

# Limited effect of the Quaternary's largest super-eruption (Toba) on land mammals from Southeast Asia

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## Abstract

The effect of the Toba super-eruption at ~74 kyr on the mammals of Southeast Asia is examined. Although few Late Pleistocene sites from Southeast Asia have been described, an analysis of those which pre- and post-date Toba reveals relatively few species became extinct following the eruption. It is suggested that species survived in refugia immediately following the eruption, and that they repopulated vast areas following a probable short period (i.e. decades to century) of environmental devastation. This study suggests that mammals are more robust at coping with catastrophic events than previously acknowledged, and questions the perceived human monopoly in overcoming ecological adversity.

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## 1. Introduction

Lake Toba, Sumatra, a  $100 \times 30$  km caldera complex, is the site of the Quaternary's largest explosive eruption (Fig. 1). This super-eruption expelled an estimated  $7 \times 10^{15}$  kg of rhyolitic magma (Rose and Chesner, 1987, 1990; Chesner and Rose, 1991) and injected  $\sim 10^{15}$  g of fine ash into the stratosphere (Zielinski et al., 1996; Bühring et al., 2000) over an estimated period of 9–14 days (Ledbetter and Sparks, 1979). Rhyolitic ash deposits have been found as far afield as the seabed between Borneo and Indochina (Bühring et al., 2000), and suspected Toba tephra have been found on the Indian sub-continent, more than 3000 km away from Sumatra (Oppenheimer, 2002). Dating of the various deposits associated with Toba has consistently returned ages of approximately  $74 \pm 2$  kyr (Oppenheimer, 2002).

Climatic impacts of the Toba eruption are related to the emission of stratospheric sulphur (Ambrose, 2003). Estimates of these emissions range from 2.3 to  $4.7 \times 10^{12}$  kg (Zielinski et al., 1996) to  $3.5 \times 10^{10}$  kg (Scaillet et al., 1998), a difference of two orders of magnitude. Atmospheric modeling using the upper range of sulphuric emission

suggests a 5–6 year period of high stratigraphic sulphate aerosol abundance (Bekki et al., 1996). Predictions of temperature changes resulting from the Toba eruption range from no more than those observed for previous ice age oscillations (Oppenheimer, 2002; Gathorne-Hardy and Harcourt-Smith, 2003) to those associated with a nuclear winter (Rampino and Ambrose, 2000; Rampino and Self, 1992, 1993). In the latter scenario, regional temperatures are expected to drop  $\sim 10$ – $15$  °C below normal, while global decreases of 3–5 °C could be expected (Rampino and Ambrose, 2000). Simulations of super-eruptions suggest that climatic conditions resulting from volcanic aerosol are strongly dependent on the season of eruption (Timmreck and Graf, 2006).

Climatic changes associated with Toba could have resulted in a volcanic winter of such magnitude as to devastate vegetation and cause a human population bottleneck (Rampino and Self, 1992, 1993; Ambrose, 1998; Rampino and Ambrose, 2000). In modeling the effects of the eruption on vegetation, Rampino and Self (1992, 1993) utilized studies of the effects of a nuclear winter on the environment (e.g. Harwell and Hutchinson, 1985; Harwell, 1984). Such studies suggest near complete decimation of above-ground tropical plants, and little better survival of deciduous and temperate forests (Harwell

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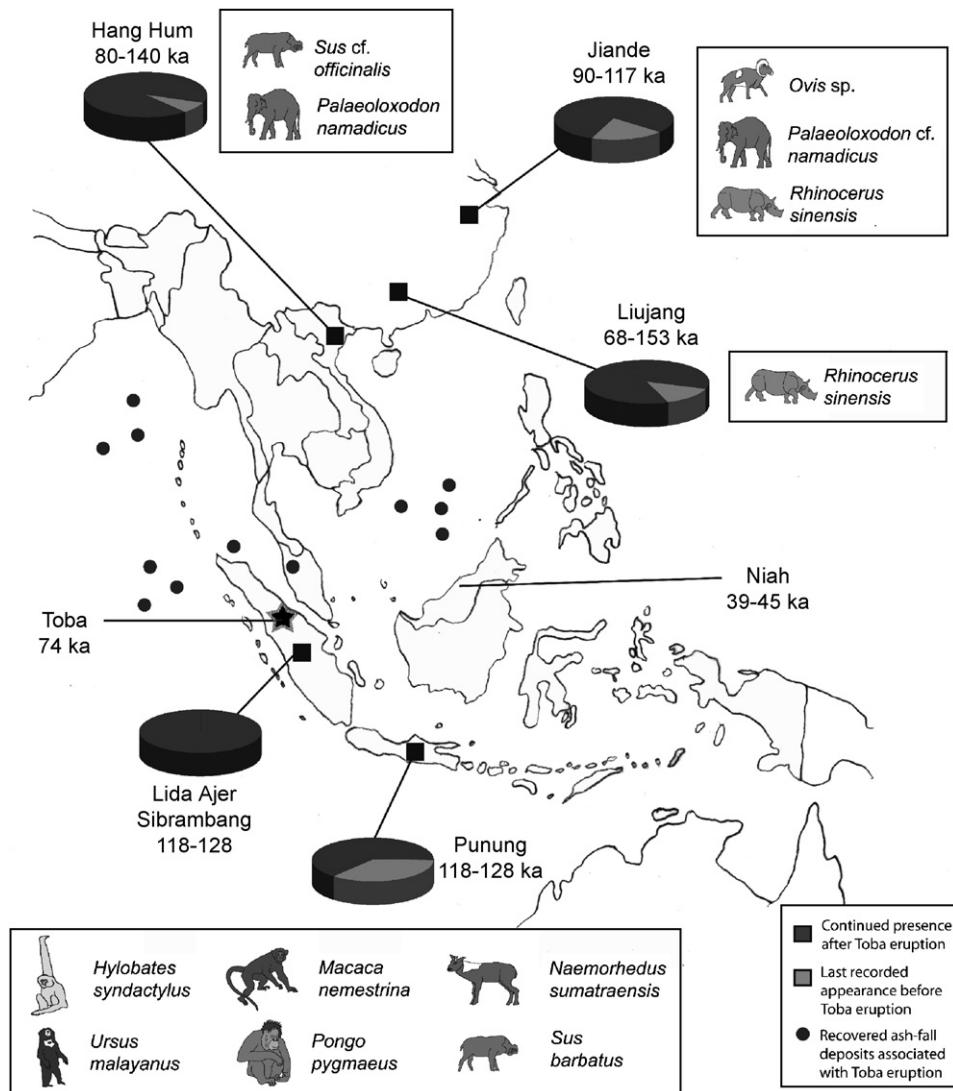


Fig. 1. Map showing the approximate locations of fossil sites preserving an extinction signature for Toba. Pie graphs represent proportion of species not represented after the eruption for each respective site. Extinct species for each country are illustrated in the boxes next to the pie graphs. Circles show recovered ash-fall deposits in the region (after Oppenheimer, 2002). Not to scale.

et al., 1985). These studies, however, have little to say on the survivability of mammals caught in nuclear winter (e.g. Hutchinson et al., 1985; Harwell et al., 1985) beyond lamenting their probable demise. Studies of the effects of volcanic super-eruptions suggest that they alone would be insufficient in producing mass extinction events (Erwin and Vogel, 1992; Prothero, 2004). However, even proponents of the volcanic winter hypothesis have not claimed mass extinctions would follow on from Toba (Ambrose, 2003). Given the magnitude and devastation associated with Toba, however, one would expect that regional extinctions would follow, especially if the ecological devastation posited for the volcanic winter were accurate. Species especially vulnerable to temperature changes and those dependent on tropical vegetation should, in particular, be adversely affected by the Toba super-eruption.

## 2. Methods

This analysis is restricted to Late Pleistocene (128–11 kyr) sites from Southeast Asia. Definitions of Southeast Asia, taxonomy and chronology follow those of Louys et al. (2007). Faunal lists were derived from the published literature (Table 1). A number of listings provide difficulties when examining whether particular taxa survived through the time of eruption, especially when analyses (such as this one) are focused at the specific level. The first of these are taxa unassigned above the level of genus. These specimens could in fact represent any member of its designated group, and thus provide limited information in terms of ecology and species extinctions. Those taxa unassigned above the level of genus are therefore omitted from the list provided here. The second involves those species assigned to genus level, but unassigned to any

Table 1

List of sites discussed in text, their respective dates and corresponding references

Faunal list	Reference (faunal list)	Age (kyr)	Reference (chronology)
Niah	Medway (1972)	39–45	Barker et al. (2007)
Hang Hum (combined faunal list from Hang Hum I and Hanh Hum II)	Olsen and Ciochon (1990)	80–140	Olsen and Ciochon (1990)
Keo Leong	Olsen and Ciochon (1990)	20–30	Olsen and Ciochon (1990)
Lida Adjer	de Vos (1983)	118–128	Based on correlation with Punung, as per de Vos (1983)
Sibrabang	de Vos (1983)	118–128	Based on correlation with Punung, as per de Vos (1983)
Kedung Brubus	van den Bergh et al. (2001)	700–800	van den Bergh et al. (2001)
Ngangdong	van den Bergh et al. (2001)	Late Pleistocene?	See text
Punung	van den Bergh et al. (2001)	118–128	Westaway et al. (2007)
Jiande	Han and Xu (1985)	90–117	Etler (1996)
Liujiang	Han and Xu (1985)	68–153	Shen et al. (2002)

particular species. This can occur for a number of reasons, including (but not limited to): (1) the material could be too incomplete to determine species, while still being informative at the generic level; (2) the author describing the material is unfamiliar with the particular group examined; or (3) it could possibly represent a new species, although not enough material is preserved to be sure. (Note these are not mutually exclusive.) Difficulties arise when trying to determine if these taxa survived the extinction: the unassigned individual may belong to an established species (either extinct or extant), or could be a new species (in which case it is likely that any such species would be extinct). Those individuals unassigned at the species level may represent the only example of that genus at that time or even in that country. Given these different scenarios, should these taxa be scored as present or absent in the Holocene? The approach taken in this study is to list taxa assigned only to the generic level at the sites from which they were recovered (Table 2). Holocene presence for those genera finding a modern representative is marked with “\*”. The final problematic listing is that of a conferred species. In this analysis a taxon designated “c.f.” is treated as the conferred species, and any Holocene presence is therefore based on that species.

The chronology of the sites was obtained from the published record (Table 1). All sites discussed have been included. Any disparity in accepted chronology is explored in the discussion. Holocene distribution of mammals was compiled from Corbet and Hill (1992), Nowak (1999), van den Bergh et al. (2001) and Tong and Liu (2004).

This analysis is restricted to large-bodied taxa, in this case represented by six orders: Artiodactyla, Proboscidea, Perrisodactyla, Carnivora, Primates and Pholidota. This was for two reasons. Firstly, most excavations described from the region, completed earlier in the last century, did not generally attach significance to microfauna, resulting in a bias towards large, charismatic species. Furthermore, large bodied taxa are easiest to recognize in the palaeontological record, leading to faunal lists where only large-bodied taxa are significantly represented. Secondly, larger

bodied taxa are more susceptible to extinction (Cardillo et al., 2005): they generally have lower reproduction rates, longer gestation periods, attain sexual maturity more slowly and have lower population densities (Cardillo et al., 2005). Recovery from a catastrophic event should favour those animals who can re-establish their population quickly.

### 3. Results

#### 3.1. Borneo

The site of Niah Great Caves, Borneo, postdates the Toba super-eruption (Table 1). Therefore, any mammals found at Niah would necessarily have survived the climatic after affects of the eruption. Of note among those taxa found at Niah are two species each of langur and macaque (*Presbytis* and *Macaca*), and one each of gibbon and orangutan (*Hylobates* and *Pongo*) (Table 2).

#### 3.2. Vietnam

The site of Hang Hum (Fig. 1), based on biochronological dating (Table 1), would pre-date the Toba eruption. Seven species recorded by Hang Hum (representing 26% of species from the site) are now extinct in Vietnam. These are the orangutan (*Pongo pygmaeus*), two species of proboscidean (*Stegodon orientalis* and *Palaeoloxodon namadicus*) the giant tapir (*Megatapirus augustus*), the extinct Chinese rhino (*Rhinoceros sinensis*) and two species of pig (*Sus lydekkeri* and *Sus officinalis*). However, of these, only *Sus officinalis*, *Palaeoloxodon namadicus* are not represented at Keo Leng (Table 2), another Vietnamese site dated well after Toba (Table 1). Therefore, the only species occurring at Hang Hum, which could be attributed to the Toba eruption is a suid and an elephant, neither of which could be considered as rainforest obligates. In addition to the species mentioned above, many species found in Hang Hum are still extant in Vietnam. These include several species of macaque and gibbon (*Macaca* and *Hylobates*),

Table 2

Species list of sites discussed in text; x represents presence, \* represents generic presence during Holocene

Table 2 (continued)

Borneo	Vietnam				Sumatra				Java				Southern China			
	Niah Caves	Hang Hum	Keo Leng	Holocene	Lida	Ajer	Sibrabang	Holocene	Kedung	Brubus	Ngangdong	Punung	Holocene	Jiande	Liujiang	Holocene
<i>Megatapirus augustus</i>		x	x											x	x	x
<i>Rhinoceros sondaicus</i>				x		x		x	x	x		x	x			x
<i>Rhinoceros sinensis</i>		x	x								x			x	x	
<i>Rhinoceros unicornis</i>								x								
<i>Dicerorhinus sumatrensis</i>	x				x	x	x	x								x
Artiodactyla																
<i>Sus barbatus</i>	x				x	x	x	x				x				
<i>Sus scrofa</i>		x	x	x	x	x	x	x				x	x	x	x	x
<i>Sus</i> sp.			x	*								x	*	x	x	*
<i>Sus</i> cf. <i>barbatus</i>																
<i>Sus</i> cf. <i>lydekkeri</i>		x	x													
<i>Sus macrognathus</i>									x		x					
<i>Sus</i> cf. <i>officinalis</i>		x	x													
<i>Hexaprotodon sivalensis</i>									x		x					
<i>Cervus unicolor</i>	x	x	x	x					x		x		*	x	x	x
<i>Cervus</i> sp.		x	x	*	x	x	*	x	x	x	x					
<i>Axis porcinus</i>				x											x	x
<i>Muntiacus muntjac</i>	x		x	x	x	x	x	x	x	x		x	x		x	x
<i>Muntiacus</i> sp.			x	*										x		*
<i>Bos frontalis</i>				x												x
<i>Bos javanicus</i>	x			x	x	x	?					x		x		
<i>Bos sauveli</i>				x												
<i>Bos palaesondaicus</i>									x		x					
<i>Bos gaurus</i>	x	x	x	x												
<i>Bubalus bubalis</i>		x	x	x		x						x	x		x	x
<i>Bubalus</i> sp.														x		*
<i>Bubalus palaeokerabau</i>									x		x					
<i>Tragulus napu</i>	x															
<i>Duboisia santeng</i>									x							
<i>Naemorhedus sumatraensis</i>		x	x	x	x	x	x	x				x			x	
<i>Epileptobos groeneveldtii</i>									x			x				
<i>Ovis</i> sp.												x				
Pholidota																
<i>Manis javanica</i>	x															
<i>Manis palaeojavanica</i>	x							x								

List drawn from references in Table 1 for Pleistocene sites and from references cited in Section 2 for Holocene.

all the Carnivora listed, the tapir (*Tapirus indicus*), pig (*Sus scrofa*), a deer (*Cervus unicolor*) and two bovids, *Bos gaurus* and *Bubalus bubalis*.

### 3.3. Sumatra

Based on faunal similarity, Lida Ajer (Fig. 1) is considered contemporaneous with Punung from Java (de Vos, 1983), which has a suggested age of 118–128 kyr (Westaway et al., 2007). Therefore it pre-dates the Toba eruption. Louys et al. (2007) incorrectly stated that the leopard *Panthera pardus* becomes extinct from Sumatra during the Late Pleistocene; however, as Meijaard (2004) points out, there are no reliable fossils of this felid from Sumatra. The only species described from Lida Ajer which could have become extinct is the bovid *Bos javanicus*, although the domesticated form of this animal is currently found on the island (Corbet and Hill, 1992). Lida Ajer therefore records at least 13 species which survived the extinction (Table 2).

Sibrabang (Fig. 1), shares the majority of its species with Lida Ajer, and as such is most likely contemporaneous (de Vos, 1983). In addition to species shared with Lida Ajer, the tiger (*Panthera tigris*), the Javan rhino (*Rhinoceros sondaicus*) and a buffalo (*Bubalus bubalis*) are also found at Sibrabang, all of which are currently extant in Sumatra.

### 3.4. Java

Java hosts two sites which likely pre-dated the Toba eruption, and therefore provide an indication of the impact of the eruption on the mammalian fauna. The first of these is Punung (Fig. 1), which has recently been dated to 118–128 kyr by luminescence and uranium (U)-series dating (Westaway et al., 2007). The second site, that of Ngangdong, is more insecurely dated. Swisher et al. (1996), on the basis of ESR and U-series dating of bovid teeth have provided an age of ~27–53 kyr, however this date has been questioned by van den Bergh (1999), who considers an age of ~135 kyr more reasonable. Certainly, the Ngangdong fauna is extremely similar to the older (0.8–0.7 Ma) Kedung Brubus fauna, sharing with it 10 (out of 11) of its species (Table 2). In addition to this, species recorded from Kedung Brubus and Ngangdong evince very different environments to those of Punung. As van den Bergh (1999) points out, it is far less parsimonious for the faunal succession and paleoenvironment of Java to shift from an archaic fauna representing an open forest environment (Kedung Brubus) to a more derived rainforest fauna (Punung), reverting back to an archaic fauna (Ngangdong), then developing the more modern fauna as represented by sites such as Wajak (see Storm (2001), for a description of Wajak). Particularly if, as van den Bergh (1999) suggests, the layer dated by Swisher et al. (1996) consists of reworked material intruding into the older, and principal fossil-bearing layers. Given these doubts on the

dating recorded by Swisher et al. (1996), and given the similarity in fauna between Kedung Brubus and Ngangdong, any further discussion of the extinctions herein will be based on the assumption that Ngangdong is older than Punung, and therefore its record of extinction cannot be associated with Toba.

Species from Punung which are no longer found on Java include a macaque (*Macaca nemestrina*), a gibbon (*Hylobates syndactylus*), the orangutan (*Pongo pygmaeus*), a bear (*Ursus malayanus*), the serow (*Naemorhedus sumatraensis*) and a pig (*Sus barbatus*) (Fig. 1). Those which continue to be found on Java following the eruption include the tiger (*Panthera tigris*), the Asian elephant (*Elephas maximus*), the tapir (*Tapirus indicus*), the Javan rhino (*Rhinoceros sondaicus*), a pig (*Sus scrofa*), a muntjac (*Muntiacus muntjak*) and a buffalo (*Bubalus bubalis*).

### 3.5. Southern China

China is host to possibly the largest number of Pleistocene sites in the region. However, the only sites examined for the purpose of this analysis are those which most likely and most closely pre-date the Toba eruption. Therefore, of the sites considered characteristic of Late Pleistocene Southern China by Han and Xu (1985), only two are considered here—Jiande and Luijiang (Fig. 1). Based on their accepted chronology (Table 1), Jiande completely pre-dates the eruption. While the range of dates for Luijiang encompasses the date of the Toba eruption, it was also most likely deposited prior to the eruption. Jiande records the extinction of two species—the archaic elephant *Palaeoloxodon namadicus* and the Chinese rhino *Rhinoceros sinensis*—the latter species representing the only extinction recorded from Luijiang (Fig. 1). Mammals present at Jiande which survived the Toba eruption include a bear (*Ursus thibetanus*), a hyena (*Crocuta crocuta*), badger (*Arctonyx collaris*), a stegodon (*Stegodon orientalis*), the giant tapir (*Megatapirus augustus*) and the giant panda (*Ailuropoda melanoleuca*). These last three mammals are also recorded at Luijiang.

## 4. Discussion

### 4.1. General discussion

A surprisingly limited number of extinctions are recorded during the time of the Toba eruption. Vietnam saw the extinction of a pig and elephant, Southern China the extinction of an elephant and a rhinoceros, while Sumatra seems to have recorded no extinctions at all. Java provides by far the largest list of extinct species: two species of monkey, one ape, one bear, one serow and a species of pig (Fig. 1).

Of significance is the fact that the vast majority of these extinctions do not involve characteristic rainforest taxa. The vast majority of animals which do become extinct

appear to be characteristic of open forests and environments, in particular the elephants and bovids.

Rainforest taxa seem to be relatively unaffected in distribution following the Toba eruption. The orangutan survived in Borneo, Vietnam and Sumatra, while the crab-eating macaque (*Macaca fascicularis*) survived in Borneo, Java and Sumatra. At least one other species of macaque, the pigtail macaque, also survives on Borneo and Sumatra. Gibbons, represented by the genus *Hylobates*, survive in Borneo, Vietnam and Sumatra. These apes are arboreal obligates, and occur predominately in evergreen and deciduous monsoon rainforests (Nowak, 1999). The Asian tapir, *Tapirus indicus*, as well as its giant relative, *Megatapirus augustus*, do not seem to have been adversely affected by the eruption, surviving in Borneo, Vietnam, Java and Sumatra in the case of the former, and Vietnam and Southern China in the case of the latter. While almost nothing is known of the ecology of the giant tapir, the little that is known of the Asian tapir suggests it has a preference for flat and damp environments and is predominantly restricted to closed forests (Novarino et al., 2005). It generally prefers secondary forest to primary and/or disturbed forests (Novarino et al., 2005), and the most serious threat to its survival remains deforestation (Holden et al., 2003).

The list of surviving fauna is not only restricted to rainforest taxa. A species of elephant (*Stegodon orientalis*) survives in Vietnam and Southern China. Several species of suids, cervids and bovids also survive, all of which are usually associated with less densely wooded environments. The fact that most carnivores survive is also not surprising given the abundance of carcasses following any catastrophe (Harwell et al., 1985), coupled with the suggested relatively short period of vegetative recovery (Harwell, 1984). The ensuing grace period for carnivores in this case would, however, be necessarily short, and any extension in the recovery time of flora (and corresponding fauna) would likely adversely affect carnivores (Harwell et al., 1985). Gathorne-Hardy and Harcourt-Smith (2003) also noted the survival of nine endemic species of rainforest obligates on the Mentawai Islands, situated 350 km south of Toba. The nature of these survivals suggest one of two possibilities, depending on whether we accept that the aftermath of the volcanic eruption can be likened to a nuclear winter and the environmental response suggested for this event.

#### 4.2. Volcanic winter

If we accept that the impact of the volcanic winter produced by a super-eruption can be likened to a nuclear winter, and that the hypothesized aftermath (see Rampino and Self, 2000, for a detailed description) will be, although highly speculative, at least within reason, then this suggests that fauna in the immediate area of the volcanic eruption are surprisingly resilient. The devastation of vegetation in the region would surely affect the vast majority of each

respective community's population, and it is likely that the surviving fauna would do so only in geographically isolated and environmentally protected refugia.

Perhaps because of the severe structural damage and ensuing human misery associated with catastrophic events, studies into the effects of catastrophes on mammals have been few (Willig and McGinley, 1999). Modern analogues to the Toba eruption are necessarily magnitudes smaller than Toba, and include the eruption of Krakatau and Mount St. Helens, and also possibly the Chernobyl disaster. The 1883 Krakatau eruption is thought to have extinguished all life on its associated islands directly following its eruption (Simkin, 1983; Gathorne-Hardy et al., 2000). In its immediate vicinity this is thought to result from the falling tephra, lava and hot gases. Heavy tephra falls are also thought to be responsible for the felling of trees within a wider area, at least 19 km (Gathorne-Hardy and Harcourt-Smith, 2003). The Mount St. Helens eruption resulted in the deaths of 5000 deer (*Odocoileus hemionus*), 1500 elk (*Cervus canadensis*), 200 black bears (*Ursus americanus*) and 15 mountain goats (*Oreamnos americanus*) (Del Moral and Grishin, 1999). In the case of the Chernobyl disaster, the first plume released by the explosion resulted in the loss of 400 ha of pine forest west of the reactor and the extermination of almost all avian and mammalian fauna within 5 km (Chesser et al., 2005).

The ability of animals to survive disturbances is dependent on the timing, magnitude and intensity of the disturbance as well as the phenotype and life history of the animal (Willig and McGinley, 1999). Studies into catastrophic disturbances have demonstrated that even the largest of these do not produce "blank slates", but leave mosaic patches of different species composition (see Platt and Connell, (2003) and references therein). Although these studies primarily deal with flora, this should equally be applicable to fauna. In fact, animal populations can recover rapidly after volcanic events, and many species thrive in post-eruption environments providing forage recovers quickly (Del Moral and Grishin, 1999; Edwards, 2005).

Many species can avoid death by hiding out in refugia. In the path of destruction produced by the Chernobyl explosion, for example, many such refugia were created from which local animal communities were able to repopulate the region (Chesser et al., 2005). Flora and fauna continue to demonstrate a surprising ability to recuperate from catastrophe; note the recolonization of Krakatau in less than 100 years (Gathorne-Hardy et al., 2000); and as Chesser states with respect to the Chernobyl disaster "ecosystems [inside the exclusion zone] have shown remarkable recovery and resilience to this insult" (Chesser, 2006, p. 7). At Mt St Helens, fauna re-entered the zone of devastation within days of the eruption, and recolonisation of the blast zone occurred within 5 years (Edwards, 2005). Extrapolating these studies to Toba, and given the low extinction signature discussed above, it would appear that fauna have an underappreciated capacity for recovery from

catastrophe. If mammals did become extinct as a result of Toba, it is likely these animals were already very much in decline, and that the eruption only pushed them over the edge. This has implications for other studies of megafauna extinctions: the hypothesis that humans were responsible for the extinction of large-bodied mammals in the Late Pleistocene in a quick blitzkrieg fashion (e.g. Martin, 1984) is rendered less likely given the ability for most animals to survive sudden and catastrophic events.

The volcanic winter hypothesis has been used as a causative model explaining the hypothesized Late Pleistocene human bottleneck (e.g. Ambrose, 1998, 2003; Rampino and Ambrose, 2000). In the scenario proposed by these authors, climatic changes resulting from the Toba eruption would have cut the global human population down to between 3000 and 10,000 individuals (Rampino and Ambrose, 2000). Recovery of humans is thought to be the result of an unprecedented adoption of cooperative skills and communication strategies (Ambrose, 2003). Evidence of population expansion of the chimpanzee at ~67 kyr is also cited as supportive evidence (Rampino and Ambrose, 2000; Ambrose, 2003). Furthermore, orangutan diversity in Borneo seems to indicate a period of recovery following the Toba eruption (Steiper, 2006, although Steiper acknowledges this could just as likely result from environmental fluctuations). Based on the current palaeontological record, however, no mammals appear to have become extinct on Sumatra immediately following the eruption, either as a result of the initial blast, or the proceeding climatic changes. While Java, Sumatra and Borneo could have been repopulated following their connection to the mainland during periods of lower sea-level following the eruption, this is not the case for the Mentawai Islands, which preserve nine rainforest endemics (Gathorne-Hardy and Harcourt-Smith, 2003). The perceived human monopoly in overcoming ecological disasters should be reconsidered. If the emerging picture from the palaeontological record is correct, then there is no need to evoke unprecedented levels of corporation within prehistoric societies when calculating the response of humans to ecological adversity. It appears many mammals in the immediate area, without the need to revert to unusual or unprecedented behaviour, were able to cope with resultant climatic changes without visible effect on their distributions.

#### 4.3. No volcanic winter

The other alternative is if the climatic and ecological damage resultant from Toba is not considered comparable to that of a nuclear disaster. While the initial impact of the blast would certainly have been catastrophic, in this case the resultant changes to climate are not seen as permanent or as global as that predicted above. The survival of many taxa, some quite sensitive to deforestation, indicates that although vegetation may have been affected by the eruption, enough trees would have survived to allow their

dependent fauna to also survive. In fact, forests are generally resilient to tephra events, since the growth form diversity of trees improves the possibility that some individuals will survive (Del Moral and Grishin, 1999). This finding casts doubts on the theory that human populations would have been reduced to a few thousand individuals as a result of the volcanic eruption (Rampino and Ambrose, 2000). If the level of deforestation and climatic impacts were not sufficient to cause major extinctions or significant range reduction in the taxa studied here, it is unlikely that it would be sufficient in and of itself to reduce the global human population as has been suggested, these being furthermore restricted to the African continent (Rampino and Ambrose, 2000). While it is possible that such a population crash could be expected for Southeast Asia, it is unlikely to have affected the populations of Eurasia or Africa to quite the same extent.

The immediate aftermath of the volcanic eruption would have been quite dire for vegetation and fauna alike, especially regionally. While the palaeontological record for Southeast Asia is still relatively scarce, it is not uninformative. The immediate period of devastation would likely be short-lived, as suggested by the high survivability of mammalian megafauna. However, there is no need to evoke Toba as the sole extinction agent: analysis of sediment cores of Indonesia suggests wetter conditions developed from 74 to 47 kyr (van der Kaars and Dam, 1995), possibly contributing to the extinction of the elephants and bovids. Thus, while the Toba eruption certainly would have produced less favourable conditions, these conditions would not have been outside the range of tolerance for most species. In fact, simulations of the climatic effects of super-eruptions suggest that although dramatic changes of climate could be expected following a the eruption event, these would be short-lived (in the order of decades), and not enough in themselves to bring about glacial conditions (Jones et al., 2005, 2007). The volcanic winter scenario is certainly possible, and is not discounted here; however, based on the survivability of the mammals studied, it is more likely that the global effects of this eruption have been overestimated.

## 5. Conclusions

The ecological aftermaths of super-eruptions are understandably difficult to examine directly. Even when massive eruptions have occurred within recorded history, their effects on mammals have been little studied. Analyses such as this one are often the only means of exploring the ecological effects of super-eruptions on fauna. While the data presented here are not as constrained as could be hoped, the results are nevertheless suggestive of a far greater resilience of mammals coping with ecological adversity. Based on the current palaeontological record, the total number of species recorded for the period of the super-eruption of Toba is small. While a mass extinction event for the region as a result of the eruption has been

discounted by a number of authors (Erwin and Vogel, 1992; Ambrose, 2003), the small number of extinctions recorded is still surprising, particularly given the ferocity of the eruption event, and its proposed ecological effects. Two different scenarios are explored in this paper based on whether these proposed ecological effects are accepted. If the volcanic winter did proceed after the eruption, then this study suggests the previously underappreciated ability of mammals to recover from catastrophic events, and has implications for other mass extinction events, especially where large-bodied taxa feature prominently. If the volcanic winter were not as dire as predicted, then it is unlikely that the human bottleneck observed was caused by the super-eruption of Toba and the resultant climate change, and that as noted by other authors (e.g. Prothero, 2004), the ecological effects of super-eruptions are not critical to mammalian extinctions.

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## References

Ambrose, S.H., 1998. Late Pleistocene human population bottlenecks, volcanic winter, and differentiation of modern humans. *Journal of Human Evolution* 34, 623–651.

Ambrose, S.H., 2003. Did the super-eruption of Toba cause a human population bottleneck? Reply to Gathorne-Hardy and Harcourt-Smith. *Journal of Human Evolution* 45, 231–237.

Barker, G., Barton, H., Bird, M., Daly, P., Datan, I., Dykes, A., Farr, L., Gilbertson, D., Harrison, B., Hunt, C., Higham, T., Kealhofer, L., Krigbaum, J., Lewis, H., McLaren, S., Paz, V., Pike, A., Piper, P., Pyatt, B., Rabett, R., Reynolds, T., Rose, J., Rushworth, G., Stephens, M., Stringer, C., Thompson, J., Turney, C., 2007. The ‘human revolution’ in lowland tropical Southeast Asia: the antiquity and behaviour of anatomically modern humans at Niah Cave (Sarawak, Borneo). *Journal of Human Evolution* 52, 243–261.

Bekki, S., Pyle, J.A., Zhong, W., Toumi, R., Haigh, J.D., Pyle, D.M., 1996. The role of microphysical and chemical processes in prolonging the climate forcing of the Toba eruption. *Geophysical Research Letters* 23, 2669–2672.

Bühring, C., Sarnthein, M., Leg 184 Shipboard Scientific Party, 2000. Toba ash layers in the South China Sea: evidence of contrasting wind directions during eruption ca 74 kyr. *Geology* 28, 275–278.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309, 1239–1241.

Chesner, C.A., Rose, W.I., 1991. Stratigraphy of the Toba Tuffs and the evolution of the Toba Caldera Complex, Sumatra, Indonesia. *Bulletin of Volcanology* 53, 343–356.

Chess, R.K., 2006. The legacy of Chernobyl: 1986 to 2006 and beyond. Briefing presented at US Capitol Building, April 27, 2006.

Chess, R., Rodgers, B., Baker, R., 2005. Temporal trends in radiation doses, survival, and recovery in wildlife populations at Chernobyl. In: Ecological Society of America 2005 Annual Meeting, Montreal, Canada (Abstract).

Corbet, G.B., Hill, J.E., 1992. The Mammals of the Indomalayan Region. Oxford University Press, New York.

Del Moral, R., Grishin, S.Y., 1999. Volcanic disturbances and ecosystem recovery. In: Walker, L.R. (Ed.), *Ecosystems of Disturbed Ground*. Elsevier Science B.V., Amsterdam, pp. 137–160.

de Vos, J., 1983. The *Pongo* faunas from Java and Sumatra and their significance for biostratigraphical and paleo-ecological interpretations. *Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen* 86, 417–425.

Edwards, J.S., 2005. Animals and volcanoes: survival and revival. In: Martí, J., Ernst, G.G.J. (Eds.), *Volcanoes and the Environment*. Cambridge University Press, Cambridge, pp. 250–272.

Erwin, D.H., Vogel, T.A., 1992. Testing for causal relationships between large pyroclastic volcanic eruptions and mass extinctions. *Geophysical Research Letters* 19, 893–896.

Etler, D.A., 1996. The fossil evidence for human evolution in Asia. *Annual Review of Anthropology* 25, 275–301.

Gathorne-Hardy, F.J., Harcourt-Smith, W.E.H., 2003. The super-eruption of Toba, did it cause a human bottleneck? *Journal of Human Evolution* 45, 227–230.

Gathorne-Hardy, F.J., Jones, D.T., Mawdsley, N.A., 2000. The recolonization of the Krakatau islands by termites (Isoptera), and their biogeographical origins. *Biological Journal of the Linnean Society* 71, 379–393.

Han, D., Xu, C., 1985. Pleistocene mammalian faunas of China. In: Wu, R., Olsen, J. (Eds.), *Palaeoanthropology and Palaeolithic Archaeology in the People’s Republic of China*. Academic Press, Orlando, pp. 267–289.

Harwell, M.A., 1984. *The Human and Environmental Consequences of Nuclear War*. Springer, New York, 179pp.

Harwell, M.A., Hutchinson, T.C. (Eds.), 1985. *Environmental Consequences of Nuclear War*, Vol. II: Ecological and Agricultural Effects. Wiley, New York, 523pp.

Harwell, M.A., Hutchinson, T.C., Cropper Jr., W.P., Harwell, C.C., 1985. Vulnerability of ecological systems to climatic effects of nuclear war. In: Harwell, M.A., Hutchinson, T.C. (Eds.), *Environmental Consequences of Nuclear War*, Vol. II: Ecological and Agricultural Effects. Wiley, New York, pp. 81–171.

Holden, J., Yanuar, A., Martyr, J.R., 2003. The Asian Tapir in Kerinci Seblat National Park, Sumatra: evidence collected through photo-trapping. *Oryx* 37, 34–40.

Hutchinson, T.C., Cropper Jr., W.P., Grover, H.D., 1985. Ecological principles relevant to nuclear war. In: Harwell, M.A., Hutchinson, T.C. (Eds.), *Environmental Consequences of Nuclear War*, Vol. II: Ecological and Agricultural Effects. Wiley, New York, pp. 3–80.

Jones, G.S., Gregory, J.M., Stott, P.A., Tett, S.F.B., Thorpe, R.B., 2005. An AOGCM simulation of the climate response to a volcanic super-eruption. *Climate Dynamics* 25, 725–738.

Jones, M.T., Sparks, R.S.J., Valdes, P.J., 2007. The climatic impact of supervolcanic ash blankets. *Climate Dynamics*.

Ledbetter, M., Sparks, R.S.J., 1979. Duration of large-magnitude explosive eruptions deduced from graded bedding in deep-sea ash layers. *Geology* 7, 240–244.

Louys, J., Curnoe, D., Tong, H., 2007. Characteristics of Pleistocene megafauna extinctions in Southeast Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 243, 152–173.

Martin, P.S., 1984. Prehistoric overkill: the global model. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson.

Medway, L., 1972. The Quaternary era in Malesia. In: Ashton, P.S., Ashton, M. (Eds.), *Miscellaneous Series*. University of Hull, University of Aberdeen, Aberdeen, Scotland, pp. 63–83.

Meijaard, E., 2004. Biogeographic history of the Javan leopard *Panthera pardus* based on a craniometric analysis. *Journal of Mammalogy* 85 (2), 302–310.

Novarino, W., Kamilah, S.N., Nugroho, A., Janra, M.N., Silmi, M., Syafri, M., 2005. Habitat use and density of the Malayan Tapir (*Tapirus indicus*) in the Taratak Forest Reserve, Sumatra, Indonesia. *Tapir Conservation* 14/2, 28–30.

Nowak, R.M., 1999. Walker's Mammals of the World. The John Hopkins University Press, London.

Olsen, J.W., Ciochon, R.L., 1990. A review of evidence for postulated Middle Pleistocene occupations in Viet Nam. *Journal of Human Evolution* 19, 761–788.

Oppenheimer, C., 2002. Limited global change due to the largest known Quaternary eruption, Toba  $\approx$  74 kyr BP? *Quaternary Science Reviews* 21, 1593–1609.

Platt, W.J., Connell, J.H., 2003. Natural disturbances and directional replacement of species. *Ecological Monographs* 73, 507–522.

Prothero, D.R., 2004. Did impacts, volcanic eruptions, or climate change affect mammalian evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 214, 283–294.

Rampino, M.R., Ambrose, S.H., 2000. Volcanic winter in the Garden of Eden: the Toba super-eruption and the Late Pleistocene human population crash. In: McCoy, F.W., Heiken, G. (Eds.), *Volcanic Hazards and Disasters in Human Antiquity*. Geological Society, America, Special Paper, vol. 345, pp. 71–82.

Rampino, M.R., Self, S., 1992. Volcanic winter and accelerated glaciation following the Toba super-eruption. *Nature* 359, 50–52.

Rampino, M.R., Self, S., 1993. Bottleneck in human evolution and the Toba eruption. *Science* 262, 1955.

Rose, W.I., Chesner, C.A., 1987. Dispersal of ash in the great Toba eruption, 75 kyr. *Geology* 15, 913–917.

Rose, W.I., Chesner, C.A., 1990. Worldwide dispersal of ash and gases from earth's largest known eruption: Toba, Sumatra, 75 kyr. *Palaeogeography, Palaeoclimatology, Palaeoecology* 89, 269–275.

Scaillet, B., Clemente, B., Evans, B.W., Pichavant, M., 1998. Redox control of sulfur degassing in silicic magmas. *Journal of Geophysical Research* 103, 23937–23949.

Shen, G., Wang, W., Wang, Q., Zhao, J., Collerson, K., Zhou, C., Tobias, P.V., 2002. U-series dating of Liujiang hominid site in Guangxi, Southern China. *Journal of Human Evolution* 43, 817–829.

Simkin, T., 1983. Krakatau, 1883—The Volcanic Eruption and its Effects. Smithsonian Institution, USA, 464pp.

Steiper, M.E., 2006. Population history, biogeography, and taxonomy of orangutans (Genus: *Pongo*) based on a population genetic meta-analysis of multiple loci. *Journal of Human Evolution* 50, 509–522.

Storm, P., 2001. The evolution of humans in Australasia from an environmental perspective. *Palaeogeography, Palaeoclimatology, Palaeoecology* 171, 363–383.

Swisher III, C.C., Rink, W.J., Antón, S.C., Schwarcz, H.P., Curtis, G.H., Suprijo, A., Widiasmoro, 1996. Latest *Homo erectus* of Java: potential contemporaneity with *Homo sapiens* in Southeast Asia. *Science* 274, 1870–1874.

Timmreck, C., Graf, H.-F., 2006. The initial dispersal and radiative forcing of a Northern Hemisphere mid-latitude super volcano: a model study. *Atmospheric Chemistry and Physics* 6, 35–49.

Tong, H., Liu, J., 2004. The Pleistocene–Holocene extinctions of mammals in China. In: Dong, W. (Ed.), *Proceedings of the Ninth Annual Symposium of the Chinese Society of Vertebrate Paleontology*. China Ocean Press, Beijing, pp. 111–119 (In Chinese with English abstract).

van den Bergh, G., 1999. The Late Neogene elephantoid-bearing faunas of Indonesia and their palaeozoogeographic implications. A study of the terrestrial faunal succession of Sulawesi, Flores and Java, including evidence for early hominid dispersal east of Wallace's line. *Scripta Geologica* 117, 1–419.

van den Bergh, G., de Vos, J., Sondaar, P., 2001. The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology* 171, 385–408.

van der Kaars, W.A., Dam, M.A.C., 1995. A 135,000-year record of vegetational and climatic change from the Bandung area, West-Java, Indonesia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 117, 55–72.

Westaway, K.E., Morwood, M.J., Roberts, R.G., Rokus, A.D., Zhao, J.-x., Storm, P., Aziz, F., van den Bergh, G., Hadi, P., Jatmiko, J.de Vos, 2007. Age and biostratigraphic significance of the Punung Rainforest Fauna, East Java, Indonesia, and implications for *Pongo* and *Homo*. *Journal of Human Evolution*.

Willig, M.R., McGinley, M.A., 1999. The response of animals to disturbance and their roles in patch generation. In: Walker, L.R. (Ed.), *Ecosystems of Disturbed Ground*. Elsevier Science B.V., Amsterdam, pp. 633–657.

Zielinski, G.A., Mayewski, P.A., Meeker, L.D., Whitlow, S., Twickler, M.S., Taylor, K., 1996. Potential atmospheric impact of the Toba mega-eruption  $\sim$ 71,000 years ago. *Geophysical Research Letters* 23, 837–840.