhstan, and subsequently introduced into Iran and Turkmenistan (Peters and Driesch, 1997). Bactrian camels provide essential resources to nomadic pastoralists, including feces collected for use as fuel, hair for rope and cloth, milk, and transport, although sheep, goats, horses and cattle have increasingly been adopted since the 1800s (Chuluunbat et al., 2014; Berger et al., 2013; Peters and Driesch, 1997; Krader, 1955). Throughout Central Asia and the Near East since antiquity, Bactrian and dromedaries have been crossed, yielding a fertile and hardy hybrid that was highly valued in the region (Potts, 2004). However, it was not allowed to breed as the offspring were aggressive. Observing “camel wrestling” contests between hybrid males is a traditional social activity that continues in Turkey (Çakırlar and Berthon, 2014). Camel racing is additionally an important traditional sport both with Bactrian camels in Central Asia and dromedaries, in the Gulf States.

Dromedaries appear to have been domesticated around 5000 ya in central Arabia from *Camelus thomasi* (Grigson et al., 1989; Spassov and Stoytchev, 2004; but see Gautier, 1966). *Camelus thomasi* occurred in northern Africa, and perhaps the Levant, into the Holocene (Grigson, 1983; Churher et al., 1999). Its extinction is attributed to the increasingly arid conditions of the Sahara after a moist period ended around 4000–5000 ya; some large animals survived in the Maghreb, but *Camelus thomasi*, along with the Atlantic gazelle and North African buffalo, disappeared (Lövei, 2007). However, it is more likely to have been incorporated into domestic herds or exterminated to prevent competition with dromedaries than to have gone extinct due to climate change alone. Subsequently dromedaries became integral parts of pastoralist cultures throughout arid and semi-arid parts of northern Africa, the Levant and India (Raziq et al., 2011; Farah et al., 2004; Mehta et al., 2007; Raziq et al., 2011; Volpato and Puri, 2014). There are many local breeds across this range, often complementary, such that one breed in a particular area is preferred for transport of goods, while another is a good source of milk and fiber (e.g. Raziq et al., 2011; Mehta et al., 2007). Transhumance in camel pastoralists systems is threatened by economic and political pressures toward sedentarization throughout Africa and Eurasia, despite recognition that camel transhumance is a robust and adaptive system in marginal

areas (Farah et al., 2004; Volpato and Puri, 2014). Thus, millennia of domestic camelid socio-ecologies are at risk of disappearance across Eurasia and Africa.

Bactrian camels are feral or free-ranging in some areas. In some Gulf States, high densities of free-ranging dromedaries result in land degradation by overgrazing (Gallacher and Hill, 2006a, b). In Australia, a small number of dromedaries that were imported during the 1800s to provide transportation across the desert, was eventually abandoned and formed a feral population that appears to have slowly increased in population to an estimated size of 1,000,000 (Spencer et al., 2012; Crowley, 2014). (While Spencer et al. (2012) notes that dromedaries have no history of being invasive species outside Australia, camelids are clearly able to migrate into suitable habitat and establish new populations). Australian dromedaries are blamed for soil degradation and reduction in water quality at watering holes (Crowley, 2014; McBurnie et al., 2015). Others argue that dromedaries are an acceptable part of modern Australian fauna, carrying out proxy functions (Crowley, 2014; Gibbs et al., 2015). Dromedary and Bactrian camels were imported to the western United States during the mid-1800s as military transport, and small feral populations existed for several years, but were eradicated before the turn of the century (Young, 1982). Llamas and alpacas, although popular as livestock and even as pets in North America and elsewhere, seem to rarely form feral populations. One exception is the Lago Peñuelas National Reserve in Chile, where feral llamas have crossed with guanacos to form “guallamas” or “llamacos,” a fertile hybrid with intermediate appearance and behaviors (pers. comm. L. Gutiérrez, pers. obs. MR-B). Guanaco were experimentally introduced as part of a naturalistic grazing scheme in sown swards in Scotland, with the conclusion that they did not compete with goats and red deer and could be raised for their fiber along with these species (Fraser and Gordon, 1997).

## 1.2. Potential ecological roles of camelids within rewilding projects

Reintroductions of camelids are already taking place in some areas and can provide insight into the challenges of camelid rewilding. The Wild Camel Protection Foundation NGO is breeding and reintroducing *Camelus ferus* in Mongolia ([www.wildcamels.com](http://www.wildcamels.com) accessed May 2015). Here, the main challenges are the low population of *Camelus ferus*, its avoidance of human presence, and the increase in anthropogenic activities in its habitat, including mining, poaching, and goat herding for cashmere production (Hare, 1997; Berger et al., 2013). In South America, reintroductions of vicuña from captive breeding facilities have been declared successful (Arzamendia et al., 2006; Bonacic et al., 2002). Guanaco are still being reintroduced sporadically into some parts of their former range, primarily in protected areas, while in other areas they are managed for sustainable harvests (Sarno et al., 1999). The main challenges to these programs include ongoing poaching, and uncontrolled feral dog populations in Chile (Donadio and Buskirk, 2006; C. Bonacic, pers. comm.).

This last challenge underscores the important role that Pleistocene history can have on reintroductions or rewilding. Since the Pleistocene, southern South American ecosystems appear have not included group-hunting pursuit predators. Group-hunting pursuit canids are only known from further north, although it is not clear what would have restricted their expansion further south: *Procyon* spp. are known from Brazil, Ecuador and northern Argentina (Prevosti et al., 2005), while the dire wolf (*Canis dirus*) ranged from North America as far south as Bolivia (Dundas, 1999). The saber toothed cat *Smilodon populator*, although likely social, was probably primarily an ambush predator, like modern lions (McCall et al., 2003; Carbone et al., 2009). *Dusicyon avus*, a large fox, and

*Arctotherium tarijense*, a bear, were omnivorous, are likely to have been solitary, and may have scavenged camelids more than they hunted them (Prevosti and Vizcaíno, 2006; Prevosti and Martin, 2013). After the end-Pleistocene/early Holocene megafauna extinction in South America, the remaining camelid species in South America were those existing south of these canids' historical range, in the Pampas, Tierra del Fuego and the southern Andes. The predator defense strategies most appropriate for ambush as opposed to pursuit, and solitary vs. group predators are different, and it is likely that South American camelids would have evolved appropriate defense mechanisms against social and solitary ambush hunters, such as *Smilodon*, pumas, jaguars, and humans. This strategy, present in guanacos (Darwin 2015 (1839); MR-B pers. obs.), consists of "predator inspection," in which the predator loses the advantage of surprise (FitzGibbon, 1994). At the same time, surviving camelid populations may have lost components of defense strategies suitable for group-hunting pursuit predators (e.g. Walther, 1969; Blumstein and Daniel, 2005), which could explain their vulnerability to feral dogs.

Rewilding introductions are distinguished from classical reintroductions by a motivation to restore ecological functions rather than populations *per se* (Svenning et al., 2015). A stumbling block in the use of camelids for rewilding is the relative lack of research on camelid functions in ecosystems. As camelids drink brackish water and eat salty plants, they may act to redistribute salts, as well as other nutrients, over the landscape (Doughty et al., 2015; Doughty et al. 2013a,b; Wolf et al., 2013). As both browsers and grazers, camelids may participate in functions such as stimulating tree growth (McNoughton, 1983; Gowda, 1997) and affecting N and P cycling rates (Schmitz, 2008; Metcalfe et al., 2014). Guanacos in particular make latrines, forming large mounds, which are likely to have ecological engineering effects. Camelids' role in transporting seeds via endo- and exo-zoochory is largely unexamined. Guanacos are reported to stimulate the germination of *Acacia caven* and *Prosopis* seeds via endozoochory (Fuentes et al., 1989). Guanacos also form trails, which could have intermediate disturbance effects or act as corridors for seed dispersal. Camelid interactions with animal species other than livestock are seemingly not researched. However, as highly selective foragers, they rarely or weakly compete with other grazers even when sharing territory with them (Migongo-Bake and Hansen, 1987; Fraser and Gordon, 1997; Borgnia et al., 2008; Acebes et al., 2012; Berger et al., 2013; Iranzo et al., 2013; Wursten et al., 2014; O'Connor et al., 2015). Thus they may either increase or decrease plant species evenness by targeting specific plants (rare or common) not eaten by other grazers in the system. They also act as prey species for large carnivores (Donadio et al., 2010). Unfortunately, many of these ecological functions are not well understood. Thus, a great deal of ecological research remains to be carried out, and rewilding may provide opportunities to do so (Svenning et al., 2015).

Here, we consider the potential costs and benefits of rewilding with camelids in deserts, semi-arid grasslands and semi-arid savannas and thorn woodlands on a global scale. Such habitats correspond to the current habitats of extant camelids as well as the past habitats of extinct camelids.

Deserts around the world hold a relatively small fraction of global biodiversity. However, their conservation is nonetheless important because deserts have many species that are uniquely adapted to extreme conditions, including for example many EDGE (Evolutionarily Distinct and Globally Endangered) species ([www.edgeofexistence.org](http://www.edgeofexistence.org); Olson and Dinerstein, 1998). While desertification is often a threat to other habitats, deserts themselves can also be threatened by increasing aridity and soil degradation or erosion, invasive species, shrub encroachment, and loss of plant diversity, and loss of pollinators and seed dispersers

(Puigdefabregas and Mendizabal, 1998; Eldridge et al., 2011; Maestre et al., 2012). Camels are the obvious choice for rewilding in the most arid regions, and the introduction histories in Australia and the western US suggest that dromedaries and Bactrian camels are both able to find suitable forage in unfamiliar habitats dominated by spiny and woody plants. Camels could probably be used to combat shrub encroachment and reduce the risk of fire. However, camels are able to eat very spiny and thorny plants, and their generalist foraging habitats combined with selective bite capacity mean that they may be prone to destroy plants that are not adapted to intensive grazing or browsing.

Semi-arid grasslands such as the Pampas, the North American prairies, or the Eurasian steppe, are important ecosystems for many large grazers including species that are endangered or that used to be much more numerous, such as the saiga *Saiga tatarica* and the American bison *Bison bison*. Grasslands can also be important habitats for migratory birds, as well as providing migratory corridors for large herbivores (Berger, 2004; Brennan and Kuvlesky, 2005). Shrub encroachment, overgrazing by livestock in pastoralist systems, desertification, and land conversion to agriculture are common conservation problems in grasslands (Bond and Parr, 2010; Henwood, 2010). All extant camelids are well suited to grassland habitats. From a compositionalist perspective, reintroducing camelids to parts of their historical range or as proxies for extinct camelids can serve to recreate the high richness of grazers typical of most grasslands. From the functionalist perspective, this can provide greater prey for large predators and assist in nutrient cycling. In addition, as camelids rarely compete directly with other grazers, they are expected to perform slightly different grazing functions, which may be unexpectedly beneficial or harmful. A likely benefit is that they can avoid competing with livestock and may thus be compatible with rewilding in areas and projects where removal of pastoralism is neither feasible nor desirable. However, using the same camelid species or breed for rewilding that is used for pastoralism in a given area is likely to create problems related to the mixing of feral and domestic populations. Where camel pastoralism is declining, wild camelids could maintain ecological benefits of camel movements over the landscape.

Finally, savannas and thorn woodlands include many different kinds of open and generally thorny woodlands around the world, such as the acacia savannas of sub-Saharan Africa, seasonally dry tropical forests and thorn woodlands (Pennington et al., 2000; van Bloem et al., 2004). Although diverse in form, these habitats in general have many endemic plant species, and a relatively high species richness (van Bloem et al., 2004). They are often threatened by strong anthropogenic influences including pasturing animals, gathering firewood, setting fires, hunting game, gathering food resources, or conversion to agriculture (van Bloem et al., 2004; Leal et al., 2005; Syampungani et al., 2009; Root-Bernstein and Jaksic, in press). These influences can lead to fragmentation, degradation and defaunation. This is the kind of habitat in which camelids evolved during the Miocene- Pleistocene, and thus they can be expected to have important ecological functions in such habitats, although unfortunately these are among the least known of camelid- environment interactions since they are currently only relevant to small populations of guanaco in the Chaco (semi-tropical seasonally dry forest) in Bolivia. Camelids could be reintroduced as seed dispersers, to provide browsing on thorny trees, or as prey for large predators. For example, a pilot rewilding project in central Chile, Proyecto REGenera (run by MR-B) aims to reintroduce guanacos to restore browsing and seed dispersal functions with the goal of restoring the "espinal" savanna silvopastoral system (Root-Bernstein and Jaksic, 2013; Landon and Root-Bernstein, 2015; Root-Bernstein et al., submitted). Conflicts with such models of rewilding are likely to include issues surrounding wild animals in

highly anthropogenic habitats, such as human-wildlife conflict and poaching.

Although this review focuses on the functional ecology and paleoecology of camelids, a thorough consideration of rewilding prospects must also consider human social and cultural interactions with the reintroduced species or proxy species. Opportunities exist to rewild camelids in areas with low densities of humans and human uses. However, many camelid reintroduction and conservation projects in South America, as well as discussions of African and Eurasian camel pastoralism, take for granted that sustainable use is part and parcel of conservation of camelid landscapes (Mehta et al., 2007; Westreicher et al., 2007; Çakırlar and Berthon, 2014; Volpato and Puri, 2014). For example, sustainable and high-welfare practices of shearing wild vicuña for their extra-fine fiber have been a focus of vicuña conservation research (Bonacic et al., 2006). Since rewilding already often blurs the line between domestic species and wild ones, e.g., by rewilding cattle and horses as proxies for aurochs and tarpan (e.g. at Oostvaardersplassen, the Netherlands; Lorimer and Driessen, 2013), camelid rewilding projects may find it pragmatic to do so as well, in the opposite direction. For example, domestic camelids could be managed in ways that allow them to carry out more ecosystem functions. This might mean reviving transhumance, mixing camelids with other grazers and browsers, or allowing a percentage of their feces to remain uncollected, for example.

## 2. Conclusions

Camelids were once highly species-rich and abundant, co-existing in savannas with a wide variety of large fauna, now mostly extinct. Along with horses, camelids were among the most successful of the large fauna that originated in North America, but went completely extinct there at the end of the Pleistocene. They are mixed browser/grazer generalists adapted to marginal habitats with an evolutionary history of spreading into new areas and coexisting alongside many other grazers and browsers. These characteristics make them potentially attractive species for rewilding for a number of purposes. We suggest that evaluations of the suitability of the various extant camelid species for rewilding be carried out on a site-by-site basis, considering the functions to be restored, the potential biotic and abiotic interactions and side-effects, and potential for social conflicts or benefits (cf. the general trophic rewilding priorities outlined by Svenning et al., 2015). Further ecological research on contributions to ecological processes would contribute to their conservation and management as well as the conservation and management of arid and semi-arid habitats around the world.

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## References

Acebes, P., Traba, J., Malo, J.E., 2012. Co-occurrence and potential for competition between wild and domestic large herbivores in a South American desert. *J. Arid Environ.* 77, 3944.

Alroy, J., 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* 292, 1893–1896.

Alvard, M.S., Kuznar, L., 2001. Deferred harvests: the transition from hunting to animal husbandry. *Am. Anthropol.* 103 (2), 295–311.

Arzamendia, Y., Cassini, M., Vilá, B., 2006. Habitat use by vicuña *Vicugna vicugna* in Laguna Pozuelos Reserve, Jujuy, Argentina. *Oryx* 40, 198.

Bacon, C., Silvestro, D., Jaramillo, C., Smith, B., Chakrabarty, P., Antonelli, A., 2015. Biological evidence supports an early and complex emergence of the Isthmus of Panama. *Proc. Natl. Acad. Sci.* 112, 6110–6115.

Belardi, J., Rindel, D., 2008. Taphonomic and archeological aspects of massive mortality processes in guanaco (*Lama guanicoe*) caused by winter stress in Southern Patagonia. *Quat. Int.* 180, 3851.

Berger, J., 2004. The last mile: how to sustain long-distance migration in mammals. *Cons. Biol.* 18 (2), 320–331.

Berger, J., Buuveibaatar, B., Mishra, C., 2013. Globalization of the cashmere market and the decline of large mammals in central Asia. *Conserv. Biol.* 27, 679–689.

Blumstein, D.T., Daniel, J.C., 2005. The loss of anti-predator behavior following isolation on islands. *Proc. R. Soc. B* 272, 1663–1668.

Bonacic, C., Macdonald, D., Galaz, J., Sibly, R., 2002. Density dependence in the camelid *Vicugna vicugna*: the recovery of a protected population in Chile. *Oryx* 36.

Bonacic, C., Feber, R., Macdonald, D., 2006. Capture of vicuñas (*Vicugna vicugna*) for sustainable use: animal welfare implications. *Biol. Conserv.* 129, 543550.

Bond, W., Parr, C., 2010. Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biol. Conserv.* 143, 23952404.

Borgnia, M., Vilá, B., Cassini, M., 2008. Interaction between wild camelids and livestock in an Andean semi-desert. *J. Arid Environ.* 72, 21502158.

Borrero, L.A., Zárate, M., Miotti, L., Massone, M., 1998. The Pleistocene–Holocene transition and human occupations in the southern cone of South America. *Quat. Int.* 49, 191–199.

Bowman, D., 2012. Conservation: bring elephants to Australia? *Nature* 482, 30.

Brennan, L.A., Kuvlesky Jr., W.P., 2005. North American grassland birds: an unfolding conservation crisis? *J. Wildl. Manag.* 69 (1), 1–13.

Brikiatis, L., 2014. The De Geer, Thulean and Beringia routes: key concepts for understanding early Cenozoic biogeography. *J. Biogeogr.* 41 (6), 1036–1054.

Çakırlar, C., Berthon, R., 2014. Caravans, camel wrestling and cowrie shells: towards a social zooarchaeology of camel hybridization in anatolia and adjacent eegions. *Anthropozoologica* 49.

Carbone, C., Maddox, T., Funston, P., Mills, M., Grether, G., Valkenburgh, B., 2009. Parallels between playbacks and Pleistocene tar seeps suggest sociality in an extinct sabretooth cat. *Smilodon*. *Biol. Lett.* 5, 81–85.

Chuluunbat, B., Charruau, P., Silbermayr, K., Khorlojav, T., Burger, P.A., 2014. Genetic diversity and population structure of Mongolian domestic Bactrian camels (*Camelus bactrianus*). *Anim. Genet.* 45, 550–558.

Churcher, C., Kleindienst, M., Schwarcz, H., 1999. Faunal remains from a Middle Pleistocene lacustrine marl in Dakhleh Oasis, Egypt: palaeoenvironmental reconstructions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 154, 301312.

Crowley, S., 2014. Camels out of place and time: Dromedaries *Camelus dromedarius* in Australia. *Anthrozoos A Multidiscip. J. Interact. People Anim.* 27, 191203.

Cui, P., Ji, R., Ding, F., Qi, D., Gao, H., Meng, H., Yu, J., Hu, S., Zhang, H., 2007. A complete mitochondrial genome sequence of the wild two-humped camel (*Camelus bactrianus ferus*): an evolutionary history of camelidae. *BMC Genomics* 8, 241.

Dantas, M.A.T., Dutra, R.P., Cherkinsky, A., Fortier, D.C., Kamino, L.H.Y., Cozzuol, M.A., et al., 2013. Paleoeology and radiocarbon dating of the Pleistocene megafauna of the Brazilian intertropical region. *Quat. Res.* 79, 61–65.

Darwin, C., 2015. *It Was Snowing Butterflies*. Penguin Classics, London, 1839.

de Melo França, L., Azevedo, L., Dantas, M., Bocchiglieri, A., Avilla, L., Lopes, R., Silva, J., 2015. Review of feeding ecology data of late Pleistocene mammalian herbivores from South America and discussions on niche differentiation. *Earth Sci. Rev.* 140, 158–165.

Dittmann, M., Hummel, J., Runge, U., Galeffi, C., Kreuzer, M., Clauss, M., 2014. Characterising an artiodactyl family inhabiting arid habitats by its metabolism: low metabolism and maintenance requirements in camelids. *J. Arid Environ.* 107, 4148.

Dompierre, H., Churcher, C.S., 1996. Premaxillary shape as an indicator of the diet of seven extinct late Cenozoic New World camels. *J. Vertebr. Paleontol.* 16 (1), 141–148.

Donadio, E., Buskirk, S., 2006. Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. *Biol. Conserv.* 127, 139–145.

Donadio, E., Novaro, A., Buskirk, S., Wursten, A., Vitali, M., Monteverde, M., 2010. Evaluating a potentially strong trophic interaction: pumas and wild camelids in protected areas of Argentina. *J. Zool.* 280, 33–40.

Donlan, J., Green, H.W., Berger, J., Bock, C.E., Bock, J.H., Burney, D.A., Estes, J.A., Foreman, D., Martin, P.S., Roemer, G.W., Smith, F.A., Soulé, M.E., 2005. Rewilding North America. *Nature* 436, 913–914.

Donlan, J., Berger, J., Bock, C.E., Bock, J.H., Burney, D.A., Estes, J.A., Foreman, D., Martin, P.S., Roemer, G.W., Smith, F.A., Soulé, M.E., Greene, H.W., 2006. Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. *Am. Nat.* 168 (5), 660–681.

Doughty, C., Wolf, A., Malhi, Y., 2013a. The impact of large animal extinctions on nutrient fluxes in early river valley civilizations. *Ecosphere* 4, 148.

Doughty, C., Wolf, A., Malhi, Y., 2013b. The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nat. Geosci.* 6, 761–764.

Doughty, C.E., Faurby, S., Svenning, J.-C., 2015. The impact of mega-fauna extinctions on savanna woody cover in South America. *Ecography* 38, 1–10.

Dundas, R., 1999. Quaternary records of the dire wolf, *Canis dirus*, in North and South America. *Boreas* 28, 375–385.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G.,

2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol. Lett.* 14, 709–722.
- FAO (Food and Agriculture Organization of the United Nations), 2001. Pastoralism in the New Millennium. FAO Animal Production and Health, Rome, Italy. Paper 150.
- Farah, K.O., Nyariki, D.M., Ngugi, R.K., Noor, I.M., Guliye, A.Y., 2004. The Somali and the camel: ecology, management and economics. *Anthropologist* 6 (1), 45–55.
- Faurby, S., Svenning, J.-C., 2015. Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Divers. Distrib.* 21, 1155–1166.
- Feranec, R., 2003. Stable isotopes, hypsodonty, and the paleodiet of *Hemiauchenia* (Mammalia: Camelidae): a morphological specialization creating ecological generalization. *Paleobiology* 40, 230–242.
- FitzGibbon, C.D., 1994. The costs and benefits of predator inspection behaviour in Thomson's gazelles. *Behav. Ecol. Sociobiol.* 34 (2), 139–148.
- França, LdM., de Azevedo, L., Dantas, M.A.T., Bocchiglieri, A., Avilla, LdS., Lopes, R.P., et al., 2015. Review of feeding ecology data of Late Pleistocene mammalian herbivores from South America and discussions on niche differentiation. *Earth Sci. Rev.* 140, 158–165.
- Fraser, M.D., Gordon, I.J., 1997. The diet of goats, red deer and South American camelids feeding on three contrasting Scottish upland vegetation communities. *J. Appl. Ecol.* 34 (3), 668–686.
- Frison, G., 1998. Paleoindian large mammal hunters on the plains of North America. *Proc. Natl. Acad. Sci. USA* 95, 14576–14583.
- Frison, G.C., Walker, D.N., Webb, S.D., Ziemens, G.M., 1978. Paleo-Indian procurement of *Camelops* on the Northern Plains. *Quat. Res.* 10, 385–400.
- Fuentes, E.R., Avilés, R., Segura, A., 1989. Landscape change under indirect effects of human use: the Savanna of Central Chile. *Landsc. Ecol.* 2 (2), 73–80.
- Gallaher, D., Hill, J., 2006a. Effects of camel grazing on the ecology of small perennial plants in the Dubai (UAE) inland desert. *J. Arid Environ.* 66, 738–750.
- Gallaher, D.J., Hill, J.P., 2006b. Effects of camel vs oryx and gazelle grazing on the plant ecology of the Dubai desert conservation reserve. Reclaiming the desert: towards a sustainable environment in Arid lands. In: Proceedings of the Third Joint UAE-Japan Symposium on Sustainable GCC Environment and Water Resources. Taylor & Francis, Abu Dhabi, UAE.
- Gasco, A.V., Marsh, E.J., 2013. Hunting, herding, and caravanning: osteometric identifications of camelid morphotypes at Khonkho Wankane, Bolivia. *Int. J. Osteoarchaeol.* 25 (5), 676–689.
- Gautier, A., 1966. *Camelus thomasi* from the northern Sudan and its bearing on the relationship *C. thomasi*: *C. bactrianus*. *J. Paleontol.* 40 (6), 1368–1372.
- Gautier, A., Makowiecki, D., Paner, H., Neer, W., 2012. Palaeolithic big game hunting at HP766 in Wadi Umm Rahau, Northern Sudan. *J. Afr. Archaeol.* 10, 165–174.
- Geraads, D., 2014. *Camelus grattardi*, sp. nov., a new camel from the Shungura formation, Omo valley, Ethiopia, and the relationships of African fossil Camelidae (Mammalia). *J. Vertebr. Paleontol.* 34, 1481–1485.
- Gibbs, L., Atchinson, J., Macfarlane, I., 2015. Camel country: Assemblage, belonging and scale in invasive species geographies. *Geoforum* 58, 56–67.
- González, B., Orozco-terWengel, P., Borries, R., Johnson, W., Franklin, W., Marín, J., 2014. Maintenance of genetic diversity in an introduced island population of guanacos after seven decades and two severe demographic bottlenecks: implications for camelid conservation. *PLoS One* 9 e91714.
- Gowda, J.H., 1997. Physical and chemical response of juvenile *Acacia tortilis* trees to browsing. *Experimental evidence. Funct. Ecol.* 11, 106–111.
- Grigson, C., 1983. A very large camel from the Upper Pleistocene of the Negev desert. *J. Archaeol. Sci.* 10, 311–316.
- Grigson, C., Gowlett, J., Zarins, J., 1989. The Camel in Arabia—A direct radiocarbon date, calibrated to about 7000 BC. *J. Archaeol. Sci.* 16, 355–362.
- Grimberg Pardo, M.P., 2010. Plan Nacional de Conservación del Guanaco (*Lama guanicoe*) en Chile 2010–2015, Macrozona Norte y Centro. CONAF, Chile.
- Hare, J., 1997. The wild Bactrian camel *Camelus bactrianus* ferus in China: the need for urgent action. *Oryx* 31, 45–48.
- Haynes, G., Stanford, D., 1984. On the possible utilization of *Camelops* by early man in North America. *Quat. Res.* 22, 216–230.
- Henwood, W.D., 2010. Toward a strategy for the conservation and protection of the world's temperate grasslands. *Gt. Plains Res. A J. Nat. Soc. Sci. Paper* 1074.
- Hubbe, A., Hubbe, M., Neves, W.A., 2013. The Brazilian megamastofauna of the Pleistocene/Holocene transition and its relationship with the early human settlement of the continent. *Earth Sci. Rev.* 118, 1–10.
- Iranzo, E., Traba, J., Acebes, P., González, B., Mata, C., Estades, C., Malo, J., 2013. Niche segregation between wild and domestic herbivores in Chilean Patagonia. *PLoS One* 8, e59326.
- Iriarte, A., 2000. Normativa legal sobre conservación y uso sustentable de vicuña y guanaco en Chile. In: González, B., Bas, F., Tala, C., Iriarte, A. (Eds.), *Manejo Sustentable de la Vicuña y el Guanaco*. SAG, PUC, FIA, Santiago, pp. 209–221.
- Jackson, S.D., Méndez, M.C., López, M.P., Jackson, S.D., Seguel, Q.R., 2005. Evaluación de un asentamiento arqueológico en el semiárido de Chile: procesos de formación, fauna extinta y componentes culturales. *Intersecc. Antropol.* 6, 139–151.
- Janis, C., Damuth, J., Thoeodor, J.M., 2004. The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 207, 371–398.
- Jepson, P., 2015. A rewilding agenda for Europe: creating a network of experimental reserves. *Ecography* 38, 001–008.
- Ji, R., Cui, P., Ding, F., Geng, J., Gao, H., Zhang, H., Yu, J., Hu, S., Meng, H., 2009. Monophyletic origin of domestic bactrian camel (*Camelus bactrianus*) and its evolutionary relationship with the extant wild camel (*Camelus bactrianus ferus*). *Anim. Genet.* 40, 377–382.
- Kaczynsky, P., Adiya, Y., Wehrden, H., Mijiddorj, B., Walzer, C., Güthlin, D., Enkhbileg, D., Reading, R., 2013. Space and habitat use by wild Bactrian camels in the Transaltai Gobi of southern Mongolia. *Biol. Conserv.* 169, 311–318.
- Kita, Z., Secord, R., Boardman, G., 2014. A new stable isotope record of Neogene paleoenvironments and mammalian paleoecologies in the western Great Plains during the expansion of C4 grasslands. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 399, 160–172.
- Kohn, M., McKay, M., Knight, J., 2005. Dining in the Pleistocene—Who's on the menu? *Geology* 33, 649–652.
- Krader, L., 1955. Ecology of Central Asian pastoralism. *Southwest. J. Anthropol.* 11 (4), 301–326.
- Le Roux, J., 2012. A review of Tertiary climate changes in southern South America and the Antarctic Peninsula. Part 2: continental conditions. *Sediment. Geol.* 247–248, 21–38.
- Leal, I.R., Cardoso da Silva, J.M., Tabarelli, M., Lacher Jr., T.E., 2005. Changing the course of biodiversity conservation in the Caatinga of Northeastern Brazil. *Conserv. Biol.* 19 (3), 701–706.
- Lindon, A., Root-Bernstein, M., 2015. Phoenix flagships: conservation values and guanaco reintroduction in an anthropogenic landscape. *Ambio* 44, 458–471.
- Lorimer, J., Driessen, C., 2013. Bovine biopolitics and the promise of monsters in the rewilding of Heck cattle. *Geoforum* 48, 249–259.
- Lorimer, J., Sandom, C., Jepson, P., Doughty, C., Barua, M., Kirby, K.J., 2015. Rewilding: science, practice and politics. *Annu. Rev. Environ. Resour.* 40, 8.1–8.24.
- Lövei, G., 2007. Extinctions, modern examples of. In: Levin, S. (Ed.), *Encyclopedia of Biodiversity*. Academic Press.
- Lucherini, M., 1996. Group size, spatial segregation and activity of wild sympatric vicuñas, *Vicugna vicugna* and guanacos *Lama guanicoe*. *Small Rumin. Res.* 20, 193–198.
- Lynch, T.F., 1983. Camelid pastoralism and the emergence of Tiwanaku civilization in the South-Central Andes. *World Archaeol.* 15 (1), 1–14.
- MacFadden, B.J., Shockey, B.J., 1997. Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. *Paleobiology* 22 (1), 77–100.
- Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., et al., 2012. Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335, 214–218.
- McBurnie, G., Davis, J., Thompson, R., Nano, C., Brim-Box, J., 2015. The impacts of an invasive herbivore (*Camelus dromedaries*) on arid zone freshwater pools: an experimental investigation of the effects of dung on macroinvertebrate colonisation. *J. Arid Environ.* 113, 69–76.
- McCall, S., Naples, V., Martin, L., 2003. Assessing behavior in extinct animals: was smilodon social? *Brain, Behav. Evol.* 61, 159–164.
- McKenna, M.C., 1966. Synopsis of Whitneyan and Arikarean camelid phylogeny. *Am. Mus. Novit.* 2253, 1–11.
- McNaughton, S.J., 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40, 329–336.
- Mehta, S.C., Bhardwaj, B., Sahani, M.S., 2007. Status and conservation of Mewari and Jaisalmeri camels in India. *Anim. Genet. Resour.* 40, 87–102.
- Mendoza, M., Janis, C., Palmqvist, P., 2006. Estimating the body mass of extinct ungulates: a study on the use of multiple regression. *J. Zool.* 270, 90–101.
- Metcalfe, D., Asner, G., Martin, R., Espejo, J., Huasco, W., Amézquita, F., Carranza-Jimenez, L., Cabrera, D., Baca, L., Sinca, F., Quispe, L., Taype, I., Mora, L., Dávila, A., Solórzano, M., Vilca, B., Román, J., Bustios, P., Revilla, N., Tupayachi, R., Girardin, C., Doughty, C., Malhi, Y., 2014. Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecol. Lett.* 17, 324–332.
- Migongo-Bake, W., Hansen, R.M., 1987. Seasonal diets of camels, cattle, sheep, and goats in a common range in eastern Africa. *J. Range Manag.* 40 (1), 76–79.
- Miller, S., 1980. Human Influence on the Distribution and Abundance of Wild Chilean Mammals: Prehistoric—present (Ph.D. thesis). University of Washington.
- Naundrup, P.J., Svenning, J.-C., 2015. A geographic assessment of the global scope for rewilding with wild-living horses (*Equus ferus*). *PLoS One* 10 e0132359.
- Navarro, L.M., Pereira, H.M., 2012. Rewilding abandoned landscapes in Europe. *Ecosystems* 15, 900–912.
- Nugent, P., Baldi, R., Carmanchahi, P., De Lamo, D., Failla, M., Ferrando, P., Funes, M., Puig, S., Rivero, S., von Thungen, J., 2006. Conservación del guanaco en la Argentina. In: Bolkovic, M.L., Ramadori, y D. (Eds.), *Manejo de Fauna Silvestre en la Argentina. Programas de uso sustentable. Dirección de Fauna Silvestre, Secretaría de Ambiente y Desarrollo Sustentable*, Buenos Aires.
- Olson, D., Dinerstein, E., 1998. The global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. *Conserv. Biol.* 12, 502–515.
- Owen-Smith, R.N., 1988. Megaherbivores: the Influence of Very Large Body Size on Ecology. University of Cambridge Press, Cambridge.
- O'Connor, D., Butt, B., Foufopoulos, J., 2015. Foraging ecologies of giraffe (*Giraffa camelopardalis reticulata*) and camels (*Camelus dromedarius*) in northern Kenya: effects of habitat structure and possibilities for competition? *Afr. J. Ecol.* 53, 183–193.
- Payne, S., Garrard, A., 1983. *Camelus* from the Upper Pleistocene of Mount Carmel, Israel. *J. Archaeol. Sci.* 10, 243–247.
- Pennington, T.R., Prado, D.E., Pendry, C.A., 2000. Neotropical seasonally dry forests and quaternary vegetation changes. *J. Biogeogr.* 27, 261–273.

- Peters, J., Driesch, A., 1997. The two-humped camel (*Camelus bactrianus*): new light on its distribution, management and medical treatment in the past. *J. Zool* 242, 651–679.
- Potts, D.T., 2004. Camel hybridization and the role of *Camelus bactrianus* in the ancient near east. *J. Econ. Soc. Hist. Orient* 47 (2), 143–165.
- Prado, J., Martínez-Maza, C., Alberdi, M., 2015. Megafauna extinction in South America: a new chronology for the Argentine Pampas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 425, 4149.
- Prevosti, F., Martín, F., 2013. Paleocology of the mammalian predator guild of Southern Patagonia during the latest Pleistocene: ecomorphology, stable isotopes, and taphonomy. *Quat. Int.* 305, 74–84.
- Prevosti, F.J., Vizcaíno, S.F., 2006. Paleocology of the large carnivore guild from the late Pleistocene of Argentina. *Acta Palaeontol. Pol.* 51 (3), 407–422.
- Prevosti, F., Zurita, A., Carlini, A., 2005. Biostratigraphy, systematics, and paleoecology of *Procyon Giebel, 1855* (Carnivora, Canidae) in South America. *J. S. Am. Earth Sci.* 20, 5–12.
- Puigdefábregas, J., Mendizabal, T., 1998. Perspectives on desertification: western Mediterranean. *J. Arid Environ.* 39 (2), 209–224.
- Raziq, A., Verdier, K., Younas, M., 2011. Rapid change of strategy is necessary for development of dromedary camel pastoralism in the Cholistan desert of Pakistan. *Pastor. Res. Policy Pract.* 1, 3.
- Reading, R.P., Mix, H., Lhagvasuren, B., Blumer, E.S., 1999. Status of wild Bactrian camels and other large ungulates in south-western Mongolia. *Oryx* 33 (3), 247–255.
- Root-Bernstein, M., Jaksic, F., 2013. The Chilean espinal: restoration for a sustainable silvopastoral system. *Restor. Ecol.* 21 (4), 409–414.
- Root-Bernstein, M., Jaksic, F., 2016. Oportunidades y desafíos para cambios adaptivos en el sistema silvopastoral de Chile central [Opportunities and challenges for adaptive change in the silvopastoral system of central Chile]. In: Postigo, J.C., Young, K.R. (Eds.), *Perspectivas socio-ecológicas, actividades productivas y cambios globales en América Latina*. In press.
- Root-Bernstein, M., Guerrero-Gattica, M., Piña, L., Bonacic, C., Svenning, J.-C., Jaksic, F.M. Prospects for a model of rewilding-inspired transhumance for the restoration of a semi-arid silvopastoral system. *Region. Environ. Change* (submitted for publication)
- Rybczynski, N., Gosse, J., Harington, C., Wogelius, R., Hidy, A., Buckley, M., 2013. Mid-Pliocene warm-period deposits in the high Arctic yield insight into camel evolution. *Nat. Commun.* 4, 1–9.
- Sandom, C.J., Hughes, J., Macdonald, D.W., 2012. Rewilding the Scottish highlands: do wild boar, sus scrofa, use a suitable foraging strategy to be effective ecosystem engineers? *Restor. Ecol.* 21 (3), 336–343.
- Sandom, C., Faurby, S., Sandel, B., Svenning, J.-C., 2014. Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proc. R. Soc. B Biol. Sci.* 281, 20133254.
- Sarno, R., Clark, W., Bank, M., Prexl, W., Behl, M., Johnson, W., Franklin, W., 1999. Juvenile guanaco survival: management and conservation implications. *J. Appl. Ecol.* 36, 937–945.
- Sato, S., 1980. Pastoral movements and the subsistence unit of the Rendille of northern Kenya: with special reference to camel ecology. *Senri Ethnol. Stud. Osaka* 6, 1–78.
- Schmitz, O., 2008. Herbivory from individuals to ecosystems. *Ecol. Evol. Syst.* 39, 133–152.
- Semperebon, G., Rivals, F., 2010. Trends in the paleodietary habits of fossil camels from the tertiary and quaternary of North America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 295, 131–145.
- Skidmore, J., Billah, M., Binns, M., Short, R., Allen, W., 1999. Hybridizing old and new world camelids: *Camelus dromedarius* x *Lama guanicoe*. *Proc. R. Soc. B Biol. Sci.* 266, 649–656.
- Soliman, M.K., 2015. Anatomical adaptations of dromedary (*Camelus dromedaries*) and ecological evolutionary impacts in KSA. In: *Proceedings, International Conference on Plant. Marine and Environmental Sciences, Kuala Lumpur, Malaysia*. Jan. 1–2, 2015.
- Spassov, N., Stoytchev, T., 2004. The dromedary domestication problem: 3000 BC rock art evidence for the existence of wild One-humped camel in Central Arabia. *Hist. Nat. Bulgarica* 16, 151–158.
- Spencer, P., Giustiniano, D., Hampton, J.O., Gee, P., Burrows, N., Rose, K., Martin, G.R., Woolnough, A.P., 2012. Identification and management of a single large population of wild dromedary camels. *J. Wildl. Manag.* 76 (6), 1254–1263.
- Surovell, T., Grund, B., 2012. The associational critique of quaternary overkill and why it is largely irrelevant to the extinction debate. *Am. Antiq.* 77, 672–687.
- Svenning, J.C., Pedersen, P.B., Donlan, C.J., Ejrnæs, R., Faurby, S., Galetti, M., Hansen, D.S., Sandel, B., Sandom, C.J., Terborgh, J.W., Vera, F.W., 2015. Science for a wilder anthropocene: synthesis and future directions for trophic rewilding research. *Proc. Natl. Acad. Sci.* 113 (4), 201502556.
- Syampungani, S., Chirwa, P., Akinnifesi, F., Sileshi, G., Ajayi, O., 2009. The miombo woodlands at the cross roads: potential threats, sustainable livelihoods, policy gaps and challenges. *Nat. Resour. Forum* 33, 150–159.
- Titov, V., Logvynenko, V., 2006. Early *Paracamelus* (Mammalia, Tylopoda) in eastern Europe. *Acta Zool. Cracoviensia Ser. A Vertebr.* 49, 163–178.
- Tulgat, R., Schaller, G.B., 1992. Status and distribution of wild Bactrian camels *Camelus bactrianus ferus*. *Biol. Conserv.* 62, 11–19.
- van Bloem, S.J., Murphy, P.G., Lugo, A.E., 2004. Tropical dry forests. In: *Encyclopedia of Forest Sciences*. Academic Press, Boston, pp. 1767–1775.
- Volpato, G., Puri, R.K., 2014. Dormancy and revitalization: the fate of ethnobotanical knowledge of camel forage among Sahrawi nomads and refugees of Western Sahara. *Ethnobot. Res. Appl.* 12, 183–210.
- Walther, F.R., 1969. Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour* 34 (3), 184–221.
- Waters, M., Stafford, T., Kooyman, B., Hills, L., 2015. Late Pleistocene horse and camel hunting at the southern margin of the ice-free corridor: reassessing the age of Wally's Beach, Canada. *Proc. Natl. Acad. Sci.* 112, 4263–4267.
- Weinstock, J., Shapiro, B., Prieto, A., Marín, J., González, B., Gilbert, M., Willerslev, E., 2009. The Late Pleistocene distribution of vicuñas (*Vicugna vicugna*) and the “extinction” of the gracile llama (*Lama gracilis*): new molecular data. *Quat. Sci. Rev.* 28, 1369–1373.
- Westreicher, C.A., Mérega, J.L., Palmili, G., 2007. The economics of pastoralism: study on current practices in South America. *Nomadic Peoples* 11 (2), 87–105.
- Wolf, A., Doughty, C., Malhi, Y., 2013. Lateral diffusion of nutrients by mammalian herbivores in terrestrial ecosystems. *PLoS One* 8, e71352.
- Wu, H., Guang, X., Al-Fageeh, M., Cao, J., Pan, S., Zhou, H., Zhang, L., Abutarboush, M., Xing, Y., Xie, Z., Alshanteqi, A., Zhang, Y., Yao, Q., Al-Shomrani, B., Zhang, D., Li, J., Manee, M., Yang, Z., Yang, L., Liu, Y., Zhang, J., Altammami, M., Wang, S., Yu, L., Zhang, W., Liu, S., Ba, L., Liu, C., Yang, X., Meng, F., Wang, S., Li, L., Li, E., Li, X., Wu, K., Zhang, S., Wang, J., Yin, Y., Yang, H., Al-Swailem, A., Wang, J., 2015. Camelid genomes reveal evolution and adaptation to desert environments. *Nat. Commun.* 5, 5188.
- Wursten, A., Novaro, A., Walker, R., 2014. Habitat use and preference by guanacos, vicuñas, and livestock in an altitudinal gradient in northwest Argentina. *Eur. J. Wildl. Res.* 60, 35–43.
- Yacobaccio, H.D., 2004. Social dimensions of camelid domestication in the southern Andes. *Anthropozoologica* 39 (1), 237–247.
- Young, J., 1982. Camels on the western range. *Rangelands* 4 (6), 248–251.
- Zazula, G., Turner, D., Ward, B., Bond, J., 2011. Last interglacial western camel (*Camelops hesternus*) from eastern Beringia. *Quat. Sci. Rev.* 30, 2355–2360.