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Special Issue: Defaunation's impact in tropical terrestrial ecosystems

The shifted baseline: Prehistoric defaunation in the tropics and its consequences for biodiversity conservation

Richard T. Corlett *

Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China

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ABSTRACT

The majority of terrestrial ecosystems outside Africa have lost megafaunal vertebrates (>44 kg) since the Middle Pleistocene and most of these extinctions can be attributed to human influence. This review assesses the likely impacts of prehistoric megafaunal extinctions in the lowland tropics and discusses the implications for contemporary conservation management. The most likely impacts include: the coextinction of parasites, a reduction in environmental heterogeneity, the release of competitors and prey (including plants), and a loss of quality and quantity in seed dispersal services. This, however, is based largely on arguments by analogy with the surviving megafauna, since the impacts of megafaunal losses are compounded in the paleoenvironmental record with changes in climate and other human impacts. Suggested conservation responses include: prioritizing the conservation of the surviving megafaunal species and reintroducing them, where possible, into parts of their former ranges; reversible experiments with the introduction of taxon substitutes outside their natural ranges; and special conservation attention to megafaunal-dependent orphans and anachronisms.

1. Introduction

The term 'shifting baseline' is used to describe the way changes to a system are measured against earlier reference states that themselves differ significantly from the original state of the system (e.g. Pauly, 1995). Although not easily quantified, shifting baselines are likely to be a particular problem for ecological studies in the tropics, where the earliest written descriptions are often <200 years old and the first quantitative studies have usually taken place in the last few decades, while significant human impacts may have started millennia or tens of millennia before. Of the two forms of shifting baseline identified by Papworth et al. (2009), personal and generational, the most relevant to the subject of this review is 'generational amnesia', where each new generation is unaware of—or, perhaps, does not take seriously—the environmental knowledge of previous generations. As Turvey et al. (2010) demonstrated for Yangtze fishing communities, loss of knowledge of even large and charismatic species can be startlingly rapid. If this can happen in China, with its exceptionally long and well-preserved written history, it is not surprising that in parts of the world without a long period of recorded history, biologists tend to work from a baseline only decades earlier.

The realization that some human impacts, including those on climate, are irreversible on a human timescale is beginning to reduce the hold that 'historical baselines' have had on ecology and conservation (e.g. Thomas, 2011), but it is still important for both scientific and practical reasons to understand how ecological systems functioned over the period when currently extant species were evolving, i.e. the last 1–3 million years. This period has experienced relatively minor changes in geography after the formation of the Panama isthmus, but wide fluctuations in global climate have driven large changes in habitats and local biotic communities. Two unidirectional changes stand out from this fluctuating picture: the origin and spread of increasingly modern humans and the loss of most of the megafauna (defined here as animals heavier than 44 kg).

There is still considerable debate about the relationship between these two changes, but the multiple coincidences of megafaunal extinctions with the local arrival of modern humans from c. 50,000 to 600 years ago make a strong case that at least these relatively recent extinctions were caused by humans, or by humans in conjunction with climate change (Lorenzen et al., 2011; Prescott et al., 2012; Brook and Barnosky, 2012). If one theory can be said to dominate in the recent literature, it is that the presence of an intelligent, social, weapon-bearing, bipedal ape changed an otherwise unexceptional glacial termination into a lethal event for many large, slow-breeding vertebrates. This theory differs considerably from Paul Martin's original 'human blitzkrieg' model, in which climate did not have a major role (Martin, 1973). Note also that each glacial cycle is unique and some authors have suggested that the unique climatic features of the last glacial termination made a

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* Tel.: +86 182 8805 9408.
E-mail address: corlett@xtbg.org.cn

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significant contribution to the unprecedented extinctions (e.g., the combination of a period of rapid cooling, high variance in temperature, and low mean temperature; Prescott et al., 2012).

Extinctions earlier in the Pleistocene (>60,000 years ago) can be more confidently attributed to climate change (e.g. in Eastern Australia; Hocknull et al., 2007), except in Africa, where early hominins may have had an impact from the early Pleistocene (Lyons et al., 2004), and Asia, where *Homo erectus* was present from 1.7 to 1.6 m years ago (Louys and Turner, 2012). The hunting abilities of *H. erectus* are still debated, but, armed with stone flakes and perhaps more perishable plant-based weapons (wooden throwing spears were used in Europe 400,000 years ago; Thieme, 1997), the first Asian hominids must surely have exploited at least the slow-moving giant tortoises and giant pangolin—all now extinct—and could plausibly have hunted much larger animals (Dennell, 2009; Louys and Turner, 2012). For example, a giant forest ape, *Gigantopithecus blacki*, coexisted with *Homo* in the forests of northern tropical and subtropical East Asia for much of the Middle Pleistocene but disappeared c. 300,000 years ago (Zhao et al., 2011). There is no evidence for hunting, but a slow-moving terrestrial ape would surely have been vulnerable. Ben-Dor et al. (2011) point out that, in comparison with smaller, faster species, elephants do not require a sophisticated hunting strategy. Corlett (2010) tentatively attributed the lack of a clear extinction spike at the time when modern humans are thought to have arrived in SE Asia (60–50,000 B.P.) to the earlier impacts of pre-modern *Homo*, as well as the initial concentration of modern humans along coasts. In contrast, Louys (2012) considered that pre-Holocene extinctions in SE Asia were primarily driven by loss of open habitats. Both authors agree, however, that the relatively few megafaunal extinctions in SE Asia hide massive range reductions in several species, including orangutans and the giant panda.

Who or what killed the megafauna, and precisely when, has received more attention than the ecological consequences of megafaunal extinctions, although there is a large and growing literature on this subject as well. The main practical justification for studying the consequences of these extinctions is that they may provide a possible model for predicting the impacts of the on-going removal of the surviving megafauna—and numerous smaller species—from most of the tropics. The focus on the last 50,000 years has meant that discussion has been largely limited to North and South America, Northern Eurasia, Australia, Madagascar, and New Zealand, with the impact of the more gradual changes in SE Asia receiving less attention.

This review takes a broader view, considering the environmental impacts—and modern-day implications for conservation management—of all tropical lowland extinctions of vertebrates >44 kg body mass from the early Middle Pleistocene (781,000 years ago), when most areas had a generally modern vertebrate fauna, to the Holocene (>2000 years ago, and thus before any recent 'baseline'). I have adopted this single, arbitrary, body-size cut-off because it is widely used in the literature and facilitates pantropical comparisons. The idea that the megafauna concept should be extended to the largest animals in any assemblage (Hansen and Galetti, 2009) makes a lot of sense for many processes, but there are also megafaunal impacts for which absolute size is important. Historical extinctions are considered in other papers in this issue.

2. Methods

Megafaunal extinctions on continents are well-documented, but species >44 kg body mass were also found on islands, including oceanic islands with no previous land connections. For example, fossils of dwarfed, but still megafaunal, proboscideans occur on many islands >100 km^2 and a distinct subspecies of Galapagos giant tortoise (*Chelonoidis nigra*) survives today on 18 km^2 Pinzón Island. I have therefore checked as many as possible of the tropical islands in this size range (18–100 km^2) and above, in the literature and on-line, for extant or extinct megafauna. Data on taxa that went extinct since the Middle Pleistocene, their time of last occurrence, and the surviving megafauna, if any, are summarized in Table 1. The literature was also searched for speculation and/or evidence for the impacts of such extinctions (Table 2) and for suggestions for mitigating adverse impacts.

3. The ubiquity of megafaunal extinctions

All continental and many island terrestrial ecosystems in the tropics are known to have lost one or more megafaunal species since the Middle Pleistocene, with most surviving species reduced in historical times to low densities (Table 1). The exceptions are remote oceanic islands that apparently never supported a megafauna (e.g. Hawaiian archipelago), less remote oceanic islands with a limited or no fossil record, and the Aldabra and the Galapagos Islands, which still support giant tortoises and have apparently not lost any other megafauna. Africa also stands out from other continental regions, since the losses there were arguably no higher than expected background levels (Smith et al., 2010). Tropical Asia, however, had significant megafaunal losses that have been overlooked in many studies because they do not show a Late Pleistocene spike (Corlett, 2010). Gaps in the spatial coverage of the fossil record mean that the presence of a megafauna cannot be confirmed for all habitats (e.g. dense rainforests in Madagascar), but their presence until recently in all major lowland habitats in Africa and Asia argues for this. Across the tropics, the losses were mostly large herbivores, the most species-rich megafaunal guild, but also included carnivores, scavengers, and, in SE Asia, the insectivorous giant pangolin. Some places lost their entire megafauna (Madagascar, the islands of the Caribbean) or most of it (Neotropics and tropical Australia), while others (Africa, tropical Asia) supported a range of megafaunal species into historical times.

4. Consequences of megafaunal extinctions

The fossil and paleoenvironmental record is rarely, if ever, good enough to detect the expected impacts of megafaunal extinctions, so much of the literature on these impacts is based on arguments by analogy with the extant megafauna, i.e. because extinct taxon X is similar to extant taxon Y, what is true for Y was also true for X (Table 2). These arguments are weakened in many cases, however, by our lack of understanding of the ecological roles of the extant species used for comparisons. On the other hand, it is reasonable to assume that the same basic biological principles applied in the past and, in particular, that large body size had the same consequences then as now.

4.1. Coextinctions of parasites

Parasites of vertebrates include helminths, arthropods, protozoans, bacteria and fungi. Host-specific parasites become extinct with their hosts, or when host population density falls below some threshold. There is insufficient information to estimate either how many parasite species each megafaunal species harbored or how many of these were host-specific, but in many cases entire host clades were lost, making it less likely that parasites survive on related hosts. Relatedness is the best predictor of shared infections in well-studied taxa (Davies and Pedersen, 2008). Tropical lowland megafaunal extinctions since the Middle Pleistocene include two whole orders of South American ungulates (Litopterna and Notoungulata), five whole families of xenarthrans (ground

Table 1
Megafaunal (>44 kg) extinctions in different tropical regions since the Middle Pleistocene.

Region	Last occurrence	Megafaunal extinctions	Survivors (until last 100–200 years)	Sources
Neotropics	Late Pleistocene	Giant tortoise, *Smilodon*, short-faced bear, ground sloths, glyptodonts, pampatheres, horses, *Toxodon*, gomphotheres, mastodons	Jaguar, tapir, capybara, boid snakes	MacFadden (2006) and Elias and Schreve (2007)
Caribbean Islands	Holocene	Giant tortoises, sloths, giant rodents	None	Steadman et al. (2005) and Turvey et al. (2007)
Galapagos Islands	Present	None (only subspecies)	Galapagos giant tortoise	
Africa	Pleistocene	Giant hyena, large bovids, giraffids, *Elephas*	Elephants, hippopotamuses, gorillas, chimpanzees, felids, hyenas, rhinoceroses, bovids, suids, equids, giraffes, pythons	Koch and Barnosky (2006)
Madagascar	Holocene	Elephant birds, giant tortoises, pygmy hippopotamus, giant lemurs	None	Burney and MacPhee (1988) and Crowley (2010)
Western Indian Ocean Islands	Holocene	Giant tortoises (Mascarenes, Seychelles, Comoros, Glorieuse)	Aldabra giant tortoise	
South Asia	Middle to Late Pleistocene	Giant tortoise, stegodon, hippopotamuses, bovids, ostrich	Elephant, felids, bears, tapir, rhinoceros, bovids, cervids, suids, pythons	Chauhan (2008)
Continental SE Asia	Middle Pleistocene to early Holocene	*Gigantopithecus* (MP); stegodon, giant tapir, hyena, orangutans	Elephant, orangutan, tiger, leopard, bears, tapir, rhinoceros, bovids, cervids, suids, pythons	Corlett (2010)
Sundaland	Late Pleistocene	Giant pangolin	As above	Corlett (2010)
Java	Middle Pleistocene	Giant tortoise, stegodon, hippopotamus, hyena	As above	Corlett (2010)
Philippine Islands (ex Palawan)	Pleistocene	Giant tortoise, stegodon, elephant, rhinoceros, *Bubalus* spp.	Bovids, suids, cervids, python	Bautista (1991) and Corlett (2010)
Sulawesi	Pleistocene	Giant tortoise, stegodon, elephant, *Celebochoerus* (Suidae)	Bovids, suids, python	van den Bergh et al. (2001) and Corlett (2010)
Wallacean Islands	Late Pleistocene	Giant tortoises, varanid lizards, stegodons	Komodo dragon	Corlett (2010)
New Guinea	Late Pleistocene	Kangaroos, diprotodontids	Cassowaries	Corlett (2010)
Tropical Australia	Late Pleistocene	Terrestrial horned turtles, terrestrial crocodile, giant varanid, giant snake, marsupial lion, kangaroos, diprotodontids	Cassowary, emu, kangaroos	Koch and Barnosky (2006) and Elias and Schreve (2007)
New Caledonia, Vanuatu, Fiji	Late Pleistocene and Holocene	Terrestrial horned turtles, terrestrial crocodiles	None	Mead et al. (2002), Molnar et al. (2002), and White et al. (2010)

sloths, glyptodonts and pampatheres), three of proboscideans (stegodons, gomphotheres and mastodons), one or more of rodents (giant hutias), and at least one each of marsupials (diprotodons) and birds (elephant birds) (Table 1). This suggests that the number of parasite extinctions (excluding microorganisms) must have been at least an order of magnitude larger than the number of megafaunal host extinctions (Dobson et al., 2008; Dunn et al., 2009).

4.2. Coextinctions of commensalists and mutualists

Host-specific mutualists and commensalists are as vulnerable as parasites, but much less common. However, the large megafaunal biomass in intact ecosystems (Owen-Smith, 1988) may have made even relative generalists quantitatively dependent on megafaunal species for their survival. Commensal feeding relationships, where a large vertebrate acts as a 'beater' for insectivorous birds are one possible example, as are dung-associated species (Tshikae et al., 2008; Campos-Arceiz, 2009) and carrion-feeders (Fox-Dobbs et al., 2006).

Most attention has focused on seed-dispersal mutualisms. Campos-Arceiz and Blake (2011) show that both African and Asian elephants have potentially unique roles in their communities as long-distance dispersal agents for seeds of all sizes, including some too large for any alternative frugivore to swallow. However, this role is well-documented only for African forest elephants and, so far, African forests also provide the best examples of species apparently dispersed only be elephants (Blake et al., 2009). Forest rhinoceroses may have had an overlapping seed-dispersal role with elephants in Asian tropical forests until their recent near-extinction, but the next largest non-ruminant mammal, the relatively widespread Malayan tapir, is unlikely to disperse large seeds from large fruits (Campos-Arceiz et al., 2012). Among other extant megafauna, seed dispersal has been studied in American tapirs (O'Farrill et al., 2012), which may disperse more large seeds than their Asian relatives, bovids and suids (largely domesticated cattle and feral pigs), which disperse mostly small (<5 mm) seeds of herbaceous species (Corlett, 1998; Matsubayashi et al., 2007), large primates (gorillas, orangutans and chimpanzees), which can move large seeds over long distances (Corlett, 1998), giant tortoises, which, because of their slow gut-passage times, move a variety of small and medium-sized seeds over long distances (<4355 m) (Blake et al., 2012), and cassowaries and emus, which disperse seeds in large fruits (<5–6 cm) for long distances (Wright, 2005; Calviño-Cancela et al., 2006; Bradford et al., 2008). All speculations about the possible role of extinct megafaunal species in seed dispersal have been based on analogies with these extant megafaunal taxa and/or the fruits they eat.

Table 2
Examples of impacts suggested for the loss of megafaunal vertebrates.

Region	Last occurrence	Taxon	Suggested impact	Evidence	Sources
Global	Late Pleistocene and Holocene	Megaherbivores > 1000 kg	Loss of vegetation mosaics & canopy gaps, changed fire regimes and nutrient cycles, decline of co-evolved plant species	Analogy	Owen-Smith (1987) and Johnson (2009)
Global	Late Pleistocene	Megaherbivores	Reduction in earth moving	Analogy	Haynes (2012)
Neotropics	Late Pleistocene	Fruit-eating megafauna	Reduced seed dispersal distances, more clumped spatial patterns, reduced geographic ranges, limited genetic variation, increased among-population structuring.	Analogy; some evidence of reduced gene flow	Guimarães et al. (2008)
Madagascar	Holocene	Giant lemurs and elephant birds	Reduction in long-distance dispersal of large and epizoochorous seeds	Analogy	Dransfield and Beentje (1995), Godfrey et al. (2008), and Crowley et al. (2011)
Mauritius	Holocene	Giant tortoises	Loss of seed dispersal services	Experimental tortoise introduction	Griffiths et al. (2011)
Tropical Australia	Late Pleistocene	Megafaunal browsers	Expansion of shrubland	Pollen records	Johnson (2006)

Extrapolating from extant to extinct giant tortoises or extant elephants to extinct proboscideans is clearly much less of a stretch than speculating on the diet and seed-dispersal role of the extinct xenarthrans, notoungulates or diprotodons. Gomphotheres, in particular, seem to have been generalist feeders with a diet similar to modern elephants (Asevedo et al., 2012). However, the need for very large herbivores to ingest very large quantities of low quality forage probably makes some seed dispersal unavoidable and comparatively nutritious fruits are unlikely to be avoided. Moreover, these animals cannot afford to reduce the rate of food intake by thorough oral processing, so even large seeds have a good chance of avoiding damage. Note that dietary strategies are more varied in medium-sized (>44 kg but <500 kg) herbivores, which can forage more selectively (Corlett and Primack, 2011), and the consequences for seed dispersal are thus less predictable.

A "megafaunal syndrome" of very large fleshy fruits (>10 cm in diameter with numerous small seeds or 4–10 cm in diameter with a few large seeds) has been identified in Africa, where they are consumed and their seeds dispersed by elephants, and Brazil, where they may have been eaten by the extinct megafauna (Donatti et al., 2007; Guimarães et al., 2008). Such fruits are also widespread in tropical Southeast Asia, where they may be consumed largely by elephants and rhinoceroses, but they have not been studied. Such very large fruits are expected to be consumed largely by mammals with a body mass >1000 kg, while those targeted at the smaller megafauna (44–1000 kg) may be considerably smaller and less distinctive.

The existence today of fruits apparently targeted at a Neotropical megafauna that has been extinct for 11,000 years has been used as evidence for a key ecological role of these animals, but at the same time undermines the idea that plants with this fruit syndrome were totally dependent on them, since they have persisted through many generations in their absence. Indeed, the degree of dependence of many animal-dispersed plants on their dispersal agents is unclear, since the seeds in fruits that remain beneath the parent plant may have a chance of establishment. If undispersed seeds can grow into adults, a plant population that has lost all its dispersal mutualists could persist beyond the lifespan of individual plants (Donatti et al., 2007; Corlett, 2007). The probability of persistence will increase if the species can spread vegetatively, or at least resprout after damage, or if alternative dispersal agents, however limited, are available. Suggested alternatives agents for megafaunal fruits include non-megafaunal frugivores, water, humans, and scatter-hoarding rodents (Donatti et al., 2007; Guimarães et al., 2008). In the Neotropics, large scatter-hoarding rodents may have played an important role in the persistence of plants with megafaunal fruit (Jansen et al., 2012), but this then invites the question: were these plant species ever really dependent on the megafauna? Unfortunately, the plant fossil record is too incomplete to assess whether other plant species, more dependent on the megafauna, have gone extinct as a result of dispersal failure. The restricted distributions of many plants with megafaunal fruits today (e.g., Dransfield and Beentje, 1995; Godfrey et al., 2008; Johnson, 2009; Muñoz-Concha and Davey, 2011) are consistent with dispersal failure but cannot prove it.

Plants with obvious megafaunal fruits make up a relatively small proportion of most tropical floras (but 30% of fleshy fruited tree species in the Brazilian Pantanal; Guimarães et al., 2008), but megafaunal extinctions may have had an impact on other, apparently less specialized, dispersal syndromes. In Madagascar, small trees and shrubs with fruits adapted for external attachment to fur or feathers are likely to have been affected by the loss of all large terrestrial and semi-terrestrial animals (Crowley et al., 2011). Plant species that depend on the incidental consumption of their fruits with foliage are also likely to have suffered from the loss of the largest and least discriminating herbivores (Johnson, 2009). More generally, any species dispersed previously by wide-ranging megaherbivores must have experienced reduced dispersal distances and increased clumping at the landscape scale.

4.3. Impacts on competitors

The loss of a huge biomass of megaherbivores would be expected to release some plant resources for surviving competitors. Conversely, feeding by megaherbivores may sometimes facilitate feeding by smaller species by increasing browse availability near the ground (Makhabu et al., 2006). However, evidence for a change in the biomass of smaller herbivores is generally lacking in the fossil record, except in Madagascar, where the abundance of animals <10 kg apparently increased dramatically after the late Holocene megafaunal extinctions (Crowley, 2010). Competitive interactions between predators can be complex and unpredictable, but one widely documented impact of the loss of top predators is 'mesopredator release', where subordinate predators released from competition with (and sometimes predation by) larger species increase impacts on their own prey and competitors (e.g. Sutherland et al., 2011; Ritchie et al., 2012). Although mesopredator release is a plausible impact of megapredator extinctions, it has not been reported from the fossil record, where its detection is likely to be confounded by other changes.

4.4. Impacts on predator-prey relationships and scavengers

Megafaunal extinctions have often included the largest carnivores in the fauna, such as *Smilodon* in the Neotropics, *Quinkana*, *Varanus priscus*, *Wonambi naracoortensis*, and *Thylacoleo carnifex* in Australia, the terrestrial crocodiles of the southwest Pacific, and the varanid lizards of Wallacea (Table 1). Theory and a variety of evidence suggest that the loss of these 'apex predators'—'trophic downgrading'—can lead to impacts that propagate as trophic cascades down through the food web (Estes et al., 2011). Assessing the impacts of these extinctions is made difficult, however, by the loss of many of their likely prey species at around the same time. Conversely, extant mega-carnivores, such as the tiger, jaguar, and Komodo dragon, have lost part of their prey base, although increases in the abundance of smaller prey may have compensated. Indeed, adults of the largest megaherbivores (>1000 kg) were presumably largely immune to predation, although their juveniles were not (Ripple and Van Valkenburgh, 2010).

Impacts of megafaunal extinctions are expected to have been greatest for predatory and scavenging taxa that specialized on extinct prey. Outside the tropics, Beringian wolves during the Late Pleistocene were morphologically different from modern North American wolves and from Pleistocene wolves from more southern regions, and may have been adapted to hunting and/or scavenging the now extinct megafauna (Hofreiter and Barnes, 2010). Pleistocene coyotes were also larger and more robust than living representatives of the same species, probably reflecting the influence of both larger prey and larger competitors (Meachen and Samuels, 2012). Scavengers may have been even more vulnerable to megafaunal extinctions since the large size and reduced vulnerability to predators of megaherbivores meant that most of their biomass was eventually available as carrion. This vulnerability is illustrated by the loss of two late Pleistocene vulture species and inland populations of California condors from southwest North America (Fox-Dobbs et al., 2006).

A focus on megafaunal prey has also been suggested on morphological grounds for many other extinct carnivores (e.g., Wroe et al., 2008), but while the Komodo dragon may have originally preyed on dwarf stegodons (Diamond, 1987), this species has survived two faunal turnovers virtually unchanged, and today its largest prey are all introduced taxa (Hocknull et al., 2009). Although direct evidence of impacts on carnivores and scavengers from megafaunal extinctions is lacking from the tropics, it is a reasonable assumption that the same ecological processes were in operation there as in the northern temperature zone.

4.5. Impacts on vegetation

In Africa, megaherbivores (>1000 kg) contribute 40–70% of the biomass in savannas, although they are only a small proportion of the species (Owen-Smith, 1988). Owen-Smith argued that, as a result of the large individual size and high total biomass, these species act as keystone herbivores, maintaining a vegetational mosaic, with open grassy patches in a climate that would support continuous woody vegetation. A recent meta-analysis of vegetation impacts by African savanna elephants confirmed that, in general, high elephant densities had a negative impact on woody vegetation, but this impact was influenced by rainfall and often site-specific (Guldemond and van Aarde, 2010). Even in wetter climates, which favor trees over grass, African forest elephants help maintain open patches. Pollen evidence for vegetation changes in the Americas following megafaunal extinctions is, in general, consistent with expectations based on analogies with African savannas, but megafaunal loss is confounded in the paleoecological record with two alternative drivers of vegetation change, climate change and new anthropogenic sources of ignition (Pinter et al., 2011). Where fire was important, an impact of megafauna loss is most likely if megaherbivores previously controlled fuel loads, although interactions between herbivores and fire regimes are complex (Johnson, 2009; Midgley et al., 2010).

In northeast Australia, megafaunal extinctions 41,000 years ago appear to have triggered the replacement of rainforest by sclerophyll vegetation through a combination of the direct effects on vegetation of reduced herbivore pressure and the indirect impact of fine fuel accumulation on fires (Rule et al., 2012). Strikingly, this study showed an impact of megafaunal extinctions on vegetation that was as large as any impact of climate change over the last glacial cycle. Although one must cautious when extrapolating the results of this one study to other areas, it does suggest that very large changes in vegetation are possible following megafaunal extinctions. While the magnitude of such changes should make them easy to detect in the pollen record, identifying the separate impacts of climate change, anthropogenic fires, and megafaunal loss may be very difficult.

More subtle impacts on vegetation are mostly from changes in plant species consumption with the replacement of relatively unselective megaherbivore grazers and browsers by more selective smaller taxa. Note, however, that even the largest surviving megaherbivore, the African savanna elephant, is very selective at the plant species level, despite consuming a much wider range of plant parts than smaller herbivores (Owen-Smith and Chafota, 2012). Conversely, plants with expensive, but now obsolete, defences against extinct megaherbivores would be expected to lose out in competition with more palatable species (Eskildsen et al., 2004; Galetti, 2004; Bond and Silander, 2007; Crowley et al., 2011). This process of 'relaxation' from megafauna-controlled to megafauna-free plant communities may take millennia (Johnson, 2009).

Changes in vegetation are, in turn, likely to impact numerous other species, positively or negatively. Large-scale exclusion experiments in East Africa, for example, showed that large herbivores significantly reduce bird diversity through their impacts on woody plant cover and invertebrate biomass (Ogada et al., 2008). Negative impacts on invertebrate abundance from the largest herbivores have also been shown in other studies in Africa (Jonsson et al., 2010). Conversely, amphibians and reptiles may benefit from increased habitat diversity in damaged woody vegetation (Pringle, 2008; Nasseri et al., 2011).

4.6. Megafauna and methane

Methane production probably occurs in all mammalian and reptilian herbivores (Franz et al., 2011). These losses scale linearly with body mass, while food intake scales to $M^{0.75}$, so as body size increases proportionately more methane is produced from each unit of food. It has been suggested that the Late Pleistocene spike in megafaunal declines resulted in a rapid loss in methane production that, in turn, helped trigger the abrupt Younger Dryas (12,800–11,500 B.P.) cooling event (Smith et al., 2010, 2011). However, the amounts involved, although significant, do not seem large enough to have had a major impact on climate and changes in carbon dioxide, rather than methane, appear to have been the primary driver of temperature changes at the end of the last glacial period (Shakun et al., 2012).

5. Conservation responses

5.1. Prioritizing the conservation of the remaining megafauna

The megafauna are special: ecologically, as highlighted above, but also in terms of their evolutionary distinctiveness, since most species have few close relatives. All the largest mammalian megafaunal species are on the top-100 list of the EDGE project (Evolutionarily Distinct and Globally Endangered; www.edgeofexistence.org) and four Asian taxa (Sumatran and Javan rhinoceroses, Asian elephant, Malayan tapir) are in the top twenty. Megafauna are also special in terms of the charisma that attracts conservation support and funding (Leader-Williams and Dublin, 2000). This support, however, contrasts strikingly with the low success rate of most conservation efforts, with almost all species currently in decline and some nearing extinction.

5.2. Reintroducing surviving megafaunal species within their natural ranges

Large vertebrates, including elephants and lions, have been translocated to many reserves in southern Africa (Hayward et al., 2007; Lindsey et al., 2012), suggesting that the reintroduction of megafaunal species within their natural range is a viable option, where habitat and animals are available. The potential for human-wildlife conflicts was greatly reduced in most of these cases by the use of appropriate fencing, financed by tourism and trophy hunting. Unfortunately, the extension of this approach to other parts of the world has been limited by shortage of habitat and/or animals, or by legal and financial issues. In tropical Asia, for example, there are no surplus animals of the two critically endangered forest rhinos, and few if any places where the numerous captive elephants (Leimgruber et al., 2008) or tigers (Luo et al., 2010) could be safely reintroduced without expensive fencing. However, the potential for reintroduction of other, less dangerous, megafaunal species (e.g., tapirs, cattle, deer) has not yet been explored. An exception is the proposal by Piper and Cranbrook (2007) to reintroduce the Malayan tapir to the Planted Forest Zone in Sarawak, which consists of 490,000 ha of primary, secondary and industrial plantation forests. Several projects are also attempting to re-establish orangutans in areas from which they have been eliminated (Corlett, 2009a).

Reintroductions are likely to be increasingly controversial the longer the species has been missing from the ecosystem, both because of the risk of disrupting a new ecological equilibrium, with unpredictable consequences, and because the animals used will necessarily lack the local adaptations and knowledge of their extinct predecessors. Where times and distances are really large, the issues merge into those considered below for species introductions outside their natural ranges.

5.3. Re-wilding with taxon substitutes

"Pleistocene re-wilding" proposes introducing extant relatives or ecological surrogates of the extinct megafauna to restore lost ecological and evolutionary processes (Galetti, 2004; Donlan et al., 2006). Given the problems caused by invasive alien vertebrates (Clout, 2002; Phillips et al., 2012), it is easy to argue that introducing species outside their native range involves too much risk for uncertain rewards (Rubenstein et al., 2006). These proposals depend on the functional equivalence of the introduced species to the extinct ones. While the high diversity of Pleistocene megafaunal communities argues against the idea that large animals are necessarily generalists, and thus substitutable, it is possible that taxa that are very different ecologically could have very similar impacts because large size constrains many aspects of an animal's biology, including diet.

The solution to this uncertainty is to carry out reversible experiments, as is currently being done with two tortoise species in Mauritius and Rodrigues (Kaiser-Bunbury et al., 2010; Griffiths et al., 2011; Waibel et al., 2012). Giant tortoises are exceptionally easily controlled, but, with appropriate fencing (Lindsey et al., 2012) or a single sex, any species could, in theory, be tested for unforeseen impacts. For short-term experiments it may be possible to use semi-domesticated animals (elephants, wild cattle), thus reducing control problems. Such experiments cannot prove that taxon substitutions are safe, since problems may take decades to appear, but they are a necessary step towards larger-scale, less easily reversible, trials.

Many megafaunal species have already been deliberately introduced by people outside their natural ranges and a proportion of these have established wild populations. Pigs, deer, and cattle are most widely introduced, but many other species have been moved outside their native range at least once, including Asian elephants, introduced to Borneo (Cranbrook et al., 2008) and the Andaman Islands (Ali, 2006). While usually viewed as pests, these casual introductions may, in some cases, have restored megafaunal processes, such as seed dispersal (e.g. the bush pig, *Potamochoerus larvatus*, in western Madagascar; Godfrey et al., 2008), and could be considered as part of a re-wilding program.

5.4. Assisted dispersal and other artificial substitutes

Guix (2009) suggests that people replaced the extinct Amazonian megafauna in dispersing some useful, large-seeded tree species that might have otherwise gone extinct or suffered range reductions at the end of the Pleistocene. Where plant movements are urgent, as they may soon be for many species exposed to anthropogenic climate change, then artificial seed dispersal (or the planting of nursery-raised seedlings) offers short-term solutions. The impacts of grazing and browsing could potentially also be imitated by artificial cutting or burning, as has been done successfully in the management of some temperate ecosystems (e.g. Middleton et al., 2006).

6. Conclusions

Caro et al. (2011), while acknowledging that "humans have had at least marginal influence on most if not all of the world's biomes", argue that large areas of the Earth's surface still support more or less intact ecosystems. This review shows that, outside Africa, this is not only untrue now, but that it has not been true during the entire period of formal scientific enquiry in the tropics. Most tropical ecosystems we study and attempt to conserve were truncated long ago by size-selective extinctions that were very likely anthropogenic. But, while these megafaunal losses must surely have had a profound influence on these ecosystems, the precise nature of this influence is still unclear. Part of the uncertainty is an inevitable consequence of studying the more or less distant past, but part also reflects our poor understanding of recent megafaunal impacts. The best-studied recent continental systems are the savannas and dry forests of southern Africa, but to extrapolate from these to wetter climates and different animal orders may not always be justified.

On balance, the most likely impacts of megafaunal extinctions, apart from the inevitable coextinction of parasites, are a reduction in environmental heterogeneity, the release of competitors and prey (including plants), and a loss of quality and quantity in seed dispersal services. None of these will be easy to detect in the paleoenvironmental record against a background of contemporary changes in climate and other human impacts. Coextinctions are irreversible, as are any species-specific impacts on mutualists, competitors and prey, but the loss of the impacts of large body size *per se* on environmental heterogeneity and seed dispersal may be mitigated by some of the responses considered above.

The megafaunal extinctions field suffers from what Baider and Florens (2006) have called the 'biopoetic approach'—appealing-sounding hypotheses based largely on suppositions—which in

Mauritius have misdirected and delayed conservation efforts for the so-called 'Dodo tree' (*Sideroxylon grandiflorum*). They argue that we should not ignore the immediate threats to a species—in this case alien plants and animals—because of speculation that the fundamental problem is the historical loss of the megafauna. There is clearly a risk that a similar misdirection of conservation effort could occur elsewhere (Rubenstein et al., 2006). Moreover, unlike Mauritius, where the loss of large vertebrates occurred relatively recently, most continental systems have already survived millennia in their truncated state, suggesting that mitigating the impact of megafaunal extinctions is not an urgent conservation problem. Rapid anthropogenic climate change may change this, however, since large-bodied animals are more likely to disperse seeds the distances needed for plants to track their climate envelope across the landscape (Corlett, 2009b; McConkey et al., 2012). Unfortunately, the increasing fragmentation of most tropical ecosystems has introduced new obstacles to plant migration even in areas with an intact disperser fauna.

Does the megafaunal extinction story have any lessons for contemporary conservation in the tropics? I suggest there are five. Firstly, ghosts, orphans and anachronisms really do exist, so there will be species that 'don't make sense' under current conditions and may need special conservation attention, such as artificial dispersal or culling of competitors. An ability to survive 11,000 years in large areas of continuous habitat does not necessarily predict persistence in modern human-dominated landscapes, or in a changing climate, so we need trials of 'assisted migration' for plant species that have lost their long-distance dispersal agents. Secondly, more resources need to be put into saving the surviving megafauna, and, where surplus animals are available, reintroducing them to suitable habitat, if necessary in fenced enclosures. It is impossible not to see the prehistoric megafaunal extinctions as a terrible tragedy and it would be unforgivable not to do all we can to avert a 21st century continuation of the process. Thirdly, re-wilding with taxon substitutes is an exciting idea with almost no scientific or practical basis. We need to do more, more varied, reversible, experiments. It will not be possible to restore modern ecosystems to pre-extinction baselines, since so many other things have changed since then, but it may be worth attempting to create, at least on an experimental basis, ecosystems that function in the same way. Fourthly, and more tentatively, I suggest that we need to look again at the causes and consequences of environmental heterogeneity, at the landscape and finer scale, in the tropics. While heterogeneity has long been valued and managed for in temperate ecosystems, tropical conservationists outside Africa have tended to view dense, uniform vegetation as most 'natural'. If, as seems likely, the extinct megafauna was responsible for maintaining a more open and varied landscape in the past, then this possibility needs to be considered in conservation management plans.

A final, but very important, lesson from the megafaunal extinction story is that letting baselines slide—as they continue to do—runs the risk that we will not notice critical losses until it is too late to do anything about them. If we let defaunated ecosystems become the 'new normal', then we will lose the motivation to prevent their spread.

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