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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

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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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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