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## Environments, terrestrial ecosystems and mammalian species: An overview of Southeast Asia in the Late Pleistocene

*Anne-Marie Bacon and Pierre-Olivier Antoine*

### Abstract

During the highly dynamic, climate-driven Pleistocene period, mammalian communities from the Indomalayan region faced major environmental changes. In the late Middle to the Late Pleistocene, the Sunda Shelf surface was particularly affected under the influence of multiple parameters—tectonic, eustatic and climatic—leading to alternating phases of exposure and flooding. The fossil faunas from the Padang Highlands in Sumatra discovered by Eugène Dubois illustrate episodes of species dispersal during the periods of exposure of land areas. Here, we analyse the assemblages of Sibrambang and Lida Ajer in the light of a selection of mammalian faunas located in continental and insular regions during two possible periods of dispersion, c. 130 ka at the Marine Isotope Stage (MIS) 6–5 transition and c. 71 ka at the beginning of MIS 4. We investigated (1) the taxonomic composition of herbivore communities in terms of archaic versus modern taxa; (2) the functions of ecosystems, based on the type of digestive physiology of herbivores (ruminant versus non-ruminant) per body mass category; and (3) the relative abundance of some Artiodactyla, Perissodactyla and Primates. Our results show that, at the time of the earliest range expansion of modern species into Sundaland c. 130 ka, diverse functional herbivore communities containing local archaic taxa coexisted in Southeast Asia. Overall, Sundaland seems to have always been less rich in large-bodied herbivore diversity compared to the Indochinese subregion, most probably reflecting the lower heterogeneity of Sundaic ecosystems, even during the period of large connections between land masses. By comparing Duoi U’Oi, Vietnam (*Homo* sp.; 70–60 ka) and Lida Ajer, Sumatra (*Homo sapiens*; 73–63 ka), two sites located at different latitudes, the results underscore the different availability to humans of herbivore prey species depending on their relative abundance in highly forested habitats.

*Keywords:* Megafauna, herbivore, Indochinese peninsula, Sundaland, mammalian communities, hominins

### Abstrak

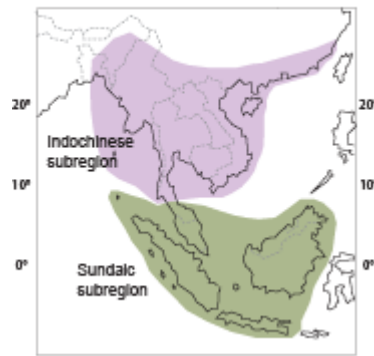
Selama periode Pleistosen yang sangat dinamis akibat pengaruh iklim, komunitas mamalia dari wilayah Indo-Melayu menghadapi perubahan lingkungan yang sangat kontras. Pada akhir Pleistosen Tengah hingga Akhir, permukaan Paparan Sunda sangat dipengaruhi oleh beberapa parameter—tektonik, eustatik, dan iklim—, yang menyebabkan perselingan fase daratan dan genang laut. Fauna dari Dataran Tinggi Padang di Sumatra yang ditemukan oleh Eugène Dubois menggambarkan episode-episode penyebaran spesies melalui periode-periode wilayah daratan yang terbuka ini. Di sini, kami menganalisis kumpulan fosil dari Sibrambang dan Lida Ajer berdasarkan seleksi fauna mamalia yang terletak di wilayah kontinental dan kepulauan, selama dua kemungkinan periode penyebaran, c. 130 ka pada transisi Tahap

Isotop Laut/*Marine Isotope Stage* (MIS) 6–5 dan c. 71 ka pada awal MIS 4. Penelitian kami meliputi (1) komposisi taksonomi komunitas herbivora; (2) fungsi ekosistem berdasarkan jenis fisiologi pencernaan (ruminansia terhadap non-ruminansia) menurut kategori massa tubuh; dan (3) kelimpahan relatif beberapa taksa Artiodactyla, Perissodactyla dan Primata. Hasil kami menunjukkan bahwa pada saat penyebaran paling awal spesies modern di Sunda c. 130 ka, beragam komunitas herbivora fungsional dengan taksa primitif lokal hidup berdampingan di Asia Tenggara. Secara keseluruhan, Sundaland tampaknya selalu kurang kaya akan keanekaragaman herbivora bertubuh besar dibandingkan dengan subkawasan Indocina, kemungkinan besar mencerminkan heterogenitas ekosistem Sunda yang lebih rendah, bahkan selama periode hubungan besar antara daratan. Dengan membandingkan Duoi U’Oi, Vietnam (*Homo* sp.; 70–60 ka) dan Lida Ajer, Sumatera (*Homo sapiens*; 73–63 ka), dua lokasi yang terletak di garis lintang berbeda, hasilnya sangat jelas menunjukkan adanya perbedaan keterdapatannya spesies mangsa herbivora bagi manusia, berdasarkan kelimpahan relatif mereka di habitat hutan lebat.

*Kata kunci:* Megafauna, herbivora, Indochina, Sundaland, komunitas mamalia, hominin

## Introduction

The deposits at Lida Ajer, Sibrambang and Djambu caves are, so far, the most prolific fossiliferous deposits recovered in the karstic caves of the Padang Highlands in Sumatra. Assemblages were collected by Eugène Dubois between 1887 and 1890 as part of his visionary project to find human ancestors in Southeast Asia (Wood 2020; Albers et al. this volume). Both the selective preservation of these remains, which consist mainly of isolated teeth of large mammals embedded in cemented breccia, and the rarity of associated hominin remains (no human bones or teeth are mentioned in the locality of Sibrambang, but Lida Ajer yielded, at that time, two human teeth), prompted Dubois to relocate to the island of Java, which had different depositional contexts and environments (Dubois 1894). From the 1940s onwards, Dirk Albert Hooijer described and inventoried the species in the abovementioned Sumatran assemblages (e.g. Hooijer 1946a, 1946b, 1947, 1948, 1960, 1962), a work continued by John de Vos (de Vos 1983; Long et al. 1996). The faunas of these caves are comparable with each other and fully modern in terms of species composition, with most of the mammals still living in Sunda (Figure 7.1). Sunda was a floristic and faunistic geographic unit whose northern limit separated it from the Indochinese subregion and was initially placed in the Malay Peninsula, close to the Isthmus of Kra, by Alfred Russel Wallace (1860). Further east, the so-called Wallace’s Line separates Sunda from Wallacea, and extends northward between the Indonesian archipelago and the Philippines, excluding Palawan, as drawn by Thomas Henry Huxley (1868). The patterns of the distribution of species throughout the Indochinese peninsula and Sunda are profoundly affected by a north–south temperature gradient, and the boundary between the regions varies according to the type of plants or animals studied, within a transitional zone between the Kangar-Pattani Line at c. 6°N and the Isthmus of Kra at c. 14°N (Woodruff 2010). How this boundary fluctuated during the Pleistocene glacial cycles is unknown, but several works have demonstrated that during the Late Pleistocene it was probably south of the Isthmus of Kra (Suraprasit et al. 2019; Tougaard and Montuire 2006; Woodruff and Turner 2009). Today, Southeast Asia has one of the highest percentages of plant and vertebrate endemic species, especially in the Sundaic and Indo-Burmese subregions (as defined by Myers et al. 2000), which have been identified as biodiversity hotspots. The biodiversity of large mammals in the Indochinese and Sundaic subregions over the last 500,000 years is still poorly known.



**Figure 7.1: Southeast Asian map showing the limits of the biogeographic Indochinese and Sundaic subregions.**

Source: Map by authors.

The age range of the historical faunas from the Padang Highlands was first estimated to be recent or Late Holocene. Based on biochronology, it was placed at c. 80–60 ka (de Vos 1983), or c. 81–70 ka according to relative dating using amino-acid racemisation (AAR) on bones (Skelton 1985). More recently, however, new dating, using coupled uranium-series (U-series) and electron spin resonance (ESR) techniques on mammalian teeth, and luminescence and U-series techniques on sediments and speleothems in various caves in Sunda, including Lida Ajer, has led to a precise chronological framework for the assemblages and thus to a precise timing for the dispersal of modern species onto the exposed continent. The new, robust age range of the fauna of Lida Ajer, c. 73–63 ka (Westaway et al. 2017), which was reconfirmed recently on the basis of the dating of the fossiliferous Unit 5 within this cave at 71–68 ka (Louys et al. 2022), postdates by about 50 ka the oldest expansion of modern taxa in Sunda. The timing of this event has been specified following the discovery of an in situ fauna at the Gunung Dawung site, also named Punung III, on Java (Storm et al. 2005; Storm and de Vos 2006), which was dated to c. 128–118 ka using luminescence and U-series methods on breccia deposits and flowstones (Westaway et al. 2007). The site, located near the village of Punung, produced a modern fauna comparable to those collected by Ralph von Koenigswald in the early 1930s (von Koenigswald 1939) in the Punung I and Punung II karstic localities (Badoux 1959).

Recently, the discovery of a faunal assemblage in a newly discovered cave of the Padang Highlands, Ngalau Gupin, with an estimated age range of 160–115 ka based on U-series and ESR dates of mammalian teeth from the breccia deposits coded NG-A (Smith et al. 2021), confirmed the antiquity of this event, which potentially extended into Marine Isotope Stage (MIS) 6 (191–130 ka; Lisiecki and Raymo 2005). Shortly before this discovery, the time range of the resulting turnover that led to the replacement of archaic taxa in Sunda was also reassessed based on a new geochronological and palaeontological study of the Ngandong site in Java (Rizal et al. 2020). Rizal et al. introduced a new chronological framework, based on U-series and ESR dating on teeth, for the vertebrate bed (facies C) in which *Homo erectus* was discovered during the 1930s. Dated to c. 117–108 ka, this bone bed still mostly contained archaic taxa endemic to the region (Rizal et al. 2020). These data suggest that this turnover took place in Java c. 120 ka, close to the oldest limits previously suggested, c. 135–70 ka (van den Bergh et al. 2001) or c. 120–90 ka (Storm et al. 2005). This timing is consistent with palaeoclimatic records for the western region of Java, which indicate shifts towards very warm and humid conditions c. 126 ka, based on sedimentological and palynological data

from the Bandung basin, Java (van der Kaars and Dam 1995). One question remains, however: did this event also coincide with an early episodic spread of *Homo sapiens* into Southeast Asia as previously proposed (Storm et al. 2005)? The modern-human nature of the single remaining tooth (an upper third premolar) from the 1930s collections from Punung has been challenged (Polanski et al. 2016), and the possible intrusion of recent human remains into older stratigraphic levels has also been suggested (Kaifu et al. 2022).

There is still a need to determine precise ages for the Djambu and Sibrambang faunas (Louys et al. this volume). The fully modern nature of Sibrambang—the collection contains more than 3,000 specimens, without any archaic elements—suggests that this site probably postdates Ngalau Gupin (c. 160–115 ka; Smith et al. 2021), but, if we accept the AAR age of c. 81–70 ka proposed for Sibrambang by Skelton (1985), it could pre-date Lida Ajer (c. 73–63 ka; Westaway et al. 2017). New investigations at Ngalau Sampit, a historical Dubois site, confirmed the presence of MIS 5 faunas on Sumatra >105 ka based on U-series/ESR dating of teeth at  $105 \pm 9$  ka and post-infrared infrared-stimulated luminescence dating of breccia at  $93 \pm 6$  ka (Duval et al. 2021).

In a recent analysis, we showed that, during the Late Pleistocene, extensive rainforests coincided with cold stages in northern latitudes of the Indochinese peninsula (Bacon et al. 2021). Indeed, our results, based on carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) records from a large spectrum of mammals from northern Laos and Vietnam, underscored that two phases of  $\text{C}_3$ -dominated vegetation occurred, during MIS 6 and MIS 4 (191–130 ka and 71–57 ka respectively; Lisiecki and Raymo 2005). In contrast, MIS 5, an interglacial stage (130–71 ka; Lisiecki and Raymo 2005), was marked by the presence of more open environments ( $\text{C}_3$ – $\text{C}_4$  intermediate forests and woodlands and  $\text{C}_4$  savanna-type habitats), in conjunction with the contraction of closed-canopy forests. The two  $\text{C}_3$  phases indicated by our results, based on the relative similarity in the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of the faunas of Coc Muoi (148–117 ka; Bacon et al. 2018a) and Duoi U’Oi (70–60 ka; Bacon et al. 2008, 2015, 2018b), have been associated with two large drops in monsoon intensity: in oxygen isotope substage 6.2 and at the onset of stage 4 respectively, based on the curves of  $\delta^{18}\text{O}$  records from the speleothems in the Sanbao, Dongee and Hulu Chinese caves (Wang Y. et al. 2008). The oldest of these climatic and vegetational shifts with extensive forests on the mainland might coincide with the end of the penultimate glacial phase at c. 130 ka, when the sea-level was low and modern faunas dispersed into Sunda, as possibly illustrated by Ngalau Gupin in the Padang Highlands (160–105 ka; Duval et al. 2021; Smith et al. 2021). However, whether this synchronicity occurred remains speculative.

The climate shift at the beginning of MIS 4 (71–57 ka), short and abrupt with a notable change in the amount of precipitation and a temperature drop of c. 5–6°C (Wang Y. et al. 2008), was severe enough to lead to a turnover of plant taxa, with dense rainforests being replaced by forests dominated by conifer (Zheng and Lei 1999). New herbivore populations that might have dispersed into the new forested biome include those of Duoi U’Oi (70–60 ka), which were better adapted to this new environment (Bacon et al. 2021). At the latitude of Duoi U’Oi in northern Vietnam, the forest expansion would have occurred in opposite phase with the savanna expansion through the central north–south corridor in Sundaland (Bird et al. 2005). In contrast, for the same time period in southwestern Sumatra, the palynological record from deep-sea cores dated to c. 71 ka does not indicate major changes in vegetation, showing a predominance of Dipterocarpaceae rainforests and a climate, which remained humid as in the preceding interglacial MIS 5 (van der Kaars et al. 2010). This underscores the sharp climatic contrast between Duoi U’Oi (70–60 ka; Bacon et al. 2015) and Lida Ajer (73–63 ka; Westaway et al. 2017).

Thus, Indochinese and Sundaic areas share a common biogeographical history (see also Heaney 1986; Woodruff 2010). In relation to the period analysed herein—from the late

Middle Pleistocene to the Late Pleistocene—simulation of the landscape evolution using various parameters, including tectonics, eustatic sea-level variations, and rainfall, has shown how the Sunda Shelf surface was affected by them, with long phases of exposure (>80% exposed) that alternated with short partially flooded (>50% exposed) and fully marine periods (Salles et al. 2021: figure 1). The faunas from Ngalau Gupin, Sibrambang and Lida Ajer in Sumatra, along with those from Punung in Java, might reflect at least two episodes of species dispersal via connected land areas; a 40 m drop in sea-level was sufficient to connect the Thai-Malay Peninsula, Sumatra, northwestern Java and Borneo (van den Bergh et al. 2001; van der Geer et al. 2021).

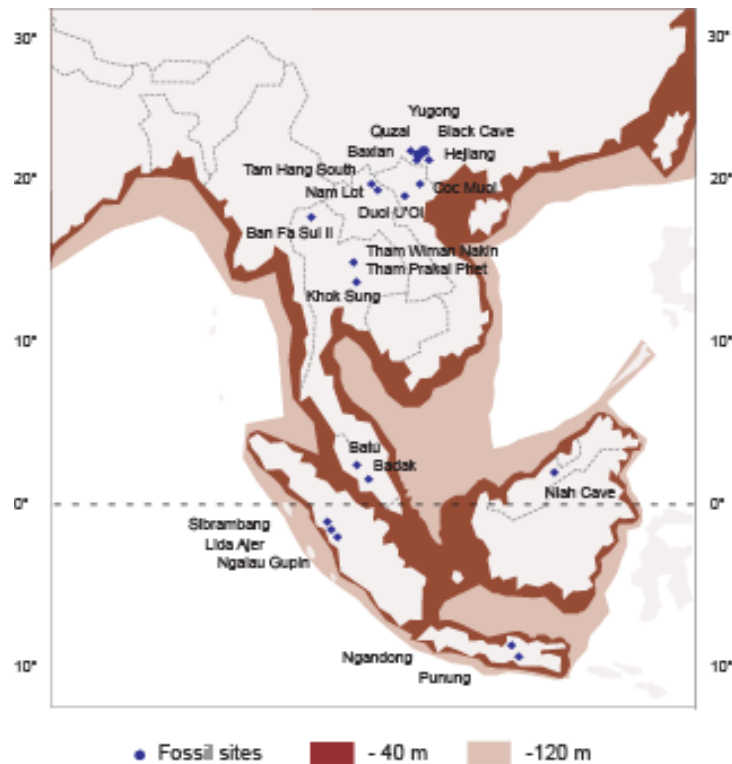
Given this background, the present chapter presents an overview of Dubois' Sumatran Pleistocene faunal assemblages—from Sibrambang and Lida Ajer—in the light of a selection of 23 mammalian faunas that inhabited continental regions (Southern China, Laos, Vietnam, Thailand and Malaysia) and insular regions (Sumatra, Java, and Borneo) at the MIS 6–5 transition and at the beginning of MIS 4. The sites examined here are limited to those with new chronologies (using various geochronological techniques on fossil remains and/or sediments) and/or that have been subjected to new investigations (carbon and oxygen isotopic analyses of mammalian teeth). Therefore, the present chapter does not deal with old collections that have already been comprehensively explored (e.g. Louys 2012; Louys and Meijaard 2010; Louys et al. 2007; Tougaard and Montuire 2006; van den Bergh et al. 2001). In undertaking this overview of past Southeast Asian mammalian faunas, we attempted to explore how terrestrial environments, ecosystems and species changed during the period c. 500–40 ka; our exploration focuses on primary consumers. We analysed the structure of communities of herbivores at various points in space and time by investigating: (1) the taxonomic composition of assemblages (archaic versus modern taxa from Artiodactyla, Perissodactyla and Proboscidea); (2) the functioning of ecosystems, based on the type of digestive physiology of herbivores (ruminant versus non-ruminant) per body mass category; and (3) the relative abundance of taxa among Artiodactyla, Perissodactyla and Primates, using the minimum number of individuals (MNI) as the best ecological indicator. For the purposes of this review, we also used carbon and oxygen isotope data from fossil faunas as complementary sources of information on palaeodiets and palaeoenvironments.

Faunal assemblages, although rare and poorly preserved, are nevertheless critical for understanding *H. sapiens*' adaptation across Southeast Asia. Therefore, this analysis also provides valuable insights into the environmental conditions during the dispersal and settlement of *H. sapiens* around 70 ka by comparing the data from Duoi U'Oi and Lida Ajer. Sediment infill chronology for Duoi U'Oi indirectly dates two hominin teeth (*Homo* sp.) to 70–60 ka (Bacon et al. 2008, 2015, 2018b), and that for Lida Ajer constrains two modern human teeth (*H. sapiens*) to 73–63 ka (Westaway et al. 2017). Our overview gave us the opportunity to compare the resource availability of herbivore species at Duoi U'Oi and Lida Ajer and, therefore, to investigate aspects of human foraging behaviour in different latitudinal conditions and different forested habitats (Bacon et al. 2021; Louys et al. 2022; Roberts et al. 2016). We also attempted to assess potential hunting pressure by predators, using mortality profiles of Rhinocerotidae, Tapiridae, Cervidae and Suidae, including novel results on Lida Ajer (for *Tapirus indicus* and *Sus* spp.).

## Materials

### Selected faunas

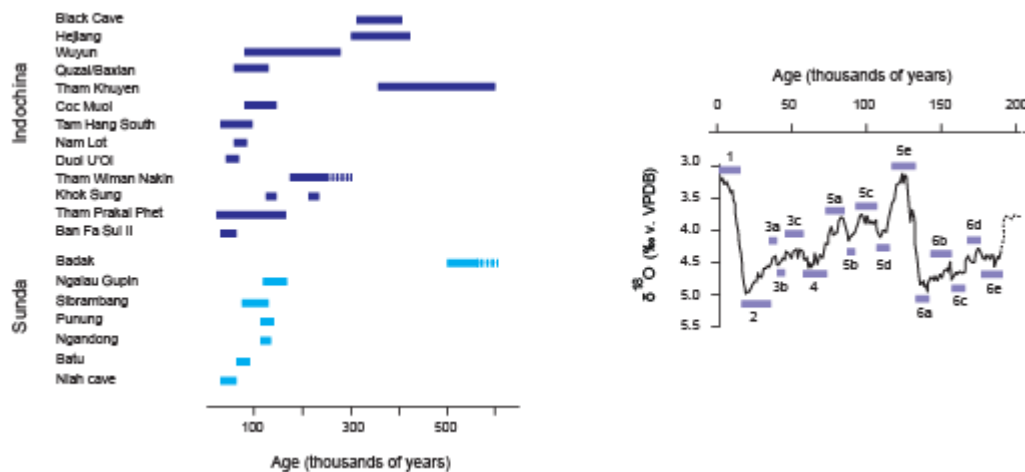
Our review surveyed published faunas from 23 Southeast Asian continental and insular sites; the details of their location and chronology are shown in Appendix 7.1 and Figures 7.2 and 7.3. The species or genus compositions of the assemblages of large mammals are listed in Appendices 7.2 and 7.3. The record of  $\delta^{18}\text{O}$  values from benthic foraminifera presented in Figure 7.3, as indicators of temperatures of oceans, shows how climates fluctuated for the last ~200,000 years, at a global scale (Lisiecki and Raymo 2005; Railsback et al. 2015).



**Figure 7.2: Locations of the Southeast Asian sites included in the study.**

Note: We have represented the extent of land area during sea-level changes of -40 m and -120 m relative to the current level (Sathiamurthy and Voris 2006).

Source: Map by authors.



**Figure 7.3: (A) Chronology of Southeast Asian sites included in the study and (B) chart of benthic foraminifera  $\delta^{18}\text{O}$  data during the Marine Isotope Substages for the last 200,000 years.**

Note: In the chart (B), the horizontal bars labelled 1, 2, 3a and so on represent the Marine Isotope Substages. On the y-axis, oxygen isotopic values are presented in delta 'δ' notation expressed as deviation ‰ compared to the International Standard Vienna Pee Dee Belemnite (VPDB).

Source: Chronology by authors; chart modified from Railsback et al. (2015: figure 3).

### Depositional contexts and composition of assemblages

With the exception of Ngandong, Java, where fossil bones are found in a terrace context formed over the Middle Pleistocene by successive alluvial deposits of the Solo River (Rizal et al. 2020), and Khok Sung, Thailand, where the bone bed is associated with the Mun River terrace deposits (Duval et al. 2019; Suraprasit et al. 2018), the faunas studied here come from breccias in a karstic context. Due to differences in depositional processes, the two sites located in river valleys yielded some complete skeletal elements, whereas the cave sites located in karsts produced isolated teeth and very occasionally bones. The latter have been associated with taphonomic and geological processes of transport and deposition inside the karsts (the taphonomic processes being the actions of biotic and abiotic agents that modified the skeletal remains). In most cases, the cave-context remains have been transported throughout the karstic network under high-energy hydrological conditions (rainfalls or river flooding) that led to the loss of the smallest elements.

This complex action of biotic and abiotic agents generated preservation biases, and assemblages from cave sites consisted of isolated teeth—the majority gnawed by porcupines—from a wide array of mammals ranging from c. 5 kg to c. 5,000 kg belonging to Artiodactyla, Perissodactyla, Proboscidea, Carnivora, Primates and Rodentia. First, the capacity of porcupines to collect a wide range of remains of predated or scavenged animals, either partial remains (mandibles of large ungulates like water buffaloes and maxillae of smaller ones like muntjacs) or complete jaws (of wild pigs) (Brain 1981) appears to be the cause of the differing quantitative representation of teeth within Artiodactyla, Perissodactyla and Proboscidea (Bacon et al. 2015). Second, the taxonomic groups also appear to be differently represented. In a previous investigation (Bacon et al. 2015), we mentioned that the species diversity of small mammals (up to c. 5 kg) is frequently underestimated, especially for carnivores and primates versus ungulates. In such assemblages, this underreported diversity coincides with the different representation of elements between groups, giving the false impression of a low abundance of small species and, conversely, a high abundance of



larger species (Louys 2012). This is particularly the case for small carnivores. Current subtropical and tropical habitats harbour the greatest richness of small carnivore species, with up to 29 inventoried species, at mid-latitudes (Corbet and Hill 1992) (Table 7.1), a level of diversity rarely found in fossil assemblages. Another bias in species diversity exists, which is of a taxonomic nature and tied to the difficulty of identifying the different species of small primates (macaques, gibbons, and langurs) and carnivores. Finally, the Dubois historical collections, particularly that of Sibrambang, may have been affected by a recovery bias due to the discarding of tooth fragments (Bacon et al. 2015).

### **Data analysed**

This review uses a combination of mostly published data and newly analysed data. The original data concern the taxonomic revision of Perissodactyla of Lida Ajer, Sibrambang and Punung, along with the estimate of dental eruption sequences and wear stages of *Tapirus indicus intermedius* and *Sus* sp. (*S. scrofa* and *S. barbatus*) from the collection of Lida Ajer. They were collected during 2013 by the authors at Naturalis Biodiversity Center, Leiden, the Netherlands. The tapir specimens in this collection include 24 permanent and 12 deciduous dental specimens, whereas the pig specimens include 78 permanent molars.

**Table 7.1: Species richness of current mammalian faunas from China, Myanmar, Vietnam, Thailand, Malaysia, Sumatra, Borneo and Java in the six orders of large mammals, following a north–south gradient.**

	Southern China 25–30° N	Central Myanmar 20–25° N	Northern Vietnam 20–25° N	Northern Thailand 15–20° N	Southern Malaysia 0–5° N	Northern Sumatra 0–5° N	Northern Borneo 0–5° N	Central Borneo 0–5° S	Central Java 5–10° S
Artiodactyla	6	10	6	8	8	7	7	3	5
Perissodactyla	—	2	1	2	2	2	1	—	1
Proboscidea	—	1	—	1	1	1	—	—	—
Carnivora	14	23	26	29	27	24	18	9	14
Primates	3	4	8	6	7	9	9	7	4
Rodentia	1	2	2	2	1	1	1	1	1

Note: Richness is defined as number of species. Among Primates, lorises and tarsiers not recovered in fossil assemblages have been excluded, as have other small mammals, such as moles, shrews, flying lemurs and bats. Among Rodentia, we included only the large rodents (*Hystrix* and *Atherurus*).

Source: Data from Corbet and Hill (1992).

## Methods

Our analysis focused on the taxonomic composition of herbivores (Artiodactyla, Perissodactyla and Proboscidea) by examining the proportion of archaic versus modern taxa at the species or genus level within each fauna, based on data listed in Appendices 7.2 and 7.3. Taxa defined at upper ranks (subfamily, family or order) have been excluded, with the exception of the Rhinocerotidae. ‘Archaic’ here means an extinct, fossil taxon, in contrast to ‘modern’, which means a current taxon, for both genera or species.

We plotted the type of digestive physiology, ruminant versus non-ruminant (hindgut fermenting herbivore) by body mass category, using the categories A (18–80 kg), B (80–350 kg), C (350–1,000 kg) and D (>1,000 kg) (Faith et al. 2019), as in a prior analysis of Southeast Asian ecosystems (Bacon et al. 2021) (Appendices 7.2 and 7.3). These indicators allowed us to describe the functional diversity of terrestrial ecosystems by time period: MIS 6 (130–123 ka) and earlier stages up to c. 500 ka, MIS 5 (123–71 ka) and MIS 4 (71–29) (Lisiecki and Raymo 2005). We also considered the carrying capacity of ecosystems to be the maximum load, that is, the largest amount of a given group of organisms that can sustainably feed using the resources locally available (Del Monte-Luna et al. 2004). We analysed the mammalian communities by period: MIS 6 (130–123 ka) and earlier stages up to c. 500 ka, MIS 5 (123–71 ka) and MIS 4 (71–29 ka) (Lisiecki and Raymo 2005).

Most of the reviewed assemblages are composed of isolated teeth; one tooth is considered here as one specimen. Therefore, to estimate the relative abundance of some Artiodactyla, Perissodactyla and Primates along a north–south latitudinal gradient, we used a MNI based on the frequency of the most common permanent and deciduous teeth, whether left or right, upper or lower, by taxon (species or genus) (Mayr 1942).

To investigate the potential signature of predators, including hominins, on prey species from Duoi U’Oi and Lida Ajer, we used a combination of published and new analysed data. The previously published data are the three-cohort profiles (showing the proportions of the juvenile, subadult and adult/mature remains) of *Rusa unicolor*, *Sus scrofa* and Rhinocerotidae for Duoi U’Oi (Bacon et al. 2015), and those of Rhinocerotidae for Lida Ajer (Bacon et al. 2018a). In these publications, we used crown height measurements as wear stages to estimate the age of *R. unicolor* individuals of Duoi U’Oi, divided into 10 age classes (10% lifespan intervals), following Klein et al. (1981). We then grouped the individuals into three cohorts: infants (< c. 1.6 years), young adults (c. 1.6–3.2 years), and mature and old adults (c. 3.2–16 years).

In the mortality profile of *S. scrofa* from Duoi U’Oi, the ages of individuals were distributed into 13 age classes [A–N], based on occlusal wear stages of lower molars (m1/m2/m3) following the criteria defined by Grant (1982). The three cohorts represented piglets (up to c. 14 months), young adults (up to c. 26 months) and mature and old adults (>6 years).

For Rhinocerotidae from Lida Ajer and Duoi U’Oi, we used wear stages of all teeth, permanent and deciduous, lower and upper, to characterise age classes following a procedure adapted from Hillman-Smith et al. (1986). The three cohorts—calves (<3 years), subadults (3–6 years) and adults (>6 years)—coincide with the age classes—0–V, VI–VIII and IX–XVI respectively—defined by these authors.

In the present analysis, we merged the juvenile and subadult cohorts of recent populations of *Rhinoceros unicornis* and *Rusa unicolor*, and of fossil samples of rhinocerotids and *R. unicolor*, in order to compare the results for two versus three cohorts for all the concerned taxa consistently, as data were merged a priori for juveniles and subadults of *Sus scrofa* from Nagarhole and Pench National Parks that we here use for comparison (Biswas and Sankar 2002; Karanth and Sunquist 1995). Given the scope of our comparisons (i.e. multiple usage

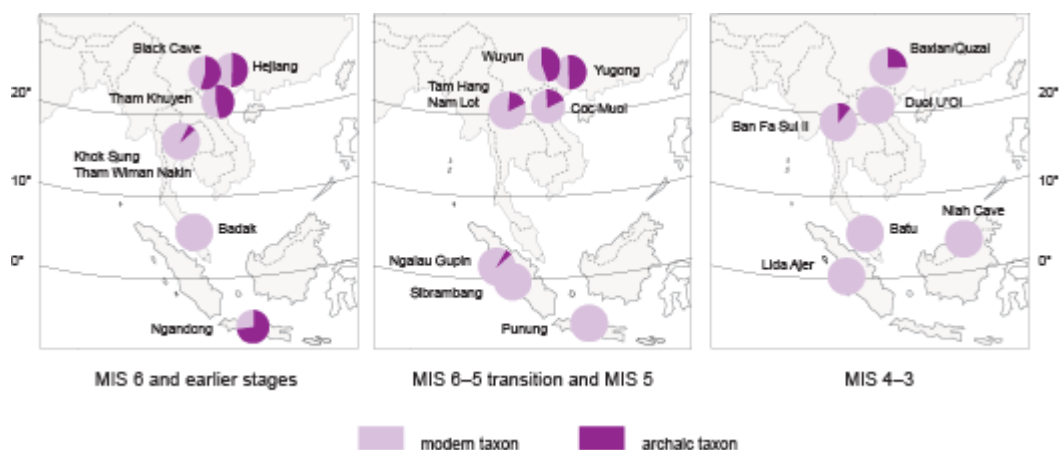
of a simple test), we did not use Bonferroni corrections for the relevant  $\chi^2$  tests, following the recommendations of Sharpe (2015).

Concerning the original age profiles of *Tapirus indicus intermedius* from Lida Ajer presented here, the age of individuals was estimated using the dental eruption sequence and wear stages defined for a natural lowland population of *Tapirus terrestris* by Maffei (2003), and the individuals were then divided into three cohorts: calves (<1 year), subadults (1–2 years), and adults (>2 years). For the pigs, *Sus* sp. (*S. scrofa* and *S. barbatus*), recovered at the site, the protocol used to build the novel age profile was the same as described by Bacon et al. (2015).

## Results

### Proportion of archaic versus modern ungulates and proboscideans

Figure 7.4 illustrates the proportion of archaic taxa versus modern ungulate and proboscidean taxa based on the data compiled in Appendices 7.2 and 7.3. For MIS 6 and earlier stages (before c. 120 ka), the fossil records from the continental sites showed various mixed compositions: 41.6% ( $n = 11$ ) of the taxa were archaic at Tham Khuyen (*Sus lydekkeri*, *Megatapirus augustus*, *Rhinoceros sinensis*, *Stegodon orientalis*, *Palaeoloxodon namadicus*), 50% ( $n = 8$ ) at Hejiang and 54.5% ( $n = 11$ ) at Black Cave (*Dicoryphochoerus ultimus*, *Megalovis guangxiensis*, *S. bijiashanensis*, *M. augustus*, *R. sinensis*, *S. orientalis*). In contrast, the taxa from sites further south on the mainland, such as Tham Wiman Naking ( $n = 15$ ) and Khok Sung ( $n = 13$ ), were 100% modern or little archaic (7.6%). In the insular Java, the Ngandong ungulate and proboscidean fauna was composed of 73% ( $n = 11$ ) archaic species (*Axis lydekkeri*, *Bibos palaeosondaicus*, *Bubalus palaeokerabau*, *Sus macrognathus*, *S. brachygnathus*, *Hexaprotodon sivajavanicus*, *Elephas hysudrindicus*, and *Stegodon trigonocephalus*) with a high level of endemism superimposed.



**Figure 7.4: Proportion of archaic taxa (extinct genera or species) versus modern taxa among ungulates and proboscideans in fossil faunas.**

Note: We considered three time periods: MIS 6 (130–123 ka) and earlier stages up to c. 500 ka, MIS 5 (123–71 ka) and MIS 4 (71–29 ka). MIS = Marine Isotope Stage.

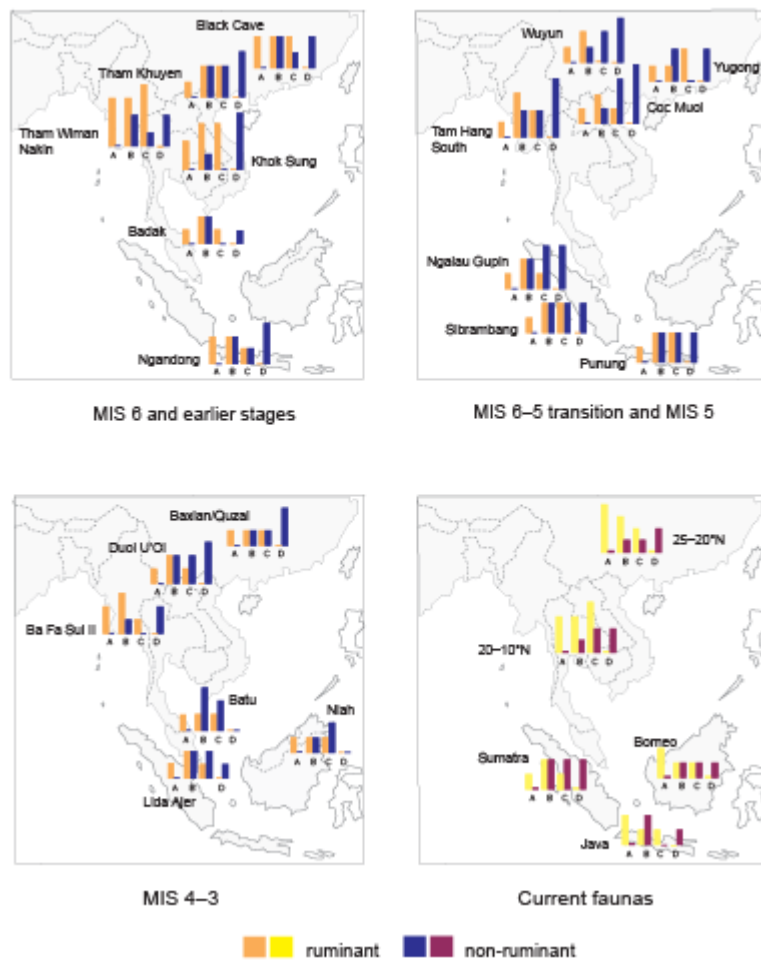
Source: Maps by authors, using data compiled in Appendices 7.2 and 7.3.

We will now consider MIS 5 and the transition from MIS 6 to MIS 5. The mainland ungulate faunas from this period were represented in various local assemblages. In China, Yugon's ungulate taxa ( $n = 8$ ) were 62.5% archaic (*M. augustus*, *S. orientalis*, *S. peii*, *S. xiaozhu*, *Leptobos* sp.) and Wuyun's ( $n = 9$ ) were 44.4% archaic (*M. augustus*, *S. orientalis*, *Tapirus sinensis*); whereas the assemblages from sites in the more southern latitudes of Laos and Vietnam harboured fewer archaic elements, with 16.6% ( $n = 12$ ) at Coc Muoi (*M. augustus*, *Stegodon* sp.), 14.2% ( $n = 14$ ) at Tam Hang South (*M. augustus* and *Stegodon* sp.) and 9% ( $n = 11$ ) at Nam Lot (*S. orientalis*). The centre of the Malay Peninsula did not contain any sites representing this transition period. On Sumatra, Ngatau Gupin's ungulate fauna showed a similarly low percentage of archaic taxa (8%,  $n = 12$ , representing a single archaic taxon, the hippopotamus *Hexaprotodon* sp.), whereas Sibrambang's appeared 100% modern. From MIS 4 onwards, the mainland herbivores were almost entirely modern, but there were some areas where *Stegodon* may have persisted locally, such as those of Ban Fa Sui II (12.5%;  $n = 8$ ) and, further north, Baxian, where *S. orientalis* and the giant tapir *M. augustus* are recorded (25%,  $n = 8$ ). It should be added, however, that the Baxian site not dated accurately could be older than MIS 4. Given the available data, the ungulate fauna on the Greater Sunda Islands, Sumatra (Lida Ajer) and Borneo (Niah) appear to have been 100% modern during this period.

### **Diversity and carrying capacity of ecosystems: Ruminants versus non-ruminants**

Figure 7.5 shows the distribution of ruminant versus non-ruminant taxa in fossil faunas by body size category, based on data compiled in Appendices 7.2 and 7.3. Despite limitations imposed by a small dataset, differences in sample size, and taxonomic constraints on the differentiation of taxa within Muntiacinae, medium-sized Cervidae and large Bovidae at the species level, three main trends emerge regarding the period studied: (1) The functional diversity of the ecosystems on the mainland was greater overall than of that on the Sunda Shelf; (2) there seems to have been a difference in the carrying capacities of ecosystems between, on the one hand, the Indochinese peninsula and, on the other hand, southern China and Sunda; and (3) there seems to have been a loss of biodiversity in large-bodied mammals from c. 70 ka onward throughout Southeast Asia. Each of these trends will now be considered in the light of our results.

First, the ecosystems on the mainland during the period MIS 6–3 were highly functionally diverse; they were dominated either by large-bodied non-ruminant herbivore taxa (*Rhinoceros*, *Dicerorhinus*, *Elephas*, *Megatapirus*, and *Tapirus* of body size categories C and D), as found in Black Cave, Tham Khuyen, Coc Muoi, Tam Hang South, Duoi U'Oi, Quzai and Baxian, or by medium-sized ruminant taxa (*Muntiacus*, *Cervus*, *Axis*, *Rucervus*, *Capricornis*, and *Naemorhedus* of body size categories A and B), as found in Tham Wiman Nakin, Khok Sung and, to a lesser extent, Ban Fa Sui II. In contrast, in Sunda, the functional diversity of the ecosystems was relatively low, as shown by the proportions of ruminant versus non-ruminant taxa.



**Figure 7.5: Distribution of ruminant and non-ruminant taxa from Southeast Asian sites in fossil and recent faunas, by body size category.**

Note: We considered three time period: MIS 6 (130–123 ka) and earlier stages up to c. 500 ka, MIS 5 (123–71 ka) and MIS 4 (71–29 ka). MIS = Marine Isotope Stage. A: 18–80 kg. B: 80–350 kg. C: 350–1,000 kg. D: >1,000 kg.

Source: Maps by authors, using data compiled in Appendices 7.2 and 7.3.

Second, the carrying capacity of ecosystems on the Indochinese peninsula was shown to be different from that of the ecosystems in southern China and Sunda. This seems to have been the case throughout the period studied. It is particularly notable for MIS 6 and earlier stages, as indicated by the numbers of ungulate and proboscidean species recorded at Khok Sung ( $n = 13$ ) and Tham Wiman Nakin ( $n = 15$ ) compared to the numbers recorded at Black Cave ( $n = 11$ ) in southern China and at Badak ( $n = 6$ ) and Ngandong ( $n = 11$ ) south of the Isthmus of Kra.

This difference remained significant during the MIS 6–5 transition, as indicated by the numbers of ungulate taxa recorded at Coc Muoi ( $n = 12$ ) and Tam Hang South ( $n = 14$ ) compared to the numbers recorded at Wuyun ( $n = 9$ ) and Yugong ( $n = 8$ ) in southern China and Punung ( $n = 9$ ) in Java.

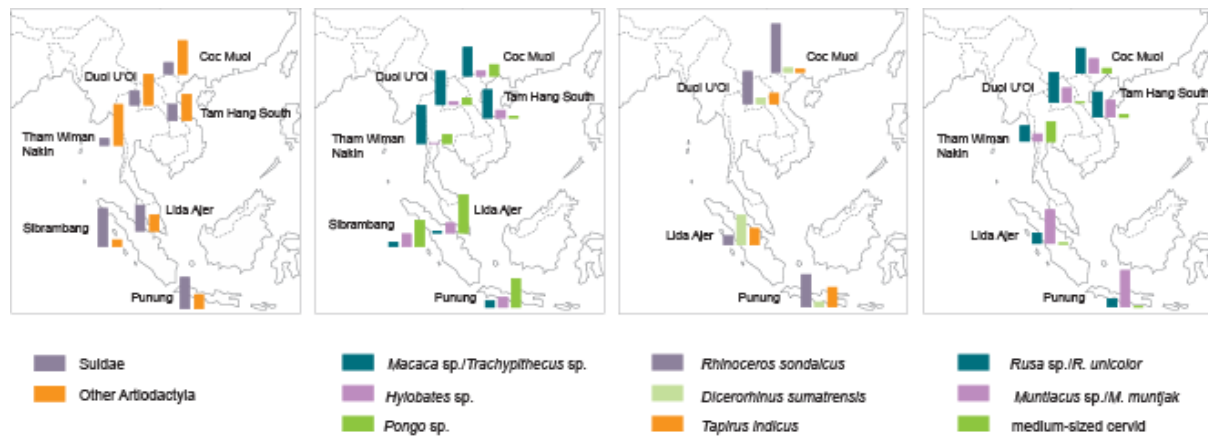
The contrast appears to have been less marked in MIS 4–3. There is not a substantial difference between the numbers of ungulate taxa recorded at Quzai/Baxian ( $n = 8$ ) and Duoi

U’Oi ( $n = 11$ ) and those recorded at Lida Ajer ( $n = 10$ ), Batu ( $n = 10$ ), Niah Cave ( $n = 6$ , without Tragulidae) and Sibrambang ( $n = 11$ ); Ngatau Gupin ( $n = 12$ , without Tragulidae) showed an ungulate diversity close to that of Sibrambang.

Third, when considering the faunas dominated by non-ruminant taxa and comparing MIS 5 and earlier stages with MIS 4–3 (see Figure 7.5 for the stages of the sites and Appendices 7.2 and 7.3 for the species details), we noted a decrease in the species diversity of large-bodied herbivores, in particular, an absence of *Megatapirus* and *Stegodon* specimens at Duoi U’Oi (MIS 4) that did not occur at Tam Hang South, Tham Khuyen or Coc Muoi. We observed a comparable difference between small to medium-sized ruminants (*Axis porcinus*, *Rucervus eldii*, and *Capricornis sumatraensis*) at Tham Wiman Nakin (MIS 6) and Ban Fa Sui II (MIS 4–3), with none recorded at the latter site. Ban Fa Sui II also had a lower diversity of large ruminants, but this result is biased because the species diversity of large Bovidae (*Bos* sp. of body size category C) could not be determined at Ban Fa Sui II, whereas four species were identified at Tham Wiman Nakin.

### Species abundance

As shown in Figure 7.6, the proportions of individuals (MNIs) were used to investigate the abundance distribution of species in fossil faunas from all the studied periods combined, within various taxonomic groups, namely Artiodactyla, Perissodactyla and Primates. The results in Table 7.2 clearly indicate differences following a north–south gradient.



**Figure 7.6: Proportions of individuals (using minimum numbers of individuals or MNIs) showing the relative abundance of taxa within taxonomic groups recorded in fossil Southeast Asian faunas from Marine Isotope Stages 6 to 3.**

Note: Data on southern Chinese faunas are not available.

Source: Maps by authors, using data compiled in Table 7.2.

The habitats at the latitudes of Sunda harboured a relative abundance of pigs (*Sus* sp., up to 85% at Sibrambang), muntjacs (*Muntiacus* sp., 73.5% at Lida Ajer), tapirs (*Tapirus indicus*, 33.3% at Punung), two-horned rhinoceroses (*Dicerorhinus sumatrensis*, 55.5% at Lida Ajer), orangutans (*Pongo* sp., 78% at Lida Ajer), and gibbons (*Hylobates* sp., 30% at Sibrambang). In contrast, the prevailing environments at the latitudes of Coc Muoi, Duoi U’Oi and Tam Hang South, on the Indochinese peninsula, were the preferred habitats of sambar (*Rusa*

*unicolor*, 65.8% at Duoi U'Oi), one-horned rhinoceroses (*R. sondaicus*, 86.3% at Coc Muoi and 66.6% at Duoi U'Oi; versus *D. sumatrensis* with 9% at Coc Muoi and 13.3% at Duoi U'Oi), and monkeys (*Macaca* sp. and *Trachypithecus* sp., 62.5% at Coc Muoi and 75% at Duoi U'Oi).

Two sites stand out within this north–south pattern: Tham Wiman Nakin, whose habitats were favourable to medium-sized cervids (44.4% versus 38.8% of large cervids), and Punung, whose results indicate a greater abundance of *R. sondaicus* (60%) than that of *D. sumatrensis* (6.6%), unlike at Lida Ajer (16.6% versus 55.5%).

Another aspect of the studied ecosystems concerns the body mass distribution of mammals. The warm, humid climates were more suitable for the smaller species within some taxonomic groups: *D. sumatrensis* (900–1,000 kg) versus *R. sondaicus* (1,500–2,000 kg) within the rhinocerotids, and *Muntiacus* sp. (20–28 kg) versus *Rusa unicolor* (180–260 kg) within the cervids (see also Francis 2008).



**Table 7.2: Relative abundance of mammalian taxa, showing minimum number of individuals (MNI) and percentages within Primates, Perissodactyla and Artiodactyla at sites in Sumatra, Java, Laos, Vietnam and Thailand.**

	Lida Ajer	Sibrambang	Punung	Coc Muoi	Duoi U'Oi	Tam Hang South	Nam Lot	Tham Wiman Nakin
Taxa	73–63 ka	~120–80 ka or 73–63 ka	128–118 ka	148–117 ka	70–60 ka	94–60 ka	86–72 ka	>169 ka
Primates								
<i>Macaca sp./ Trachypithecus sp.</i>	2 (2.4%)	17 (13.0%)	4 (16.6%)	5 (62.5%)	18 (75.0%)	10 (71.4%)	5 (83.3%)	7 (77.7%)
<i>Hylobates sp.</i>	16 (19.5%)	39 (30.0%)	6 (25.0%)	1 (12.5%)	2 (8.3%)	3 (21.4%)	—	—
<i>Pongo sp.</i>	64 (78.0%)	74 (56.9%)	14 (58.3%)	2 (25.0%)	4 (16.6%)	1 (7.1%)	1 (16.6%)	2 (22.2%)
Perissodactyla								
<i>Rhinoceros sondaicus</i>	3 (16.6%)	21 (84.0%) <sup>1</sup>	9 (60.0%)	38 (86.3%)	10 (66.6%)	5 (71.4%)	1	— <sup>2</sup>
<i>Dicerorhinus sumatrensis</i>	10 (55.5%)	—	1 (6.6%)	4 (9.0%)	2 (13.3%)	—	—	— <sup>2</sup>
<i>Tapirus indicus</i>	5 (27.7%)	4 (16.0%)	5 (33.3%)	2 (4.5%)	3 (20.0%)	2 (28.5%)	2	1
Artiodactyla								
Suidae	59 (59.5%)	244 (85.0%)	25 (60.9%)	18 (25.3%)	18 (29.0%)	15 (35.7%)	11 (37.9%)	6 (13.0%)
Other Artiodactyla	40 (40.4%)	43 (14.9%)	16 (39.0%)	53 (74.6%)	44 (70.9%)	27 (64.2%)	18 (62.0%)	40 (86.9%)
<i>Rusa sp./R. unicolor</i>	9 (26.4%)	14 (41.1%)	2 (22.2%)	17 (53.1%)	27 (65.8%)	13 (56.5%)	4 (57.1%)	7 (38.8%)
<i>Muntiacus sp./ M. muntjak</i>	25 (73.5%)	20 (58.8%)	7 (77.7%)	11 (34.3%)	14 (34.1%)	9 (39.1%)	3 (42.8%)	3 (16.6%)

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Medium-sized cervid taxa	—	—	—	4 (12.5%)	—	1 (4.3%)	—	8 (44.4%)
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Note: The taxonomic determination of Perissodactyla from Lida Ajer, Sibrambang and Punung was revised by POA based on material at Naturalis Biodiversity Center, Leiden, the Netherlands. Within Perissodactyla, *R. unicornis* (Tam Hang South, Nam Lot, Coc Muoi, Duoi U’Oi, Tham Wiman Nakin) and *Megatapirus augustus* (Coc Muoi and Tam Hang South) were also recorded.

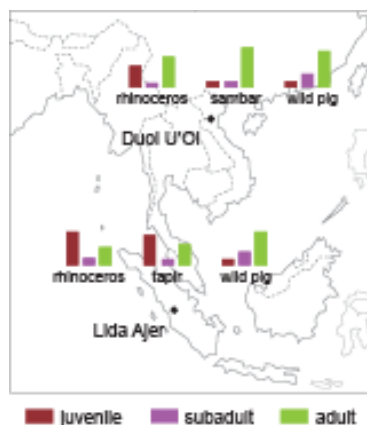
<sup>1</sup> Rhinocerotids from Sibrambang were assigned to *R. sondaicus* or *D. sumatrensis*.

<sup>2</sup> In relation to Tham Wiman Nakin, Suraprasit et al. (2021) did not find the *R. sondaicus* previously identified by Tougard (1998).

Sources: Fossil occurrence data: Tham Wiman Nakin: Suraprasit et al. (2021), Tougard (1998). With the exception of the data for Lida Ajer (authors; present study), the MNI data have been published in our earlier works (Bacon et al. 2015, 2018a).

### Mortality profiles of ungulate taxa: Duoi U’Oi versus Lida Ajer

Figure 7.7 illustrates the three-cohort (juvenile, subadult, and adult) mortality profiles of various ungulate taxa recorded at Duoi U’Oi and Lida Ajer. The distribution of individuals among the cohorts was compared to the J-shaped patterns (adult > juvenile > subadult) observed in natural populations (see Table 7.3). For some recent populations used as references, juveniles and subadults are merged, which led us to also consider two-cohort profiles: juvenile plus subadult, and adult.



**Figure 7.7:** Three-cohort (juvenile, subadult, and adult) mortality profiles of taxa (rhinoceros (*Rhinoceros*, *Dicerorhinus*), tapir (*Tapirus*), sambar (*Rusa unicolor*), and wild pig (*Sus*) from Duoi U’Oi (Vietnam) and Lida Ajer (Sumatra).

Source: Image by authors, using data compiled in Table 7.3.

The three-cohort profiles of sambar (*R. unicolor*) at Duoi U’Oi and tapir (*T. indicus intermedius*) and rhinoceros (*D. sumatrensis*) at Lida Ajer indicate selective pressures on some age classes. At Duoi U’Oi, adult sambar individuals are overrepresented, at 75% compared to 59–72% in two natural populations from Indian reserves (Biswas and Sankar 2002; Karanth and Sunquist 1995) and include only prime-adult individuals (3–9 years, c. 180–260 kg; Francis 2008). This hints at a human signature (Bacon et al. 2015) rather than the tiger (*Panthera tigris*) signature, which always contains old individuals in addition to prime-adult individuals (Karanth and Sunquist 1995).

Among the tapirs from Lida Ajer, there is a bias towards calves less than one year old: 53% compared to 25% in a natural population of *Tapirus terrestris* from Amazonian forests (Maffei 2003). (To our knowledge, no data are available for Malayan tapirs, *Tapirus indicus*.) The body weight of juveniles ranged between c. 10 and c. 160 kg (Donny et al. 2019), which suggests a selective pressure by either pack-hunting dholes (*Cuon alpinus*), small felids (*Felis temmincki*) or humans, all three having the capacity to hunt at least small tapirs, such as newborns and young calves given their body weight (Gearty 2012; Hayward et al. 2014). We will now compare the age profiles of rhinocerotids (all species combined) between sites. The distribution pattern at Duoi U’Oi coincides with that of a natural population, *R. unicornis* (Laurie et al. 1983), with no apparent bias (three-cohort or two-cohort), whereas the pattern at Lida Ajer shows an overrepresentation of juveniles (57% v. 27%). Only pack-hunting dholes

or humans could have hunted Lida Ajer's newborn rhinoceroses, which would have weighed up to 300 kg (Groves and Leslie Jr 2011).

In relation to suids, no selective pressure or taphonomic bias can be clearly assessed from either the three-cohort or the two-cohort profiles found at Duoi U'Oi (*S. scrofa*) and Lida Ajer (*S. scrofa* and *S. barbatus*).

**Table 7.3: Data and results of the three-cohort (juvenile, subadult, and adult) mortality profiles of rhinocerotids, tapirids, large cervids and suids from Duoi U'Oi (Vietnam) and Lida Ajer (Sumatra); method, tooth type and number of specimens used to estimate the ages of fossil individuals; and demographic data of the reference modern populations.**

Locality	Taxa	Method	Teeth	No.	Juvenile	Subadult	Adult	$\chi^2$	Sources
Chitwan, Nepal	<i>Rhinoceros unicornis</i>	—	—	—	27% 48% <sup>1</sup>	21%	52%	—	Laurie et al. 1983
Duoi U'Oi, Vietnam	<i>Rhinoceros sondaicus</i> , <i>Rhinoceros unicornis</i> , <i>Dicerorhinus sumatrensis</i>	wear stages	all teeth	51	37.2% 47.9% <sup>1</sup>	10.6%	52.1% 0 (>0.90)	5.04 (>0.05)	Bacon et al. 2015
Lida Ajer, Sumatra	<i>Rhinoceros sondaicus</i> , <i>Dicerorhinus sumatrensis</i>	wear stages	all teeth	77	57.4% 72% <sup>1</sup>	14.5%	28% 23.08 (<0.001)	19.34 (<0.001)	Bacon et al. 2018a
Amazonia, Bolivia	<i>Tapirus terrestris</i>	—	—	—	25% 44.5% <sup>1</sup>	19.5%	55.5%	—	Maffei 2003
Lida Ajer, Sumatra	<i>Tapirus indicus</i> <i>intermedius</i>	eruption sequence, wear stages	all teeth	36	52.7% 63.9% <sup>1</sup>	11.1%	36.1% 14.47 (<0.001)	16.29 (<0.001)	Authors
Nagarhole National Park, India	<i>Rusa unicolor</i>	—	—	—	19% 40.7% <sup>1</sup>	21.7%	59.3%	—	Karanth and Sunquist 1995

Pench National Park, India	<i>Rusa unicolor</i>	—	—	—	21%	6.8%	72.2%	—	Biswas and Sankar 2002
					27.8% <sup>1</sup>				
Duoi U'Oi, Vietnam	<i>Rusa unicolor</i>	wear stages	d4/m3	25	12%	12%	76%	N: 6.43 ( $<0.05$ ) P: 4.55 ( $>0.10$ )	Bacon et al. 2015
					24% <sup>1</sup>			N: 10.88 ( $<0.01$ ) P: 0.54 ( $>0.50$ )	
Nagarhole National Park, India	<i>Sus scrofa</i>	—	—	—	39.4% <sup>1</sup>	60.6%	—	—	Karanth and Sunquist 1995
Pench National Park, India	<i>Sus scrofa</i>	—	—	—	28.4% <sup>1</sup>	71.6%	—	—	Biswas and Sankar 2002
Duoi U'Oi, Vietnam	<i>Sus scrofa</i>	wear stages	m1/m2/m3	21	38% <sup>1</sup> (14 + 24%)	62%	—	N: 0.04 ( $>0.70$ ) P: 0.73 ( $>0.30$ )	Bacon et al. 2015
Lida Ajer, Sumatra	<i>S. scrofa</i> , <i>S. barbatus</i>	wear stages	m1/m2/m3	78	38.5% <sup>1</sup> (12.8 + 25.6%)	61.5%	—	N: 0.44 ( $>0.80$ ) P: 2.29 ( $>0.10$ )	Authors

Note: Shaded rows represent natural populations.

<sup>1</sup> Juveniles plus subadults.

$\chi^2$  values include the confidence interval. Two  $\chi^2$  values were available for *Rusa* and *Sus*: N = Nagarhole National Park; P = Pench National Park.

Juveniles and subadult percentages were merged at Nagarhole and Pench for *Sus scrofa*, which led us to consider similarly merged percentages for Duoi U'Oi and Lida Ajer juveniles and subadults assigned to *Sus* spp. for the sake of  $\chi^2$  comparison. We similarly merged the juvenile and subadult cohorts of recent populations of *R. unicornis* and *R. unicolor*, and of fossil samples of rhinocerotids and *R. unicolor*, in order to compare consistently the results for two-cohort and three-cohort profiles.

Sources: As shown in the table.

## Discussion

### Diverse functional herbivore communities

Our overview of Southeast Asian mammalian faunas shows that over the period c. 500–40 ka, communities were organised into a biogeographic pattern similar to that of today's, following a north–south temperature gradient, regarding the structure of ecosystems and their carrying capacities (Corlett 2010; Woodruff 2010). In the period before MIS 6 (c. 500–130 ka) and during the MIS 6–5 transitional period, megafaunas on the mainland were largely archaic (c. 40–60% archaic taxa versus c. 10–50% modern taxa), and there were various local associations between herbivores. The Ngandong fauna from Java is composed of c. 70% archaic endemic taxa, indicating the long-term isolation of this mammalian community due to insular conditions until c. 120 ka (Rizal et al. 2020).

At the time of the earliest range expansion of modern faunas into Sunda c. 130 ka. Diverse functional herbivore communities coexisted in the Southeast Asian mainland (Louys and Roberts 2020). Extensive savanna, open woodlands and dense forests covered the central plains of the continent, as shown by the data of Tham Wiman Nakin and Khok Sung; these extended to the southernmost boundary of the Indochinese subregion, including the Yai Ruak cave site located between the Isthmus of Kra and the Kangar-Pattani line (Suraprasit et al. 2019). These habitats were home to browsers such as rhinoceros and tapir and to a great number of small, medium-sized and large mixed-feeding and grazing cervids and bovids. Within the ruminant taxa, the great diversity of bovids (e.g. Bovinae and Caprinae) is particularly notable (Bocherens et al. 2017; Pushkina et al. 2010; Suraprasit et al. 2021). The taxonomic diversity in ungulates, including, for example, 15 taxa at Tham Wiman Nakin, reflects a high environmental heterogeneity, with notably the presence of open woodlands and savannah in the central plains of the Indochinese Peninsula that allowed greater niche partitioning between taxa (Graham et al. 1996). This contrasts with the much less diverse southern Chinese mammalian communities (Black Cave, Wuyun, Hejiang and Yugong) containing 8 to 10 ungulate taxa and reflecting conversely predominant forested environments. Some other faunas have suggested the same pattern: Ganxian Cave, with 11 taxa (Liang 2020; 360–160 ka); Zhiren Cave, with 9 taxa (Jin et al. 2009; Ge et al. 2020; 116–106 ka or 190–130 ka); Fuyan Cave, with 10 taxa (Li et al. 2013; 180–120 ka); and Mocun Cave with 12 taxa (Fan et al. 2022; 101–66 ka).

The newly recovered faunal assemblage at Ngalau Gupin in the Padang Highlands tells us more about the composition of mammalian communities in the early phase of expansion of mammals in Sunda in Sumatra at c. 130 ka (Duval et al. 2021). This expansion brought about the emergence of a new modern guild combining taxa from the mainland source area able to adapt to new, humid tropic conditions, associated with one local archaic hippopotamus *Hexaprotodon* sp. (>70 ka; direct U-series age estimated from one specimen; Smith et al. 2021). The example of the Ngalau Gupin fauna shows how climate-driven biogeographical events contributed to new associations between herbivore taxa in new communities balanced differently to the preceding ones (Barnosky 2001; Stewart 2009).

Meanwhile, in more northern latitudes, *Stegodon orientalis* and *Megatapirus augustus* belonged to herbivore communities composed of a greater diversity of large-bodied non-ruminants (rhinocerotids, proboscideans, and tapirids) living predominantly in forested landscapes (Antoine 2012; Bacon et al. 2015, 2018a; Ma et al. 2017; Rink et al. 2008; Sun et al. 2019). *Stegodon orientalis* and *M. augustus* on the mainland and *Hexaprotodon* sp. in Sunda were the last relicts of Early to Middle Pleistocene archaic megafaunas, either being browsers ( $\delta^{13}\text{C} < -14\%$ ) adapted to C<sub>3</sub>-canopy forests (Bacon et al. 2018b, 2021; Bocherens



et al. 2017; Li et al. 2017; Ma et al. 2017, 2019; Stacklyn et al. 2017; Wang W. et al. 2007), or C<sub>3</sub>–C<sub>4</sub> mixed feeders ( $\delta^{13}\text{C} > -8 \text{‰}$ ) and C<sub>4</sub> grazers ( $\delta^{13}\text{C} > -2 \text{‰}$ ) living in a predominantly open environment with large areas of swamps and/or lakes (Janssen et al. 2016; Puspaningrum et al. 2020).

The turnover of the mammalian composition in Java shows how drastic the shift was, with all the archaic endemic ungulate species found at Ngandong (Rizal et al. 2020) replaced by the modern species found at Punung (Storm and de Vos 2006). However, our data seem to indicate that this turnover did not result in a noticeable change in the diversity of ungulates within body size categories, suggesting that either the carrying capacity or the structure (or both) of the inferred ecosystems did not change so significantly. Archaic species adapted to open landscapes were replaced by their modern congeners from the mainland; these had broad ecological ranges and included large-bodied ruminants. For example, *Bubalus palaeokerabau* was replaced by *B. arnee* (Janssen et al. 2016). The relative abundance of specialised browsers such as tapirs (*T. indicus*) and of mixed feeders such as wild pigs (*Sus* sp.) or muntjacs (*M. muntjac*), as shown by our analysis, along with the relative abundance of orangutans (*Pongo pygmaeus*), gibbons (*Hylobates syndactylus*) and bears (*Helarctos malayanus*) (de Vos 1983), leaves no doubt about the presence of rainforests and associated warm, humid conditions (van der Kaars and Dam 1995). However, some evidence hints at the presence of grassy clearings within the rainforest habitat around Punung, probably associated with higher seasonality. This evidence takes two forms: the carbon isotope signal of large bovids that relied exclusively on a C<sub>4</sub> diet (Janssen et al. 2016), and, as shown in the present analysis, the predominance of *R. sondaicus* at Punung, which is known to have different ecological constraints from those of *D. sumatrensis*. Regarding the old collection from Punung studied here, however, the alternative hypothesis that it contains a mixture of elements from different stratigraphic levels remains viable (Kaifu et al. 2022).

In the biogeographical history of Southeast Asia, it is difficult to assess the effects of the other postulated turnover in the middle of the Late Pleistocene, which is much less detectable in the fossil records, as it involves modern lineages of herbivores discriminated at the infraspecific level, as shown by the Duoi U’Oi evidence from 70–60 ka (Bacon et al. 2021). This turnover of populations on the mainland was associated with a rapid climatic shift at the beginning of MIS 4 (Wang Y. et al. 2008) that had profound effects on temperatures, seasonality and vegetation, with an increase in temperate plants, which was particularly noticeable in conifers and ferns (Zheng and Lei 1999). This, in turn, affected the faunal communities, leading to the occurrence of populations better adapted to this new C<sub>3</sub>-dominated environment and the local loss of archaic taxa.

This climatic change had seemingly less impact in southern latitudes. At this time, the lowlands rainforests of Sumatra, consisting of dipterocarps, remained very humid, with precipitation over 2,000 mm per year (van der Kaars et al. 2010) that had comparatively less effect on faunal communities. In our results, the faunal communities from Southeast Asia may seem to appear more depleted of ungulates during MIS 4–3 compared with those from the previous MIS 6–5 period, but our results are not convincing due to the small size of the datasets. More evidence is needed to reliably assess the effects of this climatic episode on Southeast Asian mammalian herbivore communities.

Besides the evidently greater herbivore biomass on the mainland—either ruminants or non-ruminants depending on the carrying capacity of grassy versus forested habitats and the extent of areas and resource availability (Woodruff and Turner 2009)—overall, our results suggest a lower carrying capacity of ecosystems in the Sundaic region than in the Indomalayan region and a relative continuity there, even during the period of broad connections between land masses that led to diverse, balanced faunas, that is, faunas with large predators and a broad array of prey (as found at Niah Cave in Borneo and Sibrambang

in Sumatra). This contrast between the mainland and the islands appears more marked today due to the global decline in megafauna since c. 50 ka, which has been particularly great in insular environments (Corlett 2010; Koch and Barnosky 2006).

### **Availability of prey species to humans**

Our results indicate that the Indomalayan region experienced differing past ecological conditions depending on latitude, that affected the structure of mammalian communities. These conditions played a significant role in the abundance distribution of ungulate species and, therefore, in the availability of prey species to predators, including modern humans. The comparison between Duoi U'Oi and Lida Ajer provides some clues to this question around 70 ka. At Duoi U'Oi, in a highly forested habitat including a significant proportion of closed-canopy forests (Bacon et al. 2021), hunting pressure on the sambar deer (*R. unicolor*) was high, most probably due to its relative abundance in the environment. This abundance could explain why humans (*Homo* sp.) targeted this prey preferentially, as we suggested previously (Bacon et al. 2015). At Lida Ajer, in an environment dominated by dipterocarp rainforests (Louys et al. 2022), hunting pressure might likewise have been higher on the most abundant species, tapir (*T. indicus*) and Sumatran rhinoceros (*D. sumatrensis*), but if so, it is not possible to say if one was preferentially targeted by humans.

In relation to suids, results appear fairly similar at both sites, with no evidence of selective pressure on *S. scrofa* at Duoi U'Oi or on *S. scrofa* or *S. barbatus* at Lida Ajer. It has been demonstrated that, at Niah Cave in the forests of Borneo, during the earliest phase of occupation (from c. 50 ka), the bearded pig (*S. barbatus*) was the primary prey of humans, with no particular selection of age classes (Barker et al. 2017; Piper and Rabett 2009). The question remains as to whether humans also hunted pigs in the forests around Duoi U'Oi (Bacon et al. 2021). It is also unknown whether pigs were hunted by humans from Lida Ajer, who might have frequently encountered abundant pigs in areas of relatively open-canopy vegetation (Louys et al. 2022). Currently, due to the absence of convincing archaeological evidence (e.g. evidence of lithic or organic industry, bones with butchery marks, etc.), firm knowledge of human foraging behaviour in Southeast Asia remains elusive.

### **Conclusion**

This study investigated the composition and structure of the mammalian communities of Southeast Asia at the time of dispersal events in Sunda. Despite the limited dataset, the comparative analysis of Indochinese and Sundaic ungulate guilds provides an overview of the diversity of the ecosystems, which was strongly modulated by environmental conditions. The difference between the species-rich ungulate communities in the centre of the mainland and the less diverse ones from southern China and Sunda might reflect the degree of heterogeneity of the biomes. Comparatively, Sundaland seems to have been relatively impoverished in large-bodied species throughout the Late Pleistocene, apparently with a continuity in the carrying capacity of ecosystems. The results also illustrate the stark contrast between past and present ecosystems. In the changing climates of the Late Pleistocene, modern humans faced a wide range of rainforest conditions, and probably adapted their foraging to focus on different prey species according to their abundance.

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**Appendix 7.1: The Southeast Asian sites included in the present analysis, listed from north to south.**

Site	Country	Age	Sources
Yugong Cave	Guangxi Zuang Autonomous Region, China	late Middle Pleistocene	Dong et al. 2014; Sun et al. 2019
Black Cave	Guangxi Zuang Autonomous Region, China	404–382 ka	Shao et al. 2017
Hejiang Cave	Guangxi Zuang Autonomous Region, China	400–320 ka	Zhang et al. 2014
Wuyun Cave	Guangxi Zuang Autonomous Region, China	279–76 ka	Rink et al. 2008
Quzai Cave	Guangxi Zuang Autonomous Region, China	early Late Pleistocene	Ma et al. 2019
Baxian Cave	Guangxi Zuang Autonomous Region, China	early Late Pleistocene	Ma et al. 2017; Sun et al. 2019
Tham Kuyen	Lang Son Province, Vietnam	475 ± 125 ka	Ciochon et al. 1996; Cuong 1985
Coc Muoi Cave	Lang Son Province, Vietnam	148–117 ka	Bacon et al. 2018a, 2021
Duoi U’Oi Cave	Hoà Binh Province, Vietnam	70–60 ka	Bacon et al. 2008, 2015, 2018b, 2021
Tam Hang South	Huaphan Province, Laos	94–60 ka	Bacon et al. 2015, 2021
Nam Lot Cave	Huaphan Province, Laos	86–72 ka	Bacon et al. 2015, 2021
Tham Wiman Nakin	Chaiyaphum Province, Thailand	>169 ± 15 ka	Esposito et al. 1998, 2002; Suraprasit et al. 2021; Tougard 1998
Tham Prakai Phet	Chaiyaphum Province, Thailand	169–19 ka	Esposito et al. 1998, 2002; Filoux et al. 2015; Tougard 1998
Khok Sung	Nakhon Ratchasima Province, Thailand	217 ka or 130 ka	Duval et al. 2019; Suraprasit et al. 2018

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Ban Fa Sui II (Levels 2e–2f)	Chiang Mai Province, Thailand	55–46 ka	Zeitoun et al. 2019
Batu (group of three caves)	Selangor, Peninsular Malaysia	66–33 ka	Ibrahim et al. 2013
Badak Cave	Selangor, Peninsular Malaysia	>500 ka	Ibrahim et al. 2013
Ngalau Gupin	Sumatra	160–115 ka	Smith et al. 2021
Lida Ajer	Sumatra	73–63 ka	Long et al. 1996; Louys 2012; Westaway et al. 2017
Sibrambang	Sumatra	128–118 ka or 73–63 ka	Westaway et al. 2007, 2017
Ngandong	Java	117–108 ka	Rizal et al. 2020
Gunung Dawung (Punung III)	Java	128–118 ka	Storm et al. 2005; Storm and de Vos 2006; Westaway et al. 2007
Niah Cave	Sarawak, Malaysia, Borneo	From c. 50 ka to Holocene 46–34 ka ‘Deep skull’ layer	Barker et al. 2007, 2017

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Source: Authors.

**Appendix 7.2: List of taxa (Artiodactyla, Perissodactyla and Proboscidea), dietary strategy (ruminant versus non-ruminant), body size category, and occurrence in the Indochinese subregion at the reviewed sites and in current faunas.**

Taxon	Common name	Dietary strategy	Body size category	Yugong	Black Cave	Hejiang Cave	Wuyun Cave	Quzai/Baxian	Tham Khuyen	Coc Muoi	Duoi U'Oi	Tam Hang South	Nam Lot	Tham Wimnan Nakin	Tham Prakai Phet	Khok Sung	Ban Fa Sui II	Current faunas 25°–20° N	Current faunas 20°–10° N
<i>Cervus</i> sp.	Deer	R <sup>1</sup>	B <sup>2</sup>	x	x	x													
<i>Cervus nippon</i>	Sika	R	B														cf.	x <sup>3</sup>	
<i>Rusa unicolor</i>	Sambar deer	R	B	x		cf.		x	cf.	x	x	x	x	x	x	x	x	x	x
<i>Axis porcinus</i>	Hog deer	R	A											x	x				x
<i>Axis axis</i>	Chital	R	A													x			
<i>Rucervus eldii</i>	Eld's deer	R	B									(?)		x		(?)		x	x
<i>Muntiacus</i> sp.	Muntjac	R	A	x	x	x	x	x		x				x	x				
<i>Muntiacus muntjak</i>	Red muntjac	R	A						x		x	x	x			x	x	x	x
<i>Muntiacus feae</i>	Fea's muntjac	R	A																x
<i>Muntiacus rooseveltorum</i>	Roosevelt's muntjac	R	A																x
<i>Megalotis guangxiensis</i> *	Extinct bovid	R	C		x	x													
<i>Leptobos</i> sp.*	Extinct bovid	R	C	x															
<i>Bos</i> sp./ <i>Bibos</i> sp.	Large bovid	R	C	x	x	x		x			x		x				x		
<i>Bos javanicus</i>	Banteng	R	C											x	x			x	x



<i>Elephas</i> sp.	Elephant	NR	D						x	x	x	x	x
<i>Stegodon orientalis</i> *	Extinct stegodontid	NR	D	x	x	x	x			x	x		x
<i>Stegodon</i> sp.*	Extinct stegodontid	NR	D	x					x				x

\* Extinct taxa.

<sup>1</sup> Digestive physiology: R = ruminant, NR = non-ruminant.

<sup>2</sup> Body size categories: A 18–80 kg, B 80–350 kg, C 350–1,000 kg, D >1,000 kg (Faith et al. 2019). Body mass of modern species from Francis (2008).

<sup>3</sup> The current faunas are those from the studied latitudinal zone during the pre-industrial period (c. mid-nineteenth century) (Corbet and Hill 1992).

Sources: Fossil occurrence data from the following sources. Yugong: Dong et al. (2014), Sun et al. (2019). Black Cave: Shao et al. (2017). Hejiang Cave: Zhang et al. (2014). Wuyun: Rink et al. (2008). Quzai: Ma et al. (2019). Baxian: Ma et al. (2017), Sun et al. (2019). Tham Khuyen: Cuong (1985). Coc Muoi: Bacon et al. (2018a). Duoi U’Oi: Bacon et al. (2008). Tam Hang South: Bacon et al. (2015). Nam Lot: Bacon et al. (2015). Tham Wiman Nakin: Suraprasit et al. (2021), Tougard (1998). Tham Prakai Phet: Filoux et al. (2015), Tougard (1998). Khok Sung: Suraprasit et al. (2018). Ban Fa Sui II: Zeitoun et al. (2019).

**Appendix 7.3: List of taxa (Artiodactyla, Perissodactyla and Proboscidea), dietary strategy (ruminant versus non-ruminant), body size category, and occurrence in the Sundaic subregion at the reviewed sites and in current faunas.**

Taxon	Common name	Dietary strategy	Body size category	Badak	Batu	Ngalau Gupin	Sibrambang	Lida Ajer	Niah Cave	Ngandong	Punung	Current faunas 10° N – 5° S	Current faunas 5°–10° S
<i>Tragulus</i> sp.	Mousedeer	R <sup>1</sup>	-			x			x <sup>6</sup>				
<i>Tragulus napu</i>	Greater mousedeer	R	-						x				
<i>Rusa unicolor</i>	Sambar deer	R	B <sup>2</sup>	x	x	(?)			x			x (S, B) <sup>3</sup>	
<i>Rusa</i> sp.	Deer	R	B				x	x		x	x		
<i>Cervus timorensis</i>	Javan rusa	R	B										x (J)
<i>Axis lydekkeri</i> *	Extinct cervid	R	A							x			
<i>Axis kuhlii</i>	Bawean deer	R	A										x (J)
<i>Muntiacus</i> sp.	Muntjac	R	A			x							
<i>Muntiacus muntjak</i>	Red muntjac	R	A	x	x	x	x	x	x	x	x	x (S, B)	x (J)
<i>Muntiacus atherodes</i>	Bornean yellow muntjac	R	A									x (B)	
<i>Bibos palaeosondaicus</i> *	Extinct bovid	R	C							x			
<i>Bos/Bubalus</i> sp.	Large bovid	R	C	x	x	(?)					(?)		
<i>Bos javanicus</i>	Banteng	R	C				x	x	x			x (B)	x
<i>Bos gaurus</i>	Gaur	R	C									x	
<i>Bubalus bubalis</i> ( <i>B. arnee</i> )	Water buffalo	R	C				x	x			x <sup>5</sup>		
<i>Bubalus palaeokerabau</i> *	Extinct bovid	R	C							x			

<i>Capricornis sumatraensis</i>	Southern serow	R	B	x	x	x	x	x		x	x (S)
<i>Sus macrognathus</i> *	Extinct suid	NR	B							x	
<i>Sus brachygnathus</i> *	Extinct suid	NR	B							x	
<i>Sus</i> sp.	Suid	NR	B	x	x	x				x	
<i>Sus scrofa</i>	Wild pig	NR	B	x	x	x	x	x		x <sup>5</sup>	x (S) x
<i>Sus verrucosus</i>	Javan warty pig	NR	B								x (J)
<i>Sus barbatus</i>	Bearded pig	NR	B		x	x	x	x	x		x (S, B)
<i>Hexaprotodon</i> sp.*	Extinct hippopotamid	NR	C			x					
<i>Hexaprotodon sivajavanicus</i> *	Extinct hippopotamid	NR	C							x	
<i>Rhinoceros sondaicus</i>	One-horned rhinoceros	NR	D	(?)		(?)	x <sup>4</sup>			x	x <sup>4</sup> x (S, B) x (J)
<i>Rhinoceros unicornis</i>	Indian rhinoceros	NR	D	(?)		(?)					
<i>Dicerorhinus sumatrensis</i>	Two-horned rhinoceros	NR	C	(?)	x	(?)	(?) <sup>4</sup>	x <sup>4</sup>	x		x <sup>4</sup> x (S, B)
<i>Tapirus indicus</i>	Malayan tapir	NR	C		x	x	x <sup>4</sup>	x <sup>4</sup>	x		x <sup>4</sup> x (S)
<i>Elephas maximus</i>	Asian elephant	NR	D				x	x		cf.	x (S)
<i>Elephas</i> sp.	Elephant	NR	D			x					
<i>Elephas hysudrindicus</i> *	Extinct elephantid	NR	D							x	
<i>Stegodon trigonocephalus</i> *	Extinct stegodontid	NR	D							x	

\* Extinct taxa.

<sup>1</sup> Digestive physiology: R = ruminant, NR = non-ruminant.

<sup>2</sup> Body size categories: A 18–80 kg, B 80–350 kg, C 350–1,000 kg, D >1,000 kg (Faith et al. 2019). Body mass of modern species from Francis (2008).

<sup>3</sup> The current faunas are those from the studied latitudinal zone during the pre-industrial period (c. mid-nineteenth century) (Corbet and Hill 1992). B = Borneo; S = Sumatra; J = Java.

<sup>4</sup> Perissodactyls revised by POA who identified *Tapirus indicus intermedius* at Sibrambang and Lida Ajer.

<sup>5</sup> Taxon cited in Louys (2012), missing in Storm et al. (2005).



<sup>6</sup> Taxon cited in Barker et al. (2017), missing in Louys (2007). Tragulidae are below the body size categories selected in the manuscript.

Sources: Fossil occurrence data from the following sources. Batu and Badak: Ibrahim et al. (2013). Ngalau Gupin: Smith et al. (2021). Lida Ajer and Sibrambang: Long et al. (1996), Louys (2012). Niah Cave: Barker et al. (2017). Ngandong: Rizal et al. (2020). Punung, represented by Punung III and Gunung Dawung: Storm et al. (2005), Storm and de Vos (2006).





<i>Felis temmincki</i>	Asian golden cat																	cf.			X	X		
<i>Felis teilhardi</i>	Extinct felid					X																		
<i>Prionailurus bengalensis</i>	Leopard cat																		cf.			X	X	
<i>Neofelis nebulosa</i>	Clouded leopard									X												X	X	
<i>Crocuta Crocuta/ C. ultima</i>	Spotted hyena																		X	X	X			
<i>Hyaena</i> sp.	Hyenas					X																		
<i>Helarctos malayanus</i>	Sun bear							X	X	X	X											X	X	
<i>Ursus thibetanus</i>	Asian black bear	X	X		X	X	X	X	X	X	X	X	X	X							cf.	X		
<i>Ursus</i> sp.	Bears					X																X		
<i>Ailuropoda baconi</i>	Extinct panda	X			X		X	X						X										
<i>Ailuropoda melanoleuca</i>	Giant panda		X		X				X				X		X					cf.	X			
<i>Macaca</i> sp.	Macaques		X	X	X	X	X	X	X	X			X	X	X							X		
<i>Macaca nemestrina</i>	Pig-tailed macaque																					cf.	X	X
<i>Macaca mulatta</i>	Rhesus macaque																					cf.	X	X
<i>Trachypithecus/ Presbytis</i> sp.	Langurs				X	X				X	X	X		X										
<i>Rhinopithecus</i> sp.	Langurs		X			X	X																	

<i>Nomascus</i> sp.	Gibbons		X		X	X				
<i>Hylobates</i> sp.	Gibbons	X					X	X	X	
<i>Pongo</i> sp.	Orangutans	X			X	X	X			X
<i>Pongo pygmaeus</i>	Bornean orangutan			X			X	X	X	cf.
<i>Gigantopithecus blacki</i>	Extinct ape	X	X							
<i>Homo</i> sp.	Humans						X		X	

The current faunas are those from the studied latitudinal zone in the pre-industrial period (c. mid-nineteenth century).

Source: Fossil occurrence data from the following sources. Yugong: Dong et al. (2014), Sun et al. (2019). Black Cave: Shao et al. (2017). Hejiang Cave: Zhang et al. (2014). Wuyun: Rink et al. (2008). Quzai: Ma et al. (2019). Baxian: Ma et al. (2017), Sun et al. (2019). Tham Khuyen: Cuong (1985). Coc Muoi: Bacon et al. (2018). Duoi U’Oi: Bacon et al. (2008). Tam Hang South: Bacon et al. (2015). Nam Lot: Bacon et al. (2015). Tham Wiman Nakin: Suraprasit et al. (2021), Tougard (1998). Tham Prakai Phet: Filoux et al. (2015), Tougard (1998). Khok Sung: Suraprasit et al. (2018). Ban Fa Sui II: Zeitoun et al. (2019). Current faunas: Corbet and Hill (1992:161–227, 409–413).





<i>Hylobates muelleri</i>	Müller's gibbon		cf.		X	B
<i>Pongo pygmaeus</i>	Bornean orangutan		X		X	S
<i>Pongo abelii</i>	Sumatran orangutan	cf.			X	B
<i>Pongo</i> sp.	Orangutans	X				
<i>Homo erectus</i>	Extinct <i>Homo erectus</i>				X	
<i>Homo sapiens</i>	Modern humans		X	X	X	X

<sup>1</sup> Taxon cited in Kaifu et al. (2022) in complement to Louys (2012) and Storm et al. (2005).

<sup>2</sup> Taxon cited in Barker et al. (2017) in complement to Louys (2007).

<sup>3</sup> B = Borneo; S = Sumatra; J = Java; TM = Thai-Malay Peninsula.

The current faunas are those from the studied latitudinal zone in the pre-industrial period (c. mid-nineteenth century).

Source: Fossil occurrence data from the following sources. Batu and Badak: Ibrahim et al. (2013). Ngalau Gupin: Smith et al. (2021). Lida Ajer and Sibrambang: Long et al. (1996), Louys (2012). Niah Cave: Barker et al. (2017). Ngandong: Rizal et al. (2020). Punung III, Gunung Dawung, Java: Storm et al. (2005), Storm and de Vos (2006). Current faunas: Corbet and Hill (1992:161–227, 409–413).



