The Indochinese–Sundaic zoogeographic transition: a description and analysis of terrestrial mammal species distributions

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ABSTRACT

Aim We describe the distributions of mammal species between the Indochinese and Sundaic subregions and examine the traditional view that the two faunas show a transition near the Isthmus of Kra on the Thai–Malay peninsula.

Location Species distributions are described along a 2000-km transect from 20° N (northernmost Thailand) to 1° N (Singapore).

Methods For the 325 species of native non-marine mammals occurring along the transect we used published records to provide a database of their distributional records by degree of latitude.

Results Along the transect we found 128 Indochinese species with southern range limits, 121 Sundaic species with northern range limits, four un-assignable endemics and 72 widespread species. In total, 152 southern and 147 northern range limits were identified, and their distribution provides no evidence for a narrow faunal transition near the Isthmus of Kra (10°30′ N) or elsewhere. Range limits of both bats and non-volant mammals cluster in northernmost peninsular Malaysia (5° N) and 800 km further north, where the peninsula joins the continent proper (14° N). The clusters of northern and southern range limits are not concordant but overlap by 100–200 km. Similarly, the range limits of bats and non-volant mammals cluster at slightly different latitudes. There are 30% fewer species and range limits in the central and northern peninsula (between 6 and 13° N), and 35 more widely distributed species have range gaps in this region. In addition, we found 70 fewer species at the southern tip of the peninsula (1° N) than at 3–4° N.

Main conclusions The deficiencies of both species and species range limits in the central and northern peninsula are attributed to an area effect caused by repeated sea-level changes. Using a new global glacioeustatic curve developed by Miller and associates we show that there were > 58 rapid sea-level rises of > 40 m in the last 5 Myr that would have resulted in significant faunal compression and local population extirpation in the narrow central and northern parts of the peninsula. This new global sea-level curve appears to account for the observed patterns of the latitudinal diversity of mammal species, the concentration of species range limits north and south of this area, the nature and position of the transition between biogeographical subregions, and possibly the divergence of the faunas themselves during the Neogene. The decline of species diversity at the southern end of the transect is attributed to a peninsula effect similar to that described elsewhere.

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INTRODUCTION

Ever since Alfred Russel Wallace (1869), biogeographers have recognized a major transition on the Thai–Malay peninsula near the Isthmus of Kra (10°30′ N), where the faunas of the Indochinese and Sundaic zoogeographic subregions meet. In forest-associated birds there is a 50% turnover at the species level (Hughes *et al.*, 2003; Round *et al.*, 2003). Botanists recognize a similar but even more significant transition *c.* 500 km further south, where the plants of the Southeast Asiatic and Malayan floristic provinces meet (van Steenis, 1950; Good, 1964; Keng, 1970; Whitmore, 1984, 1998; Ashton, 1992; Richards, 1996; Baker *et al.*, 1998; Morley, 2000; Wikramanayake *et al.*, 2002). The turnover in plant genera on the peninsula is greater than that at the eastern edge of the Sundaic subregion (Woodruff, 2003a), where Wallace's Line marks the boundary between the Oriental and Australian zoogeographic regions. Although the eastern *regional* biogeographical transition has been the subject of numerous studies (Whitmore, 1981, 1987; Hall & Holloway, 1998; Metcalfe *et al.*, 2001; Heaney, 2004), the north-western transition between the Sundaic and the continental Indochinese *subregions* has been largely ignored. This north-western transition is not well characterized, and the underlying cause(s) of the divergence of the Indochinese and Sundaic biotas remains unknown. Building on our preliminary analysis of the bird species distribution patterns (Hughes *et al.*, 2003; Round *et al.*, 2003; Woodruff, 2003a,b), we here consider the distribution patterns of extant mammals. According to tradition, the mammalian transition also occurs near the Isthmus of Kra (Chasen, 1940; Musser & Newcomb, 1983; Cranbrook, 1988; Lekagul & McNeely, 1988; Corbet & Hill, 1992; Chaimanee, 1998; Francis, 2001; Tougard, 2001; Luo *et al.*, 2004; Sodhi & Brook, 2006), but this has never been formally documented.

With over 500 species, the mammal fauna of Southeast Asia is sufficiently rich to support geographic analyses. Estimates of national terrestrial mammal species diversity are: Thailand, 251 species; peninsular Malaysia, 210; Vietnam, 273 and Myanmar (Burma), 300 (WCMC, 1992; Sterling *et al.*, 2006; SAMD, 2007). The general features, ranges and natural history of these animals have been characterized by a century of enquiry and a number of books document the fauna (Chasen, 1940; Medway, 1983; Lekagul & McNeely, 1988; Corbet & Hill, 1992; Francis, 2001, 2008; Parr, 2003). The taxonomic constitution of this diverse fauna is summarized in Table 1.

The Neogene history of Southeast Asia in now known in sufficient detail to allow for reliable inference of the role of geographic events in faunal distributions. Early geographic reconstructions of the emergent Sunda shelf (Sundaland) by Wallace (1876) and Molengraaff (1922), in combination with more recent discussions (Whitmore, 1987, 1998; Hall & Holloway, 1998; Woodruff, 2003b; Hope *et al.*, 2004; Bird *et al.*, 2005; Hope, 2005; Harrison *et al.*, 2006; Meijaard & Groves, 2006; Harrison & Chivers, 2007), have provided a general palaeoenvironmental overview. Although many details remain controversial, the main features of geography and sea-level change relevant to the following discussion are widely accepted.

MATERIALS AND METHODS

We created a database of distributional records for each of the 325 species of native non-marine mammals living along a 2000-km geographic transect from 20 to 1° N latitude, from the northernmost point of Thailand to Singapore (see Appendix S1 in Supporting Information). Domesticated and fossil species were excluded although the ultimate need for the consideration of the latter is discussed below. We arranged the higher taxa in Tables 1 and 2 and Appendix S1 following Wilson & Reeder (2005), except that species within a genus are arranged alphabetically.

The transect varied in width from *c.* 50 km at the Isthmus of Kra to 300 km. Its continental section includes the hill country of the Thai–Myanmar borderlands, the central valley of Thailand, and the western edge of the Khorat plateau including Khao Yai National Park (Fig. 1). For discussion purposes we divide the transect into four parts: the *mainland* or *continental*
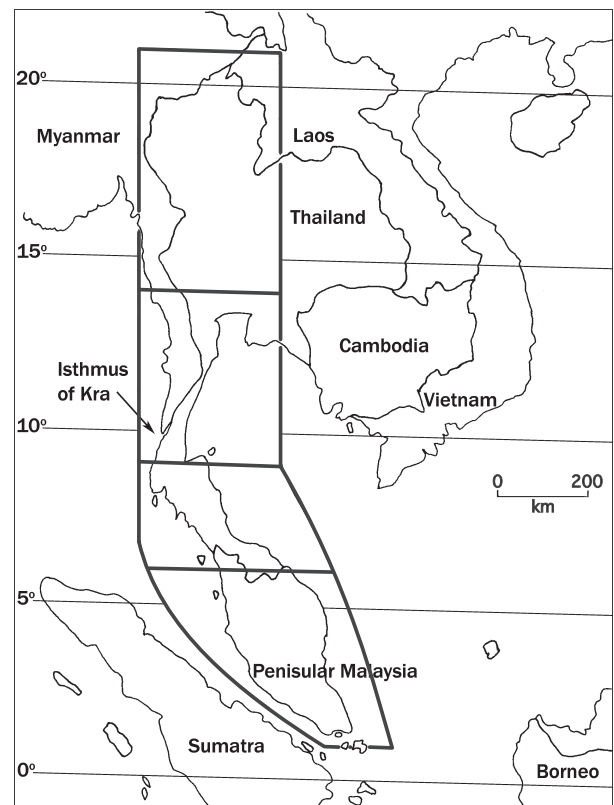

Figure 1 Geographic position of the transect between Indochinese and Sundaic zoogeographic subregions. The transect extends from 21° N to the equator and the Isthmus of Kra (at 10°30′ N) and marks the traditional boundary between subregions. Dark lines separate the four sections of the transect: continental section (13°30′–21° N), northern peninsula (9–13°30′ N), central peninsula (6–9° N) and southern peninsula (0–6° N, including Singapore).

Table 1 Systematic representation of 325 mammal species present in historical times along the transect.

Order/Suborder	No. of species	Species in Thailand	Species in peninsular Malaysia
Proboscidea			
Elephants	1	1	1
Scandentia			
Treeshrews	4	3	3
Dermoptera			
Colugos	1	1	1
Primates			
Loris (2 species), macaques (6), leaf monkeys (7), gibbons (5)	20	16	10
Rodentia			
Sciuromorpha, squirrels (17), flying squirrels (15)	32	27	25
Myomorpha, rats and mice	45	39	26
Hystricomorpha, porcupines	3	2	3
Subtotal rodents	*80*	*68*	*54*
Lagomorpha			
Hares	1	1	0
Erinaceomorpha			
Gymnures	2	2	2
Soricomorpha			
Shrews: moles	15	13	11
Chiroptera			
Pteropodidae, fruit and nectar bats	21	18	16
Rhinolophidae, horseshoe bats	21	18	16
Hipposideridae, leaf-nosed bats	22	15	20
Megadermatidae, false vampire (2), Rhinopomatidae, mouse-tailed (1), Craseonycteridae, hog-nosed (1), Emballonuridae, sheath-tailed (5), Nycteridae, slit-faced (1), Molossidae, free-tailed bats (4)	14	11	11
Vespertillionidae	64	49	40
Subtotal bats	*142*	*111*	*103*
Pholidota			
Pangolins	2	2	1
Carnivora			
Cats (9), weasels (4), badgers (2), otters (4), civets (12), dogs (2), bears (2), mongoose (3)	38	35	28
Perissodactyla			
Tapir, rhinoceros	3	3	3
Artiodactyla			
Pigs (2), cattle (6), mousedeer (2), deer and muntjak (6)	16	15	9
Total	325	271	226

section (14–20° N), the *northern peninsula* (9–13° N, southern boundary running between Phuket and Surat Thani), the *central peninsula* (6–9° N, southern boundary at the Thai–Malaysian border), and the *southern peninsula* (1–6° N, including Singapore).

We used the published print and electronic literature to infer extant mammal distribution patterns 100–500 years ago, before humans altered them significantly. For almost all species we began with the specimen-based schematic maps prepared by Corbet & Hill (1992) and revised these with data in the Southeast Asian Mammal Database (SAMD, 2007), which provides more current distributional data. We have adopted all the taxonomic changes made in the SAMD but used larger geographic ranges when we judged the historical evidence from Corbet and Hill to be reliable, as, for example, in the cases of the Javan rhinoceros (*Rhinoceros sondaicus*) and Schomburgk's deer (*Cervus schomburgki*). We extended a few ranges based on reports not yet incorporated in SAMD (Hirai *et al.*, 2002; Meijaard, 2003; Geissmann *et al.*, 2004). Range limits were recorded to the nearest degree of latitude. Our methods and distributions are thus very similar to those used by Francis (2008) in his excellent field guide.

We looked for evidence of an Indochinese–Sundaic mammal faunal transition and, in particular, we focused on

Table 2 Taxonomic diversity along the transect. The number of southern and northern species range limits and the percentage of species exhibiting range limits (from Appendix S1) are shown.

Order	No. of species	No. of species with range limits	Percentage of species with range limits	Southern range limits	Northern range limits
Proboscidea	1	0	0	0	0
Scandentia	4	4	100	1	3
Dermoptera	1	1	100	0	1
Primates	20	20	100	13	14
Rodentia					
Sciuridae	32	29	91	13	19
Muridae	45	37	82	27	18
Hystricidae	3	1	33	0	1
Lagomorpha	1	1	100	1	0
Erinaceomorpha	2	1	50	0	1
Soricomorpha	15	14	93	13	5
Chiroptera					
Macrochiroptera	21	18	86	5	17
Microchiroptera	121	90	74	57	53
Pholidota	2	2	100	1	1
Carnivora	38	20	53	12	8
Perissodactyla	3	1	33	0	1
Artiodactyla	16	13	81	9	5
Total	325	252	78	152	147

establishing the latitudinal position of historical species range limits *along the transect*. In some analyses and discussion we have excluded range limits at 1° N and at 20° N, the terminal cells in the series – the former because it constitutes a hard habitat edge today, and the latter because it lies close to the largely unsurveyed area where Myanmar, Laos and China meet, and current records there could be revised by up to 200 km in the future. Many species found on the transect have different distributional limits further east in Laos, Cambodia and Vietnam, or further south in Sumatra, Java and Borneo, but these data were excluded from analyses except where they clearly indicate that a species' true latitudinal range limit lay beyond the range of the transect.

Terms and ages for geological periods follow the cited authorities. The abbreviations Myr/kyr and Ma/ka are used to mean million/thousand years and million/thousand years ago, respectively.

RESULTS

Table 1 describes the systematic representation of mammals present along the transect. Of the 325 species, 80% belong to three taxa: bats (142 species, 44% of the total), rodents (80 species, 25%), and carnivores (38 species, 12%). All of the 13 mammalian orders present, except for Proboscidea, have at least one range limit along the transect. Four taxa exhibited the bulk of the limits: Microchiroptera, 90; Muridae, 37; Sciuridae, 29; Carnivora, 20 (Table 2). The Thai fauna (> 6° N) is 20%

more species-rich than that of peninsular Malaysia (≤ 6° N) but we attribute this, in part, to there being 1300 km of transect in Thailand and only 600 km in peninsular Malaysia.

Latitudinal changes in species diversity are summarized in Table 3 and Fig. 2. Although one might expect a steady increase in species numbers towards the equator (Lomolino *et al.*, 2006), the data show a more complex pattern. Figure 2 shows a trimodal pattern, with diversity peaks at 3–5° N (hills of peninsular Malaysia), at 12–15° N (northernmost peninsula and forest block north of Kanchanaburi), and at 19° N (mountains of north Thailand). There is a distinct trough from 6 to 14° N, with the lowest overall diversity at 10–12° N (northern peninsula between Ranong and Prachup Khiri Khan). This pattern is the same in bats and non-volant mammals, but non-volant mammals contribute more to this local decline than bats. The reverse is the case for the second decline observed at 16° N. The greatest species diversity occurs between 3 and 6° N, with the peak for non-volant mammals occurring at 3–6° N and that for bats at 4–6° N. Figure 2 also shows a 34% decline in total species numbers from north to south in the southern peninsula, from 188–198 species per degree at 3–5° N to 128 species at 1° N.

Summarizing the distribution patterns of the 325 species presented in Appendix S1, three major patterns are represented: 128 species (39%) are Indochinese and have southern range limits somewhere along the transect; 121 species (37%) are Sundaic and have northern range limits along the transect; and 72 species (22%) are widespread, occurring in both subregions. An additional four species have their entire ranges within the transect: two are not clearly assignable to either the Indochinese or the Sundaic subregion (*Hipposideros lekaguli*, *Hesperoptenus blanfordi*) and two are restricted-range endemics in the central peninsula (*Eptesicus demissus*, *Hypsigo lophurus*). This summary conceals two important phenomena. First, the data in Appendix S1 show internal gaps in the ranges of 65 species. Some gaps are inconsequential but others may be biologically significant. Thirty-five species (11%) have distributional gaps of 200–300 km in the northern or central peninsula (e.g. *Petinomys setosus*, *Atherurus macrourus*, *Megaderma lyra*, *Pardofelis marmorata*). Such geographically consistent internal gaps are ignored in the following tabulations of range limits but are important to our subsequent discussion. Second, more than 70 species are not present at the southern end of the peninsula, where they would be expected to occur (e.g. *Chiropodomys gliroides*, *Trichys fasciculata*, *Hypsugo macrotis*, *Lutrogale perspicillata*, *Neofelis nebulosa*). Of these, 47 species occur in the southern peninsula at 3–4° N and are known to occur further south elsewhere but are not present at 1° N (20 species) or at both 1 and 2° N (27 species). An additional 25 species not known to occur further south elsewhere occur in the southern peninsula at 3–4° N but have not been recorded at 1 or 2° N (19 species) or at just 1° N (six species). Many of these 72 species probably ranged south to 1° N in the past (see Discussion).

A consideration of the position of the species range limits and geographic replacement of 128 Indochinese species by 121

Table 3 Latitudinal changes in species diversity and distribution of northern and southern species range limits along the transect.

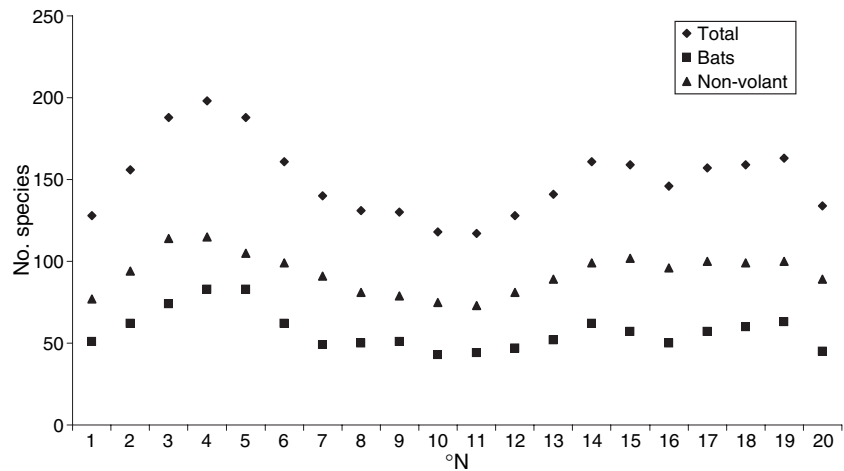| Latitude	Mammal species (n)			Southern range limits			Northern range limits			Overall range limits		
	Total	Bats	Other	Bats	Other	All	Bats	Other	All	Bats	Other	All
20	134	45	89	1	0	1	0	0	0	1	0	1
19	163	63	100	3	3	6	6	7	13	9	10	19
18	159	60	99	2	4	6	2	1	3	4	5	9
17	157	57	100	7	4	11	4	3	7	11	7	18
16	146	50	96	0	3	3	1	3	4	1	6	7
15	159	57	102	5	4	9	5	6	11	10	10	20
14	161	62	99	5	11	16	6	1	7	11	12	23
13	141	52	89	4	8	12	1	3	4	5	11	16
12	128	47	81	3	6	9	1	3	4	4	9	13
11	117	44	73	1	5	6	1	0	1	2	5	7
10	118	43	75	2	5	7	1	5	6	3	10	13
9	130	51	79	2	3	5	7	5	12	9	8	17
8	131	50	81	2	1	3	3	5	8	5	6	11
7	140	49	91	0	2	2	4	13	17	4	15	19
6	161	62	99	0	4	4	6	8	14	6	12	18
5	188	83	105	6	0	6	12	10	22	18	10	28
4	198	83	115	5	1	6	5	4	9	10	5	15
3	188	74	114	7	12	19	4	0	4	11	12	23
2	156	62	94	4	5	9	0	0	0	4	5	9
1	128	51	77	3	9	12	1	0	1	4	9	13
Total (n)	325	142	183	62	90	152	70	77	147	132	167	299

Figure 2 Latitudinal changes in mammal species diversity along the transect, based on data in Appendix S1.

Sundaic species shows that: (1) there is no marked species turnover at or near the Isthmus of Kra (10°30′ N); (2) the distribution of Indochinese range limits does not mirror that of Sundaic limits – each group has a different pattern; and (3) 76/121 (63%) of the Sundaic species do not extend north of 8° N, and 73/128 (57%) of the Indochinese species do not extend south of 11° N, leaving an anomalous low turnover pattern in the northern and central peninsula. To analyse this phenomenon in more detail we now present the range-limit data in a series of histograms.

Fig 3 shows the latitudinal distribution of the 299 range limits by latitude seen in these 325 species. There are 152 southern and 147 northern limits; these include the limits for

the 253 clearly Indochinese or Sundaic species, and both the northern and southern limits of species with more restricted ranges along the transect (data in Appendix S1 and Tables 2 and 3). The data are shown in Fig. 3 as the percentage of the range limits in each zone but will first be discussed in terms of absolute numbers (Table 3). If the range limits were distributed uniformly along the transect we would expect 15.0 limits per degree of latitude, 7.6 southern limits of Indochinese species and 7.4 northern limits of Sundaic species. In fact, we observe substantial variation in the number of limits per degree: 1–19 for southern limits and 0–22 limits for northern limits. The distribution of limits is not uniform but rather bimodal or multimodal (limits at 1 and 20° excluded, χ^2,
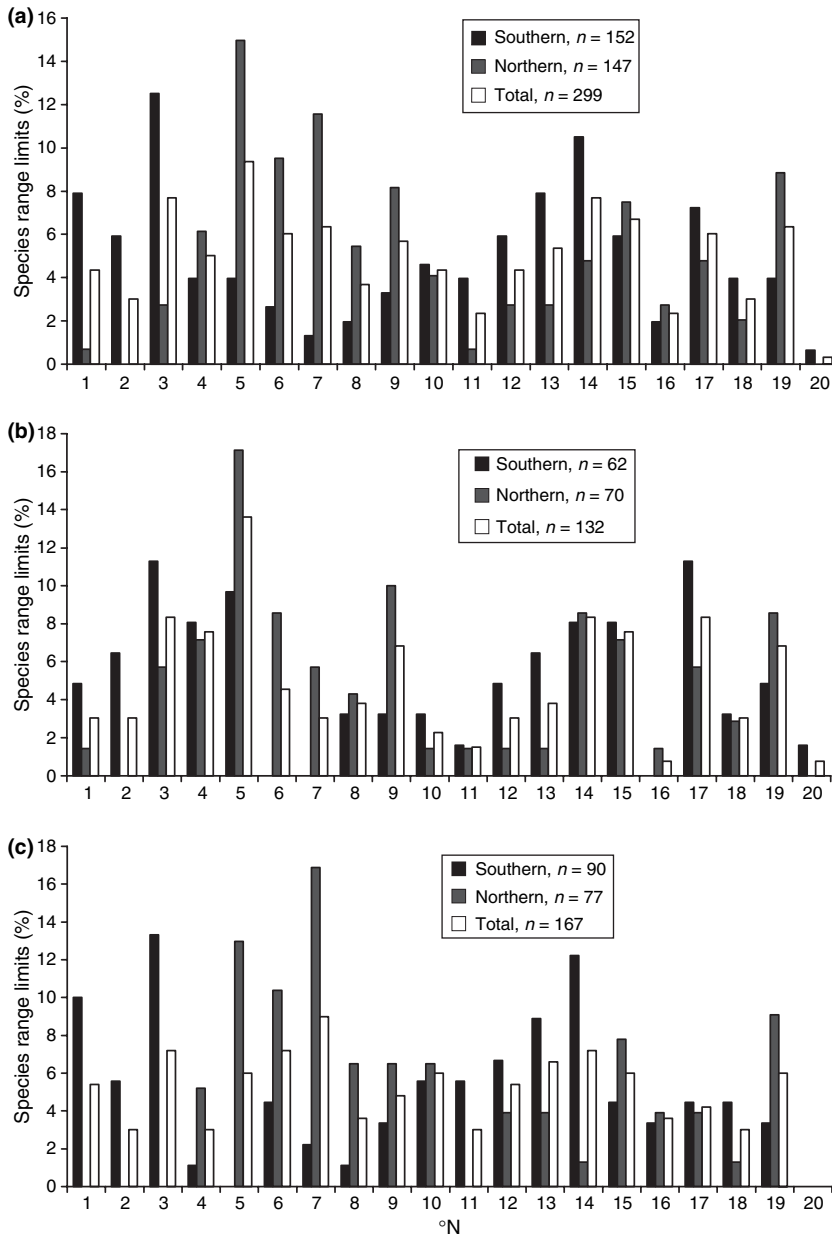
Figure 3 Latitudinal distribution of the number of mammal species range limits along the transect for (a) all mammals, (b) bats and (c) non-volant mammals. The data from Appendix S1 are shown as the percentage of total range limits in each latitudinal degree (100 km) zone.

d.f. = 17, P = 0.003, remains significant with Bonferroni correction). The maximum number of range limits occurs in two areas: in northernmost peninsular Malaysia between 5 and 6° N (28 limits vs. 15 expected, P = 0.001, z-test) and just north of where the peninsula joins the continent proper, from 14 to 16° N (43 limits vs. 30 expected, P = 0.022). At the lowest point in the trough between these two clusters, in the northern part of the peninsula (11–12° N), there are only seven range limits (15 expected, P = 0.013). Only five species (3%) have northern range limits between 11 and 14° N (27 expected, P < 0.001), and there are fewer southern limits than expected from 4 to 12° N (P = 0.002) and at 16° N (P = 0.045).

The pattern we observe in absolute numbers of limits per degree of transect is accentuated if one considers the percentage of the range limits in each zone (Table 3, Fig. 3a).

Combined northern and southern range limits vary between 2% and 9% per degree and peak at 5–6° N (9%) and 14–16° N (7–8%). Northern range limits vary between 1% and 15% per degree and peak at 5° N (15%) and 15° N (8%). Southern limits vary between 1% and 13% per degree and peak at 3° N (13%) and 13–15° N (8–11%). Again, we see greater variability in the northern range-limit distribution and a non-concordance (and overlap) of the peaks in southern and northern limits. In the northern cluster of range limits, the peaks of the northern range limits are concentrated 100 km north of the peaks of the southern range limits. In the southern cluster of range limits, the peaks of the northern range limits are c. 200 km north of the peaks of the southern range limits.

These all-species histograms obscure the fact that a small fraction of the limits are less informative with respect to the discussion of the faunal transition, as they involve local

endemics. Appendix S1 shows that there are five species restricted to a single latitudinal degree (*Niviventer hinpoon*, *Eptesicus demissus*, *Hypsugo lophurus*, *Myotis oreias*, *Murina rozendaali*) and eight others restricted to two degrees – five in the southern peninsula, two in the central peninsula, and six north of the peninsula between 13 and 16° N. However, these few local endemics do not substantially affect the distributional patterns of range limits.

The overall distribution patterns discussed above are made up of two very different groups of mammals: 142 bats (with 132 range limits) and 183 non-volant species (with 167 range limits; Table 3). We therefore re-analysed the data separately for bats (Fig. 3b) and other mammals (Fig. 3c). We found that, similar to the pattern seen for all species, total range limits for bats exhibit a multimodal pattern ($P < 0.001$), with a peak at 5–6° N ($P < 0.001$) and secondary clusters of limits further north at 14–16° N ($P = 0.034$) and 17–18° N ($P = 0.069$). The overall distribution of range limits in non-volant mammals is not significantly different from uniform ($P = 0.395$), but distributions of southern ($P = 0.002$) and northern ($P < 0.001$) limits are both uneven. The locations of the peaks of both northern and southern range limits differ somewhat between bats and other mammals. Southern range limits in bats are fairly uniformly distributed along the transect: the distribution is only marginally significantly different from even ($P = 0.0491$), and not significantly different following Bonferroni correction. Northern limits show peaks at 5–6° N ($P < 0.001$) and at 14–15° N ($P = 0.133$). In contrast, for non-volant mammals the southern peaks cluster at 3° N ($P < 0.001$) and 13–15° N ($P < 0.001$), and the northern limits cluster at 5–8° N ($P < 0.001$). Neither bats nor non-volant mammals have a transition (a cluster of species range limits) associated with the Isthmus of Kra.

DISCUSSION

The mammal distributional data and patterns

Our analysis of mammalian species distributions reveals four intriguing patterns: (1) there is a peak in species range limits between the central and southern parts of the Thai–Malay peninsula (5–6° N); (2) a second peak in range limits occurs where the peninsula meets the mainland (13–16° N); (3) few species and range limits occur in the central and northern peninsula (8–12° N); and (4) fewer species than expected occur near the southern end of the peninsula (1–2° N). (Cattulo *et al.* (2008) independently reported the last two patterns while this paper was in press.) We will now offer explanations for these features. The issues involving the non-concordance of the northern and southern range limits of all mammals, and of limits of bats and non-volant mammals will be interesting topics for future analyses.

Overall, the mammal faunas of Indochina and Sundaland appear more similar to one another than are the avifaunas of these two subregions (Hughes *et al.*, 2003). At higher taxonomic levels there is no marked distinction between the

mammal faunas of Thailand and of peninsular Malaysia (Table 1). In fact, some species used to characterize one or other subregion occur in both; for example, the Sumatran rhinoceros, tapir and orangutan are not strictly Sundaic, as all occurred in Indochina in historical times. Nevertheless, there is a substantial turnover at the species level in many genera (see Appendix S1 and below). In this discussion we first note the limitations of our database, and then interpret our results, focusing on the historical causes of faunal differentiation.

Our database has several limitations. First, it is based on a mix of records in European and North American museums but is by no means exhaustive: a comprehensive review of all available specimens will undoubtedly change a few range limits. Moreover, as many of the records are more than 50 years old it should not surprise us if some museum specimens were misidentified. Systematic revisions and on-the-ground surveys are underway and cryptic species are to be expected, especially in some groups (Baker & Bradley, 2006; Guillen-Servent & Francis, 2006; Kingston *et al.*, 2006). We ignored subspecific taxonomy but note that there are large numbers of nominal subspecies in some species; for example, *Callosciurus erythraeus* (44 nominal taxa), *C. notatus* (36) and *Rattus rattus* (> 51 in Southeast Asia alone). The vast majority of these subspecies were named *c.* 100 years ago and, following the arguments of Wilson & Brown (1953), probably have little merit in defining evolutionarily significant units. Some such taxa will, however, undoubtedly be elevated to species rank as a result of ongoing morphometric, karyotypic and molecular genetic analyses (e.g. Endo *et al.*, 2004; Hayashida *et al.*, 2007), and this will, in turn, increase the number of range limits that require consideration by perhaps 10%. However, we do not expect that changes in species designations will substantially alter our findings.

We also recognize that the transect has not been uniformly surveyed but that correction for observational effort is not feasible. Some areas have never been well studied, including the region along the Thai–Malaysian border (5°30′–6°30′ N) and the area where Myanmar and Laos share a border between 20 and 21° N. Another area has not been surveyed for over 40 years: the entire Tenasserim extension of Myanmar from 10 to 17° N. These three areas are of significance to our analyses, but, although the dearth of recent information is unfortunate, the gaps in coverage are unlikely to be filled soon. In contrast, other regions are comparatively well known, including the area around Kuala Lumpur (3° N; Medway, 1983), Khlong Saeng Wildlife Sanctuary (9° N; Nakasathien, 1989; Lynam, 1997) and Khao Yai National Park, Thailand (14° N; Kaewprom, 2004; Lynam *et al.*, 2006; Suzuki *et al.*, 2006, 2007).

Geographic ranges can change rapidly. Overhunting in the last few hundred years has caused range collapses of more than 1000 km in Sumatran rhino, Javan rhino, giant panda, concolor gibbon and tapir (Tougard & Montuire, 2006). Deforestation has fragmented formerly continuously distributed populations throughout the lowlands. Land clearing for rice farming in central and north-east Thailand over the last

few thousand years, coupled with hunting, has contributed to the extirpation of hog deer and Eld's deer, and to the extinction of Thailand's endemic Schomburgk's deer. Further south, extensive rubber plantations in Thailand and Malaysia have had similar undocumented but generally negative impacts on numerous species since the 1940s. Such rapid changes have two implications for the current analysis. First, the ranges reported herein may not be the historical ranges of interest of some taxa, and, in the few cases where historical data are available, these were considered. Second, many published range maps are misleading as they show continuously distributed populations where today there may be only a few isolated populations remaining. In this regard, some of the SAMD (2007) maps, which plot suitable habitat for a particular species, provide an important advance.

At first glance, it might appear that we have documented yet another case for which species diversity increases towards the equator (Lomolino *et al.*, 2006). We report 134 mammal species at 20° N and 198 species at 4° N. Parenthetically, we can also note that there are 102 mammal species at 22° N (Xishuanbanna, China) (Zhang, 2000; Smith *et al.*, 2008) and > 222 species in Borneo (centred on the equator) (Payne *et al.*, 1985). This gradient is not simple, however, and it deviates from a monotonic latitudinal increase in three locations. First, there appears to be a peninsula effect in the far south, resulting in a decline in diversity from 198 species at 4° N to 128 species at 1° N. A similar effect has been found in many groups of animals in other peninsulas, including Florida, Baja California, Iberia, Italy, Korea and Cape York (references in Lomolino *et al.*, 2006). One problem with this peninsula effect hypothesis is that Bird *et al.* (2006) suggest that the Straits of Singapore are only 125 kyr old and the effect must therefore be very recent. Second, there is a significant reduction in species diversity in the central and northern parts of the peninsula (7–14° N). In addition, 35 species (11%) have distributional gaps in the northern or central peninsula. If there were a simple latitudinal gradient in diversity we would expect *c.* 175 species at 10–12° N; instead we observe only 117–118 species, which is 33% fewer than expected. The deficiency is greater among non-volant mammals than among bats. Third, there is a minor deficiency (9%) of species at 16° N on the continent mainland that is more pronounced in bats than in other mammals. This region, the hills to the west of Tak, is less well surveyed, and this deficiency may be an artefact of sampling effort. Despite these three exceptions to apparent general increase in species richness towards the equator we must note that the habitat cells being compared are not of equal area. In this first exploration of the latitudinal pattern we have not corrected for the fact that the continental sample areas are larger than some cells in the peninsula. A follow-up study in the author's laboratory, based on the digital records of SAMD (2006) and the newly available IUCN database (Schipper *et al.*, 2008), takes such available habitat differences into account (Luke Gibson, personal communication).

The mammalian pattern reported here is different from that described earlier for birds along a portion of the same transect

(6–19° N; Hughes *et al.*, 2003). In forest-associated birds there is a major transition between Sundaic and Indochinese faunas, with 47% of total species limits occurring between 11 and 15° N vs. only 19% in the mammals. Neither bats nor non-volant mammals show range-limit distributions similar to that of birds. One might expect bats to have patterns of range limits similar to those of birds because of their comparable vagility, but the pattern in bats is in fact more similar to that of the non-volant mammals. As noted above, 11% of the mammals have gaps in their distribution in the northern and central peninsula; these 35 species occur in continental Thailand and in peninsular Malaysia but have not been recorded in historical times in the upper half of the peninsula. Similar gaps were reported among 13% of the birds studied previously (Hughes *et al.*, 2003; Round *et al.*, 2003).

Repeated sea-level changes as a cause of the mammal pattern

We now turn to the larger question of what caused the divergence of the Indochinese and Sundaic faunas. It is widely believed that only significant and persistent geographic barriers to dispersal can produce faunal divergence. Woodruff (2003b) surveyed the literature and found that no geophysical or climatic barrier had ever been proposed, and hypothesized that previously unrecognized marine transgressions could account for the avian pattern described with his colleagues (Hughes *et al.*, 2003; Round *et al.*, 2003). He identified two periods when seaways submerged the northern and southern ends of the central peninsula: when global sea levels reached +100 m from 4 to 5 Ma and +100–150 m from 15 to 20 Ma. His reconstruction of Neogene sea levels was based on the Exxon Production Research Company (Exxon) global eustatic curve derived from proprietary seismic studies of coastal sediments (Vail *et al.*, 1977; Vail & Hardenbol, 1979; Haq *et al.*, 1987). Recently, Miller *et al.* (2005) published a new global curve that validates the Exxon curve with respect to the number and timing of sea-level events, but shows that the earlier estimates of amplitude are at least 2.5 times too high. This advance negates Woodruff's (2003b) reconstruction and we accordingly offer the following revision.

The Miller *et al.* (2005) sea-level curve is also based on the sedimentary sequence unconformities (when one erosional or non-depositional surface is replaced by another) observed in five New Jersey coastal boreholes, and spans the Phanerozoic, the last 543 Myr. Unconformities reflect changes in sea levels and local tectonics, but concordance of sequence ages in geographically disparate localities are interpreted as indicators of global eustatic change. Miller *et al.* used a quantitative method called backstripping to distinguish the contributions of glacioeustacy, sedimentoeustasy, tectonoeustasy (at least on passive or stable continental margins) and thermosteric (temperature) effects. Their results are concordant with data from elsewhere in the world and with those obtained from other sea-level proxies. The Miller *et al.* curve is radically different in appearance to the Exxon curve used by Woodruff
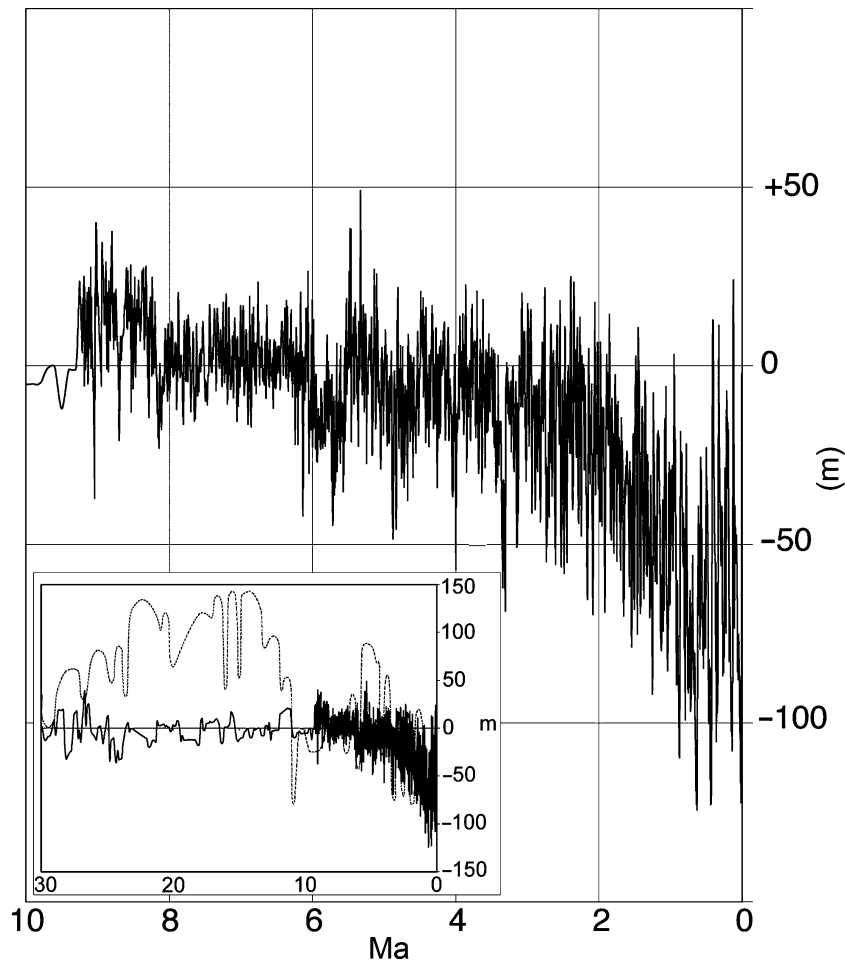
Figure 4 Global sea-level curve for the last 10 Myr based on the method of Miller *et al.* (2005). Inset shows the Miller curve (solid line) and the earlier Exxon curve (Haq *et al.*, 1987) (dotted line) for the last 30 Myr. (Curves drawn from best-estimate data in Miller *et al.*, 2005, Supplement: Table.)

(2003b) and many others since 1977 (Fig. 4). In particular, it provides no evidence for +100 m highstands during the last 25 Myr.

Since the analysis presented below was completed, an independent review of the Miller *et al.* (2005) curve (and others) based on ocean basin dynamics has appeared (Müller *et al.*, 2008). The Müller *et al.* geophysical analysis corrects for substantial regional (New Jersey) subsidence over the last 70 Myr but does not negate the following discussion or conclusions. The Müller *et al.* analysis shows that Cretaceous sea levels were higher than estimated by Miller *et al.* (2005), but the two curves are reconciled over the biogeographically relevant last 25 Myr. Müller *et al.* (2008) do not consider the effects of global ice so their recalibration of the global curve cannot be used further here.

The Miller *et al.* (2005) sea-level curve for the last 9 Myr shown in Fig. 4 is based on the analysis of the oxygen isotopic records in the fossil skeletons of benthic foraminifera from two deep-sea cores (ODP 846 and 982). The ratio of ^{18}O to ^{16}O is temperature-dependent and serves as a proxy for ice volume and therefore sea levels (Lambeck & Chappell, 2001). The

general features of this curve are concordant with oxygen isotope patterns seen in an averaged 'stack' of 57 deep-sea cores over the last 5 Myr (Lisiecki & Raymo, 2005). The periodic rises and falls of sea level are found consistently across many cores and oceans. Miller *et al.* estimated the sea-level equivalents of each of the 1800 points (stable isotopic ratios) in their curve and dated the record by curve fitting to the orbital time-scale (the Milankovitch curve based on 100,000-year cycles in the Earth's orbit), and also to reversals in the Earth's magnetic field and to biostratigraphy. There are errors associated with each determination (typically ± 15 m), and two recent highstands are illustrative. First, as shown in Fig. 4, the sample from core 846 for 130 ka gave a sea-level estimate of +24 m. This estimate is probably spurious as most other lines of evidence point to a +4–6 m highstand between 128 and 116 ka (MIS 5e; Siddall *et al.*, 2007). These lower estimates are based on data from radiometrically dated fossil coral reefs elevated above sea level in the Bahamas, Barbados, Bermuda and New Guinea, and from sedimentary evidence from the mid-Atlantic coast of the USA (Wright *et al.*, 2008). The +6 m estimate is also supported by research specifically on the last

Table 4 Tertiary sea levels and fluctuations estimated from Miller *et al.* (2005: Supporting Information, Table S1, best estimate). The data comprise sea-level estimates for every 5000 years between 0 and 9.3 Ma and every 100,000 years thereafter. Means were calculated from these data and ranges may actually be greater, given the gaps in the record. Fleeting highstands of < +2 m and <1 kyr were ignored.

Age (Ma)	Mean sea level (m)	Sea level range (m)	Highstands > +0 m			Rapid sea level rises (m)		Duration (kyr) of lowstands of > −60 m
			Number	Duration	% of period	> 40	> 80	
43–63	+56	+20 to +133	1	20 Myr	100	3	1	0
30–43	+18	−12 to +54	4	1.3 Myr	95	4	0	0
20–30	−4	−36 to +39	9	3.4 Myr	34	3	0	0
10–20	−1	−18 to +21	7	4.0 Myr	40	0	0	0
9–10	+8	−36 to +40	6	205 kyr	21	1	0	0
8–9	+9	−23 to +38	14	775 kyr	78	2	0	0
6–8	+1	−42 to +26	> 42	1.12 Myr	56	1	0	0
5.5–6	−7	−45 to +19	6	< 29 kyr	< 0.01	2	0	0
5–5.5	+8	−28 to +49	14	255 kyr	51	3	0	0
4–5	−8	−48 to +21	> 16	222 kyr	0.02	5	0	0
3–4	−11	−67 to +22	> 18	135 kyr	0.01	7	0	< 15
2–3	−16	−70 to +25	17	160 kyr	0.02	14	1	15
1–2	−38	−92 to +10	5	19 kyr	< 0.01	16	2	185
0–1	−62	−120 to +10	4	23 kyr	< 0.01	6	7	530

interglacial conditions (Otto-Bliesner *et al.*, 2006; Overpeck *et al.*, 2006; Siddall *et al.*, 2007). Second, the reverse error probably applies to the +10 m highstand shown in Fig. 4 at *c.* 400 ka (MIS 11: 395–415 ka). There is evidence from Atlantic sites that sea levels rose briefly to +20–22 m at the end of the interglacial (Hearty *et al.*, 1999; Hearty & Kaufman, 2000). This is currently the maximum highstand for which there is reasonable evidence in the last 1.5 Myr.

Miller *et al.*'s (2005) results, as they affect the issues under discussion here, are summarized in Table 4. The mean sea level column in Table 4 shows that four stages can be recognized in the last 63 Myr. First, for 20 Myr during the Palaeocene and Eocene (63–43 Ma) global sea levels averaged +56 m above today's level. Second, mean sea levels then fell for 13 Myr until 30 Ma, when they reached levels within 10 m of today's. The third stage, spanning 25 Myr from 30 to 5 Ma, was characterized by mean sea levels that fluctuated within 10 m of contemporary levels. Finally, during the fourth stage, spanning the last 5 Myr, mean sea levels have remained below today's level, and have declined gradually to an average of −62 m during the last million years.

Today, a highstand of +50 m would almost breach the northern end of the central peninsula between Krabi and Surat Thani (Fig. 5e), and a highstand of +70 m would also flood the southern end of the central peninsula between Kangar and Songkla. Such transgressions would connect the Gulf of Thailand to the Andaman Sea and create multiple narrow, shallow marine barriers to land mammal dispersal. Mean sea levels were +56 m during the period 43–63 Ma, and fluctuated between +20 and +133 m. From 51.7 to 53.6 Ma mean sea levels remained above +74 m, and on six other occasions during the early Tertiary exceeded +60 m. This suggests that the central peninsula comprised an island chain for significant periods during the early Tertiary and was never as extensive as it is today. Early Indochinese mammals would have had to island-hop across the central peninsula to reach the pre-Tertiary mountains of peninsular Malaysia, Sumatra (itself an archipelago until the Pliocene), Java and Borneo. This first high-sea-level stage of the Tertiary transitioned into the second stage 43 Ma, when mean global sea levels started a 13-Myr decline to levels similar to today's. During this time span (30–43 Ma; middle and late Eocene and early Oligocene), mean sea levels were +18 m (fluctuating between −12 and +54 m) and were probably never again high enough to breach the central peninsula.

The third stage of Tertiary sea-level history commenced *c.* 30 Ma and was characterized by mean sea levels fluctuating within 10 m of today's level (Fig. 4). Throughout the Oligocene and Miocene the peninsula was probably similar to today's in its basic geographic extent and physiography (Hall, 2001, 2002; Woodruff, 2003b). Although the peripheral areas of Southeast Asia (Sumatra and the Philippines) have changed dramatically during this period, the Thai–Malay Peninsula has existed for 100 Myr, and sea-level changes, rather than large-scale tectonic changes, have controlled its basic appearance. Extensive ever-wet rain forest and more seasonal forests have dominated the region since *c.* 20 Ma (Whitmore, 1998; Woodruff, 2003b). There was ample land and time for the dispersal and range extension of Indochinese mammals south into Malaysia and, as we will explain below, out to today's Sundaic islands. We are more concerned with north-to-south dispersal than with the reverse, as the eastern end of Sundaland (marked by Wallace's line) constituted a relatively hard barrier to land mammals throughout the Cenozoic (Hall, 2001, 2002). However, we also recognize that opportunities for overland dispersal in the reverse direction occurred whenever sea levels fell below *c.* −30 m, as they have done repeatedly since *c.* 6 Ma.
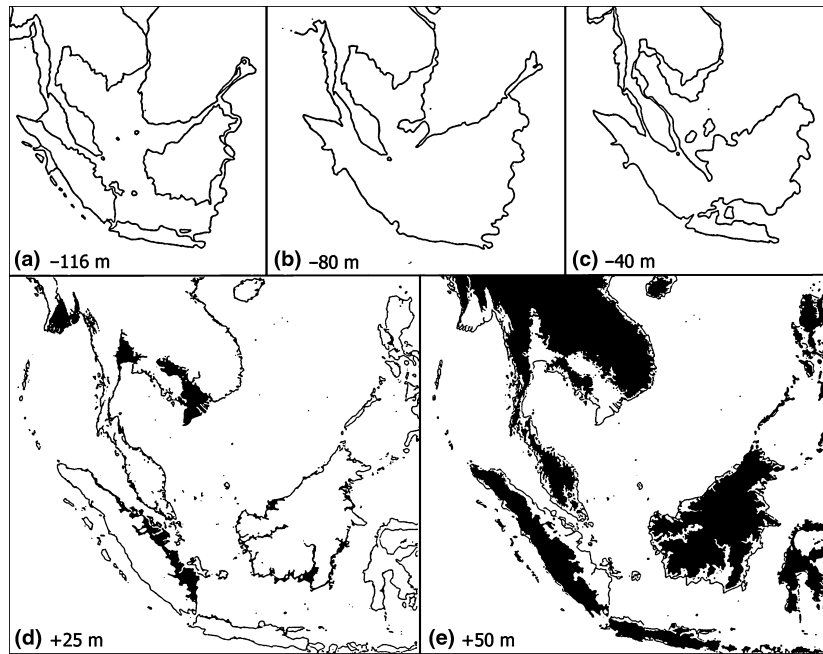
Figure 5 Schematic maps showing the extent of Sundaland when sea levels, relative to today's, were at (a) −116 m, (b) −80 m, (c) −40 m, (d) +25 m and (e) +50 m. Map (a) shows the extent of Sundaland during the Last Glacial Maximum *c.* 20 ka and on two other occasions during the last million years (Fig. 4). The current positions of the Southeast Asian mainland and major islands are shown. During the last 1 Myr, sea levels fluctuated widely around −62 m and reached −80 m (map b) on at least a dozen occasions. Map (c) shows the sea level at −40 m, the average position of the coast 1–2 Ma, with half of the Sunda Shelf exposed. Map (d) shows the +25 m transgression (shaded) of numerous earlier Pliocene and late Miocene highstands. Finally, map (e) shows the extent of the brief +50 m transgression *c.* 5.4 Ma (land above +50 m shaded); this event, the maximal transgression during the last 10 Myr, does not appear to have breached the central peninsula. [Maps (a) to (c) redrawn from Sathiamurthy & Voris (2006) (see source and original full colour maps for details); maps (d) to (e) prepared by Kathryn Woodruff, from Woodruff & Woodruff (2008).]

The fourth stage of sea-level history began *c.* 5 Ma and continued until very recently. During this period mean sea levels remained below today's level and declined gradually to an average of −62 m over the last 1 Myr. Because sea level declines to below −40 m will expose half of the Sunda shelf (Sathiamurthy & Voris, 2006) (Fig. 5c), the peninsula became an insignificant fraction of the habitat available to mammals, especially during the last 2 Myr. During most of that period, the Indochinese and Sundaic faunas would have been in broad geographic contact across two million km^2 of emergent surrounding plains. Only during Pleistocene highstands did anything like a peninsula appear, and then, for one with today's coastline, for only 42 kyr or 2% of the last 2 Myr.

This substantial revision of the palaeogeographic history of the Thai–Malaysian peninsula provides no clear physical barrier to account for the divergence of Indochinese and Sundaic species pairs. The narrow seaway that occurred for a few million years 50 Ma is irrelevant to the evolution of today's species. Similarly, there is no simple explanation for the concordance of species range limits at 5–7 or 13–14° N based on the consideration of mean sea levels during the Neogene. However, a closer examination of the eustatic curve suggests a likely explanation for both issues. We here propose that the dramatic and repeated fluctuations in sea level during the last 5 Myr will account for these observations.

To see how sea-level fluctuations might account for the differentiation of Indochinese and Sundaic species pairs and the concordance of species range limits one needs to consider the impact of each glacioeustatic cycle. In the last such cycle, beginning *c.* 130 ka, sea levels fell gradually and episodically from +6 m (isotopic stage 5e, 120 ka) to *c.* −122 m (Fig. 5a; stage 2, 18–20 ka). Since then, sea levels rose quickly until they reached today's level *c.* 6 ka. This rise of > 100 m in less than 12,000 years had a very dramatic effect on the mammals inhabiting Southeast Asia. According to Sathiamurthy & Voris (2006), the total area of Sundaland above sea level shrank from 4,709,397 to 2,342,826 km^2, a decrease of 50% (Fig. 5a). Although the rise was very rapid in a geological sense and exceeded 20 m kyr^{-1}, most mammals would have had no difficulty adjusting to a 20 mm $year^{-1}$ transgression. Even the maximum transgression of 20 m in 200 years *c.* 14,600 yr BP, or 100 mm $year^{-1}$, was biologically trivial. It is unlikely that many mammal populations were 'drowned away', except for some trapped on the originally large South China Sea islands between peninsular Malaysia and Borneo (the Anambas, Natuna Besar and Natuna Selatan archipelagos; Meijaard, 2003). Most mammals would have had ample time to move away from the edge and inland towards higher ground. The resulting faunal compression may have led to intensified competition and, in some isolated habitat patches, to population

extinction and even species extirpation. Under the equilibrium model of island biogeography we would expect a gradual loss of species with shrinking area (MacArthur & Wilson, 1967; Heaney, 1984, 1986). This may account for the observed reduction in species numbers in the narrowest parts of the peninsula today. Faced by the rising sea level, many mammals living on the vast Sundaic plains would have moved north to the continent or west to the hills of the peninsula. Those in the latter category would have found themselves restricted to very small habitat patches if they ended up in the northern or central peninsula. Those that moved into the larger and more mountainous southern peninsula would have enjoyed far more area (the peninsula was broadly connected to Sumatra until sea levels rose above −40 m) and greater topographic relief (hills exceeding 2000 m). But all would have encountered a resident fauna that had inhabited the peninsula for millions of years.

Although the last glacioeustatic cycle's impact is useful in illustrating the principal effect of a rapid sea-level rise it will alone not account for our biogeographical observations. To understand both species numbers and distributions in this area we must consider the impact of multiple rapid rises of sea level (Fig. 4, Table 4). There were seven transgressions of > 80 m in the last 1 Myr. In addition, there were six rapid rises of 40–80 m. In the fourth phase of Tertiary sea-level history, in the last 5 Myr there have been 10 rapid rises of > 80 m and 48 rapid rises of 40–80 m. We hypothesize that these 58 rapid rises, coupled with the eight that preceded them 4–6 Ma, account for the current patterns of mammal species distribution. Although we view rapid rises of > 40 m as significant for peninsular mammals, we note that there were many more smaller rapid rises of 20–40 m that may amplify the overall impact of the larger rises.

Each rapid rise began from a different depth and consequently resulted in a different reduction in habitat area. For this reason we suspect that rapid rises that began from below −40 m would have had the greatest impact. Such rapid rises from below −40 m dominate the eustatic pattern for the last 3 Myr but occurred at lower frequency back to 6.1 Ma. At sea levels of −40 m the sea would have retreated from both the east and west coasts of the present peninsula, resulting in an isthmus broadly connected to the mainland in the north and to Sumatra–Java–Borneo in the south (Fig. 5c). The area associated with today's peninsula doubled. Both the South China Sea and the Gulf of Thailand remained extensive open water. In contrast, by −60 m the Gulf of Thailand had disappeared and by −80 m the South China Sea had retreated over 500 km and the Sunda shelf had emerged between Borneo and Vietnam (Fig. 5b). We focus here on −40 and −80 m geographic patterns because a rapid rise from the former would have halved the habitat of peninsular mammals, and most rises of > 40 m would have had an even greater impact. Sathiamurthy & Voris (2006) calculated the total additional land exposed with each 10 m drop in sea level but their estimates are based on the entire Sundaland region. A study of their reconstructions shows that when just the focal region (the peninsula) is

considered, different estimates would emerge depending on how the local region's boundaries are set. Nevertheless, a sea-level drop to −40 m would have doubled the peninsula's area, a drop to between −50 and −60 m would have added the greatest area of land relevant to peninsular mammals, and drops to below −80 m would have had little additional local impact.

The above discussion has been premised on the idea that today's coastlines have great antiquity and are a proper basis for palaeobiological reconstructions. In fact they are not, as biologists have long appreciated (Wallace, 1869; Woodruff & Woodruff, 2008). In addition to the seashore retreats discussed above there have been repeated marine transgressions during the last 10 Myr. Figure 4 shows 31 transgressions of +10 to 20 m during the last 4 Myr. Figure 5d shows the maximal areal extent of these brief transgressions (at +25 m) on today's peninsula. These transgressions had only a minor impact on land area (< 10% reductions) except in the central peninsula and the far south. In the central peninsula, between the towns of Krabi, Surat Thani and Nakhon si Thammarat, the transgressions halved the peninsula's width. Although the duration of such transgressions was very short, with each episode lasting hundreds not thousands of years, their ecological impact was locally catastrophic. The brief higher transgressions between 5 and 6 Ma (to +49 m) had little additional areal impact (Fig. 5e). The Holocene highstand of +2.5 m would have had virtually no impact. Together, these multiple brief transgressions would have amplified the general effect of the rapid sea-level rises but they themselves were not responsible for the overall divergence of the Indochinese and Sundaic faunas.

Our work shows that modern mammal distribution patterns have three features that are linked: (1) the peaks in species range limits north of the northern peninsula, (2) the peaks south of the central peninsula, and (3) the fall in species diversity in the central and northern peninsula. We hypothesize that an area effect accounts for these observations. A 70% reduction in habitat area in the north and central peninsula could account for the observed 30% decline in species number (MacArthur & Wilson, 1967; as applied to Southeast Asian mammals by Heaney, 1984, 1986). We do not know the ages of most of the extant Southeast Asian mammal species under discussion but assume that they are comparable to those in better-dated faunas, and that most species originated in the last 2–4 Myr (Avise, 2000). We hypothesize that most of the species were in place two or more million years ago, and that multiple rapid sea-level rises are the one unusual phenomenon affecting this regional fauna during this time period. We hypothesize that the > 50 episodes of significant faunal compression onto the peninsula account for the accumulation of species borders at the geographic edges of the more stable areas, both at the northern end of the large mountainous southern peninsula and at the northern end of the peninsula itself. The reduced numbers of mammal species in between these areas is probably the result of a repetitively imposed area effect.

Reconstructing Neogene mammal distribution patterns

Although the effects of sea-level change on habitat area appear highly significant to us, we recognize that other factors must also be considered in explaining today's mammal distribution patterns. We conclude this discussion by noting the need for consideration of four additional factors likely to be important in the final solution of the issues raised: palaeoenvironments, the role of individual species ecology, the fossil record, and the genetic variation and phylogeography of today's populations. Future discussions will also have to begin with the premise that the present geography of this region is not a simple key to the past: today's high sea levels and warm-wet climates are highly unusual and have prevailed for less than 3% of the last few million years.

In the above palaeogeographic reconstruction we have implied that the emergent Sunda shelf constituted an equal opportunity for range expansion of all mammals: it certainly did not. Forest-associated mammals would be far more attuned to the differences between perhumid rain forest, and seasonal, monsoonal and mangrove forest than we have allowed. The current determinants of the distribution of representative members of these plant associations have only recently come under investigation (Baltzer et al., 2007, 2008). The past distribution and species composition of these plant associations would have changed with each cool-dry hypothermal and warm-wet hyperthermal phase, and these climatic cycles have been becoming progressively cooler since the Pliocene. Furthermore, much of the flat Sunda plain may have been vegetated by Pinus savanna woodland or grassland, and not by rain forest (Whitmore, 1987, 1998; Heaney, 1991; Taylor et al., 1999; Morley, 2000, 2007; Kershaw et al., 2001, 2007; Gathorne-Hardy et al., 2002; Hope et al., 2004; Hope, 2005). Mammals restricted to primary rain forest could have crossed these plains along riparian forest corridors or could have become isolated by ecological barriers (Gorog et al., 2004). The areal extent and distribution of savanna and rain forest (and rain forest refugia) are still controversial (Sun et al., 2000, 2003; Taylor et al., 2001; Meijaard, 2003; Bird et al., 2005; Tougard & Montuire, 2006; Kershaw et al., 2007; Morley, 2007), but the implications of these palaeoenvironmental changes need to be coupled with the impact of the area changes. Habitat requirements are clearly significant to some species' distribution patterns and responses to change (see Meijaard, 2003), and should be taken into account in future analyses.

Although habitat availability (for example limestone outcrops) may determine the distribution of some species, habitat selection is rarely a fixed trait in mammals, and palaeogeographic reconstructions based on the ecology of living populations can be misleading. Ecological niches, fundamental and realized, can change over time. Similarly, niches of widely distributed species may vary geographically. An example of the latter involves the lesser gymnure, Hylomys suillus, which ranges from China to Borneo: Bornean populations are exclusively montane (> 1000 m) but elsewhere the species ranges down to sea level. Similar niche shifts have been reported in several species of Indochinese birds that range south towards the equator (Round et al., 2003). A full understanding of current species range limits requires the investigation of the plasticity or conservatism of each species niche (Wiens & Graham, 2005). It must also address the denial of the niche concept in neutral theories (e.g. Hubbell, 2001). Some of these ideas are being tested by comparing niches of conspecific populations in species-poor and species-rich areas of the transect (L. Gibson and D.S.Woodruff, in preparation).

Repetitive range compression will also leave a mark on the genetic structure of today's populations. Genetic drift in small isolated populations will rob them of their genetic variability. Interestingly, several authors have reported evidence consistent with repeated demographic bottlenecks in a variety of taxa in this region (Inger & Voris, 1993; Cannon & Manos, 2003). As proposed for the avifauna (Woodruff, 2003b), a molecular clock approach could be used to date the divergence of the Indochinese and Sundaic faunas. Candidate mammalian genera with species-pairs appropriate for such an analysis include Nycticebus, Tupaia, Macaca, Callosciurus, Hylopetes, Rattus, Niviventer, Hipposideros and Prionailurus. Our prediction that Indochinese–Sundaic species pairs diverged following repeated range disruption in the central and northern peninsula 1–4 Ma can be tested. The resolving power of phylogeographic analyses is well illustrated by recent examples in Southeast Asian rodents (Mercer & Roth, 2003; Gorog et al., 2004), primates (Brandon-Jones, 1996; Tosi et al., 2002; Harrison et al., 2006; Steiper, 2006; Ziegler et al., 2007; Roos et al., 2008), bats (Thabah et al., 2006), frogs (Emerson et al., 2000; Inger & Voris, 2001), arachnids (Su et al., 2006; Warrit et al., 2006), insects (Pramual et al., 2005; Quek et al., 2007) and freshwater prawns (De Bruyn et al., 2005; De Bruyn & Mather, 2007).

Future discussions must also take into account the growing body of information on fossil mammals and their distribution. Although we did not incorporate this evidence in our analysis as so many of the fossils are undated, we recognize that this situation is changing rapidly. Chaimanee (1998), Chaimanee & Jaeger (2000a,b), Bacon et al. (2006) and Tougard & Montuire (2006) have made significant progress in elucidating the Pliocene–Pleistocene evolution of rodents and should be consulted for references to the broader palaeontological literature. Murine rodents are important regional palaeoenvironment indicators and their data can be interpreted to reconstruct the past extent of forest and savanna communities. The fossil record shows that the transition between Indochinese and Sundaic rodents lay south of the Isthmus of Kra during parts of the Pleistocene, and that more than a dozen species previously ranged further north or further south than they do today. Chaimanee also identified five genera of rodents no longer present in the area. Tougard (2001) and Tougard & Montuire (2006) have reviewed the evidence for mammal movements between the Indochinese and Sundaic subregions during the Pleistocene, and these analyses again underscore how different mammal communities were in this region in the not so distant past. The reconstruction of the history of today's

mammals in this area will also be incomplete until the impacts of the disappearance of the megafauna are understood (see, for example, Tougard *et al.*, 1996; Van den Bergh *et al.*, 2001; Corlett, 2006, 2007; Hill *et al.*, 2006; Louys *et al.*, 2007; Louys, 2008). The megafauna of the region included proboscideans (*Stegodon* and *Palaeloxodon*), hippopotamus (*Hexaprotodon*), hyenas (*Crocuta* and *Pachycrocuta*), giant panda (*Ailuropoda*), tapirs (*Tapirus* and *Megatapirus*), rhinoceroses (*Rhinoceros* and *Dicerorhinus*), giant pangolin (*Manis*) and giant primates (*Pongo* and *Gigantopithecus*). Their regional extirpation or extinction is less related to the arrival of *Homo erectus* (*c.* 1.9 Ma) than it is to that of *H. sapiens* (*c.* 70 ka). Similarly, a meteor's impact 793 ka just east of our transect (near Ubon Ratchathani in eastern Thailand) has to be assessed as it may have killed mammals over an area half the size of Sundaland (Hope, 2005; Meijaard & Groves, 2006). The cataclysmic eruption of Mt Toba, Sumatra, *c.* 74 ka, albeit along the western edge of the region, appears to have had a limited effect on mammals (Louys, 2007). The ever-improving dating of the region's fossils, coupled with the demonstrable association of orbital forcing with climate and sea levels (Vrba, 1992; Dynesius & Jansson, 2000; Van Dam *et al.*, 2006), provide a better framework for the consideration of these complex interactions.

Finally, several contrasting hypotheses that were developed to explain species-richness patterns elsewhere (reviewed by Hortal *et al.*, 2008) should now be examined for their applicability to the situation on the Thai/Malay peninsula. Competitive replacement models (Case & Taper, 2000), which appear relevant to the avian transition, are clearly not going to explain the mammal pattern. By contrast, the habitat theory hypotheses developed by Vrba (1992) to explain the Central American mammal interchange appear highly relevant to the Indochinese–Sundaic mammal transition, albeit on a lesser taxonomic scale. Habitat theory models, in which habitats shift, shrink or disappear in response to cyclical climatic change, lead to a set of evolutionary hypotheses that can be tested by comparing, for example, the differential survival of extant rain forest, savanna, grassland, lowland and montane species. Similarly, the differential dispersal of Sundaic and Indochinese species merits attention: were the overland dispersal opportunities from Indochina to Borneo comparable to those from Sundaland back to the mainland, as suggested for two groups of primates (Ziegler *et al.*, 2007; Roos *et al.*, 2008)? In turn, the answers to such questions have implications for projecting the response of today's species to ongoing climate changes. Interesting as such discussions will be, they lie beyond the scope of the present paper.

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REFERENCES

Ashton, P.A. (1992) Plant conservation in the Malaysian region. *In harmony with nature* (ed. by Y.S. Kheong and L.S. Win), pp. 86–93. Malay Nature Society, Kuala Lumpur.

Avise, J.C. (2000) *Phylogeography: the history and formation of species*. Harvard University Press, Cambridge, MA.

Bacon, A.M., Demeter, F., Duringer, P., Rousse, S., Dodo, Y., Matsumura, H., Long, V.T., Nguyen Kim Thuy, N.K., Huong, N.T.M. & Anezaki, T. (2006) Records of murine rodents (Mammalia, Rodentia) in the Pleistocene localities of Tan Vinh and Ma U'Oi (northern Vietnam) and their implications to past distribution. *Annales de Paléontologie*, **92,** 367–383.

Baker, R.J. & Bradley, R.D. (2006) Speciation in mammals and the genetic species concept. *Journal of Mammalogy*, **87,** 643–662.

Baker, W.J., Coode, M.J.E., Dransfield, J., Dransfield, S., Harley, M.M., Hoffmann, P. & Johns, R.J. (1998) Patterns of distribution of Malesian vascular plants. *Biogeography and geological evolution of Southeast Asia* (ed. by R. Hall and J.D. Holloway), pp. 243–258. Backhuys, Leiden.

Baltzer, J.L., Davies, S.J., Noor, N.S.M., Kassim, A.R. & LaFrankie, J.V. (2007) Geographical distributions in tropical trees: can geographical range predict performance and habitat association in co-occurring tree species? *Journal of Biogeography*, **34,** 1916–1926.

Baltzer, J.L., Davies, S.J., Bunyavejchewin, S. & Noor, N.S.M. (2008) The role of desiccation tolerance in determining tree species distributions along the Malay–Thai Peninsula. *Functional Ecology*, **22,** 221–231.

Bird, M.I., Taylor, D. & Hunt, C. (2005) Environments of insular Southeast Asia during the last glacial period: a savanna corridor in Sundaland? *Quaternary Science Reviews*, **24,** 2228–2242.

Bird, M.I., Pang, W.C. & Lambeck, K. (2006) The age and origin of the Straits of Singapore. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **241,** 531–538.

Brandon-Jones, D. (1996) The Asian Colobinae (Mammalia: Cercopithecidae) as indicators of Quaternary climatic change. *Biological Journal of the Linnean Society*, **59,** 327–350.

Cannon, C.H. & Manos, P.S. (2003) Phylogeography of the southeast Asian stone oaks (*Lithocarpus*). *Journal of Biogeography*, **30**, 1–17.

Case, T.J. & Taper, M.L. (2000) Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *The American Naturalist*, **155**, 583–605.

Cattulo, G., Masi, M., Falcucci, A., Maiorano, L., Rondinini, C. & Biotani, L. (2008) A gap analysis of Southeast Asian mammals based on habitat suitability models. *Biological Conservation*, **141**, 2730–2744.

Chaimanee, Y. (1998) Plio-Pleistocene rodents of Thailand. Biodiversity Research and Training Program, Bangkok.

Chaimanee, Y. & Jaeger, J.-J. (2000a) Occurrence of *Hadromys humei* (Rodentia: Muridae) during the Pleistocene in Thailand. *Journal of Mammalogy*, **81**, 659–665.

Chaimanee, Y. & Jaeger, J.-J. (2000b) Evolution of *Rattus* (Mammalia, Rodentia) during the Plio-Pleistocene in Thailand. *Historical Biology*, **15**, 181–191.

Chasen, F.W. (1940) A handlist of Malaysian mammals: a systematic list of the mammals of the Malay Peninsula, Sumatra, Borneo and Java, including adjacent small islands. *Bulletin of the Raffles Museum*, **15**, 1–209.

Corbet, G.B. & Hill, J.E. (1992) *The mammals of the Indomalayan region: a systematic review*. Oxford University Press, Oxford.

Corlett, R.T. (2006) Megafaunal extinctions in tropical Asia. *Tropinet*, **17**, 1–2.

Corlett, R.T. (2007) The impact of hunting on the Mammalian fauna of tropical Asian forests. *Biotropica*, **39**, 292–303.

Cranbrook, Earl of (1988) Mammals: distribution and ecology. *Key environments. Malaysia* (ed. by Earl of Cranbrook), pp. 146–166. Pergamon, Oxford.

De Bruyn, M. & Mather, P.B. (2007) Molecular signatures of Pleistocene sea-level changes that affected connectivity among freshwater shrimp in Indo–Australian waters. *Molecular Ecology*, **16**, 4295–4307.

De Bruyn, M., Nugroho, E., Hossain, M.M., Wilson, J.C. & Mather, P.B. (2005) Phylogeographic evidence for the existence of an ancient biogeographic barrier: the Isthmus of Kra seaway. *Heredity*, **94**, 370–378.

Dynesius, M. & Jansson, R. (2000) Evolutionary consequences of changes in species geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences USA*, **97**, 9115–9120.

Emerson, S.B., Inger, R.F. & Iskandar, D. (2000) Molecular systematics and biogeography of the fanged frogs of Southeast Asia. *Molecular Phylogenetics and Evolution*, **16**, 131–142.

Endo, H., Fukuta, K., Kimura, J., Sasaki, M., Hayashi, Y. & Oshida, T. (2004) Phylogenetic relationships among populations of the mouse deer in the Southeast Asian region from the nucleotide sequence of cytochrome *b* gene. *Mammal Study*, **29**, 119–123.

Francis, C.M. (2001) *A photographic guide to mammals of South-East Asia*. New Holland, London.

Francis, C.M. (2008) *A field guide to the mammals of Thailand and South-East Asia*. Asia Books, Bangkok.

Gathorne-Hardy, F.J., Syaukani, Davies, R.G., Eggleston, P. & Jones, D.T. (2002) Quaternary rainforest refugia in southeast Asia: using termites (Isoptera) as indicators. *Biological Journal of the Linnean Society*, **75**, 453–466.

Geissmann, T., Groves, C.P. & Roos, C. (2004) The Tenasserim lutung, *Trachypithecus barbei* (Blyth 1847) (Primates: Cercopithecidae): description of a live specimen, and a reassessment of phylogenetic affinities, taxonomic history, and distribution. *Contributions to Zoology*, **73**, 271–282.

Good, R. (1964) *The geography of the flowering plants*, 3rd edn. Longman, London.

Gorog, A.J., Sinaga, M.H. & Engstrom, M.D. (2004) Vicariance or dispersal? Historical biogeography of three Sunda shelf murine rodents (*Maxomys surifer*, *Leopoldamys sabanus* and *Maxomys whiteheadi*). *Biological Journal of the Linnean Society*, **81**, 91–109.

Guillen-Servent, A. & Francis, C.M. (2006) A new species of bat of the *Hipposideros bicolor* group (Chiroptera: Hipposideridae) from central Laos, with evidence of convergent evolution with Sundaic taxa. *Acta Chiropterologica*, **8**, 39–61.

Hall, R. (2001) Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. *Faunal and floral migrations and evolution in SE Asia–Australasia* (ed. by I. Metcalfe, J.M.B. Smith, M. Morwood and I. Davidson), pp. 35–56. Balkema, Lisse.

Hall, R. (2002) Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions and animations. *Journal of Asian Earth Sciences*, **20**, 353–434.

Hall, R. & Holloway, J.D. (eds) (1998) *Biogeography and geological evolution of Southeast Asia*. Backhuys, Leiden.

Haq, B.U., Hardenbol, J. & Vail, P.R. (1987) Chronology of fluctuating sea levels since the Triassic. *Science*, **235**, 1156–1167.

Harrison, M.E. & Chivers, D.J. (2007) The orang-utan mating system and the unflanged male: a product of increased food stress during the late Miocene and Pliocene? *Journal of Human Evolution*, **52**, 275–293.

Harrison, T., Krigbaum, J. & Manser, J. (2006) Primate biogeography and ecology on the Sunda Shelf islands: a paleontological and zooarchaeological perspective. *Primate biogeography* (ed. by S.M. Lehman and J.G. Fleagle), pp. 331–372. Springer, New York.

Hayashida, A., Endo, H., Sasaki, M., Oshida, T., Kimura, J., Waengsothorn, S., Kitamura, N. & Yamada, J. (2007) Geographical variation in skull morphology of gray-bellied squirrel *Callosciurus caniceps*. *Journal of Veterinary Medical Science*, **69**, 149–157.

Heaney, L.R. (1984) Mammalian species richness on islands on the Sunda Shelf, Southeast-Asia. *Oecologia*, **61**, 11–17.

Heaney, L.R. (1986) Biogeography of the mammals of Southeast Asia: estimates of colonization, extinction, and speciation. *Biological Journal of the Linnean Society*, **28**, 127–165.

Heaney, L.R. (1991) A synopsis of climatic and vegetational change in Southeast Asia. *Climatic Change*, **19**, 53–61.

Heaney, L.R. (2004) Conservation biogeography in oceanic archipelagoes. *Frontiers of biogeography* (ed. by M.V. Lomolino and L.R. Heaney), pp. 345–360. Sinauer, Sunderland, MA.

Hearty, P.J. & Kaufman, D.S. (2000) Whole-rock aminostratigraphy and Quaternary sea-level history of the Bahamas. *Quaternary Research*, **54,** 163–173.

Hearty, P.J., Kinder, P., Cheng, H. & Edwards, R.L. (1999) A +20 m middle Pleistocene sea-level highstand (Bermuda and the Bahamas) due to partial collapse of Antarctic ice. *Geology*, **27,** 375–378.

Hill, C., Soares, P., Mormina, M., Macaulay, V., Meehan, W., Blackburn, J., Clarke, D., Raja, J.M., Ismail, P., Bulbeck, D., Oppenheimer, S. & Richards, M. (2006) Phylogeography and ethnogenesis of Aboriginal Southeast Asians. *Molecular Biology and Evolution*, **23,** 2480–2491.

Hirai, H., Hirai, Y., Kawamoto, Y., Endo, H., Kimura, J. & Rerkamnuaychoke, W. (2002) Cytogenetic differentiation of two sympatric tree shrew taxa found in the southern part of the Isthmus of Kra. *Chromosome Research*, **10,** 313–327.

Hope, G. (2005) The Quaternary in Southeast Asia. *The physical geography of Southeast Asia* (ed. by A. Gupta), pp. 24–37. Oxford University Press, Oxford.

Hope, G., Kershaw, A.P., van der Kaars, S., Xiangjun, S., Liew, P.-M., Heusser, L.E., Takahara, H., McGlone, M., Miyoshi, N. & Moss, P.T. (2004) History of vegetation and habitat change in the Austral–Asian region. *Quaternary International*, **118–119,** 103–126.

Hortal, J., Rodriguez, J., Nieto-Diaz, M. & Lobo, J.M. (2008) Regional and environmental effects on the species richness of mammal assemblages. *Journal of Biogeography*, **35,** 1202–1214.

Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.

Hughes, J.B., Round, P.D. & Woodruff, D.S. (2003) The Sundaland–Asian faunal transition at the Isthmus of Kra: an analysis of resident forest bird species distributions. *Journal of Biogeography*, **30,** 569–580.

Inger, R.F. & Voris, H.K. (1993) A comparison of amphibian communities through time and from place to place in Bornean forests. *Journal of Tropical Ecology*, **9,** 409–433.

Inger, R.F. & Voris, H.K. (2001) The biogeographical relations of the frogs and snakes of Sundaland. *Journal of Biogeography*, **28,** 863–891.

Kaewprom, W. (2004) *Responses to burning and edge effects of small mammals at Khlong E Tao Substation, Khai Yai National Park*. MSc Thesis, King Mongkut's University of Technology, Thonburi, Thailand.

Keng, H. (1970) Size and affinities of the flora of the Malay Peninsula. *Journal of Tropical Geography*, **31,** 43–56.

Kershaw, A.P., Penny, D., Kaars, S., van der Anshari, G. & Thamotherampillai, A. (2001) Vegetation and climate in lowland Southeast Asia at the last glacial maximum. *Faunal and floral migration and evolution in SE Asia–Australasia* (ed. by I. Metcalfe, J.M.B. Smith, M. Morwood and I. Davidson), pp. 227–236. Balkema, Lisse.

Kershaw, A.P., van der Kaars, S. & Flenley, J.R. (2007) The Quaternary history of Far Eastern rainforests. *Tropical rainforest responses to climate change* (ed. by M.B. Bush and J.R. Flenley), pp. 77–115. Springer, Berlin.

Kingston, T., Lim, B.L. & Zubaid, A. (2006) *Bats of Krau Wildlife Reserve*. University Kebangsaan Malaysia, Bangi.

Lambeck, K. & Chappell, J. (2001) Sea level change through the last glacial cycle. *Science*, **292,** 679–686.

Lekagul, B. & McNeely, J.A. (1988) *Mammals of Thailand*, 2nd edn. Saha Karn Bhaet, Bangkok.

Lisiecki, L.E. & Raymo, M.E. (2005) A Pliocene–Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. *Paleoceanography*, **20.** Article No. PA1003, doi:10.1029/2004PA001071.

Lomolino, M.V., Riddle, B.R. & Brown, J.H. (2006) *Biogeography*, 3rd edn. Sinauer, Sunderland, MA.

Louys, J. (2007) Limited effect of the Quaternary's largest super-eruption (Toba) on land mammals from Southeast Asia. *Quaternary Science Reviews*, **26,** 3108–3117.

Louys, J. (2008) Quaternary extinctions in Southeast Asia. *Mass extinction – the danger around us* (ed. by A.M.T. Elewa), pp. 159–189. Springer, Heidelberg.

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

Luo, S.J., Kim, J.H., Johnson, W.E., van der Walt, J., Martenson, J., Yuhki, N., Miquelle, D.G., Uphyrkina, O., Goodrich, J.M., Quigley, H.B., Tilson, R., Brady, G., Martelli, P., Subramaniam, V., McDougal, C., Hean, S., Huang, S., Pan, W., Karanth, U.K., Sunquist, M., Smith, J.L.D. & O'Brien, S.J. (2004) Phylogeography and genetic ancestry of tigers (*Panthera tigris*). *Public Library of Science Biology*, **2,** 2275–2293.

Lynam, A.J. (1997) Rapid decline of small mammal diversity in monsoon evergreen forest fragments in Thailand. *Tropical forest remnants* (ed. by W.F. Laurance and R.O. Bierregaard), pp. 222–240. Chicago University Press, Chicago.

Lynam, A.J., Round, P.D. & Brockelman, W.Y. (2006) *Status of birds and large mammals in Thailand's Dong Phayayen – Khao Yai forest complex*. Biodiversity Research & Training Program, Bangkok.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Medway, L. (1983) *The wild mammals of Malaya (Peninsular Malaysia and Singapore)*. Oxford University Press, Kuala Lumpur.

Meijaard, E. (2003) Mammals of south-east Asian islands and their Late Pleistocene environments. *Journal of Biogeography*, **30,** 1245–1257.

Meijaard, E. & Groves, C.P. (2006) The geography of mammals and rivers in mainland Southeast Asia. *Primate biogeography* (ed. by S.M. Lehman and J.G. Fleagle), pp. 305–329. Springer, New York.

Mercer, J.M. & Roth, V.L. (2003) The effects of Cenozoic global change on squirrel phylogeny. *Science*, **299,** 1568–1572.

Metcalfe, I., Smith, J.M.B., Morwood, M. & Davidson, I. (eds) (2001) *Faunal and floral migrations and evolution in SE Asia–Australasia*. Balkema, Lisse.

Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N. & Pekar, S.F. (2005) The Phanerozoic record of global sea-level change. *Science*, **310**, 1293–1298.

Molengraaff, G.A.F. (1922) *De geologie der zeen van de Nederlandsch Oost-Indie archipel*. Nederlandsch Aardrijkokundig Genootschap, Amsterdam.

Morley, R.J. (2000) *Origin and evolution of tropical rain forests*. J. Wiley, Chichester.

Morley, R.J. (2007) Cretaceous and Tertiary climate change and the past distribution of megathermal rainforests. *Tropical rainforest responses to climate change* (ed. by M.B. Bush and J.R. Flenley), pp. 1–31. Springer, Berlin.

Müller, R.D., Sdrolias, M., Gaina, C., Steinberger, B. & Heine, C. (2008) Long-term sea-level fluctuations driven by ocean basin dynamics. *Science*, **319**, 1357–1362.

Musser, G.G. & Newcomb, C. (1983) Malaysian murids and the giant rat of Sumatra. *Bulletin of the American Museum of Natural History*, **174**, 329–598.

Nakasathien, S. (1989) Chiew Larn Dam wildlife rescue operation. *Oryx*, **23**, 146–154.

Otto-Bliesner, B.L., Marshall, S.J., Overpeck, J.T., Miller, G.H., Hu, A. & CAPE Last Interglacial Project members (2006) Simulating Arctic climate warmth and icefield retreat in the last interglaciation. *Science*, **311**, 1751–1753.

Overpeck, J.T., Otto-Bliesner, B.L., Miller, G.H., Muhs, D.R., Alley, R.B. & Kiehl, J.T. (2006) Paleoclimatic evidence for future ice-sheet instability and rapid sea-level rise. *Science*, **311**, 1747–1750.

Parr, J.W.K. (2003) *A guide to the large mammals of Thailand*. Sarakadee Press, Bangkok.

Payne, J., Francis, C.M. & Phillipps, K. (1985) *A field guide to the mammals of Borneo*. World Wildlife Fund, Kuala Lumpur.

Pramual, P., Kuvangkadilok, C., Baimai, V. & Walton, C. (2005) Phylogeography of the black fly *Simulium tani* (Diptera: Simuliidae) from Thailand as inferred from mtDNA sequences. *Molecular Ecology*, **14**, 3989–4001.

Quek, S.P., Davies, S.J., Ashton, P.S., Itino, T. & Pierce, N.E. (2007) The geography of diversification in mutualistic ants: a gene's-eye view into the Neogene history of Sundaland rain forests. *Molecular Ecology*, **16**, 2045–2062.

Richards, P.W. (1996) *The tropical rain forest: an ecological study*, 2nd edn. Cambridge University Press, Cambridge.

Roos, C., Nadler, T. & Walter, L. (2008) Mitochondrial phylogeny, taxonomy and biogeography of the silvered langur species group (*Trachypithecus cristatus*). *Molecular Phylogenetics and Evolution*, **47**, 629–636.

Round, P.D., Hughes, J.B. & Woodruff, D.S. (2003) Latitudinal range limits of resident forest birds in Thailand and the Indochinese–Sundaic zoogeographic transition. *Natural History Bulletin of the Siam Society*, **51**, 69–96.

SAMD [Southeast Asian Mammal Databank] (2006) *Ecological data set and GIS based models: a tool for biodiversity based conservation in Southeast Asia*. Instituto di Ecologia Applicata, Rome, Italy. Available at: http://www.ieaitaly.org/samd/ (used June 2007; reviewed January 2008).

Sathiamurthy, E. & Voris, H.K. (2006) Maps of Holocene sea level transgression and submerged lakes on the Sunda Shelf. *Natural History Journal of Chulalongkorn University*, **2**(Suppl.), 1–43. Maps available at: http://www.field museum.org/research_collections/zoology/zoo_sites/seamaps/mapindex1.htm.

Schipper, J. & 130 co-authors (2008) The status of the world's mammals: diversity, threat, and knowledge. *Science*, **322**, 225–230.

Siddall, M., Chappell, J. & Potter, E.K. (2007) Eustatic sea level during past interglacials. *The climate of past interglacials* (ed. by F. Sirocko, M. Claussen, M.F. Sanchez Goni and T. Litt), pp. 74–92. Elsevier, Amsterdam.

Smith, A.T., Xie, Y., Hoffmann, R.S., Lunde, D., MacKinnon, J., Wilson, D.E. & Wozencraft, W.C. (eds) (2008) *A guide to the mammals of China*. Princeton University Press, Princeton, NJ.

Sodhi, N.S. & Brook, B.W. (2006) *Southeast Asian biodiversity in crisis*. Cambridge University Press, Cambridge.

van Steenis, C.G.G.J. (1950) The delimitation of Malesia and its main plant geographical divisions. *Flora Malesiana I*, **1**, lxx–lxxv.

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.

Sterling, E.J., Hurley, M.M. & Minh, L.D. (2006) *Vietnam. A natural history*. Yale University Press, New Haven.

Su, Y.C., Chang, Y.H., Lee, S.C. & Tso, I.M. (2006) Phylogeography of the giant wood spider (*Nephila pilipes*, Araneae) from Asian–Australian regions. *Journal of Biogeography*, **34**, 177–191.

Sun, X., Li, X., Luo, Y. & Chen, X. (2000) The vegetation and climate at the last glaciation on the emerged continental shelf of the South China Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **160**, 301–316.

Sun, X., Luo, Y., Huang, F., Tian, J. & Wang, P. (2003) Deep-sea pollen from the South China Sea: Pleistocene indicators of East Asian monsoon. *Marine Geology*, **201**, 97–118.

Suzuki, S., Kitamura, S., Kon, M., Poonswad, P., Chuailua, P., Plongmai, K., Yumoto, T., Noma, N., Maruhashi, T. & Wohandee, P. (2006) Foraging activity patterns of frugivorous or omnivorous animals on the forest floor of a tropical seasonal forest in Thailand, with reference to seasonal changes. *Natural History Bulletin of the Siam Society*, **54**, 177–194.

Suzuki, S., Kitamura, S., Kon, M., Poonswad, P., Chuailua, P., Plongmai, K., Yumoto, T., Noma, N., Maruhashi, T. & Wohandee, P. (2007) Fruit visitation patterns of small mammals on the forest floor in a tropical seasonal forest of Thailand. *Tropics*, **16**, 17–29.

Taylor, D., Saksena, P., Sanderson, P.G. & Kucera, K. (1999) Environmental change and rain forests on the Sunda Shelf:

drought, fire and the biological cooling of biodiversity hotspots. *Biodiversity and Conservation*, **8,** 1159–1177.

Taylor, D., Yen, O.H., Sanderson, P.G. & Dodson, J. (2001) Late Quaternary peat formation and vegetation dynamics in a lowland tropical swamp; Nee Soon, Singapore. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **171,** 269–287.

Thabah, A., Rossiter, S.J., Kingston, T., Zhang, S., Parsons, S., Mya, K.M., Zubaid, A. & Jones, G. (2006) Genetic divergence and echolocation call frequency in cryptic species of *Hipposideros larvatus* s.l. (Chiroptera: Hipposideridae) from the Indo-Malayan region. *Biological Journal of the Linnean Society*, **88,** 119–130.

Tosi, A.J., Morales, J.C. & Melnick, D.J. (2002) Y-chromosome and mitochondrial markers in *Macaca fascicularis* indicate introgression with Indochinese *M. mulatta* and a biogeographic barrier in the Isthmus of Kra. *International Journal of Primatology*, **23,** 161–178.

Tougard, C. (2001) Biogeography and migration routes of large mammal faunas in South-East Asia during the Late Middle Pleistocene: focus on the fossil and extant faunas from Thailand. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **168,** 337–358.

Tougard, C. & Montuire, S. (2006) Pleistocene paleoenvironmental reconstructions and mammalian evolution in South-East Asia: focus on fossil faunas from Thailand. *Quaternary Science Reviews*, **25,** 126–141.

Tougard, C., Chaimanee, Y., Suteethorn, V., Triamwichanon, S. & Jaeger, J.J. (1996) Extension of the geographic distribution of the giant panda (*Ailuropoda*) and search for the reasons for its progressive disappearance in Southeast Asia during the latest Middle Pleistocene. *Comptes Rendus de l'Academie des Sciences, IIA Sciences de la Terre et des Planetes*, **323,** 973–979.

Vail, P.R. & Hardenbol, J. (1979) Sea-level changes during the Tertiary. *Oceanus*, **22,** 71–79.

Vail, P.R., Mitchum, R.M. & Thompson, S. (1977) Seismic stratigraphy and global changes of sea-level, Part 4: global cycles of relative changes of sea-level. *American Association of Petroleum Geologists Memoir*, **26,** 83–133.

Van Dam, J.A., Aziz, H.A., Sierra, M.A.A., Hilgen, F.J., van den Hoek Ostende, L.W., Lourens, L.J., Mein, P., van der Meulen, A.J. & Pelaez-Campomanes, P. (2006) Long-period astronomical forcing of mammal turnover. *Nature*, **443,** 687–691.

Van den Bergh, G., Vos, J. & Sondaar, P.Y. (2001) Late Quaternary palaeogeography of mammal evolution in the Indonesian archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **171,** 385–408.

Vrba, E.S. (1992) Mammals as a key to evolutionary theory. *Journal of Mammalogy*, **73,** 1–28.

Wallace, A.R. (1869) *The Malay Archipelago*. Macmillan, London.

Wallace, A.R. (1876) *The geographical distribution of animals*. Macmillan, London.

Warrit, N., Smith, D.R. & Layprayoon, C. (2006) Genetic subpopulations of *Varroa* mites and their *Apis cerana* hosts in Thailand. *Apidologie*, **37,** 19–30.

WCMC (World Conservation Monitoring Centre) (1992) *Global biodiversity: status of the earth's living resources*. Chapman & Hall, London.

Whitmore, T.C. (ed.) (1981) *Wallace's line and plate tectonics*. Oxford University Press, Oxford.

Whitmore, T.C. (1984) *Tropical rainforests of the Far East*, 2nd edn. Oxford University Press, Oxford.

Whitmore, T.C. (ed.) (1987) *Biogeographical evolution of the Malay archipelago*. Oxford University Press, Oxford.

Whitmore, T.C. (1998) *An introduction to tropical rain forests*. Oxford University Press, New York.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Reviews of Ecology Evolution & Systematics*, **36,** 519–539.

Wikramanayake, E., Dinerstein, E., Loucks, C., Olson, D., Morrison, J., Lamoreux, J., McKnight, M. & Hedao, P. (2002) *Terrestrial ecoregions of the Indo-Pacific: a conservation assessment*. Island Press, Washington, DC.

Wilson, E.O. & Brown, W.L. (1953) The subspecies concept and its taxonomic applications. *Systematic Zoology*, **2,** 97–111.

Wilson, D.E. & Reeder, D.M. (eds) (2005) *Mammal species of the world*, 3rd edn. Johns Hopkins University Press, Baltimore, MD.

Woodruff, D.S. (2003a) Location of the Indochinese–Sundaic biogeographic transition in plants and birds. *Natural History Bulletin of the Siam Society*, **51,** 97–108.

Woodruff, D.S. (2003b) Neogene marine transgressions, paleogeography and biogeographic transitions on the Malay Peninsula. *Journal of Biogeography*, **30,** 551–567.

Woodruff, D.S. & Woodruff, K.A. (2008) Paleogeography, global sea level changes and the future coastline of Thailand. *Natural History Bulletin of the Siam Society*, **56**(2)**,** 1–24.

Wright, J.D., Miller, K.G., Sheridan, R.E., Uptegrove, J., Cramer, B.S. & Browning, J.V. (2008) Late Pleistocene sea level on the U.S. mid-Atlantic margin: implications to eustasy and deep-sea temperature. *Global and Planetary Change SEALAIX*, doi: 10.1016/j.gloplacha.2008.03.013.

Zhang, R. (2000) *Distribution of mammalian species in China*. China Forestry Publishing, Beijing.

Ziegler, T., Abegg, C., Meijaard, E., Perwitasari-Farajallah, D., Walter, L., Hodges, J.K. & Roos, C. (2007) Molecular phylogeny and evolutionary history of Southeast Asian macaques forming the *M. silenus* group. *Molecular Phylogenetics and Evolution*, **42,** 807–816.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Current and probable historical distributions of species recorded by degree of latitude.

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BIOSKETCHES

David Woodruff has conducted collaborative research on the evolution and conservation of animal species in Thailand for 20 years. A noninvasive study of genetic erosion in mammal populations in fragmented rain forest patches near the Isthmus of Kra led to the preparation of a series of analyses on the Indochinese–Sundaic biogeographical transition, the fifth of which is presented here. Webpage: http://www-biology.ucsd.edu/faculty/woodruff.html.

Leslie Turner completed her Master's at Duke University, where she studied primate evolutionary genetics, and her PhD at the University of California San Diego (2007), where she studied reproductive protein evolution and speciation in deer mice (*Peromyscus*). She is continuing to pursue research on the genetic basis of reproductive isolation in rodents as a post-doctoral fellow at Harvard University and the Max Planck Institute.

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