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ORIGINAL ARTICLE

Palaeoecology of Southeast Asian megafauna-bearing sites from the Pleistocene and a review of environmental changes in the region

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ABSTRACT

Aim To reconstruct the palaeoenvironments of megafauna-bearing sites from Pleistocene Southeast Asia, and to describe general environmental changes in the region.

Location Indochina and Sundaland, including Myanmar, Laos, Vietnam, Cambodia, Thailand, the Malay Peninsula, Borneo, Sumatra and Java.

Methods This study reconstructs the habitat types of 25 Pleistocene sites in Southeast Asia through a synecological (community-based) method. This method specifically targets medium- and large-bodied mammals, and ecovariables that could be directly assessed from species lists were chosen. The methods allow the reconstruction of fossil sites as closed (continuous tree cover), mixed (heterogeneous tree cover) and open (very limited to no tree cover) through discriminant functions analysis of community guild structure.

Results Four Pleistocene sites can confidently be assigned to one of the three habitat types. Tam Hang (south), a Middle Pleistocene site from Laos, is classified as mixed. Ban Fa Suai, a Middle Pleistocene site from Thailand, is also classified as mixed. Trinil, a Middle Pleistocene site from Java, is classified as open. Lastly, Hang Hum II, a Late Pleistocene site from Vietnam, is classified as open. Insufficient species are present in the fossil faunas of remaining sites to allow statistically confident habitat assignment. Nevertheless, conditional habitat assignments can be achieved, and these are largely congruent with other palaeoenvironmental evidence.

Main conclusions Medium- and large-bodied mammals are the most frequently recovered mammals from Pleistocene sites in Southeast Asia. Previous palaeoenvironmental reconstructions of these sites have been hampered by this body size bias, as well as by limited site and faunal descriptions. However, our analysis demonstrates that reconstructions can still be achieved for megafauna-bearing sites in the region. The reconstructions suggest that through much of the Pleistocene, Southeast Asia had significant areas of mixed habitats, and that the widespread distribution of rain forests, such as found today, was a relatively rare phenomenon.

Keywords
Discriminant functions analysis, ecovariable, mammals, megafauna, palaeoenvironment, palaeontology, Quaternary, Southeast Asia, synecology.

INTRODUCTION

Southeast (SE) Asia (Fig. 1) is one of the most species-rich areas in the world (Myers *et al.*, 2000), with, for example, *c.* 13% of all mammal species occurring on about 1% of the world's land mass. This species richness is probably the result of the region's dynamic geological past (Holloway & Hall, 1998), and relatively stable environmental conditions, which

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Figure 1 Southeast Asia, showing the locations of the fossil sites considered in this study.

resulted in many speciation opportunities and relatively few extinction events (e.g. Whitmore, 1987; Meijaard, 2004; Louys, 2007, 2008; Louys *et al.*, 2007). In fact, few taxonomic groups disappeared from SE Asia or became extinct in the Pleistocene, although some that did include proboscideans (*Stegodon* and *Palaeoloxodon*), carnivorans (*Crocuta* and *Pachycrocuta*) and hippopotamus (*Hexaprotodon*) (Louys *et al.*, 2007). The faunas of SE Asia are subdivided into a number of zoogeographic subregions, of which two, the Indochinese and Sundaic (*sensu* Lekagul & McNeely, 1988), are the subject of the present study. The biogeography of these subregions remains at best partially understood; this is partly a result of the intense geological activity in this highly fragmented region, which has led to complex patterns of species diversity (e.g. Heaney, 1984, 1986; Ruedi, 1996), as well as of the limited information currently available on palaeo-faunas and -floras (Woodruff & Turner, 2009).

Some recent research has, however, begun to shed light on the palaeobiogeography, palaeoecology and palaeontology of the SE Asian region (e.g. Heaney, 1991; van den Bergh *et al.*, 2001; Tougard, 2001; Bacon *et al.*, 2004; Meijaard, 2004; Zeitoun *et al.*, 2005; Storm & de Vos, 2006; Louys, 2008; Meiri *et al.*, 2008; Westaway *et al.*, 2009a,b). Owing in large part to the presence of hominins in the region from the beginning of the Pleistocene, some attempts have been made to understand regional palaeohabitats and palaeoenvironments. One of the best sources of information on palaeoenvironments, particularly as it applies to early humans, is that of the mammalian fauna associated with them, and SE Asia is no exception. In fact, the use of fossil faunas from SE Asia to infer palaeoenvironments and palaeobiogeography enjoys a long history (e.g. Dubois, 1908; Colbert, 1943). Until recently, however, all attempts at palaeoenvironmental reconstruction in the region have been qualitative and based on the presence or absence of one or a small number of species (e.g. Medway, 1977; de Vos *et al.*, 1994; van den Bergh *et al.*, 2001). Although such studies can be quite informative, they fail to make use of the faunal community preserved in an integrated way.

Multivariate synecological analyses, on the other hand, rely on comparisons between faunal communities in order to reconstruct palaeoenvironments. These methods examine the presence or abundance of taxonomic or ecological groups within a community, and allow the association of differences in representation with particular habitat types (e.g. Reed, 1997; Sandrock *et al.*, 2007; Louys *et al.*, 2009). A synecological analysis on SE Asian sites was recently carried out by Tougard & Montuire (2006), who attempted to reconstruct Pleistocene environments of the region using cenograms (rank-ordered graphs of body sizes in a community). However, because cenograms rely on the full spectrum of body mass distributions to reconstruct palaeoenvironments (see Legendre, 1986, 1989 and Travouillon & Legendre, 2009 for a discussion of this methodology), the heavy bias towards larger mammals in SE Asian fossil deposits makes the use of this method problematic for the region. This bias is in part due to many SE Asian excavations having being undertaken at the beginning of the last century, and therefore before modern excavation techniques, which screen and retain remains of smaller species, were developed. In the case of modern excavations, taphonomic bias (see, for example, Bacon *et al.*, 2008a), as well as a dearth of micromammal specialists in the region, continue to produce a large-bodied bias. This bias hampers palaeoenvironmental reconstructions in the region, such that Tougard & Montuire (2006) were only able to assign a single palaeohabitat with any confidence to a single fossil fauna out of the seven they examined, that of Thum Wimam Nakin, Thailand.

Analytical methods that seek to reconstruct the palaeoenvironments of SE Asian sites must be equipped to deal with a large body size bias. Synecological analyses based on the proportions of species classified into ecological categories have been shown to be useful in reconstructing past environments (e.g. Reed, 1998; Mendoza *et al.*, 2005). In addition, these analyses can be conducted using only the large-bodied subset of the entire fossil community, and as such do not suffer from the limitations affecting cenogram analyses. Furthermore, because SE Asia has suffered relatively few Pleistocene extinctions, modern faunal communities provide good comparative models for extinct ones. However, these types of analyses are subject to taphonomic limitations (Soligo & Andrews, 2005) as well as requiring the preservation of a minimum number of species (Louys *et al.*, 2009). For example, Louys *et al.* (2009) calculated that to differentiate with confidence between closed and mixed habitats, a site must contain at least 32 species, between mixed and open at least 12 species, and between closed and open at least eight species. Unfortunately, the target of 32 species is achieved in only a few sites in SE Asia. Nonetheless, classifications based on fewer species can provide an indication of environments present, especially when they are placed within a larger palaeoecological context (Louys *et al.*, 2009). Palaeoenvironments of most SE Asian sites from the Pleistocene will therefore be proposed based on a synecological analysis of medium- and large-bodied mammals (≥ 1 kg, termed here ‘megafauna’) examined in the context of other palaeoecological information. The results presented herein represent the first palaeoenvironmental reconstructions for many SE Asian sites on the basis of multivariate synecological methods. Furthermore, the ecological variables chosen for this analysis not only allow such reconstructions to be achieved relatively ‘materials-free’ for this understudied region, but also provide insights as to the evolution of faunal community structure concomitant with environmental changes.

MATERIALS AND METHODS

Modern species lists and habitat descriptions

Multivariate synecological approaches to palaeoenvironmental reconstruction rely on modern faunal communities as a basis of comparison with fossil faunas. We used the species lists from 25 Asian nature reserves and national parks, where possible taxonomic bias in those lists had been controlled for (Louys *et al.*, 2009). Each protected area represents one of three habitat types. Closed habitats are represented by protected areas with complete forest cover; mixed habitats have heterogeneous forest cover – significant treeless areas can be present in these protected areas; and open habitats are almost completely bereft of trees (Louys *et al.*, 2009). Species used in this analysis are listed in Appendix S1 in the Supporting Information. The geographical positions of the natural protected areas can be found in Louys *et al.* (2009).

Fossil sites

The palaeontological literature was examined for faunal lists from select Pleistocene SE Asian sites. Species from the following sites were included: Myanmar (Colbert, 1943): Mogok Caves, Irrawady beds; Thailand (Pope *et al.*, 1981; Tougard, 1998; Zeitoun *et al.*, 2005): Thum Wiman Nakin, Thum Phra Khai Phet, Kao Pah Nam, Ban Fa Suai; Laos (Fromaget, 1936; Arambourg & Fromaget, 1938): Tam Hang (north), Tam Hang (south) [previously referred to as Tam Nang (e.g. Arambourg & Fromaget, 1938); however, this was a typographical corruption of Tam Hang (A-M. Bacon, CNRS Paris, pers. comm., 2009; see also Bacon *et al.*, 2008a)]; Vietnam (de Vos, 1983; Olsen & Ciochon, 1990): Keo Leng, Tham Khuyen, Tham Hai, Lang Trang, Tham Om, Hang Hum I & II; Cambodia (Beden & Guérin, 1973): Phnom Loang; Malay Peninsula (Medway, 1972): Kinta Valley; Borneo (Medway, 1960, 1972): Niah Caves; Sumatra (de Vos, 1983): Lida Ajer, Sibrambang; Java (Hooijer, 1975; de Vos, 1983; Aimi & Aziz, 1985; van den Bergh *et al.*, 1996, 2001): Ci Saat, Trinil, Kedung Brubus, Kali Glagah, Punung. Geographical locations of these sites are presented in Fig. 1; species used in the analysis are listed in Appendix S2. These sites were chosen as they all occur on continental SE Asia – that is, they are currently on the continent, or were connected to continental areas during Pleistocene periods of lower sea-level. Faunal communities from continental sites have similar faunas, body size ranges and diversity to the modern communities sampled. Oceanic parts of SE Asia that possess island communities, such as Sulawesi and the Phillipines, are therefore not included in this analysis.

Discriminant functions analysis

To assign extinct taxa to ecological variables that have previously been published (e.g. Reed, 1998; Mendoza *et al.*, 2005) requires access to original fossils, or at least to detailed descriptions of individual specimens. It was not possible to get access to all SE Asian fossil faunas within the scope of this study, and for some sites this fossil material is incomplete. Detailed anatomical descriptions of fossils from SE Asia are rare, and in some cases descriptions of fossil material by early excavators were either perfunctory or even non-existent. The variables defined in this study have been chosen such that they can be determined, in almost all cases, directly from species lists themselves. They are based where possible on extant members of the fossil species. In the case of extinct species or where information was missing for extant species, they are based on the most closely related taxa, within the same genus wherever possible. Because of this, these variables cannot be considered 'taxon-free' or 'phylogeny-free'. To truly achieve such a designation, extinct fauna in such an analysis would need to be subjected to a taxon-free ecomorphic study or similar treatment in order to determine palaeobiology. For reasons mentioned above, this cannot be done for many SE Asian sites. In any case, as far as synecological studies are concerned, we eschew the use of the terms 'taxon-free' or 'phylogeny-free', and prefer instead to refer to the variables as ecological ('ecovariables'). All ecological information for extant species was obtained from Nowak (1999).

Ecological variables were determined for each species using three basic categories. First, each species was placed in one of five body size classes according to average body mass (cf. Andrews *et al.*, 1979; Gagnon, 1997; Andrews & Humphrey, 1999; Soligo & Andrews, 2005), and as such are comparable. The body size categories are: tiny (A) < 1 kg; small (B) 1–10 kg; medium (C) 10–45 kg; large (D) 45–180 kg; and very large (E) > 180 kg. Taxa belonging to body weight category A are excluded from further analysis here: they are not adequately represented in faunal lists from Pleistocene sites in SE Asia. In addition, small mammals show increased levels of endemism relative to larger mammals, in particularly those occurring in montane regions of SE Asia (e.g. Heaney, 1984, 1986). As the modern and fossil sites examined in this study largely reflect lowland (as opposed to montane) communities, tiny-bodied (body size category A), endemic taxa are again not applicable in this study.

The second category was that of trophic guild: specifically, primary (P) and secondary (S) consumers (as in, for example, Soligo & Andrews, 2005). Secondary consumers are hypercarnivores, carnivores, piscivores, omnivores, insectivores, as well as any other trophic guild in which non-plant matter makes up a significant part of the diet. Primary consumers are those whose intake of non-plant matter is very small or non-existent.

The final category groups species on the basis of their arboreality. Those species spending some to all of their time in trees are classified as arboreal (A), and thus this category includes scansorial species. Terrestrial species (T) are defined as those that spend no time in trees (i.e. strictly terrestrial). Again, where information on arboreality was not available, it was estimated by comparison with closest related taxa. Note that the term 'arboreal', as applied herein, implies potential, not strict, arboreality. Although some species may have been incorrectly classified (owing to the limited amount of ecological information available for many extant SE Asian mammals), the use of multivariate analyses ensures that, unless the majority of species are incorrectly classified, ecologically meaningful results will still be obtained.

Sixteen ecological categories were established by combining the remaining four body weight categories, the two trophic categories and the two locomotor categories (see Appendix S3). However, two of these categories are unfilled by either extant or extinct species considered herein (very large, arboreal primary and secondary consumers). Therefore, a total of 14 ecological categories were used throughout the analyses. Species from each nature reserve and national park discussed in Louys *et al.* (2009) were therefore allocated to these categories, and percentage representation was calculated (see Appendix S1 and Table 1, respectively). These ecological variables were subjected to a principal components analysis (PCA) in order to verify that the habitat groupings defined by Louys *et al.* (2009) were reflected by the ecological categories defined above. This analysis was run on PAST software (Hammer *et al.*, 2001). In addition to confirming groupings, an examination of the loadings for each of the components allows a determination of which ecological variables characterize each habitat type. Changes from one habitat type to another should be reflected in changes to these loadings.

A canonical discriminant functions analysis (DFA) calculates the relationships between variables belonging to pre-defined groups in order to assign unknown variables to those groups. The most often used variables in palaeoecological analyses are either taxonomic (e.g. Sandrock *et al.*, 2007; Louys *et al.*, 2009) or ecological (e.g. Reed, 1998; Mendoza *et al.*, 2005). Taxonomic variables are not used in the following study. Although a range of habitat types are represented by the natural protected areas discussed above, those reserves and parks sampled from SE Asia are exclusively closed. In contrast, open habitats are represented exclusively by Chinese parks and reserves. Therefore, in order to avoid a potential zoogeographical bias in the analysis, ecological variables were preferred over taxonomic.

Fossil taxa from the 25 sites in SE Asia were likewise defined by the ecological variables (see Appendix S2 and Table 2). Percentages were standardized for both modern and fossil lists

Table 1 Proportional representation of medium- and large-bodied mammalian communities found in select national parks and reserves in Asia, broken down according to ecological guilds. B, small; C, medium; D, large; E, very large; A, arboreal; T, terrestrial; P, primary consumer; S, secondary consumer.

Reserve/Park	Classification	BPA	BPT	BSA	BST	CPA	CPT	CSA	CST	DPA	DPT	DSA	DST	EPT	EST
Ailaoshan	Closed	0.14	0.07	0.14	0.1	0.1	0.21	0.14	0	0	0	0	0.03	0.03	0.03
Changshanerhai	Closed	0.09	0.18	0.14	0.09	0.09	0.05	0.14	0	0	0.05	0.05	0.05	0.09	0
Gaolingong	Closed	0.07	0.1	0.14	0.1	0.14	0.1	0.1	0.03	0	0	0.03	0.07	0.07	0.03
Maolan	Closed	0.11	0.16	0.11	0.16	0.05	0.26	0	0	0	0	0.05	0.05	0	0.05
Medong	Closed	0	0.05	0.05	0.16	0.16	0.26	0.05	0	0	0.05	0.05	0.05	0.11	0
Sai Yok	Closed	0.14	0.06	0.11	0.08	0.08	0.08	0.11	0.03	0	0	0.03	0.11	0.14	0.03
Khao Yai	Closed	0.09	0.09	0.16	0.13	0.03	0.06	0.13	0.06	0	0	0.03	0.09	0.09	0.03
Kaeng Krachan	Closed	0.09	0.09	0.15	0.03	0.09	0.09	0.09	0.09	0	0	0.03	0.09	0.15	0.03
Erawan	Closed	0.09	0.09	0.13	0.13	0.09	0.07	0.11	0.02	0	0.02	0.02	0.09	0.11	0.02
Kerinci Seblat	Closed	0.16	0.09	0.18	0.09	0.04	0.04	0.13	0.09	0	0	0	0.04	0.09	0.04
Dinghushan	Mixed	0	0.06	0.13	0.31	0	0.13	0.13	0.06	0	0	0.06	0.06	0	0.06
Fanjingshan	Mixed	0.09	0.09	0.09	0.18	0.09	0.15	0.09	0.09	0	0	0.03	0.09	0	0.03
Wuyishan	Mixed	0.03	0.13	0.1	0.2	0.07	0.13	0.13	0.07	0	0	0.03	0.07	0	0.03
Funiushan	Mixed	0	0.08	0.17	0.21	0	0.21	0.04	0.13	0	0	0.04	0.08	0	0.04
Nujiang	Mixed	0.09	0.09	0.15	0.18	0.06	0.12	0.03	0.12	0	0.03	0.03	0.09	0.03	0
Tianmushan	Mixed	0	0.07	0.11	0.21	0.04	0.18	0.14	0.11	0	0	0.04	0.07	0	0.04
Yellow River	Mixed	0	0.25	0.25	0.25	0	0	0	0.25	0	0	0	0	0	0
Maojingba	Mixed	0	0.08	0.08	0.25	0	0.08	0	0.17	0	0	0.08	0.17	0	0.08
Yunwushan	Mixed	0	0.13	0.13	0.38	0	0	0	0.25	0	0	0	0.13	0	0
Longqi	Mixed	0.05	0.14	0.14	0.14	0.05	0.1	0.1	0.05	0	0.05	0.05	0.1	0	0.05
Poyang	Mixed	0	0.14	0.29	0.14	0	0.07	0.14	0.14	0	0	0	0	0	0.07
Baima Xueshan	Open	0.13	0	0.13	0	0.13	0.25	0.13	0	0	0.25	0	0	0	0
Bogdhad	Open	0	0	0.11	0.11	0	0.11	0	0	0	0.33	0	0.11	0.22	0
Jiuzhaigou	Open	0.1	0	0.1	0.1	0	0.2	0	0	0	0.3	0.1	0	0.1	0
Altun Mountain	Open	0	0.13	0.06	0.13	0	0.13	0	0.06	0	0.19	0	0.19	0.13	0

by taking the square-root of the raw values. The standardized values from modern habitats were used to define the discriminant functions, calculated using SPSS Standard Version, Release 11.0.1 (http://www.spss.com). The functions were cross-validated by leaving one reserve or park out, re-running the analysis using the remainder of the protected areas, and classifying the omitted reserve. The discriminant functions were then used to classify all Pleistocene sites. To assess the accuracy of palaeoecological predictions for Pleistocene sites on the basis of fossil fauna compositions, we compared these results with palaeoecological reconstructions obtained in other ways and available in the scientific literature.

RESULTS

Species analysis

The results of the PCA (Fig. 2) confirmed the characterization of the three habitat types as established in Louys *et al.* (2009) on the basis of the ecological variables defined in this paper. In particular, the first two components [explaining 43% and 19% of the variation, respectively (Table 3)] best separated the different habitat types. Negative values of PC 1 were generally indicative of closed and open habitats, with the more negative values associated with open habitats. Positive values for this component were generally indicative of mixed habitats. PC 2 most clearly differentiated closed habitats from mixed and open habitat types, with the latter values negative or close to zero. An analysis of the biplot and loadings for these two components (Fig. 2; Table 3) suggested that the variable DPT (large terrestrial primary consumers) helped separate open habitats; BPT (small terrestrial primary consumers), BSA (small arboreal secondary consumers), BST (small terrestrial secondary consumers), CST (medium terrestrial secondary consumers) helped separate mixed habitats; and BPA (small arboreal primary consumers), CPA (medium, arboreal primary consumers), CSA (medium arboreal secondary consumers) helped separate closed habitats, whereas DPT (large terrestrial primary consumers) and DST (large terrestrial secondary consumers) separated mixed/open from closed habitats.

An examination of the PCA results showed that open habitats, such as those represented by grasslands and deserts, were characterized by the smallest number of ecological variables. The variables separating open habitats from all other habitats were large, terrestrial primary consumers (Fig. 2; Table 3). These results were congruous with that expected: that open habitats would have a greater relative proportion of larger, terrestrial primary consumers, especially grazers. This variable was also a selected ecological variable with regard to

Table 2 Proportional representation of medium- and large-bodied mammalian communities found in select Pleistocene fossil sites in Southeast Asia, broken down according to ecological guilds. B, small; C, medium; D, large; E, very large; A, arboreal; T, terrestrial; P, primary consumer; S, secondary consumer.

Pleistocene site	No. megafauna species	BPA	BPT	BSA	BST	CPA	CPT	CSA	CST	DPA	DPT	DSA	DST	EPT	EST
Tham Khuyen	27	0.04	0.11	0.04	0.07	0.07	0.04	0	0.04	0.04	0.15	0	0.07	0.22	0.11
Tham Hai	20	0	0.05	0.05	0.1	0.05	0	0	0.05	0.05	0.25	0.05	0.1	0.2	0.05
Tham Om	31	0	0.06	0.1	0.1	0.03	0.16	0.03	0.03	0	0.13	0.03	0.06	0.23	0.03
Hang Hum 1	25	0	0.08	0.08	0.08	0.04	0	0.04	0.12	0	0.12	0.04	0.08	0.2	0.12
Hang Hum 2	19	0	0.11	0.11	0	0.05	0	0.05	0.05	0.05	0.16	0.05	0.05	0.26	0.05
Lang Trang	21	0.05	0.05	0	0.1	0.05	0.1	0.05	0.05	0.05	0.1	0.05	0.14	0.19	0.05
Keo Leng	24	0.04	0.08	0.04	0.08	0.13	0.13	0	0	0.04	0.13	0	0.04	0.17	0.13
Kali Glagah	11	0	0	0	0.09	0	0	0	0	0	0.27	0	0	0.45	0.18
Ci Saat	9	0	0	0	0	0	0.22	0	0	0	0.33	0	0	0.33	0.11
Trinil	21	0.05	0.05	0	0	0.05	0.1	0.05	0.05	0	0.24	0	0.05	0.29	0.1
Kedung Brubus	23	0.04	0.04	0	0.04	0.04	0.04	0.04	0	0	0.13	0.04	0.09	0.39	0.09
Punung	18	0.11	0.06	0	0	0.11	0.11	0.06	0	0.06	0.06	0	0.11	0.22	0.11
Kinta Valley	8	0	0	0	0.13	0	0	0	0	0	0.13	0	0	0.63	0.13
Niah	22	0.14	0.09	0.05	0.09	0.09	0.05	0.14	0	0.05	0.09	0.05	0.05	0.09	0.05
Lida Ajer	18	0.22	0.06	0	0	0.11	0.11	0	0	0.06	0.11	0	0.06	0.17	0.11
Sibrambang	20	0.2	0.05	0	0	0.05	0.1	0	0	0.05	0.1	0	0.1	0.25	0.1
Thum Wimam Nakin	29	0.07	0.03	0.07	0.1	0.03	0.07	0	0.03	0.03	0.21	0	0.03	0.24	0.07
Thum Phra Khai Phet	8	0	0	0	0	0	0.25	0	0.13	0	0.25	0	0	0.25	0.13
Ban Fa Suai	34	0.03	0.03	0	0.06	0.03	0.18	0	0.03	0.03	0.18	0	0.09	0.26	0.09
Kao Pah Nam	7	0	0.14	0	0	0	0	0	0.14	0	0.29	0	0.14	0.29	0
Phnom Loang	11	0	0	0	0.09	0	0.09	0	0.09	0.09	0.18	0	0.09	0.36	0
Mogok Caves	8	0	0.13	0	0	0	0	0	0	0	0.25	0	0	0.5	0.13
Irrawaddy beds	19	0	0	0	0	0	0	0	0	0	0.16	0	0	0.79	0.05
Tam Hang (north)	13	0	0.08	0	0	0.08	0	0	0	0.08	0.08	0.08	0.15	0.38	0.08
Tam Hang (south)	36	0	0.06	0.11	0.03	0.08	0.14	0	0.08	0.03	0.08	0	0.08	0.22	0.08

the DFA (Table 4), again highlighting this characteristic of open habitats.

Closed habitats were differentiated from open and mixed habitats by large representation in three variables (Fig. 2; Table 3). All of these were arboreal categories (small and medium primary consumers, and medium secondary consumers). Smaller proportions of large terrestrial primary and secondary consumers differentiated between closed and mixed/open habitats along PC 2. Of the ecological variables helping to separate closed habitats, only medium arboreal secondary consumers were selected by the DFA in the classification of habitats (Table 4).

Mixed habitats were separated in the PCA by large proportions of four ecological variables: small terrestrial primary consumers, small secondary consumers, both arboreal and terrestrial, and medium terrestrial secondary consumers (Fig. 2; Table 3). Of these only the proportion of small and medium terrestrial secondary consumers was selected by the DFA in differentiating between habitats (Table 4). We note that no large mammals were necessary in differentiating mixed habitats. The bias in most SE Asian fossil sites towards larger and more iconic species may therefore provide a potential bias against a mixed habitat classification.

On the basis of these results, some expectations of changes in the proportions of the ecological variables can be determined across suspected ecological changes. In particular, the presence of a central savanna corridor running through the middle of Sundaland, as proposed by a number or researchers (e.g. Heaney, 1991; Meijaard, 2003; Bird *et al.*, 2005), should be traceable through an ecological analysis of fossil faunas. A change from a closed (e.g. rain forest) habitat to either a mixed or an open (e.g. open forest or grassland) habitat should be reflected by a significant decrease in the proportion of medium arboreal secondary consumers. Mammals from Pleistocene sites described by this variable include medium-sized cats (e.g. *Catopuma* and *Prionailurus* species), the pangolin (*Manis*), the clouded leopard (*Neofelis*) and the binturong (*Arctictis*). Concomitant with these are relative increases in the proportions of large and very large terrestrial primary consumers, and small and medium terrestrial secondary consumers. Mammals from Pleistocene sites described by these variables include the dhole (*Cuon*), Asian spotted hyena (*Crocuta*), as well as cervids, bovids, rhinos and elephants.

Differentiating between open and mixed habitats is more difficult than differentiating between closed and open habitats. Although component 2 in the PCA separates closed habitats,

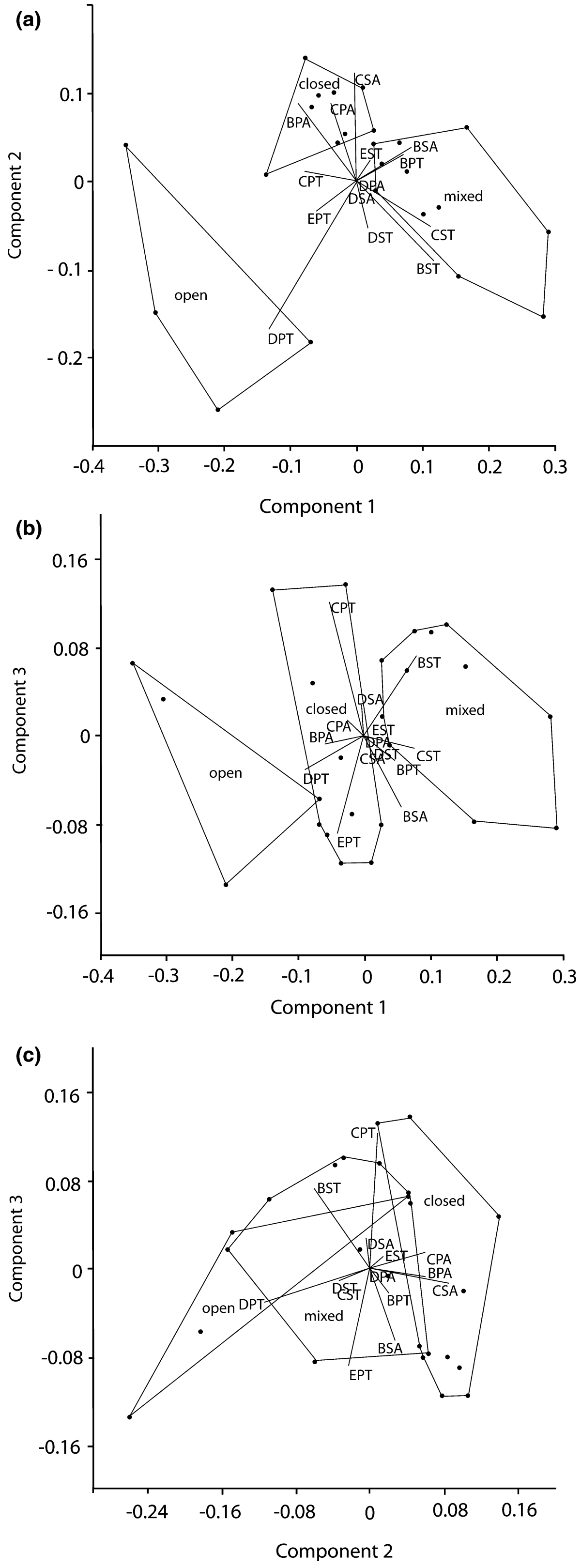

Figure 2 Principal components analysis (PCA) and biplot of modern reserves and parks in Asia using ecological characteristics of their mammal faunas. (a) PC 1 versus PC 2; (b) PC1 versus PC 3; (c) PC 2 versus PC 3. B, small; C, medium; D, large; E, very large; A, arboreal; T, terrestrial; P, primary consumer; S, secondary consumer.

Table 3 Principal components analysis of modern medium- and large-bodied mammalian communities found in select Asian national parks and reserves, with communities broken down according to ecological guilds. Eigenvalues, percentage variance and principal components (PC) loading for the first three principal components are listed. B, small; C, medium; D, large; E, very large; A, arboreal; T, terrestrial; P, primary consumer; S, secondary consumer.

Ecological category	PC 1	PC 2	PC3
Eigenvalue	0.02315	0.010194	0.007198
Percentage variance accounted for	42.775	18.835	13.299
BPA	−0.3263	0.3207	−0.0397
BPT	0.2528	0.1088	−0.1243
BSA	0.3011	0.1408	−0.3479
BST	0.4228	−0.3239	0.3873
CPA	−0.1462	0.3201	0.07771
CPT	−0.2869	0.04314	0.649
CSA	−0.0203	0.4429	−0.06991
CST	0.4047	−0.1861	−0.05982
DPA	3.99×10^{-24}	6.97×10^{-21}	7.84×10^{-19}
DPT	−0.4847	−0.6055	−0.1614
DSA	−0.0221	−0.02196	0.1508
DST	0.06011	−0.1915	−0.05152
EPT	−0.2212	−0.1248	−0.4704
EST	0.0663	0.07741	0.06015

Table 4 Discriminant functions analysis of modern medium- and large-bodied mammalian communities found in select Asian national parks and reserves, with communities broken down according to ecological guilds and values standardized. Canonical discriminant function coefficients are listed. B, small; C, medium; D, large; E, very large; A, arboreal; T, terrestrial; P, primary consumer; S, secondary consumer.

	Function	
	1	2
BST	1.029	−0.260
CSA	0.799	−0.309
CST	1.207	0.530
DPT	0.731	1.213
EPT	−1.183	−0.399

it does not separate mixed from open habitats. Nevertheless, significant relative changes between the proportions of large terrestrial primary consumers and small and medium terrestrial secondary consumers should indicate a transition from mixed to open habitat.

The results of the DFA of modern faunas are shown in Fig. 3 and Table 4. Five variables were selected by the DFA as useful in classification, these being BST (small terrestrial secondary consumers), CSA (medium arboreal secondary consumers), DPT (large terrestrial primary consumers), CST (medium terrestrial secondary consumers) and EPT (very large terrestrial primary consumers). The first function calculated accounted

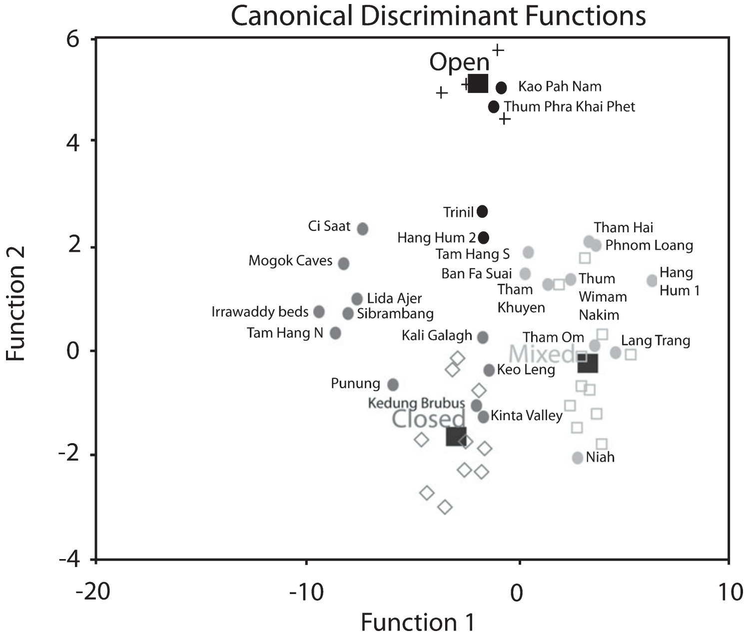

Figure 3 Discriminant functions analysis showing the classification of select Southeast Asian Pleistocene sites (circles). Colour scheme: dark grey circles represent closed; light grey circles represent mixed; black circles represent open habitat classifications. Dark grey diamonds represent closed; light grey squares represent mixed; and black crosses represent open modern parks and reserves. Black solid squares represent the group centroids for each habitat type.

for 62.1% of the variance observed (0.953 canonical correlation), and the second accounted for 37.9% of the variance (0.926 canonical correlation). All reserves were correctly reclassified in the leave-one-out cross-validation analysis. Each fossil site was subsequently allocated to a habitat on the basis of these functions (Table 5).

Palaeoenvironmental classification

The sites of Thum Phra Khai Phet and Kao Pah Nam (Thailand) are classified as open habitats. Although these sites have sufficient numbers of species to differentiate between open and closed habitats, they do not have enough to allow differentiation between open and mixed environments. On the basis of their discriminant scores, however, they are more likely to represent open than mixed habitats. Trinil and Hang Hum II are also classified by the DFA as open, although an examination of their position relative to the habitat group centroids shows that they fall much closer to mixed habitats than the aforementioned Thai sites. They preserve, however, sufficient numbers of species to differentiate between open and mixed habitats, and as such should be classified as open.

Only two sites could confidently be allocated to a mixed habitat: Tam Hang (south), Laos and Ban Fa Suai, Thailand. Their positions are, however, close to those of Trinil and Hang Hum II, both classified as open sites. These four sites therefore in all likelihood preserve a gradation from more open habitats (Trinil and Hang Hum II) to slightly more wooded habitats [Tam Hang (south) and Ban Fa Suai], on the basis of the mammals present.

All other sites, classified as either mixed or closed habitats, do not preserve sufficient numbers of species for them to be confidently attributed to either habitat. What can be determined, however, is that these sites, with the exception of Ci Saat, Mogok Caves and Kinta Valley, are unlikely to represent open habitats. These last three sites, although preserving sufficient numbers of species to differentiate between closed and open habitats, do not preserve sufficient numbers to differentiate between mixed and open and mixed and closed habitats, therefore making unambiguous classifications difficult to establish.

DISCUSSION

Sundaland

Java

The climate of Java during much of the Miocene is thought to have been wet and warm, and land would have been covered mostly by rain forest and peat-swamps (Morley, 1991, 2000; Whitten *et al.*, 1996). During the Late Miocene and Pliocene, cooler and drier conditions probably prevailed (Morley, 1999; Morley *et al.*, 2000), with climatic drying and concomitant expansion of savanna in the Central Java region suggested at the Pliocene–Pleistocene boundary (Rahardjo, 1999). This change in vegetation is not reflected in our data, which suggest that both the Early Pleistocene Ci Saat (*c.* 1200 ka; van den Bergh *et al.*, 2001) and Kali Glagah faunas in Central Java are classified as representing closed habitats (although Ci Saat may represent mixed or open habitats and Kali Glagah mixed habitats). Ci Saat has previously been interpreted to represent a more open habitat on the basis of pollen evidence (de Vos *et al.*, 1994), and a similar palaeoenvironment was suggested for the Early Pleistocene Mojokerto region, where pollen indicates extensive grassland with hardly any trees (R. Morley, Palynova, Indonesia, pers. comm., 12 April 2003). However, an examination of Ci Saat's position relative to the group centroids for the habitats (Fig. 3) shows that its position

Table 5 Habitat allocations of select Pleistocene fossil sites found in Southeast Asia based on a discriminate functions analysis of modern medium- and large-bodied mammalian communities found in Asian national parks and reserves, with communities broken down according to ecological guilds and values standardized. Other habitat possibilities are listed for sites where the number of taxa in that site does not reach the minimum number required to differentiate confidently between habitat types. Possible oxygen isotope stages (OIS) corresponding to each site are also indicated.

Period	Country	Site	Primary DF classification	Other DF habitat possibilities (more likely/less likely)	Age (ka)	Chronological reference	Glacial/Interglacial (OIS)
Early Pleistocene	Myanmar	Irrawaddy beds	Closed	Mixed			
Early Pleistocene	Java	Ci Saat	Closed	Mixed/Open	~1200	van den Bergh *et al.* (2001)	?Glacial (OIS36)
Early Pleistocene	Java	Kali Glagah	Closed				
Middle Pleistocene	Myanmar	Mogok Caves	Closed	Mixed/Open			
Middle Pleistocene	Cambodia	Phnom Loang	Mixed	Closed			
Middle Pleistocene	Java	Trinil	Open		~900	van den Bergh *et al.* (2001)	?Intergacial (OIS23)
Middle Pleistocene	Java	Kedung Brubus	Closed	Mixed	~700–800	van den Bergh *et al.* (2001)	Largely Glacial (OIS17-20)
Middle Pleistocene	Laos	Tam Hang (south)	Mixed				
Middle Pleistocene	Laos	Tam Hang (north)	Closed	Mixed			
Middle Pleistocene	Malaysia	Kinta Valley	Closed	Mixed/Open			
Middle Pleistocene	Thailand	Kao Pah Nam	Open	Mixed	~690	Pope *et al.* (1981)	?Interglacial (OIS17)
Middle Pleistocene	Thailand	Thum Wimam Nakin	Mixed	Closed	169	Esposito *et al.* (2002)	Glacial (OIS6)
Middle Pleistocene	Thailand	Thum Phra Khai Phet	Open	Mixed	169	Based on correlation with Thum Wiman Nakin, as per Tougard (2001)	Glacial (OIS6)
Middle Pleistocene	Thailand	Ban Fa Suai	Mixed				
Middle Pleistocene	Vietnam	Tham Om	Mixed	Closed	140–250	Olsen & Ciochon (1990)	?Glacial (OIS6,8)/?Interglacial (OIS7)
Middle Pleistocene	Vietnam	Tham Khuyen	Mixed	Closed	475	Ciochon *et al.* (1996)	Boundary between glacial (OIS12) and interglacial (OIS13)
Middle Pleistocene	Vietnam	Tham Hai	Mixed	Closed	475	Based on correlation with Tham Khuyen, as per Olsen & Ciochon (1990)	Boundary between glacial (OIS12) and interglacial (OIS13)
Late Pleistocene	Borneo	Niah	Mixed	Closed	39–45	Barker *et al.* (2007)	Interglacial (OIS3)
Late Pleistocene	Java	Punung	Closed	Mixed	128	Westaway *et al.* (2007)	Interglacial (OIS5)
Late Pleistocene	Sumatra	Lida Ajer	Closed	Mixed	128	Based on correlation with Punung, as per de Vos (1983)	Interglacial (OIS5)
Late Pleistocene	Sumatra	Sibrambang	Closed	Mixed	128	Based on correlation with Punung, as per de Vos (1983)	Interglacial (OIS5)
Late Pleistocene	Vietnam	Hang Hum I	Mixed	Closed	80–140	Olsen & Ciochon (1990)	?Interglacial (OIS5)/?Glacial(OIS4,6)
Late Pleistocene	Vietnam	Hang Hum II	Open		80–140	Olsen & Ciochon (1990)	?Interglacial (OIS5)/?Glacial(OIS4,6)
Late Pleistocene	Vietnam	Lang Trang	Mixed	Closed	128	Based on correlation with Punung, as per de Vos (1983)	Interglacial (OIS5)
Late Pleistocene	Vietnam	Keo Leng	Closed	Mixed	20–30	Olsen & Ciochon (1990)	?Glacial (OIS2)/?Interglacial (OIS3)

approaches that of open habitats. Mixed habitats, with some forest but also significant open (i.e. grassland) areas, are more probable for these sites. These habitats can occur in areas with long dry seasons, where abrupt forest to open grassland ecotones can arise, possibly maintained by natural fire. This interpretation is supported by palaeosol studies of the Solo Basin, central Java (Bettis *et al.*, 2009), which indicate an increased duration of the dry season during the early part of the Pleistocene. Extensive forest areas remain in wetlands, around rivers, and on mountain slopes, with drier areas kept open by fire and grazing. This seems to be confirmed by the presence of species such as *Chiropodomys gliroides*, which indicate a forested environment at the time of the early Pleistocene Satir fauna, whereas wide-toothed species of mouse (*Mus* sp.) suggest the presence of grasslands (van der Meulen & Musser, 1999). The different vegetation zones would have shifted with the increasingly severe glacial cycles that characterize much of the Pleistocene and which would have contracted and expanded forests and mixed areas inversely with more open ones (Meijaard, 2004).

Trinil's (*c.* 900 ka; van den Bergh *et al.*, 2001) classification in our analysis largely agrees with previous palaeoenvironmental reconstructions. The almost intermediate position of Trinil between open and mixed habitats in the DFA suggests primarily grassland conditions, but does not specifically exclude the presence of some trees. On the basis of the large numbers of bovids present at the site, the predominant vegetation was previously classified as open woodland (de Vos *et al.*, 1994; van den Bergh *et al.*, 2001; Storm, 2001). Finds of *Leptoptilos* cf. *dubius* (an adjutant stork) and *Ephippiorhynchus* cf. *asiaticus* (black-necked stork of mainland Asia – but not Sundaland – and Australia) suggest the presence of grassy areas, mud banks, mangroves, swamps, or open and lightly wooded areas, which also seems to fit the picture for *Pavo muticus* (green peafowl) habitat (MacKinnon & Phillipps, 1993; Simpson & Day, 1996). The open environment reconstructed in this analysis is confirmed by the presence of the wide-toothed species of rat (*Rattus* sp. A), from Trinil (van der Meulen & Musser, 1999), which was presumably a grassland species.

The Trinil conditions changed during the deposition of the Kedung Brubus sediments, when a wave of Asiatic mammals entered the region, probably during a glacial maximum (Musser, 1982). The Kedung Brubus fauna, which has been dated at 0.8–0.7 or 1.3–0.8 Ma (see van den Bergh *et al.*, 2001; Larick *et al.*, 2001), brought in several new medium- to large-sized mammals [*Rhinoceros unicornis* (Indian rhinoceros), *Tapirus indicus* (Malayan tapir), *Manis palaeojavanica* (giant tapir), *Pachycrocuta brevirostris* (giant hyena), *Lutrogale palaeoleptonix* (otter)] (Aimi & Aziz, 1985; Bandet *et al.*, 1989; van den Bergh *et al.*, 2001). Although allocated to a closed habitat, we cannot discount, owing to the low number of taxa preserved, that Kedung Brubus may represent a mixed environment such as open woodland. This latter interpretation would be more congruent with previous qualitative analyses that describe the Middle Pleistocene environments of Java as very diverse with tall evergreen forests, shrubby or woodland vegetation, and extensive grasslands, reminiscent of a mosaic of forest, scrub and grassland, such as seen today in the wetter, hillier parts of East Africa (e.g. western Uganda) or India (Medway, 1972; de Vos *et al.*, 1994; van den Bergh *et al.*, 2001), as well as with the open/mixed forest reconstructions of the Middle Pleistocene deposists of the Sangiran dome (Bouteaux, 2005).

Climatic conditions at the beginning of the Late Pleistocene are considered to have been drier than today. Around 135 ka, annual precipitation on Java, inferred from palaeosol development, is estimated to have been 750–1000 mm (van der Kaars & Dam, 1995, 1997), whereas today annual rainfall amounts to between 1500 and 2000 mm (Whitten *et al.*, 1996). However, between 126 and 81 ka, very warm and humid conditions prevailed, with up to 2000 mm of annual precipitation. The site of Punung, dated at between 128 ± 15 and 118 ± 3 ka (Westaway *et al.*, 2007), preserves for the first time characteristic rain forest taxa [e.g. *Symphalangus* (siamang), *Pongo* (orangutan), *Catopuma* (golden cat), *Helarctos* (Malayan sun bear) and *Tapirus* (Malay tapir)] (Storm *et al.*, 2005). The palaeoenvironmental reconstruction for this fauna by the DFA is unsurprisingly that of a closed forest. At around 81 ka the vegetation in the Bandung plain changed from closed freshwater swamp forest to open herbaceous swamp, dominated by grasses and sedges, suggesting a reduction in annual precipitation to *c.* 1000 mm (Smit-Sibinga, 1947; van der Kaars & Dam, 1995, 1997; van der Kaars, 1998 cited in Sun *et al.*, 2000). However, between 74 and 47 ka, slightly warmer and wetter conditions existed.

Sumatra

Late Pleistocene environments of Sumatra were warm and wet, similar to those at present, if perhaps a little drier (Maloney & McCormac, 1996). The sites of Lida Ajer and Simbrambang, Sumatra, from the Late Pleistocene, share the same classification as Punung, which is not surprising because they share a high level of taxonomic similarity (de Vos, 1983). Furthermore, the faunas from these sites are essentially modern – neither Lida Ajer nor Simbrambang records any extinctions (Louys, 2007) – and it is expected that these faunas would correspond to Sumatra's present-day predominant vegetation types, namely closed forests.

Borneo

Early Miocene coals in the Maliau Basin in Sabah, Borneo, suggest warm everwet climates (Tjia *et al.*, 1990). The conifers *Phyllocladus* and *Podocarpus* first appear in the Late Pliocene of Borneo, with the former arriving at the Pliocene–Pleistocene transition, indicating either cooler climates and/or substantially higher mountains in Borneo than at present (Muller, 1971). As elsewhere in the region, the increasingly severe glacials of the Pliocene–Pleistocene resulted in occasionally more open vegetation types in an evergreen matrix.

These patterns are especially clear in Late Pleistocene Borneo, for which several sources suggest considerably colder temperatures and reduced rainfall (Thomas, 1987; Thorp *et al.*, 1990). These conditions, for example those in the penultimate glacial period, are characterized by the expansion of montane vegetation, the contraction of lowland cover and a reduction of mangrove vegetation (Jirin, 1993). In east and south Borneo, dated charcoal finds suggest that the coastal area was more continental and drier than at present; forest formations were more seasonal and probably had a temporary fire-climax character (Goldammer & Seibert, 1989). Grasslands or wooded savannas also appear to have been present (Caratini & Tissot, 1988). This would be congruent with the faunal evidence from Niah Cave (39–45 ka, Barker *et al.*, 2007). In our analysis, Niah Cave is classified as a mixed habitat, although not enough species are preserved at this site to enable it to be confidently distinguished from a closed habitat. The fauna from Niah Caves occupies a unique position in the DFA, and is strongly indicative of a mixed habitat, most probably including woodlands and grasslands. This classification agrees with previous qualitative reconstructions on the basis of fauna (e.g. Medway, 1977; Harrison, 1996) and flora (e.g. Barker *et al.*, 2007). By contrast, Majid (1982) suggested that, at the height of the last glacial maximum, the Niah area in Sarawak was covered by deciduous monsoon forest, a drier forest type but not as open as suggested by other authors. The data from the literature are, however, equivocal about the predominant vegetation characteristics of Late Pleistocene Borneo. Visser *et al.* (2004) found evidence based on lignin phenol ratios in coastal sediments that indicated that Late Pleistocene vegetation in eastern Borneo did not significantly change from tropical rain forest during the last two glacial periods, relative to subsequent interglacial periods. Furthermore, pollen records suggest that during the Last Glacial Maximum (LGM) the upper Kapuas area in west Borneo was probably covered in rain forest, very similar to that found during the mid-Holocene (Anshari *et al.*, 2001; Kershaw *et al.*, 2001). Moreover, pollen data from peat swamps in the Sebangau area in south Borneo (Page *et al.*, 1999) indicate that the climate remained relatively warm and wet during the LGM. These mixed signals from various data sets may suggest that there was significant spatial and temporal variation in the palaeoenvironments of Borneo during the Late Pleistocene. This would not be unlike the present-day situation, in which rainfall patterns and concomitant vegetation types vary widely, longitudinally as well as elevationally.

Malay Peninsula

The coal composition of Pliocene–Early Pleistocene deposits in the Kepong and Kluang-Niyor Basins (Stauffer, 1973) and the Merapoh Basin (Hing & Leong, 1990) indicates that these deposits were derived mainly from woody and herbaceous plants as well as from spore-bearing plants, as would have been found in a tropical forest dominated by angiosperms and to a lesser extent by gymnosperms (Hing & Leong, 1990). Based on palaeobotanical data, Morley (1999) suggested that *Pinus* savanna was probably widespread on the Malay Peninsula at 660, 480, 200 and 22 ka. All of these, apart from 200 ka, are periods of low sea-level and presumably drier, slightly cooler conditions (see Meijaard, 2004 for an overview). During the interstadials, the climate in the lowlands of the Malay Peninsula was probably similar to that prevailing today, as suggested by pollen found at interglacial deposits dated at *c.* 80 and 55 ka (Kamaludin & Azmi, 1997). Elsewhere, Ayob (1970) provided carbon-dated peat and wood samples from deposits containing pollen indicating perhumid vegetation; these samples were dated at *c.* 36.4 and 41.2 ka, indicating that before the LGM an evergreen vegetation type existed in this area close to present-day Kuala Lumpur. Price *et al.* (1997) suggested that bauxite formation on the Malay Peninsula took place continuously from 115 ka to the present, which would suggest mostly warm and wet conditions. It therefore appears that vegetation zones along the peninsula shifted from open woodlands to closed deciduous and evergreen rain forest with the changing climatic patterns of the glacial–interglacial fluctuations. The fauna from the Kinta Valley represents one of the few discoveries of Pleistocene fossils on the Malay Peninsula. It is classified by the DFA as representing a closed habitat, although a mixed habitat is also likely. However, the dating of this site is not well constrained: although assigned to the Middle Pleistocene based on the presence of *Palaeoloxodon* (e.g. Hooijer, 1963; Medway, 1972), on the basis of geological evidence the site could well be Late Pleistocene in age (Kamaludin *et al.*, 1993; Thorp & Thomas, 1993; Kamaludin & Azmi, 1997; Teeuw *et al.*, 1999). Muhammad *et al.* (2002) report an age of 228 ka for a Kinta Valley vertebrate fossil, but it is unclear how that particular fossil relates to the fauna described by Hooijer (1963). It is unfortunate that neither the age nor the habitat type of this site can be constrained on the basis of current data, as the Kinta Valley site lies on the proposed savanna corridor of Heaney (1991).

Mainland SE Asia

Mammalian fossil assemblages in Yunnan Province, southern China, indicate that between the Early and Middle Pliocene a mixed forest and open bush–grassland vegetation existed, with several carnivores typical of forested areas, and ungulate species suggesting more open, grassy vegetation (Pan, 1993). Slightly wetter conditions seem to have prevailed further east and south-east of Yunnan. Reconstructions of the climate and vegetation of this area in the Middle Pliocene (3 Ma) indicate that there was a considerable expansion of evergreen forest in southern China, whereas mainland SE Asia was covered mostly by rain forest, possibly with patches of deciduous forest in the area of present-day Myanmar (Dowsett *et al.*, 1994).

The Middle–Late Pleistocene in the eastern parts of SE Asia saw some considerable changes in vegetation distribution. For instance, Zheng & Lei's (1999) palaeoenvironmental data for the

Leizhou Peninsula, north of Hainan Island, suggest significant changes over the last 400 kyr. Starting with slightly drier and cooler conditions than today around 400 ka, there was a change to a wetter and warmer climate with predominant evergreen oak forest between 340 and 280 ka. When mean annual temperatures were more than 4°C lower than today, between 280 and 240 ka, a substantial increase in typical montane conifer forest elements occurred. The Middle to Late Pleistocene saw fluctuations in vegetation with the waxing and waning of glacials and interglacials, with open vegetation peaking around the LGM, when mean temperatures dropped between 5 and 6°C and dense forests were transformed to grassland or savanna (Zheng & Lei, 1999). This scenario fits with data from Ferguson (1993), who reported an extremely cold and arid phase at the end of the Pleistocene (20–15 ka) for China. In Jiangxi Province, central–south-east China, the Late Pleistocene climate (between 12.8 and 10.5 ka) was also drier and cooler than today's, and the subtropical, mixed deciduous–evergreen broad-leaved forest, which is now in the area, was reduced and herbaceous cover expanded (Jiang & Piperno, 1999).

Overall, mainland SE Asia appears to have been cooler and more seasonal than today during much of the Pleistocene. The dominant vegetation type for mainland SE Asia during this period appears to have been evergreen, semi-evergreen and coniferous forests, with varying amounts of grasses and other herbaceous vegetation. The results of our mammal fauna analysis are in general agreement with these overall patterns, although mostly indefinite about exactly which vegetation types the faunas correspond to.

Myanmar

Palaeobotanical data from India and from Myanmar indicate that a rich tropical to subtropical vegetation covered the region *c.* 5 Ma under a prevailing warm humid climate (several references in Poole & Davies, 2001). During the Pliocene, however, an increasingly arid climate, engendered by the rising Himalayas, caused a change in the vegetation of this region (Poole & Davies, 2001). The vegetation changes are also reflected in faunal turnovers in southern Asia: browsers are replaced by grazers, and rodents show considerable turnover (Barry *et al.*, 1985; Quade *et al.*, 1989). These palaeoenvironmental changes are also reflected in northern Thailand, where coals in Middle Miocene sediments indicate a peat swamp, fluvial or lacustrine environment, whereas no coal has been found in Late Miocene, Pliocene and Quaternary sediments (Morley *et al.*, 2000), probably indicating a climate that was either too cool or too dry for coal formation. Evidence for grasslands is very limited through most of the Pliocene, but subsequently shows a marked increase during the Early Pleistocene, indicating the expansion of savanna vegetation, which, together with evidence of charred grass cuticle, suggests it was subject to burning (Morley, 1999). Our classifications of Mogok Caves and the Irrawaddy faunas as representing closed habitats are probably a result of the limited number of taxa from these sites, and the classification of mixed or open would be more consistent with the interpretations discussed above. Furthermore, the climatic fluctuations of the Pleistocene would have resulted in expanding and contracting forests within a more open vegetation matrix. As the age of the Pleistocene faunas remains unresolved, it might be that they relate to the warmer and more humid phases of the Pleistocene, which would have coincided with more forested environments.

Thailand

Thick laterites of Pliocene–Early Pleistocene age in the Lower Central Plain of Thailand (Thiramongkol, 1986) indicate seasonality in a generally humid tropical climate (Whittow, 1984). Based on rodent fossil distributions, Chaimanee (1998) reconstructed Late Pliocene–Early Pleistocene palaeoenvironments for several locations in Thailand. The site of Khao Samngam (99°42′ E, 13°27′ N) probably had an environment with some mixed vegetation, with grasslands in the floodplain and forests on the surrounding limestone hills. Of the SE Asian Middle Pleistocene sites, only Kao Pah Nam (*c.* 690 ka, Pope *et al.*, 1981) and Thum Phra Khai Phet (*c.* 169 ka, see Table 5) are classified as open habitats. It should be noted, however, that both these sites are represented by relatively small numbers of species (although they are not the only sites to exhibit such low species numbers). The palaeoenvironment of Kao Pah Nam was interpreted by Pope *et al.* (1981, p. 161) as 'relatively open, dry dipterocarp woodland'. However, this description would be more congruent with our mixed habitat description, as opposed to the open classification obtained. Thum Phra Khai Phet has been considered, on the basis of taxonomic similarity, to be contemporaneous with Thum Wimam Nakin (Tougard, 1998, 2001). In our analysis, this latter site (Thum Wimam Nakin) is classified as representing a mixed habitat, which agrees with previous palaeoenvironmental reconstructions suggesting that it represents 'a slightly open forested environment' (Tougard & Montuire, 2006). Thus, the classification of Thum Phra Khai Phet as open is also likely to be a result of the inadequate number of large-bodied taxa preserved at the site (Table 2), which prohibits differentiation between open and mixed habitats. Ban Fa Suai, the only Middle Pleistocene site from Thailand to preserve more than 32 species, is confidently assigned as mixed.

Vietnam and Cambodia

Vietnam and Cambodia have received little previous palaeoecological attention. The three Middle Pleistocene Vietnamese sites examined in this analysis [Tham Khuyen (475 ka, Ciochon *et al.*, 1996), Tham Hai (475 ka, see Table 5), Tham Om (140–250 ka, Olsen & Ciochon, 1990)] are each classified in our analysis as mixed, but they do not preserve sufficient species to enable us to distinguish confidently between mixed and closed habitats. Of these three sites, Tham Om is the most southern, and with 31 species is actually quite likely to be correctly classified. With respect to the DFA, it is closest to that of the mixed habitat group centroid. In terms of age, at 140–250 ka (Olsen & Ciochon, 1990), it is closest to that of Tham Wimam Nakin, Thailand, which is also considered a mixed habitat. The site of Phnom Loang, Cambodia, is also classified as mixed habitat, but again too few species are preserved to rule out the possibility that it may represent a closed habitat. The discriminant functions calculated for this site are almost identical to those of Tham Hai, Vietnam, suggesting that these two sites sample the same habitat. Middle Pleistocene megafaunal communities across Indochina are therefore reconstructed by the DFA as most probably representing mixed habitats, that is, heterogeneous habitats consisting of patches of grassland and forest, most probably of the dry evergreen type. These include sites in Cambodia (Phnom Loang), Thailand (Thum Wimam Nakin, Ban Fa Suai) and Vietnam (Tham Om, Tham Khuyen, Tham Hai). The present-day vegetation in this area, prior to human disturbance, is dense evergreen forest.

Bacon *et al.* (2008b) suggested a humid forested area with some open areas for the Late Pleistocene site of Duoi U'Oi (*c.* 66 ka), whereas the site of Ma U'Oi (*c.* 49 ka) in northern Vietnam showed drier and more open conditions (Bacon *et al.*, 2006). Between 62 and 28 ka and between 28 and 19 ka, the reworking and redeposition of aeolian sands along the south-eastern Vietnam coast points to reduced vegetation cover and to landscape instability in this area (Murray-Wallace *et al.*, 2002). In our analysis, Late Pleistocene sites from Vietnam represent a variety of habitat types. Interestingly, the only site to preserve sufficient numbers of species to enable a habitat type to be confidently assigned is Hang Hum II (80–140 ka, Olsen & Ciochon, 1990), which is classified as open. An examination of the discriminant functions shows that Hang Hum II is the furthest 'open' site from the open habitat group centroid. On the basis of its discriminant functions, it is quite close to Tam Hang (south), a site confidently assigned as mixed. The faunas preserved in these two sites therefore most likely represent an ecotone between mixed and open habitats. Other sites from Vietnam are classified as either mixed (Hang Hum I, Lang Trang) or closed [Keo Leng (20–30 ka, Olsen & Ciochon, 1990)]; however, the numbers of species preserved at these sites mean that they can be excluded confidently only from being open.

Laos

The palaeoenvironmental reconstructions for Laos represent some of the first for this country. Tam Hang (south) is one of two sites confidently assigned, on the basis of both DFA and species numbers, as a mixed habitat. However, its position relative to the DFA group centroids also reveals that in character it approaches some open sites. Therefore, it is herein interpreted as a mixed habitat with significant open areas. This reconstruction is at odds with the palaeoenvironmental interpretations of Bacon *et al.* (2008a), who suggest that this site is more indicative of closed forests. Interestingly, Tam Hang (north) is classified as a closed habitat; however, the small number of species preserved at this site makes this classification uncertain, and it may also in fact represent a mixed habitat.

CONCLUSIONS

Our results indicate that, throughout much of the Pleistocene, SE Asia was characterized by a heterogenous vegetation complex, with habitats comprising a mix of both woodlands and grasslands. The Sundaic subregion was dominated by mixed habitats during most of the Early and Middle Pleistocene, certainly for Java; and evidence for closed habitats during this period is seen only in the Malay Peninsula. Both the faunal evidence and other palaeoenvironmental studies demonstrate changes of vegetation structure with glacial and interglacial cycles during the Late Pleistocene, with glacial periods associated with drier and more mixed habitats, and interglacials with more humid, closed habitats. Evidence for environmental changes in the Indochinese subregion is more limited, but consistently indicates the dominance of mixed habitats through most of the Pleistocene; support for extensive closed habitats in this subregion is found only for the Pliocene and the end of the Late Pleistocene.

Our study of habitat types of 25 Pleistocene sites in SE Asia through synecological methods is in general agreement with the overall palaeoenvironmental information obtained from other sources and through different methods. This indicates that our approach can provide useful additional information on palaeoenvironments where only mammal fossils are available. Even when insufficient numbers of fauna are present at a site, the position of that site with regard to the centroids of closed, mixed and open vegetation provides an indication of the overall vegetation type present. Although our analysis does not directly predict certain environmental factors (for example relative precipitation), when our results are placed within a regional palaeoenvironmental framework this method can provide significant new insights into palaeoenvironmental changes over time. Not only is such information of considerable use in the study of the evolution of faunas in relation to environmental changes, but with the presently rapid changes in global climate, an understanding of palaeoenvironments in relation to palaeoclimates can help us to predict the impacts that such changes might have on the distribution of present-day species.

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REFERENCES

Aimi, M. & Aziz, F. (1985) Vertebrate fossils from the Sangiran Dome, Mojokerto, Trinil and Sambungmacan areas. *Quaternary geology of the hominid fossil bearing formations in Java. Report of the Indonesia–Japan Joint Research Project*

CTA-41, 1976-1979 (ed. by N. Watanabe and D. Kadar), pp. 155–198. Geological Research and Development Centre, Bandung, Indonesia.

Andrews, P. & Humphrey, L. (1999) African Miocene environments and the transition to early hominines. *African biogeography, climate change, and human evolution* (ed. by T.G. Bromage and F. Schrenk), pp. 282–300. Oxford University Press, Oxford.

Andrews, P., Lord, X. & Evans, E.M.N. (1979) Patterns of ecological diversity in fossil and modern mammalian faunas. *Biological Journal of the Linnean Society*, **11,** 177–205.

Anshari, G., Kershaw, A.P. & van der Kaars, S. (2001) A Late Pleistocene and Holocene pollen and charcoal record from peat swamp forest, Lake Sentarum Wildlife Reserve, West Kalimantan, Indonesia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **171,** 213–228.

Arambourg, C. & Fromaget, J. (1938) Le gisement quaternaire de Tam Nang (Chaîne Annamitique septentrionale). Sa stratigraphie et ses faunes. *Comptes Rendus de l'Académie des Sciences*, **207,** 793–795.

Ayob, M. (1970) Quaternary sediments at Sungei Besi, West Malaysia. *Bulletin of the Geological Society of Malaysia*, **3,** 53–61.

Bacon, A.-M., Demeter, F., Schuster, M., Long, V.T., Thuy, N.K., Antoine, P.-O., Sen, S., Nga, H.H. & Huong, N.M. (2004) The Pleistocene Ma U'Oi cave, northern Vietnam: palaeontology, sedimentology and palaeoenvironments. *Geobios*, **37,** 305–314.

Bacon, A.-M., Demeter, F., Rousse, S., Long, V.T., Duringer, P., Antoine, P.-O., Thuy, N.K., Mai, B.T., Huong, N.T.M., Dodo, Y., Matsumura, H., Schuster, M. & Anezaki, T. (2006) New palaeontological assemblage, sedimentological and chronological data from the Pleistocene Ma U'Oi cave (northern Vietnam). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **230,** 280–298.

Bacon, A.-M., Demeter, F., Tougard, C., de Vos, J., Sayavongkhamdy, T., Antoine, P.-O., Bouasisengpaseuth, B. & Sichanthongtip, P. (2008a) Redécouverte d'une faune pléistocène dans les remplissages karstiques de Tam Hang au Laos: Premiers résultats. *Comptes Rendus Palevol*, **7,** 277–288.

Bacon, A.-M., Demeter, F., Duringer, P., Helm, C., Bano, M., Long, V.T., Thuy, N.T.K., Antoine, P.-O., Mai, B.T., Huong, N.T.M., Dodo, Y., Chabaux, F. & Rihs, S. (2008b) The Late Pleistocene Duoi U'Oi in northern Vietnam: palaeontology, sedimentology, taphonomy and palaeoenvironments. *Quaternary Science Reviews*, **27,** 1627–1654.

Bandet, Y., Semah, F., Sartono, S. & Djubiantono, T. (1989) Premier peuplement par les mammifères d'une région de Java Est, à la fin de Pliocène: âge de la faune du Gunung Butak, près de Kedungbrubus (Indonésie). *Comptes Rendus de l'Académie des Sciences Paris, série II. Mécanique, Physique, Chimie, Sciences de l'univers, Sciences de la Terre*, **308,** 867–870.

Barker, G., Barton, H., Bird, M. *et al.* (2007) The 'human revolution' in lowland tropical Southeast Asia: the antiquity and behaviour of anatomically modern humans at Niah Cave (Sarawak, Borneo). *Journal of Human Evolution*, **52,** 243–261.

Barry, J.C., Johnson, N.M., Raza, S.M. & Jacobs, L.L. (1985) Neogene mammalian faunal change in southern Asia: correlations with climatic, tectonic, and eustatic events. *Geology*, **13,** 637–640.

Beden, M. & Guérin, C. (1973) Le gisement de vertébrés du Phnom Loang (province du Kampot, Cambodge). Faune pléistocène moyen terminal. *Travaux et Documents de l'O.R.S.T.O.M*, **27,** 1–97.

van den Bergh, G.D., de Vos, J., Sondaar, P.Y. & Aziz, F. (1996) Pleistocene zoogeographic evolution of Java (Indonesia) and glacio-eustatic sea level fluctuations: a background for the presence of *Homo*. *Bulletin of the Indo-Pacific Prehistory Association*, **14,** 7–21.

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

Bettis, E.A., III, Milius, A.K., Carpenter, S.J., Larick, R., Zaim, Y., Rizal, Y., Ciochon, R.L., Tassier-Surine, S., Murray, D., Suminto & Bronto, S. (2009) Way out of Africa: Early Pleistocene paleoenvironments inhabited by *Homo erectus* in Sangiran, Java. *Journal of Human Evolution*, **56,** 11–24.

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

Bouteaux, A. (2005) *Paléontologie, paléoécologie et taphonomie des mammifères du Pléistocène moyen ancien du site à hominidés de Sangiran (Java central, Indonésie)*. PhD Thesis, Muséum National d'Histoire Naturelle de Paris, Paris.

Caratini, C. & Tissot, C. (1988) Paleogeographical evolution of the Mahakam delta in Kalimantan, Indonesia during the Quaternary and late Pliocene. *Review of Palaeobotany and Palynology*, **55,** 217–228.

Chaimanee, Y. (1998) Plio-Pleistocene rodents of Thailand. *Thai Studies in Biodiversity*, **3,** 1–303.

Ciochon, R.L., Long, V.T., Larick, R., González, L., Grün, R., de Vos, J., Yonge, C., Taylor, L., Yoshida, H. & Reagan, M. (1996) Dated co-occurrence of *Homo erectus* and *Gigantopithecus* from Tham Khuyen Cave, Vietnam. *Proceedings of the National Academy of Sciences USA*, **93,** 3016–3020.

Colbert, E.H. (1943) Pleistocene vertebrates collected in Burma by the American Southeast Asiatic expedition. *Transactions of the American Philosophical Society*, **32,** 395–429.

Dowsett, H., Thompson, R., Barron, J., Cronin, T., Fleming, F., Ishman, S., Poore, R., Willard, D. & Holtz, T.J. (1994) Joint investigations of the Middle Pliocene climate I: PRISM palaeoenvironmental reconstructions. *Global and Planetary Change*, **9,** 169–195.

Dubois, E. (1908) Das geologische Alter der Kendeng- oder Trinil-fauna. *Tijdschrift van het Koninklijk Nederlandsch Aardrijkskundig Genootschap*, **2,** 1235–1270.

Esposito, M., Reyss, J.-L., Chaimanee, Y. & Jaeger, J.-J. (2002) U-series dating of fossil teeth and carbonates from Snake Cave, Thailand. *Journal of Archaeological Science*, **29,** 341–349.

Ferguson, D.K. (1993) The impact of Late Cenozoic environmental changes in East Asia on the distribution of terrestrial plants and animals. *Evolving Landscapes and Evolving Biotas of East Asia since the Mid-Tertiary: proceedings of the Third Conference on the Evolution of the East Asian Environment* (ed. by N.G. Jablonski and S. Chak-Lam), pp. 145–196. Centre of Asian Studies, Hong Kong.

Fromaget, J. (1936) Sur la stratigraphie des formations récentes de la Chaine annamitique septentrionale et sur l'existence de l'Homme dans le Quaternaire inférieur de cette partie de l'Indochine. *Comptes Rendus de l'Académie des Sciences*, **203,** 738–741.

Gagnon, M. (1997) Ecological diversity and community ecology in the Fayum sequence (Egypt). *Journal of Human Evolution*, **32,** 133–160.

Goldammer, J.G. & Seibert, B. (1989) Natural rain forest fires in Eastern Borneo during the Pleistocene and Holocene. *Naturwissenschaften*, **76,** 518–520.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: Palaeontological Statistics software package for education and data analysis. *Palaeontologia Electronica*, **4,** 9, http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Harrison, T. (1996) The palaeoecological context at Niah Cave, Sarawak: evidence from the primate fauna. *Bulletin of the Indo-Pacific Prehistory Association*, **14,** 90–100.

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 mammals in SE Asia: estimates of rates 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.

Hing, T.T. & Leong, L.K. (1990) Environmental placer gold deposits in northern Pahang. *Bulletin of the Geological Society of Malaysia*, **26,** 1–11.

Holloway, J.D. & Hall, R. (1998) SE Asian geology and biogeography: an introduction. *Biogeography and geological evolution of SE Asia* (ed. by R. Hall and J.D. Holloway), pp. 1–23. Backhuys Publishers, Leiden.

Hooijer, D.A. (1963) Report upon a collection of Pleistocene mammals from tin-bearing deposits in a limestone cave near Ipoh, Kinta Valley, Perak. *Federated Museum Journal*, **7,** 1–5.

Hooijer, D.A. (1975) Quaternary mammals west and east of Wallace's line. *Netherlands Journal of Zoology*, **25,** 46–56.

Jiang, Q. & Piperno, D.R. (1999) Environmental and archaeological implications of a Late Quaternary palynological sequence, Poyang Lake, southern China. *Quaternary Research*, **52,** 250–258.

Jirin, S. (1993) Palynology of Late Quaternary sediments of piston-core KL-139 from Sabah Trough, East Malaysia (abstract). *Warta Geologi*, **19,** 117.

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

van der Kaars, W.A. & Dam, M.A.C. (1997) Vegetation and climate change in West-Java, Indonesia during the last 135,000 years. *Quaternary International*, **37,** 67–71.

Kamaludin, H. & Azmi, H.Y. (1997) Interstadial records of the last glacial period at Pantai Remis, Malaysia. *Journal of Quaternary Science*, **12,** 419–434.

Kamaludin, H., Nakamura, T., Price, D.M., Woodroffe, C.D. & Fuji, S. (1993) Radiocarbon and thermoluminescence dating of Old Alluvium from a coastal site in Perak, Malaysia. *Sedimentary Geology*, **83,** 199–210.

Kershaw, A.P., Penny, D., van der Kaars, S., 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. A.A. Balkema Publishers, Lisse, The Netherlands.

Larick, R., Ciochon, R.L., Zaim, Y., Sudijono, Suminto, Riza, Y., Aziz, F., Reagan, M. & Heizler, M. (2001) Early Pleistocene ^{40}Ar/^{39}Ar ages for Bapang Formation hominins, Central Java, Indonesia. *Proceedings of the National Academy of Sciences USA*, **98,** 4866–4871.

Legendre, S. (1986) Analysis of mammalian communtities from the late Eocene and Oligocene of southern France. *Palaeovertebrata*, **16,** 191–212.

Legendre, S. (1989) Les communautés de mammifères du Paléogène (Eocène et Oligocène) d'Europe occidentale: structures, milieu et évolution. *Münchner Geowissenschaftliche Abhandlungen*, **16,** 1–110.

Lekagul, B. & McNeely, J.A. (1988) *Mammals of Thailand*. Association for the Conservation of Wildlife, Bangkok, Thailand.

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* (ed. by A.M.T. Elewa), pp. 159–189. Springer-Verlag, Heidelberg.

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

Louys, J., Travouillon, K.J., Bassarova, M. & Tong, H. (2009) The use of natural protected areas in palaeoecological analyses: assumptions, limitations and application. *Journal of Archaeological Science*, **36,** 2274–2288.

MacKinnon, J. & Phillipps, K. (1993) *A field guide to the birds of Borneo, Sumatra, Java, and Bali*. Oxford University Press, Oxford.

Majid, Z. (1982) The West Mouth, Niah in the prehistory of Southeast Asia. Special Monograph No. 3. *The Sarawak Museum Journal*, **31,** 1–200.

Maloney, B.K. & McCormac, F.G. (1996) Palaeoenvironments of North Sumatra: a 30,000 year old pollen record from Pea Bullok. *Bulletin of the Indo-Pacific Prehistory Association*, **14,** 73–82.

Medway, Lord (1960) The Malay Tapir in late Quaternary Borneo. *Sarawak Museum Journal*, **9,** 356–360.

Medway, Lord (1972) The Quaternary mammals of Malesia: a review. *Transactions of the Second Aberdeen–Hull Symposium on Malesian Ecology, Hull* (ed. by P. Ashton and M. Ashton), pp. 63–98. University of Hull Department of Geography Miscellaneous Series 13, Hull, UK.

Medway, Lord (1977) The Niah excavations and an assessment of the impacts of early man on mammals in Borneo. *Asian Perspectives*, **20,** 51–69.

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

Meijaard, E. (2004) *Solving mammalian riddles. A reconstruction of the Tertiary and Quaternary distribution of mammals and their palaeoenvironments in island South-East Asia*. PhD Thesis, School of Archaeology and Anthropology, The Australian National University, Canberra.

Meiri, S., Meijaard, E., Wich, S.A., Groves, C.P. & Helgen, K.M. (2008) Mammals of Borneo – small size on a large island. *Journal of Biogeography*, **35,** 1087–1094.

Mendoza, M., Janis, C.M. & Palmqvist, P. (2005) Ecological patterns in the trophic-size structure of large mammal communities: a 'taxon-free' characterization. *Evolutionary Ecology Research*, **7,** 505–530.

van der Meulen, A.J. & Musser, G.G. (1999) New paleontological data from the continental Plio-Pleistocene of Java. *Elephants have a snorkel!* (ed. by J.W.F. Reumer and J. de Vos), pp. 361–368. *Deinsea* (Jaarbericht van het Natuurmuseum Rotterdam), Vol. 7, Rotterdam.

Morley, R.J. (1991) Tertiary stratigraphic palynology in Southeast Asia: current status and new directions. *Bulletin of the Geological Society of Malaysia*, **28,** 1–36.

Morley, R.J. (1999) Palynological evidence for Tertiary plant dispersals in the SE Asian region in relation to plate tectonics and climate. *Biogeography and geological evolution of SE Asia* (ed. by R. Hall and J.D. Holloway), pp. 211–234. Backhuys Publishers, Leiden.

Morley, R.J. (2000) *Origin and evolution of tropical rain forests*. John Wiley & Sons, Ltd, Chichester, UK.

Morley, R.J., Lelono, E.B., Nugrahaningsih, L. & Hasjim, N. (2000) LEMIGAS Tertiary Palynology Project: aims, progress and preliminary results from the Middle Eocene to Late Pliocene of Sumatra and Java. *Geological Research and Development Centre, Paleontology Series*, **10,** 27–47.

Muhammad, R.F., Yoshida, D., Tani, A. & Smart, P.L. (2002) Implications of electron spin resonance and uranium-series dating techniques on speleotherms in the Kinta and Lenggong Valleys, West Malaysia. *Advances in ESR Applications*, **18,** 19–26.

Muller, J. (1971) Palynological evidence for change in geomorphology, climate, and vegetation in the Mio-Pliocene of Malesia. *Transactions of the Second Aberdeen–Hull Symposium on Malesian Ecology, Hull* (ed. by P. Ashton and M. Ashton), pp. 6–32. University of Hull Department of Geography Miscellaneous Series 13, Hull, UK.

Murray-Wallace, C.V., Jones, B.G., Nghi, T., Price, D.M., Vinh, V.V., Tinh, T.N. & Nanson, G.C. (2002) Thermoluminescence ages for a reworked coastal barrier, southeastern Vietnam: a preliminary report. *Journal of Asian Earth Sciences*, **20,** 535–548.

Musser, G.G. (1982) The Trinil rats. *Modern Quaternary Research SE Asia*, **7,** 65–85.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403,** 853–858.

Nowak, R.M. (1999) *Walker's mammals of the world*. The Johns Hopkins University Press, London.

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

Page, S.E., Rieley, J.O., Shotyk, Ø.W. & Weiss, D. (1999) Interdepence of peat and vegetation in a tropical peat swamp forest. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **354,** 1885–1897.

Pan, Y. (1993) The relationships between Late Cenozoic mammalian faunas from Yuanmou and their environment. *Evolving landscapes and evolving biotas of East Asia since the Mid-Tertiary* (ed. by N.G. Jablonski and S. Chak-Lam), pp. 207–220. Centre of Asian Studies, Hong Kong.

Poole, I. & Davies, C. (2001) *Glutoxylon* Chowdhury (Anacardiaceae): the first record of fossil wood from Bangladesh. *Review of Palaeobotany and Palynology*, **113,** 261–272.

Pope, G.G., Frayer, D.W., Liangchareon, M., Kulasing, P. & Nakabanlang, S. (1981) Palaeoanthropological investigations of the Thai–American expeditions in northern Thailand (1978–1980): an interim report. *Asian Perspectives*, **21,** 147–163.

Price, G.D., Valdes, P.J. & Sellwood, B.W. (1997) Prediction of modern bauxite occurrence: implications for climate reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **131,** 1–13.

Quade, J., Cerling, T.E. & Bowman, J.R. (1989) Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature*, **402,** 163–166.

Rahardjo, A.T. (1999) Perubahan iklim dan batas umur Pliosen – Plistosen berdasarkan analisis forminifera dan palinologi di daerah Mojoroto, Mojokerto – Jawa Timur. *Buletin Geologi*, **31,** 1–14.

Reed, K.E. (1997) Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution*, **32,** 289–322.

Reed, K.E. (1998) Using large mammal communities to examine ecological and taxonomic structure and predict vegetation in extant and extinct assemblages. *Paleobiology*, **24,** 384–408.

Ruedi, M. (1996) Phylogenetic evolution and biogeography of Southeast Asian shrews (genus *Crocidura*: Soricidae). *Biological Journal of the Linnean Society*, **58,** 197–219.

Sandrock, O., Kullmer, O., Schrenk, F., Juwayeyi, Y.M. & Bromage, T.G. (2007) Fauna, taphonomy, and ecology of the Plio-Pleistocene Chiwondo Beds, Northern Malawi. *Hominin environments in the East African Pliocene: an assessment of the faunal evidence* (ed. by R. Bobe, Z. Alemseged and A.K. Behrensmeyer), pp. 315–332. Springer, Dordrecht.

Simpson, K. & Day, N. (1996) *Field guide to the birds of Australia*. Penguin Books Australia Ltd, Ringwood, Australia.

Smit-Sibinga, G.L. (1947) De jongste bodembewegingen in en om de Java Zee en de eustatische beweging van de zeespiegel. *Tijdschrift Nederlandsch Aardrijkskundig Genootschap*, **64,** 455–465.

Soligo, C. & Andrews, P. (2005) Taphonomic bias, taxonomic bias and historical non-equivalence of faunal structure in early hominid localities. *Journal of Human Evolution*, **49,** 206–229.

Stauffer, P.H. (1973) Cenozoic. *Geology of the Malay Peninsula (West Malaysia and Singapore)* (ed. by D.J. Gobbett and C.S. Hutchison), pp. 143–176. John Wiley and Sons, New York.

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

Storm, P. & de Vos, J. (2006) Rediscovery of the Late Pleistocene Punung hominin sites and the discovery of a new site Gunung Dawung in East Java. *Palaeobiodiversity and Palaeoenvironments*, **86,** 271–281.

Storm, P., Aziz, F., de Vos, J., Kosasih, D., Baskoro, S., Ngaliman & van den Hoek Ostende, L.W. (2005) Late Pleistocene *Homo sapiens* in a tropical rain forest fauna in East Java. *Journal of Human Evolution*, **49,** 536–545.

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.

Teeuw, R.M., Rhodes, E.J. & Perkins, N.K. (1999) Dating of Quaternary sediments from Western Borneo, using optically stimulated luminescence. *Singapore Journal of Tropical Geography*, **20,** 181–192.

Thiramongkol, N. (1986) Neotectonism and rate of uplift in the eastern margin of the lower central plain of Thailand. *Proceedings of the Workshop on Economic Geology, Tectonics, Sedimentary Processes and Environment of the Quarternary in Southeast Asia. Haay Yai, 3–7 February 1986* (ed. by N. Thiramongkol), pp. 35–44. Department of Geology, Chulalongkorn University, Bangkok, Thailand.

Thomas, M.F. (1987) Quaternary sedimentation in W. Kalimantan (Indonesian Borneo). *Tropical Geomorphology Newsletter*, **4,** 23.

Thorp, M.B. & Thomas, M.F. (1993) Discussion: Late Pleistocene sedimentation and landform development in western Kalimantan (Indonesian Borneo). Reply by the authors. *Geologie en Mijnbouw*, **71,** 363–368.

Thorp, M.B., Thomas, M.F., Martin, T. & Whalley, B. (1990) Late Pleistocene sedimentation and landform development in western Kalimantan (Indonesian Borneo). *Geologie en Mijnbouw*, **69,** 133–150.

Tjia, H.D., Komoo, I., Lim, P.S. & Surat, T. (1990) The Maliau basin, Sabah: Geology and tectonic setting. *Bulletin of the Geological Society of Malaysia*, **27,** 261–292.

Tougard, C. (1998) *Les faunes de grands mammifères du Pléistocène moyen terminal de Thaïlande dans leur cadre phylogénétique, paléoécologique et biochronologique*. PhD Thesis, Université Montpellier II, Montpellier.

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.

Travouillon, K.J. & Legendre, S. (2009) Using cenograms to investigate gaps in mammalian body mass distributions in Australian mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **272,** 69–84.

Visser, K., Thunell, R. & Goni, M.A. (2004) Glacial–interglacial organic carbon record from the Makassar Strait, Indonesia: implications for regional changes in continental vegetation. *Quaternary Science Reviews*, **23,** 17–27.

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

de Vos, J., Sondaar, P.Y., van den Bergh, G.D. & Aziz, F. (1994) The *Homo* bearing deposits of Java and its ecological context. *Courier Forschung-Institut Senckenberg*, **171,** 129–140.

Westaway, K.E., Morwood, M.J., Roberts, R.G., Rokus, A.D., Zhao, J.-x., Storm, P., Aziz, F., van den Bergh, G., Hadi, P., Jatmiko & de Vos, J. (2007) Age and biostratigraphic significance of the Punung Rain forest Fauna, East Java, Indonesia, and implications for *Pongo* and *Homo*. *Journal of Human Evolution*, **53,** 709–717.

Westaway, K.E., Roberts, R.G., Sutikna, T., Morwood, M.J., Drysdale, R., Zhao, J.-X. & Chivas, A.R. (2009a) The evolving landscape and climate of western Flores: an environmental context for the archaeological site of Liang Bua. *Journal of Human Evolution*, **57,** 450–464.

Westaway, K.E., Sutikna, T., Saptomo, W.E., Jatmiko, Morwood, M.J., Roberts, R.G. & Hobbs, D.R. (2009b) Reconstructing the geomorphic history of Liang Bua, Flores, Indonesia: a stratigraphic interpretation of the occupational environment. *Journal of Human Evolution*, **57,** 465–483.

Whitmore, T.C. (1987) *Biogeographical evolution of the Malay Archipelago*. Clarendon Press, Oxford.

Whitten, T., Soeriaatmadja, R.E. & Afiff, S.A. (1996) *The ecology of Java and Bali*. Periplus Editions, Singapore.

Whittow, J. (1984) *Dictionary of physical geography*. Penguin Books, London.

Woodruff, D.S. & Turner, L.M. (2009) The Indochinese–Sundaic zoogeographic transition: a description and analysis of terrestrial mammal species distributions. *Journal of Biogeography*, **36,** 803–821.

Zeitoun, V., Seveau, A., Forestier, H., Thomas, H., Lenoble, A., Laudet, F., Antoine, P.-O., Debruyne, R., Ginsberg, L., Mein, P., Winayalai, C., Chumdee, N., Doyasa, T., Kijngam, A. & Nakbunlung, S. (2005) Découverte d'un assemblage faunique à *Stegodon–Ailuropoda* dans une grotte du Nord de la Thaïlande (Ban Fa Suai, Chiang Dao). *Comptes Rendus Palevol*, **4,** 255–264.

Zheng, Z. & Lei, Z.Q. (1999) A 400,000 year record of vegetational and climatic changes from a volcanic basin, Leizhou Peninsula, southern China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **145,** 339–362.

SUPPORTING INFORMATION

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

Appendix S1 Species and ecovariables from natural protected areas used in the analyses.

Appendix S2 Species and ecovariables from fossil sites used in the analyses.

Appendix S3 Description and examples of ecological categories used in the analyses.

BIOSKETCHES

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