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ORIGINAL ARTICLE

Mentawai's endemic, relictual fauna: is it evidence for Pleistocene extinctions on Sumatra?

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ABSTRACT

Aim The four Mentawai islands, south-west of Sumatra, have long been isolated from the remainder of Sundaland, resulting in a high level of endemism. We examined the distribution of 151 species of the Mentawai Islands in Sundaland and assessed various processes that may have resulted in the various biogeographical patterns.

Location Southeast Asia, particularly the Mentawai Islands and nearby large landmasses (Sumatra, Java, Borneo and Peninsular Malaysia).

Methods We compared the faunal composition of the Mentawai Islands for selected taxa (43 mammals, 92 reptiles and 16 amphibians) with that of the four nearby large landmasses of Sundaland using morphological comparisons and the most recent molecular phylogenetic analyses available in the literature. These comparisons yielded sister taxa, which were used to simulate species absence data for the four Sundaland landmasses under several scenarios to investigate how patterns of species absence could have arisen.

Results In contrast to our expectations, several Mentawai species did not have their closest relatives on neighbouring Sumatra, but rather on the more distant Borneo, Java or Peninsular Malaysia. For mammals, the similarity between species from Mentawai and Borneo was greater than that observed between species from Mentawai and Sumatra. We conclude that the relationships represent traces of species historically distributed throughout Sundaland that became extinct in Sumatra during the Pleistocene. For reptiles and amphibians the observed pattern of species absences generally resembled the simulated pattern expected under the scenario of absence rates increasing with landmass isolation, whereas for mammals we observed more species than expected missing from Java and Sumatra, and fewer than expected from Borneo.

Main conclusions The potential extinctions on Sumatra probably had two causes: changes of climate and vegetation during the Pleistocene and environmental impacts from the Toba supervolcanic eruption.

Keywords
Biogeography, extinction, immigration, mammals, palaeoclimate, Southeast Asia, Sunda Shelf, Toba volcanic eruption.

INTRODUCTION

The peculiarity of the Sunda Shelf was noticed as early as 1869 by Alfred Russel Wallace, who commented on the shallowness of the sea that separates Java, Sumatra, Borneo and Peninsular Malaysia:

> … it is when we examine the zoology of these countries that we find what we most require – evidence of a very striking character that these great islands must have once formed a part of the continent, and could only have been separated at a very recent geological epoch.
>
> (Wallace, 1869)

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Today we understand that during much of the Pliocene and Pleistocene, until as recently as 10,000 years ago (ka), Sumatra, Borneo, Java and present-day Malay Peninsula formed a single large landmass called 'Sundaland' (Molengraaff, 1916). Falling and rising sea levels during glacial cycles led to the alternating emergence and submergence of land bridges among islands and the mainland (Voris, 2000). Since Wallace's time, modern animal distribution patterns have often been viewed as the result of Pleistocene faunal movements across a united Sunda Shelf (e.g. Heaney, 1986; Brandon-Jones, 1996; Ruedi, 1996). However, molecular systematic studies have shown that Pleistocene land bridges alone do not satisfactorily explain the distribution of and the phylogenetic relationships among species in and around the shelf area. Instead, they indicate the importance of a deep history of vicariant evolution (e.g. Brandon-Jones, 1996; Meijaard & Groves, 2004; Wilting *et al.*, 2007, 2011; Patou *et al.*, 2010).

These vicariant patterns were probably influenced by drier and cooler climate periods on the Sunda Shelf (e.g. Heaney, 1991; Brandon-Jones, 1996; Wurster *et al.*, 2010), which resulted in a reduction of humid tropical forest areas, restricting rain forest-dwelling species to refugia and hindering their dispersal across periodically exposed land bridges (e.g. Bird *et al.*, 2005; Patou *et al.*, 2010). For example, a 'savanna corridor' composed of open vegetation types running north–south through Sundaland has been suggested for the Last Glacial Maximum (LGM; Heaney, 1991; Bird *et al.*, 2005; Piper *et al.*, 2011). However, past palaeoenvironmental conditions remain a matter of debate; for example, a retrospective climate model by Cannon *et al.* (2009) indicates that forest-covered areas were substantially larger during the LGM than they are today (not accounting for human deforestation), as the greater land exposure on the Sunda Shelf at times of low sea levels created more lowland areas for forest growth. Nevertheless, these forests – particularly those on newly exposed Sunda Shelf – may have been substantially different in composition and structure from present-day forests (Cannon *et al.*, 2009).

Meijaard (2003) used the distribution of mammal species across the many small shelf islands to derive general patterns for the presence/absence of species on Sundaic islands. He assumed that if forest-dependent species still occur on some islands, those islands must have been forested at the time when they became isolated, and thus he identified areas that must have remained forested throughout the Late Pleistocene

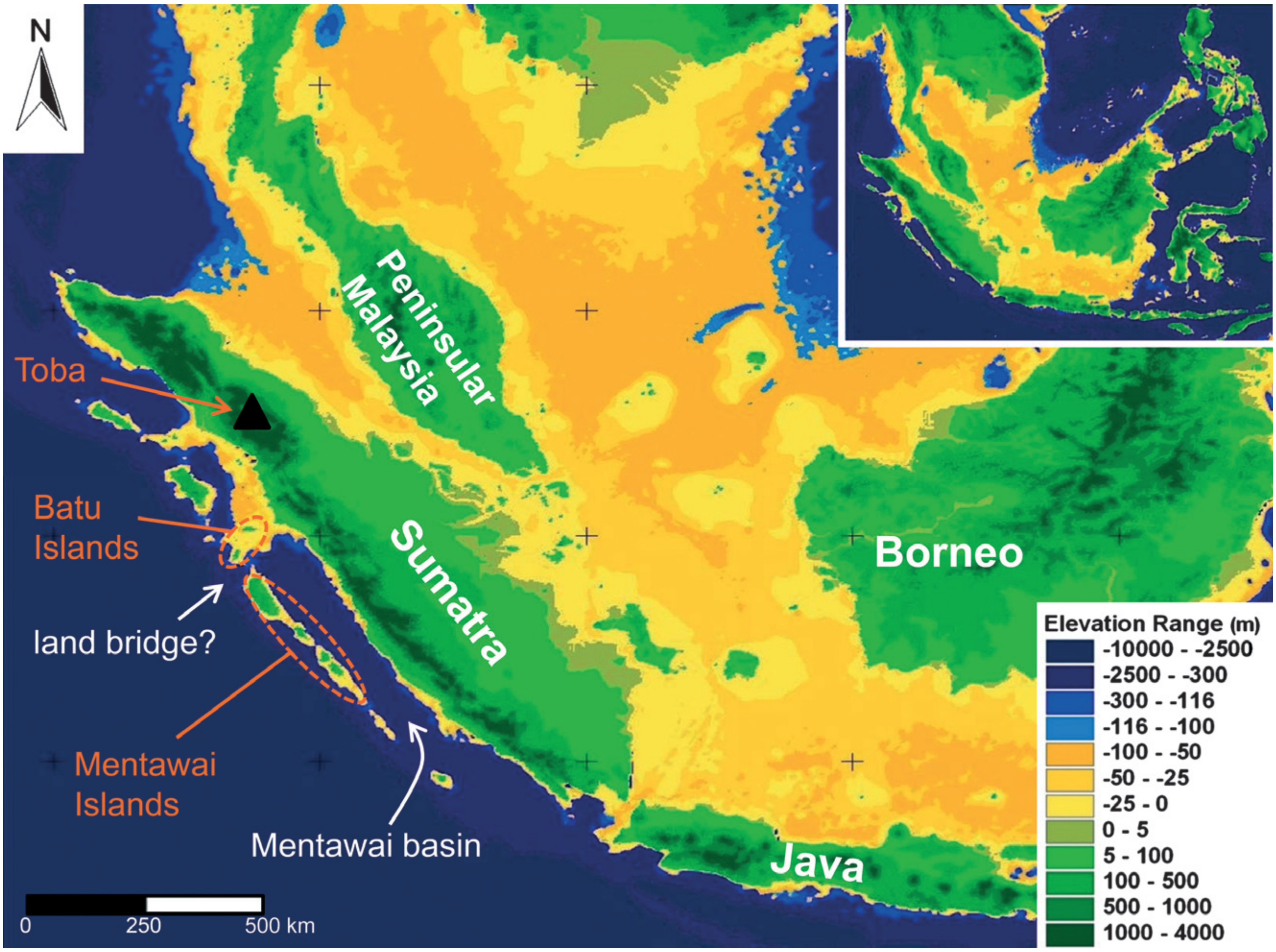

Figure 1 Map of the Sunda Shelf, 100 m below present-day sea level, *c.* 15.6 ka. Map adapted and modified from The Field Museum of Natural History 2006 (Voris, 2000; Sathiamurthy & Voris, 2006).

(Meijaard, 2003). The most remarkable of these small islands are the four Mentawai islands: Siberut, Sipora, North Pagai and South Pagai (also and henceforth called 'the Mentawais'). Situated 85–135 km off the coast of west Sumatra, Indonesia, within 0°55′ to 3°20′ S and 98°31′ to 100°40′ E (Fig. 1), they encompass a total land area of about 6000 km^2, with the most northern island, Siberut, being the largest (*c.* 4000 km^2). The faunal composition of the Mentawais, especially that of mammals, was first studied in detail from collections made by E. Modigliani (cited in Thomas, 1895) and W.L. Abbott (cited in Miller, 1903), and later by C.B. Kloss (Chasen & Kloss, 1928). These collections revealed a highly distinct fauna that included endemic species and involved interesting disjunct patterns of distribution of Sundaic mammal lineages (Chasen & Kloss, 1928; Banks, 1961). In the late 1970s more studies were conducted, focusing on diurnal mammals such as primates and squirrels (e.g. Whitten, 1980). Currently, about 17 endemic mammal species and a greater number of endemic subspecies and subpopulations are recognized in the Mentawai fauna (Corbet & Hill, 1992; Wilson & Reeder, 2005).

The Mentawais have been separated from Sumatra since the mid-Pleistocene (Batchelor, 1979; Dring *et al.*, 1990) by the 1500-m-deep Mentawai Basin (Fig. 1). Several Pliocenic and Pleistocenic subsidences in the basins west of Sumatra (Izart *et al.*, 1994) render Late Neogene land connections between the Mentawais and Sumatra unlikely, even at times when sea levels were low enough to interconnect the rest of Sundaland (Voris, 2000; Whitten *et al.*, 2000). Within the last 500 kyr (perhaps for much longer), only Siberut, the most northern of the four Mentawai islands, could have been physically linked to Sumatra through the Batu Islands by a land bridge across the Siberut Strait (Batchelor, 1979; Dring *et al.*, 1990), which is 55-km wide today (Fig. 1). However, the stretch of water deeper than the approximate maximum sea-level drop (< 125 m) during Pleistocene glacial maxima (Rohling *et al.*, 1998; Hanebuth *et al.*, 2000) is only about 10-km wide, potentially permitting an indirect Mentawai–Sumatra bridge during the LGM (Inger & Voris, 2001; Meijaard, 2003). Nevertheless, the high level of endemism found on the Mentawais, especially for mammals, indicates limited migration between the Mentawais and Sundaland via the Batu Islands. This is supported by evolutionary divergence time estimates (1–3 Ma) of some endemic Mentawaian taxa relative to Sumatran and other Sundaic populations (Table 1).

Table 1 Divergence time estimates of some Mentawaian mammals.

	Divergence time (Myr)	References
Simias/*Nasalis*	1.1–1.8	Roos *et al.* (2011)
Paradoxurus hermaphroditus lignicolor/*P. h. philippinensis*	*c.* 3.5	Patou *et al.* (2010)
Hemigalus derbyanus minor/*H. d. derbyanus*	*c.* 2.7	A. Wilting & J. Fickel (unpublished data)*
Presbytis potenziani/*Presbytis* spp.	*c.* 3.2 2.6	Meijaard & Groves (2004), Meyer *et al.* (2011)
Hylobates klossii/*Hylobates moloch*	2.0–2.8 2.8	Israfil *et al.* (2011), Chan *et al.* (2010)
M. pagensis – (*M. siberu*/*M. nemestrina*/*M. leonina*/*M. silenus*)	2.4–2.6	Ziegler *et al.* (2007)
Macaca siberu/(*M. nemestrina*/*M. leonina*/*M. silenus*)	1.5–1.7	Ziegler *et al.* (2007)
Sundasciurus fraterculus/*S. lowii*	1.5–3.1	den Tex *et al.* (2010)

*We estimated the divergence time based on 350 bp of cytochrome *b* (n = 3 Mentawai; n = 57 Borneo/Sumatra/Peninsular Malaysia); and net-between-clade-means genetic distances using the split between *Chrotogale* and *Hemigalus* at 20.1 Ma (Patou *et al.*, 2008) as the calibration date.

In mammals, the recorded insular distributions and delineations of species and subspecies boundaries point to a secondary north–south biogeographical break within the Mentawai Archipelago, situated between Siberut and the southern three Mentawai islands Sipora, North Pagai and South Pagai. The latter show closer faunal resemblance to each other and fewer occurrences of Sumatran lineages than Siberut (Table 2; Chasen & Kloss, 1928; Corbet & Hill, 1992), reflecting their greater isolation.

In addition to its species-level endemism, it is notable that the Mentawais harbour several mammalian lineages that are lacking from neighbouring Sumatra but are found elsewhere on the Sunda Shelf. An example is the gibbon species-pair *Hylobates klossii* (endemic to the Mentawais) and *H. moloch* (endemic to Java; Chan *et al.*, 2010; Israfil *et al.*, 2011). Most Mentawaian mammal lineages are, however, shared exclusively with Borneo. The monotypic colobid genera *Simias* (*S. concolor*, the simakobu of the Mentawais) and *Nasalis* (*N. larvatus*, the proboscis monkey of Borneo) – both often placed in the same genus *Nasalis* (Corbet & Hill, 1992) – constitute a distinctive phylogenetic monkey lineage of the Mentawais and Borneo (Whittaker *et al.*, 2006). The treeshrew species-pair *Tupaia longipes* (Borneo and satellite islands) and *T. chrysogaster* (Mentawais) also constitute a distinctive phylogenetic branch that is not known from Sumatra (Roberts *et al.*, 2011). Large-bodied species of the tree-mouse genus *Chiropodomys* are recorded from forests on the Mentawais (*C. karlkoopmani*) and on Borneo (*C. major*) [as well as on Palawan and adjacent islands (*C. calamaniensis*), an archipelago with Bornean affinities – see Esselstyn *et al.*, 2010 and Piper *et al.*, 2011 for reviews on Palawan's biogeographical affinities], but not from Sumatra (Musser, 1979). The larger dawn-bat, *Eonycteris major*, is known only from Borneo and the Mentawais [records from Sipora (Zoological Museum Berlin ZMB 50002) and North Pagai (American Museum of Natural History AMNH 103319), identifications confirmed by K.M.H.], not from Sumatra (with the closely related – possibly conspecific – *E. robusta* occurring in the oceanic Philippines). Palm civets of the genus *Paradoxurus* are found throughout the islands of the Malay Archipelago, but the distinctive endemic palm civet of the Mentawais, *P. hermaphroditus lignicolor*, is the sister lineage to *P. h. philippinensis*, the subspecies of palm

Table 2 List of Mentawaian mammal species including their sister-taxa and their current distribution in the Sunda Shelf.

	The Mentawais	Siberut	Sipora	North Pagai	South Pagai	Sister-taxa	Sumatra	Malaya	Java	Borneo	References
Scandentia (treeshrews)											
Ptilocercus lowii	x	x					x	x		x	
Tupaia chrysogaster	x		x	x	x	*T. longipes*				x	Roberts *et al.* (2011)
Tupaia glis	x	x					x	x	x		
Primates (primates)											
Hylobates klossii	x	x	x	x	x	*H. moloch*			x		Chan *et al.* (2010), Israfil *et al.* (2011)
Macaca pagensis	x		x	x	x	*Macaca siberu*/ *M. nemestrina*	x	x		x	Roos *et al.* (2003)
Macaca siberu	x	x				*M. nemestrina*	x	x		x	Roos *et al.* (2003)
Presbytis potenziani	x	x	x	x	x	*P. comata*/ *P. melalophos*/ *P. rubicunda*	x	x	x	x	Meyer *et al.* (2011)
Simias concolor	x	x	x	x	x	*Nasalis larvatus*				x	Whittaker *et al.* (2006)
Cervidae (deer)											
Rusa unicolor	x	x	x	x	x		x	x		x	
Pholidota (pangolins)											
Manis javanica	x	x		x	x		x	x	x	x	
Carnivora (carnivorans)											
Aonyx cinerea	x	x					x	x	x	x	
Hemigalus derbyanus	x	x	x		x		x	x		x	
Paradoxurus hermaphroditus lignicolor	x	x	x	x	x	*P. hermaphroditus philippinensis*				x	Patou *et al.* (2010)
Muridae (rats and mice)											
Chiropodomys karlkoopmani	x	x		x		*C. major*/ *C. calamianensis*				x	Musser & Carleton (2005)
Leopoldamys siporanus	x	x	x	x	x	*L. sabanus*	x	x	x	x	Corbet & Hill (1992)
Maxomys pagensis	x	x	x	x	x	*M. surifer*	x	x	x	x	Corbet & Hill (1992), Musser & Carleton (2005)
Rattus lugens	x	x	x	x	x	*R. tiomanicus*	x	x	x	x	Corbet & Hill (1992), Musser & Carleton (2005)
Sciuridae (squirrels)											
Hylopetes sipora	x		x			Uncertain					
Iomys sipora	x		x	x		*I. horsfieldii*	x	x		x	Corbet & Hill (1992)
Petaurista petaurista	x	x	x				x	x	x	x	
Petinomys lugens	x	x	x	x		*P. hageni*	x			x	Corbet & Hill (1992)
Callosciurus melanogaster	x	x	x	x	x	Uncertain					
Lariscus obscurus	x	x	x	x	x	*L. insignis*	x	x	x	x	Chasen, 1940, Corbet & Hill (1992)
Sundasciurus fraterculus	x	x	x	x	x	*S. lowii*	x	x		x	Corbet & Hill (1992)
Chiroptera (bats)											
Cynopterus sphinx	x	x	x	x			x	x	x	x	
Eonycteris major	x		x	x						x	Identifications by K.M.H. (see text)
Macroglossus sobrinus	x	x	x	x			x	x	x		
Pteropus hypomelanus	x	x	x				x	x		x	
Pteropus vampyrus	x	x	x	x	x		x	x	x	x	
Rousettus amplexicaudatus	x		x	x			x	x	x	x	
Emballonura monticola	x	x	x				x	x	x	x	
Megaderma spasma	x	x					x	x	x	x	
Rhinolophus affinis	x	x	x	x	x		x	x	x	x	
Rhinolophus pusillus	x			x			x	x	x	x	
Hipposideros bicolor	x			x			x	x	x	x	
Hipposideros breviceps	x			x		*H. galeritus*	x	x	x	x	Hill (1963)
Hipposideros cervinus	x		x	x			x	x		x	
Hipposideros diadema	x		x				x	x	x	x	

Table 2 Continued

	The Mentawais	Siberut	Sipora	North Pagai	South Pagai	Sister-taxa	Sumatra	Malaya	Java	Borneo	References
Hipposideros larvatus	x			x			x	x	x	x	
Myotis ater	x		x					x		x	
Myotis muricola	x		x				x	x	x	x	
Myotis hasseltii	x				x		x	x	x	x	
Kerivoula hardwickii	x	x	x				x	x	x	x	
No. mammal species	43	28	31	28	18		34	34	25	38	
Similarity (percentage of species shared with the Mentawais)							83	83	61	93	

civet in Borneo/Palawan, rather than to palm civet populations in Sumatra (Patou *et al.*, 2010). The Borneo–Mentawai link is not just a zoological one but is found also in plants; a recent study observed a similar pattern in orchids of the genus *Phalaenopsis* (Tsai *et al.*, 2010).

The absence of many mammal lineages from Sumatra that are instead shared between the Mentawais and other areas of the Sunda Shelf, particularly Borneo, is both striking and unexpected. Some of these apparent absences may result from a lack of collecting effort on Sumatra. The fauna of this island, especially with regard to smaller vertebrates, is relatively poorly known in comparison to those of Borneo, Java and the Malay Peninsula. Fewer specimens from fewer localities are represented in museums world-wide, and very few major collections have been made in recent decades (K.M.H., pers. obs.). However, while the absence of some small mammals might conceivably be explained by lack of survey efforts in Sumatra (e.g. the common forest fruit bats *Balionycteris maculata* and *Dyacopterus spadiceus* were just recently recorded there, see Danielsen *et al.*, 1997; Helgen *et al.*, 2007), Sumatra's large mammal fauna is well known. The island possesses several well-studied national parks, has a history of intensive primate field studies, and has been the site of some of the most intensive camera trapping efforts undertaken in tropical forests (summarized in Duckworth *et al.*, 2009). Historical declines and local extinctions of larger mammal species (such as that of the Javan rhinoceros, *Rhinoceros sondaicus*) have been well documented (Corbet & Hill, 1992). Thus, the presence of *Nasalis/Simias* monkeys on Sumatra, or that of a gibbon species related to *Hylobates klossii/H. moloch*, would probably not have been overlooked. Therefore, these and various other distinctions between the Mentawaian and Sumatran faunas that we documented in our comparisons must be considered real differences requiring an explanation.

Here, we analyse the mammal fauna of the Mentawais in relation to that on nearby landmasses. Further, we compare the findings for mammals with distribution patterns of reptiles and amphibians, which have different modes of dispersal. Our objective was to examine patterns in the historical distribution of species in Sundaland and to discuss environmental changes that may have resulted in the observed distribution of species within the Sunda Shelf and in the unique and enigmatic modern mammal fauna of the Mentawai Archipelago.

MATERIALS AND METHODS

We compared the species list of mammals, amphibians and reptiles of the Mentawai Islands with the inventory of species on the four nearby larger landmasses: Sumatra, Java, Borneo and Peninsular Malaysia. Our analysis included 43 mammal, 16 amphibian and 92 reptile species (in total 151) that are known to occur on the Mentawais. For the mammals the main sources were the Conservation Master Plan for Siberut prepared by WWF (1980), Heaney (1986), Corbet & Hill (1992), Meijaard (2003), Wilson & Reeder (2005), and the IUCN Red List of Threatened Species (IUCN, 2010). However, to update taxonomic relationships and species occurrences for mammals we used primary and more recent sources (Table 2). Information for amphibians and reptiles was taken from Teynié *et al.* (2010). For mammal species endemic to Mentawai we attempted to identify their closest relatives on the nearby landmasses (as far as they were known) to determine species-pairs of sister-taxa. For 15 endemic Mentawaian mammals, a sister-taxon could be identified. Identification was based on the most recent molecular phylogenetic analyses available in the literature, or, if those were lacking, on morphological comparisons. The latter were used to identify the closest ecological vicars of Mentawai species, which in the absence of better information we regarded to be their most likely closest relatives (details in Table 2). Pairs of well-established sister-taxa were treated as 'single species' in the analysis of similarity between the Mentawai Islands and the various landmasses. When the phylogenetic relationships of Mentawaian endemics to species of the other landmasses could not be sufficiently resolved we excluded these species from further analyses, for example if several species were described in the same genus but lack of phylogenetic resolution did not allow the identification of the closest relative of the Mentawaian endemics. For all non-endemics, we recorded the landmasses on which they occurred. Similarity itself was measured as the number of species/species-pairs shared between the Mentawais and the other four landmasses.

To understand the current pattern of absence of Mentawaian species from any of the other investigated landmasses we performed a simulation study. We assumed that Mentawaian species should have been present throughout Sundaland at times when it formed a single landmass, so that absence of one of these species today on either landmass would represent an extinction event. This assumption surely holds true for Sumatra, as species/species-pairs occurring on one of the other landmasses and the Mentawais must have occurred on neighbouring Sumatra as well. However, this assumption might be violated to some extent for Peninsular Malaysia and Borneo, and to a greater extent for Java. The climate and vegetation on Java (seasonal, open vegetation) differed the most from that of the Mentawais (mainly evergreen rain forest) throughout the Pleistocene (Bird *et al.*, 2005; Cannon *et al.*, 2009), and geographical barriers such as rivers could have prevented species dispersal. We therefore refer to results in terms of species absence, rather than extinction, keeping in mind that for Sumatra absences can be interpreted as extinctions.

For mammals, reptiles and amphibians, we first determined the number of non-endemic Mentawaian species absent from one, two or three of the four landmasses. We then assigned to these species which landmasses they were missing from by randomly selecting one, two or three of the landmasses without replacement, and in the end counted how many species were absent on each landmass. We repeated this procedure 10,000 times and compared this 'expected number of missing species' with the number actually observed on each landmass. We simulated four scenarios (Table 3; see Appendix S1 in Supporting Information for the simulation code). (a) Equal probabilities of absence for all four landmasses, assuming that species had the same probability of being absent anywhere. (b) The probability of absence on a landmass was related to the distance to the other landmasses (a species extinct on a landmass could re-immigrate from a neighbouring landmass); we used the sum of the minimum distances from each landmass to all others (including the Mentawais) scaled to 1 as the probability of a species missing from the respective landmass. (c) The probability of absence on a landmass was related to the degree of connectivity with the other landmasses. It is assumed that a more open 'savanna-like' vegetation covered the exposed shelf between Sumatra and Borneo during the glacial maxima (Heaney, 1991; Bird *et al.*, 2005), but an evergreen forest corridor between Borneo and Sumatra was also considered (Cannon *et al.*, 2009), which would have aided the dispersal of forest-dwelling species between these islands. To consider this potential rain forest corridor we reduced the minimum distance between Borneo and Sumatra by half and recalculated the probabilities as described under scenario b. (d) Especially on Sumatra, where recent species survey efforts have been lower than on Borneo and Peninsular Malaysia, and possibly also on Java, existing species may have been overlooked and were therefore falsely classified as absent. Although we believe that this may be the case mainly for the herpetofauna, and only to a lesser extent be valid for mammals (see above), we repeated our simulation, multiplying the probability of a species missing from Sumatra with a 'sampling bias factor', $f = 2$ (so that 'missing' encompasses both true absence and failure to have been recorded) and re-scaled the resulting values to 1. For each scenario we present the mean 'expected number of missing species' ± standard deviation (SD).

RESULTS

Out of the 151 species investigated, 25 were endemic to the Mentawais (17%). Seventeen of them were mammals (40% of all mammals; Table 2) and eight were reptile species (9% of all reptiles; Teynié *et al.*, 2010). None of the 16 amphibian species was endemic to the Mentawais (Teynié *et al.*, 2010).

Out of the 41 mammalian species/species-pairs with known phylogenetic relationships, all but three also occurred on Borneo (93%), whereas only 34 (83%), 25 (61%) and 34 (83%) were recorded for Sumatra, Java and Peninsular Malaysia, respectively (Fig. 2b). Five mammalian species/species-pairs from the Mentawais had their closest relative not on Sumatra but exclusively on Borneo (two of these species also occurred in the Philippines), one species on Peninsular Malaysia and Borneo, and one – Kloss's gibbon, *H. klossii* (Chan *et al.*, 2010; Israfil *et al.*, 2011) – exclusively on Java (Table 2).

In comparison to the mammals, Sumatra shared 78 of the 84 reptile species (with known relationships) with the Mentawais (93%), Peninsular Malaysia shared 70 species (83%), Borneo 67 (80%) and Java 53 (63%; Fig. 2c). With regard to the amphibians, Sumatra shared 15 out of the 16 species with the Mentawais (94%), whereas Java, Borneo and Peninsular Malaysia shared only four (25%), seven (44%) and nine (56%) species with the Mentawai Islands, respectively (Fig. 2d).

Simulation results showed that, assuming an equal probability of absence on all four landmasses, the expected number of non-endemic Mentawaian species missing on all landmasses was 8.22 (± 1.9) for mammals, 17 (± 2.6) for reptiles and 6.26 (± 1.6) for amphibians. For all taxonomic groups, the distance and connectivity-based models resulted in low expected numbers of missing species for Sumatra, which had the lowest cumulative distance to all other landmasses, and high expected numbers for Borneo, which had the highest cumulative distance, even after considering a potential rain forest corridor between Borneo and Sumatra (Table 3, Fig. 3a–c). The observed numbers of missing species of amphibians and reptiles were similar to the expected values generated under the distance and connectivity models, except for Java where numbers were higher than expected. The outcome was different for mammals: the observed number of mammal absences was higher than expected on Sumatra and Java and lower than expected on Borneo (Fig. 3a).

DISCUSSION

In the deep past, extinction of species was mostly a natural process, and species or populations living on small islands (such as the Mentawais) become extinct at a much higher rate than those distributed over a larger range (such as the larger Sunda

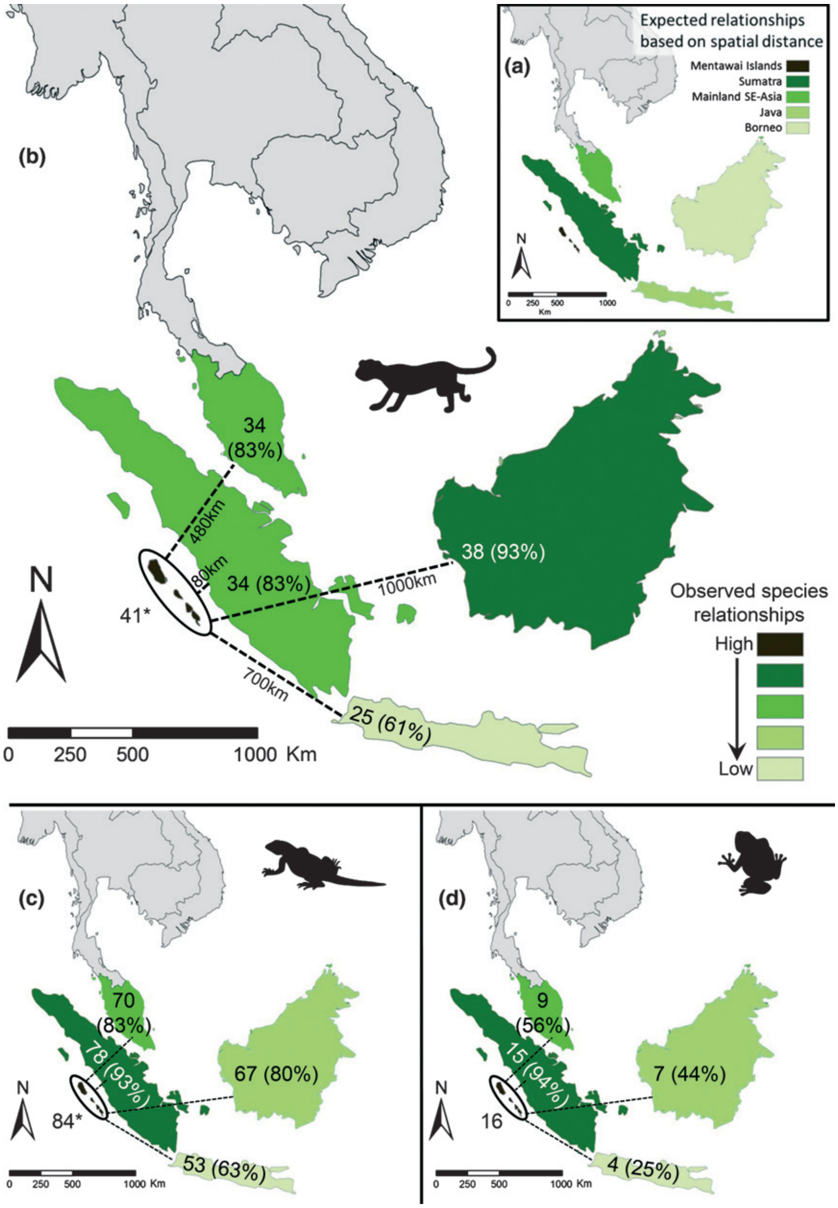

Figure 2 Relationships among the fauna of the Mentawai Islands and their nearby landmasses. Colours indicate closeness of observed relationships from high (dark green) to low (light green). (a) Expected relationships based on a simple spatial proximity similarity model, (b) observed relationships for mammals, (c) observed relationships for reptiles, (d) observed relationships for amphibians. *Only species with a resolved phylogenetic relationship were included.

islands; MacArthur & Wilson, 1967; Heaney, 1986; Burkey, 1995). Based on spatial proximity we expected the Mentawaian fauna to have their closest relatives first and foremost on Sumatra.

Regarding reptiles and amphibians, the Mentawai Islands indeed shared most of their species (or closest related species) with Sumatra. However, for mammals the pattern was quite different (Fig. 2): the relationship of Mentawaian mammals to those on Borneo is much closer (sharing all but three species/species-pairs) than the one to those on Sumatra.

Differences in distribution between the mammal fauna and the herpetofauna might be explained by the respective abilities of these groups to cross saltwater barriers and establish stable populations (i.e. on the Mentawais). Protected by their scaly epidermis, many reptiles are able to tolerate saline waters (Inger & Voris, 2001), and thus can cross channels either by swimming or on rafts of floating vegetation. In addition, females of some species are able to store sperm prior to ovulation and some of others are able to reproduce parthenogenetically, enabling them to establish a new population even if reaching new shores alone. Amphibians, however, are very sensitive to saline waters and have been regarded as relatively poor dispersers across major ocean barriers (Savage, 1973). Nevertheless, amphibians can cross oceans by rafts (Vences *et al.*, 2004), and in the Malay Archipelago

Table 3 Input values for simulation scenarios in which the relative probabilities (*P*) of a non-endemic Mentawaian species missing from Sumatra, Peninsular Malaysia, Java or Borneo were determined based on: (1) the relative cumulative minimum distances [*D* (km)] of a landmass to all others; (2) the degree of connectivity; and (3) the sampling bias, in which probabilities from (2) were multiplied by a sampling bias factor (*f*).

	Species missing			Distance		Connectivity*		Sampling bias†	
Landmass	Mammals	Reptiles	Amphibians	*D*	*P*	*D*	*P*	*f*	*P*
Sumatra	7	6	1	589	0.089	369	0.060	2	0.114
Peninsular Malaysia	7	14	7	1854	0.281	1854	0.301	1	0.285
Java	16	31	12	1873	0.284	1873	0.304	1	0.285
Borneo	3	17	9	2278	0.345	2058	0.334	1	0.314

*The distance between Sumatra and Borneo was reduced (divided by 2), assuming a rain forest corridor between these two islands (Cannon *et al.*, 2009) facilitating species dispersal.

†Reflecting the lower recent sampling effort on Sumatra than on other landmasses.

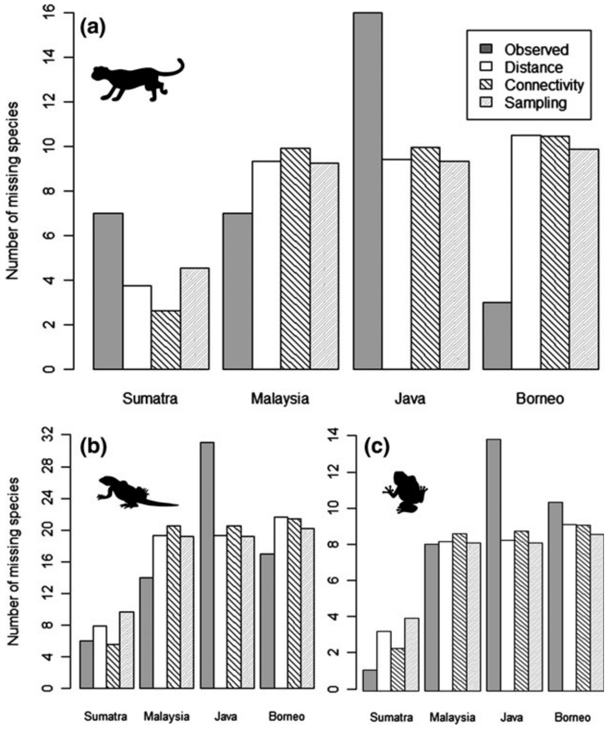

Figure 3 Number of non-endemic Mentawai species (a, mammals; b, reptiles; c, amphibians) missing on Sumatra, Peninsular Malaysia, Java and Borneo; observed versus expected when the probability of absence is relative to the cumulative minimum distance from a landmass to all others (Distance); the same as before, but dividing the distance between Sumatra and Borneo by 2, assuming a rain forest corridor aiding species dispersion (Connectivity); multiplying the probability of absence for Sumatra under the Connectivity model by 2, assuming a lower sampling effort on the island (Sampling).

amphibians have repeatedly crossed deep-water straits such as denoted by the Wallace and Huxley lines (Evans *et al.*, 2003), albeit such crossings probably being very rare. Although the low number of amphibians known from the Mentawais and the general lack of taxonomic research on those species hamper general conclusions about this group, the narrowing of the Siberut Strait to only about 10 km during the LGM may have allowed Sundaland amphibians and especially reptiles to raft from the Batu Islands to the Mentawais and/or vice versa. In contrast to the herpetofauna, mammals (with the exception of bats) have greater difficulties in crossing saltwater barriers and thus in establishing new populations, owing to their low tolerance to hypothermia (by cold ocean waters), to high salinity, and to dehydration. Thus, compared with reptiles, the relationship between the non-volant mammals of the Mentawai Islands and those of the neighbouring landmasses should reflect a more ancient pattern of isolation, with very few dispersal events.

In our simulation study for the less well-studied herpetofauna, the observed pattern of species absences generally resembled the expected pattern under scenario b of 'extinction increasing with landmass isolation' (Fig. 3a–c). Only on Java were more species absent than expected, perhaps owing to the major climatic and vegetational differences prevailing between Java and the Mentawais for most of the Pleistocene (open dryland versus evergreen rain forest; Bird *et al.*, 2005; Cannon *et al.*, 2009). These findings, especially those from Java, call into question the assumption used in the simulation, namely that all species originally occurred on all islands, because it does not take into consideration that absence includes both species that went extinct and species that never occurred there (e.g. because of environmental constraints).

Similar to the herpetofauna, simulations for mammals revealed that more Mentawaian species than expected were absent on Java. Surprisingly, the same was observed for Sumatra. Connectivity (opportunity for migration) could not have caused the observed pattern, as the centrally located Sumatra has the highest connectivity of the landmasses investigated (Table 3). In line with its highest connectivity was the low level of endemism for mammals on Sumatra (*c.* 7%, excluding Mentawai endemics) compared with Borneo (*c.* 24%) and Java (*c.* 12%, including Bali; Heaney, 1986; Natus, 2005). The consideration of a sampling bias on Sumatra – recognizing a lower survey effort – also did not sufficiently explain the observed pattern of mammal species absences, thus indicating higher extinction rates for Sumatra. In contrast to Java and Sumatra, far fewer mammals than expected were absent on Borneo – a surprising result given Borneo's location.

For some Mentawaian endemic species the phylogenetic relationships with other Sunda Shelf species are currently unresolved, rendering it impossible to determine their closest relatives on the nearby larger landmasses. Although these endemics may have been isolated sufficiently long to have evolved on the Mentawai Islands themselves, another scenario is also conceivable, as was proposed for the Mentawai langur (*Presbytis potenziani*). The latter may have originally evolved on Sumatra, spread to the Mentawais – when the islands were indirectly connected to Sumatra in the Plio-Pleistocene – and later became extinct on Sumatra (Meijaard & Groves, 2004). Further molecular studies might overcome the problem of the incomplete fossil record from Sumatra and reveal whether Mentawaian endemics evolved on the small Mentawais (as neoendemics) or on larger landmasses such as Sumatra (as palaeoendemics).

Additional support for higher extinction rates on Sumatra stems from the fact that Sumatra is also not part of the distribution range of many other ('non-Mentawaian') mammals that otherwise occur widely in mainland Asia and other parts of Sundaland, for example the banteng *Bos javanicus* (mainland Asia, Java and Borneo), the leopard *Panthera pardus* (mainland Asia and Java), and ferret badgers, *Melogale* spp. (mainland Asia, Java and Borneo).

Based on available information, our present hypothesis is that some areas on the Sunda Shelf, such as Sumatra, experienced more local extinctions within the last few 100 years than other regions, such as Borneo. Here we propose two, not mutually exclusive, scenarios to explain the potentially increased extinction rates.

Scenario 1. Changes of climate and vegetation

The hitherto most common scenario to explain faunal changes in the Sunda Shelf assumes a key role for cooler and drier climates during Pleistocene glacial periods (e.g. Heaney, 1991; Brandon-Jones, 1996; Bird *et al.*, 2005; Wurster *et al.*, 2010). However, while some authors suggest the persistence of monsoon and evergreen forests during glacial periods – similar to those found there today (e.g. Taylor *et al.*, 1999) – others argue for a corridor of savanna-like vegetation across the centre of the Sunda Shelf during these times (Heaney, 1991; Bird *et al.*, 2005; Piper *et al.*, 2011). The consequences of these two types of vegetation on fauna would have been quite different: glacial open mixed habitats would have restricted the spread of forest-restricted species, confining them to refugia, whereas the persistence of evergreen forests would have allowed their occurrence across Sundaland. It was argued that Late Pleistocene glacial periods were associated with drier and more mixed habitats in Sundaland, whereas interglacials allowed more humid and closed habitats (Louys & Meijaard, 2010). Because forest-restricted mammals in Sundaland currently live only on islands believed to have always been covered by forests, but are absent from islands that were part of the proposed drier corridors (Meijaard, 2003), we find it unlikely that during the glacial maxima evergreen forests similar to those found today persisted throughout Sundaland. Whether seasonal deciduous forests (Cannon *et al.*, 2009) or open savanna-like vegetation (Heaney, 1991; Bird *et al.*, 2005) dominated across the central parts of the shelf, either type of vegetation would have strongly limited the dispersal of rain forest-restricted mammals such as the Mentawaians.

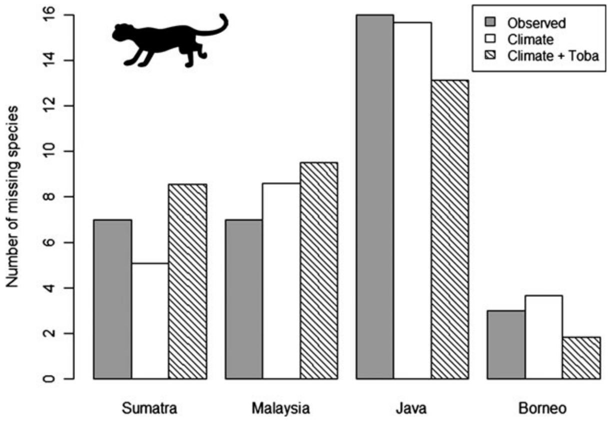

Figure 4 Number of non-endemic Mentawai mammal species missing on Sumatra, Peninsular Malaysia, Java and Borneo; observed versus expected when multiplying probabilities of absence from the Connectivity model with a factor (*c*) representing differences in forest cover due to climate (Climate); and when multiplying the probabilities of the climate model with a factor representing the effect of the Toba volcano [Climate (*c*) + Toba (*t*)]. Climate: Java $c = 4$, Sumatra $c = 2$, Borneo $c = 0.25$; Climate + Toba: Sumatra $t = 4$, Peninsular Malaysia $t = 2$.

To investigate whether climate and vegetation changes during the LGM could have caused the absence of species, we included the 'predicted land cover' (scenario c; of Cannon *et al.*, 2009) in our absence simulation. We simulated a decreased probability of a species being absent on Borneo and an increased probability of it being absent on Java and Sumatra (Fig. 4). We observed a distribution of expected absences that resembled the observed values more closely than in the other models (Fig. 3a), and found indications that the receding glacial forest cover on Sumatra could not have been the sole cause for extinctions on this island. Environmental changes during the Pleistocene may thus partly explain the observed distribution patterns among mammals.

Scenario 2. Toba supervolcanic eruption

Environmental conditions were influenced not just by global climatic changes but also by the Toba volcano, located in the northern part of Sumatra (Fig. 1), which erupted *c.* 73.5 ka. This megablast was the second largest explosive eruption known in Phanerozoic history (Ambrose, 1998). Its consequences for flora and fauna in the Sunda Shelf are, however, controversial (Louys, 2007; Williams *et al.*, 2009; Haslam & Petraglia, 2010; Williams, 2011). So far, only the extinction of one large mammal species, the banteng in Sumatra, has been linked to the eruption (Louys, 2007), but post-catastrophe re-colonization events on Sumatra may have obscured previous local extinctions. Such a post Toba-eruption re-colonization was suggested for the Sumatran orangutan, *Pongo abelii* (e.g. Nater *et al.*, 2011); the tiger, *Panthera tigris* (Luo *et al.*, 2004); the common palm civet, *Paradoxurus hermaphroditus* (Patou *et al.*, 2010); and the Sunda clouded leopard, *Neofelis diardi* (Wilting *et al.*, 2011). The slightly wetter and warmer climate after the eruption (van der Kaars & Dam, 1995; Gingele *et al.*, 2002) probably facilitated the growth and expansion of forests, allowing the spatial expansion back into Sumatra of species that had survived the eruption in areas outside Sumatra. Phylogeographical studies of additional Sundaic species could test if Sumatran populations demonstrate a much more recent origin than neighbouring source populations.

Another possible legacy of the Toba blast is the zoogeographical boundary running across Sumatra from south-west to north-east through Lake Toba (Whitten *et al.*, 2000). Various Sumatran mammals are confined in their distribution to either the north (e.g. Thomas's langur, *Presbytis thomasi*; white-handed gibbon, *Hylobates lar*) or the south (e.g. Horsfield's tarsier, *Tarsius bancanus*; Whitten *et al.*, 2000; Nater *et al.*, 2011). This transition lends tentative support to the re-colonization of Sumatra after the Toba impact.

We incorporated the Toba eruption into the climate simulation of species absence, as the two factors are complementary. Based on the occurrence/distribution of the Youngest Toba Tuffs, the Toba blast had its highest impact on Sumatra and was less severe on Peninsular Malaysia. As no ash layers were found on Java and Borneo, these islands were treated in our approach as 'not affected by the Toba eruption'. The simulation indicated that the synergy of climate changes + Toba eruption consequences may generate a pattern of species absences on each of the islands similar to that observed (except for Java, but see above; Fig. 4).

Quantifying the consequences of changing climate and the Toba eruption in this way is unavoidably subjective: these simulations merely illustrate that if these two factors resulted in higher rates of species extinction on some of the landmasses, patterns of species absences similar to the ones observed could have arisen. These scenarios did not include the varying soil compositions across the shelf, which may also have influenced biogeographical differences in Sundaland (e.g. Slik *et al.*, 2011). Faunal dynamics (i.e. species immigration) may also have impacted the absence of lineages on Sumatra, either directly (resource competition, interference and prey–predator relationships) or indirectly (e.g. introduction of new pathogens). 'Mainland Asian' mammal lineages occurring on Sumatra but not elsewhere in Sundaland are indicators for Sumatra's function as a Plio-Pleistocenic faunal crossroad. Such lineages include genera (e.g. *Arctonyx* as a montane badger versus *Melogale*, Helgen *et al.*, 2008) and species (e.g. presence of the gibbon *Hylobates lar*).

CONCLUSIONS

In contrast to what would be expected by spatial proximity, many contemporary Mentawaian mammal species do not have their closest relatives on Sumatra. Moreover, the Mentawais feature several other widely distributed Sunda Shelf species that have disjunct distributions in that they do not occur on Sumatra. We therefore propose that less stable environmental and geological conditions on Sumatra resulted in a higher extinction risk there. Nevertheless, the absence of a comprehensive fossil record renders our hypothesis about large-scale extinctions on Sumatra speculative. Competing scenarios for population extinctions in Sumatra will be hard to disentangle, in particular as their causes may be complementary.

Our study of the faunal relationships of the Mentawais with nearby landmasses discloses a clear connection between mammals of Borneo and the Mentawais. The relict Mentawaian fauna therefore provides valuable insights into the biogeography and evolution of species in the Sunda Shelf, perhaps in particular offering a window into the faunal composition of Sumatra's recent past, now overwritten by that island's environmental, tectonic and faunal dynamics. Our discussion on the causes of potential Pleistocene extinctions on Sumatra expands current discussion on species extinction risks. Understanding the Pleistocene history of species in Sundaland may help us to predict and evaluate the consequences of rapid environmental changes (mainly climate and habitat) in this biodiversity hotspot.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Code to simulate species absence on Sumatra, Malaysia, Java and Borneo in R under different scenarios.

BIOSKETCH

Andreas Wilting integrates in his work results obtained from field research (mainly camera-trapping on Borneo), predicted distribution modelling and phylogenetic approaches to gain further information on the past, current and potential future distributions of carnivores on the Sunda Shelf. He and the co-authors have a great interest in the biogeography and phylogeography of mammals on the Sunda Shelf and in the evolutionary history that led to the observed distribution patterns.

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