

## Quaternary rainforest refugia in south-east Asia: using termites (Isoptera) as indicators

F. J. GATHORNE-HARDY<sup>1,2\*</sup>, SYAUKANI<sup>3</sup>, R. G. DAVIES<sup>1</sup>, P. EGGLETON<sup>1</sup>  
and D. T. JONES<sup>1</sup>,

<sup>1</sup>Termite Research Group, Entomology Department, The Natural History Museum,  
Cromwell Road, London, SW7 5BD, UK

<sup>2</sup>Division of Life Sciences, King's College London, Franklin-Wilkins Building,  
150 Stamford Street, London, SE1 8WA, UK

<sup>3</sup>Syiah Kuala University, Darussalam, Banda Aceh, Aceh, Indonesia

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In south-east Asia, during Quaternary glaciations, increased seasonality and sea level decreases of ~120 m caused considerable fragmentation of the rainforest. It is believed that most of the region's core was covered with savannah vegetation, and rainforest was confined to a few refugia. We investigated the geographical extent of the savannah vegetation and the positions of the refugia, using a combination of palynological, geological, fossil and termite data. Our results show that during the Last Glacial Maximum, most of Thailand, Peninsula Malaysia, western and southern Borneo, eastern and southern Sumatra, and Java were probably covered by savannah. Rainforest refugia were probably present in northern and eastern Borneo, northern and western Sumatra and the Mentawai islands. We also discuss a possible complete history of the region. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 75, 453–466.

ADDITIONAL KEYWORDS: Borneo – climate – Indonesia – Java – Malaysia – pleistocene – savannah – Siberut – Sumatra – Thailand.

### INTRODUCTION

The rainforests of south-east Asia are among the most biologically diverse areas in the world (Myers *et al.*, 2000). They are a dynamic ecosystem and it is thought they were considerably affected by Quaternary glaciations (van der Kaars & Dam, 1995; Morley, 2000). Most of the vegetation during these glaciations was probably a mixture of savannah and patchy deciduous forest (Morley, 2000). Obligate rainforest species are likely to have been confined to a few refugia in northern Borneo, northern Sumatra and the Mentawai islands (Brandon-Jones, 1998). During interglacial periods rainforest recolonized the region (van der Kaars & Dam, 1995; Morley, 2000).

The extent of vegetation change and the sites of lowland rainforest refugia have never been fully inves-

tigated. Here we use termite data to determine refugia locations and try to assess their geographical limits. We used palynological, geological, fossil and current plant and mammal distribution data to define potential refugium sites, and examined termite survey data from these areas to assess the suitability of termites as indicators of Quaternary climate change. Termite data from a complete survey of the region were then examined to provide an indication of the possible extent of the rainforest refugia.

Termites are the most important arthropod decomposers in tropical rainforests (Wood & Sands, 1978; Collins, 1983, 1989) and are vital in maintaining decomposition processes (Collins, 1989; Wood, 1988) and nitrogen and carbon cycles (Tayasu *et al.*, 1997). They are thought to be a key source of soil heterogeneity (Donovan *et al.*, 2001b) and are at their highest diversity in lowland tropical rainforests (Collins, 1989; Eggleton, 2000).

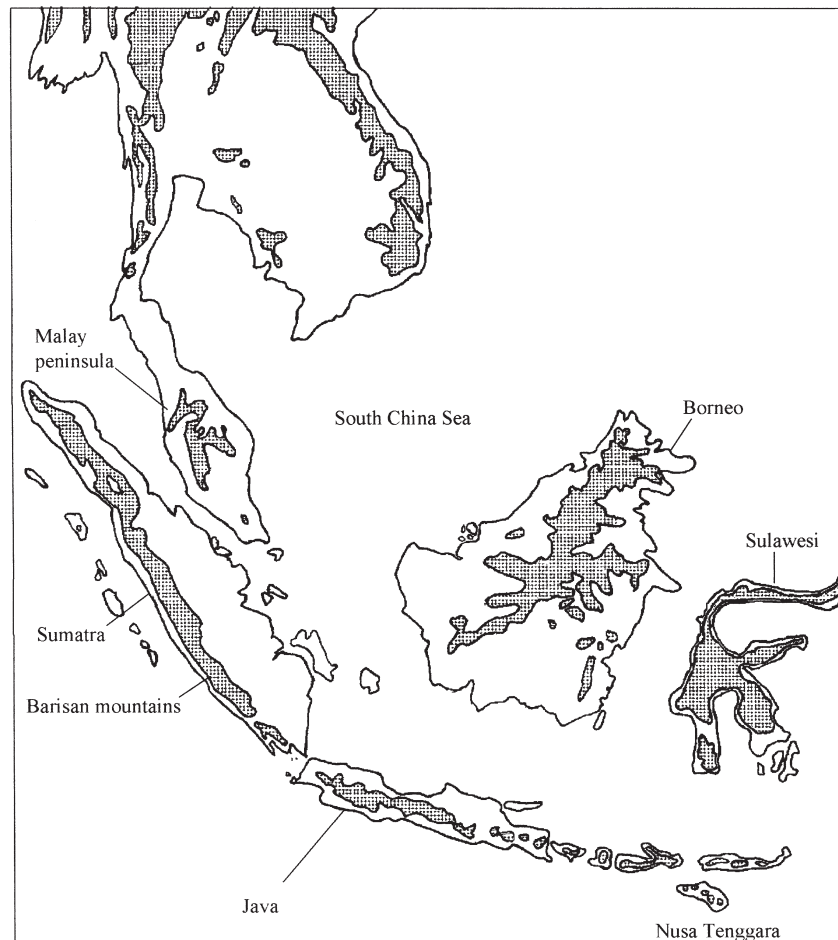
\*Corresponding author. E-mail: fgh@nhm.ac.uk

Termites eat dead wood from almost all plant species and live in most soil types (Collins, 1989; F. J. Gathorne-Hardy, pers. observ.). South-east Asian termites are species-poor when compared to the Neotropics and Afrotropics (except for the high diversity of the *Termes/Capritermes* group), which makes them relatively taxonomically tractable (Davies, 2001). Termites are easily sampled (Jones & Eggleton, 2000). They are sensitive to disturbance, especially to forest canopy loss (Eggleton *et al.*, 1996, 1997; Dibog *et al.*, 1999; Gathorne-Hardy, Syaokani & Eggleton, 2001). Recovery is very slow (Gathorne-Hardy, *et al.*, 2001), and they are generally poor at crossing biogeographical barriers (Abe, 1984; Gathorne-Hardy *et al.*, 2000a; Gathorne-Hardy, Jones & Mawdsley, 2000b). Termite composition is known to reflect historical patterns (Eggleton, Williams & Gaston, 1994; Eggleton, 2000; Davies, 2001), making them ideal organisms with which to investigate the ongoing effects of Quaternary climate change (Fig. 1).

#### QUATERNARY CLIMATE CHANGE IN THE SUNDA REGION

##### *Monsoons*

The climate of south-east Asia is primarily governed by monsoon winds (Whitmore, 1984). The winter or north-west monsoon is caused by air from cold high pressure areas in Siberia and the Tibetan plateau blowing to the hot low pressure zone over Australia. The monsoon picks up water from the West Pacific Warm Pool and the South China Sea (SCS) and is the cause of most of the rainfall in the Sunda region (Whitten *et al.*, 1984, 1996; MacKinnon *et al.*, 1997; An, 2000). The summer or south-east monsoon works in the opposite way to the winter one, it picks up water from the Indian ocean, causing rain in the summer months (An, 2000). However, the mountains of Nusa Tenggara, Java and the Barisan range of Sumatra cause a rain-shadow effect, making the summer a relatively dry season for most of the region (Whitten *et al.*, 1984; MacKinnon *et al.*, 1997).



**Figure 1.** Map showing mountainous areas of south-east Asia. Shaded areas = land above 500 m altitude.

During higher latitude glacials the northern summer was much colder than during interglacials; the atmospheric pressure was higher over continental Asia which led to a reduced summer monsoon (An, 2000). The winter monsoon was probably stronger than it is now (An, 2000). This reduction of the summer monsoon probably caused an increase in seasonality during Oxygen Isotope Stages (OIS) 4, 3 and 2.

#### Temperature

The temperature in south-east Asia of OIS 5 was probably similar to that of today, or at times a little higher (Pelejero *et al.*, 1999) or a little lower (Lee, Wei & Chen, 1999; Pelejero *et al.*, 1999). In OIS 4 and 3, temperature declined by between 2°C (Pelejero *et al.*, 1999) and 4°C (van der Kaars & Dam, 1995), the former being more likely. During OIS 2, the last glacial maximum (LGM), was 3–7°C lower than at present. The consensus is that the decrease at sea level was ~4°C (Morley, 2000).

#### Sea level

Bard, Hamelin & Fairbanks (1991), Shackleton (1987), Haq, Hardenbol & Vail (1987) and Pirazzoli *et al.* (1991) have estimated sea levels for pre-Holocene times. These estimates are inevitably open to error at

a smaller scale (Shackleton, 1987); although they use different methods, in general the estimates agree with each other. During interglacials the sea level was approximately the same as it is now, during OIS 3 and 4 it dropped by ~40–50 m (or more). Sea level was ~120 m lower than present sea level at the LGM (Shackleton, 1987; Pirazzoli *et al.*, 1991; Voris, 2000), exposing approximately 1 800 000 km<sup>2</sup> of the Sunda shelf.

The expansion of the exposed Sunda shelf in the LGM, preventing the winter monsoon from picking up moisture from the SCS, probably led to increased drought in the central part of the Sunda region. This drought and increased seasonality is thought to have changed the vegetation of the central part of the Sunda shelf, causing it to become savannah-like (Medway, 1972; Morley, 2000).

#### Evidence for climate change

Palynological, geological, fossil and modern animal distributions all provide evidence of Pleistocene climate change. Table 1 shows sites for which there is direct evidence of climate change affecting the biota of south-east Asia. In most of these areas it is thought that the flora changed to a savannah or wooded savannah system.

**Table 1.** Evidence for climate change in south-east Asia during the Quaternary

Site	Period	Author	Change and evidence
Bandung basin, W. Java, indicating local climate	80–10 kya	van der Kaars & Dam (1995)	Palynological evidence for increased seasonality, reduced rainfall and colder temperatures (down to 7.2°C lower than now) and increased grassland
Lombok ridge, indicating climate of north-western Australia	300–244, 190–130, 38–12 kya	Kaars (1991)	Palynological evidence of drier climates at these times, with increased grassland
Subang airport, near Kuala Lumpur, Malay peninsula, indicating local climate	Mid-Pleistocene	Morley (2000)	Palynological evidence for a drier, grass- <i>Pinus</i> savannah system
Peninsula Malaysia, the north coast of Java, Java sea	Late-Pleistocene	Verstappen (1997)	Geological evidence indicates seasonal, savannah-like system
Southern and northern Sumatra, Sarawak	Pleistocene	Verstappen (1992)	Geological evidence indicates seasonal, savannah-like system
Malay Peninsula and West Kalimantan	Oxygen Isotope stage 3	Thomas (2000)	Geological evidence indicates seasonal, savannah-like system
Java	250 kya	Medway (1972)	Large fossil grazing herbivores, needing savannah vegetation to live

*Areas of continuing rainforest*

Although the whole of south-east Asia is likely to have felt the effects of the increased seasonality of OIS 4, 3 and 2, many areas of everwet rainforest remained.

Stuijts (1993) and Newsome & Flenley (1988) found no evidence of increased seasonality in their pollen cores from the Barisan Mountains and West Java. It is likely that these areas had sufficient moisture to remain as rainforest for two reasons: (1) proximity to the continental shelf and therefore to the sea, even at low sea levels, allowing convergent rainfall with moisture from the sea; and (2) altitude, allowing the interception of the weak summer monsoon, fog, and as they are cold, forcing precipitation. Northern Borneo probably also stayed everwet, for the same reason.

Around montane rainforest patches, lowland rainforest probably survived as well. As explained above, the lowland areas probably received enough moisture (both directly from convergent rainfall from both the sea and from mountains, as well as gaining water from runoff from the mountains). The temperature at the LGM dropped by  $\sim 4^{\circ}\text{C}$  (Morley, 2000) bringing the altitudinal zones downhill by approximately 700 m (assuming a lapse rate of  $0.6^{\circ}\text{C}$  per 100 m increase in altitude). Lowland rainforest is typically found up to 700–800 m (Richards, 1996), so it is probable that lowland rainforest could continue through the LGM, especially at the base of large mountains. It is likely that lowland forest migrated onto the newly exposed Sunda shelf wherever possible (Morley, 2000). Rainforest is thought to have continued through the Quaternary in many areas (Table 2).

## METHODS

## SAMPLING SITES

Termites have previously been sampled using a standardized transect technique in Thailand (Davies, 1997), Peninsula Malaysia (Jones & Brendell, 1998), Sabah (Eggleton *et al.*, 1997), Java and Way Kambas in Lampung, southern Sumatra (Gathorne-Hardy *et al.*, 2000b), Jambi in central Sumatra, Tabalong in South Kalimantan (Jones & Prasetyo, in press), and northern Sumatra (Gathorne-Hardy *et al.*, 2001).

In the summer of 2000, Gathorne-Hardy and Syaokani sampled the termites of Siberut, Bukit Barisan National Park in Lampung, Barito Ulu in Central Kalimantan and Gunung Palung National Park in West Kalimantan. The sites were chosen so that in total, all of the putative refugia and non-refugia were surveyed.

Much of the sampling has been carried out over either disturbance or altitudinal gradients (Davies, 1997; Eggleton *et al.*, 1997; Gathorne-Hardy *et al.*, 2001), giving an additional insight into the effects of these environmental variables on termites.

## SAMPLING METHODS

A standardized transect method was used (Davies, 1997; Jones & Eggleton, 2000; Jones, 2000). Jones & Eggleton (2000) have demonstrated that the method gives a representative sample of both the taxonomic composition and the functional group composition of the local termite assemblage. Straight belt-transects,

**Table 2.** Evidence for rainforest refugia in south-east Asia during the Quaternary

Area of continuing forest	Time	Author	Evidence for forest and amount of change
Sumatran highlands (1500 m a.s.l.)	31–13 kya	Newsome & Flenley (1988)	Palynological evidence of montane forest migrating downhill during colder times
Situ Bayongbong, W. Java (1300 m a.s.l.)	17–10 kya	Stuijts (1993)	Palynological evidence of montane forest migrating downhill
Mentawai islands	Quaternary	F. J. Gathorne-Hardy & H. Harcourt-Smith, in prep.	High rate of non-volant mammal endemism indicates continuous lowland rainforest
Sarawak, Brunei and Sabah	Quaternary	Ashton (1972, 1995) & Morley (2000)	Inter riverian endemism of dipterocarps indicates continuous lowland rainforest
Niah caves, Sarawak	40 kya	Cranbrook (2000)	Fossils of <i>Presbytis</i> and <i>Pongo</i> indicate tall evergreen forest
Punung caves, East Java	80–60 kya	van den Bergh (1999)	Fossils of <i>Hylobates</i> and <i>Pongo</i> indicate lowland rainforest
Mentawai islands, northern Sumatra, West Java and northern Borneo	80–10 kya	Brandon-Jones (1998)	Present day primate distributions indicate lowland rainforest refugia

100m × 2m, were laid at random throughout the forest, incorporating habitat heterogeneity. All transects were divided into 20 sections, each 5 m long, and in each section one man-hour was spent searching for termites. Within each section the following four microhabitats for termites were examined. (1) Approximately 12 areas of surface soil of ~50 cm<sup>2</sup> and 10 cm deep with associated leaf litter were scraped up and examined for termites. (2) Dead wood with a diameter of <1 cm was broken open and termites removed. (3) Tree trunks and buttress roots were examined, particular attention was paid to the deep accumulations of litter and organic-rich soil between buttresses. Any carton sheeting or runways were scraped off and examined, up to a height of 2 m. (4) Nests were opened and termites collected.

Termites of both soldier and worker castes were collected, if both were present, and stored in 90% ethanol. Alates were excluded because their presence does not necessarily imply the presence of a viable colony.

#### IDENTIFICATION AND FEEDING GROUP CLASSIFICATION

The termites collected were identified at the Natural History Museum (BMNH), London. They will be lodged at the Bogor Zoology Museum, Indonesia with duplicates at Syiah Kuala University, Banda Aceh, Indonesia and at the BMNH. Specimens were identified to species or, where this proved impossible, to numbered morphospecies. These were numbered in accordance with Tho (1992), material from Danum Valley Conservation Area (Eggleton *et al.*, 1997, 1999) and the Maliau Basin in Sabah (Jones, 2000), Jambi (D. J. Jones, unpubl. data), and from Pasoh Forest Reserve in Peninsular Malaysia (Jones & Brendell, 1998). Several taxonomic changes have been made (Gathorne-Hardy, 2001).

Termites were placed into one of four feeding groups according to worker morphological characters, i.e. shape of pronotum, mandible and enteric valve characters (Donovan *et al.*, 2001a). The feeding groups are numbered sequentially as their principal food source becomes more humified: I, wood, litter and grass feeders (all lower termites); II, wood, litter and grass feeders (some of the higher termites); III, very decayed wood or high organic content soil; and IV, low organic content soil. A full list of termite genera and their feeding group assignments can be found in Donovan *et al.* (2001a).

Termites were also placed into one of nine functional taxonomic groups following Davies (2001). These represent a combination of the taxonomic and functional position of the termite species. For analyses, termites of feeding group IV were amalgamated with those of

group III, as there are so few group IV feeders in the region.

#### ENVIRONMENTAL VARIABLES

Environmental data were collected for each transect. The following variables were analysed for their effect upon the termite composition:

- Rainfall. Mean annual rainfall measured in mm (from field station records or published records).
- Altitude. Measured by an altimeter or from a map (25 m contours).
- Disturbance. The level of disturbance was scored on a scale of 1–4: 1, primary forest; 2, old secondary/regenerating closed canopy forest; 3, young secondary/regenerating forest with disturbed canopy; 4, very badly disturbed forest.
- Modern island size, i.e. island size at present sea levels. Thailand (north of the Kra ecotone) was taken to be part of the same ecological 'island' as the Indian/Burmese/Indochinese forest area. Pasoh is south of the Kra ecotone, so the island size is approximately the same area as Peninsula Malaysia.
- Log<sub>10</sub> (modern island size).
- Log<sub>10</sub> (area of forest where the transect was run). Estimated from vegetation maps or taken from site descriptions.
- Log<sub>10</sub> (distance to forest edge). The distance from each transect to the edge of the forest (Table 3).

#### DATA ANALYSIS

All data are expressed as numbers of encounters (hits) per taxonomic unit per transect. The number of hits acts as a surrogate for abundance (Gathorne-Hardy *et al.*, 2001).

We analysed the data at a functional taxonomic group level in order to minimize the effects of possible alpha-taxonomic mistakes and species patchiness. Where two transects had been run at one site we amalgamated them and took the means of the number of encounters. As almost all termite functional taxonomic groups were found in every site, it was appropriate to use linear response models to analyse the data. Because the process of standardizing species data causes rare species to dominate the analysis (Jongman, Ter Braak & van Tongeren, 1995), we downweighted the two rarest functional taxonomic groups, the Kalotermitidae and the Apicotermitinae (both <3 hits transect<sup>-1</sup>).

As the effects of altitude are well known, and they are known not to correspond directly to height a.s.l. (Gathorne-Hardy *et al.*, 2001), we removed all non-lowland (>800 m a.s.l.) sites from the analysis.

**Table 3.** Table showing sampling sites and environmental variables. \*D, disturbance measured on a scale of 1–4

Site	Code	Site description	Longitude (decimal)	Latitude (decimal)	D* (1–4 scale)	Log10 modern island size (km <sup>2</sup> )	Modern island size (km <sup>2</sup> )	Altitude (m)	Rainfall (mm)	Log10 (area)	Log10 (edge)
Thailand, Khao Sok	ThKhSo	Secondary forest with bamboo	98.00	8.90	3	6.2886	1943645	500	1700	3.1764	3.080
Thailand Doi Sutep-Pui National Park	ThDoSuFP	Fire-protected dry deciduous dipterocarp forest	100.00	18.80	3	6.2886	1943645	575	1100	3.1764	3.080
Thailand Doi Sutep-Pui National Park	ThDoSuB	Burnt dry deciduous dipterocarp forest	100.00	18.80	3	6.2886	1943645	480	1100	3.1764	3.080
Thailand, Khao Yai National Park	ThKhYa	Primary evergreen rainforest	101.37	14.33	1	6.2886	1943645	780	4000	3.1764	3.080
Peninsula Malaysia, Pasoh Forest Reserve	PMPas1	Primary evergreen rainforest	102.3	2.98	1	5.1182	131286	100	2000	2.4786	2.904
Sabah, Danum Valley Conservation Area	SaDanOS1	Old logged (18 ya) evergreen forest	117.8	4.97	3	5.8711	743247	50	2700	3.0004	3.301
Sabah, Danum Valley Conservation Area	SaDanPF1	Primary evergreen rainforest	117.8	4.97	1	5.8711	743247	50	2700	3.0004	3.301
Central Kalimantan, Barito Ulu Research Station	BU1ry	Primary evergreen rainforest	116.93	0.1	1	5.8711	743247	150	3800	4	3.301
Central Kalimantan, Barito Ulu Research Station	BU2ndry	Old secondary evergreen forest (57 ya)	116.93	0.1	2	5.8711	743247	150	3800	4	2.699
West Kalimantan, Gunung Palung National Park	GP	Primary evergreen rainforest	110.12	-1.22	1	5.8711	743247	50	4300	2.954	4.255
South Kalimantan, Tabalong District Logging Concession	Tabysf	Young logged (2 ya) evergreen forest	115	-2	4	5.8711	743247	450	3000	2.954	4.255

South Kalimantan, Tabalong District Logging Concession	Tabosf	Old logged (15 ya) evergreen forest	115	−2	3	5.8711	743 247	630	3000	2.954	4.255
Sumatra, Leuser Ecosystem, Ketambe Field Station	SuKet500	Primary evergreen rainforest	97.65	3.68	1	5.62697	423 611	500	3125	3.9543	3.477
Sumatra, Leuser Ecosystem, Suaq Belimbing Field Station	SuSuaq	Primary evergreen rainforest	97.65	3.05	1	5.62697	423 611	125	3231	3.9543	3.477
Sumatra, Leuser Ecosystem, MRT Logging Concession	SuMRT	Primary evergreen rainforest	97	3.18	1	5.62697	423 611	200	3231	3.9543	3.001
Sumatra, Leuser Ecosystem, Bukit Lawang	SuBuLaw1	Primary evergreen rainforest	98.12	3.53	1	5.62697	423 611	350	4675	3.9543	3.3015
Sumatra, Leuser Ecosystem, Lokop	SuLokop	Primary evergreen rainforest	97.53	4.42	1	5.62697	423 611	500	1700	3.9543	3.0009
Sumatra, Jambi province	SuJaPF	Primary evergreen rainforest	102.1	−1.08	1	5.62697	423 611	76	3000	1.0414	2.7796
Sumatra, Jambi province	SuJaLogF	Young logged (3 ya) evergreen forest	102.1	−1.08	4	5.62697	423 611	85	3000	1.041	1.324
Sumatra, Way Kambas National Park	SuWK	Primary evergreen rainforest	105.67	−4.67	3	5.62697	423 611	20	2000	4.989	2
Sumatra, Bukit Barisan Selatan National Park	BBar	Primary evergreen rainforest	104.5	−5.8	1	5.62697	423 611	200	3250	3.562	3
Siberut National Park	SibT1	Primary evergreen rainforest	98.98	−1.35	1	3.65128	4 480	100	3320	3.279	3
Java, Ujung Kulon National Park	JaUjKuIn	Primary evergreen rainforest	105.5	−6.83	1	5.10209	126 500	200	3140	3.7782	3.0009
Java, Pangandaran Nature Reserve	JaPangI1	Old secondary evergreen forest (70 ya)	109	−7.72	3	5.10209	126 500	75	3196	0.778	3.115

We first ran a reducing analysis (RDA), analysing those sites for which there is evidence for savannah in the LGM (Java, Way Kambas near Palembang, Gunung Palung in West Kalimantan, and Pasoh near to Subang), and those for which there is evidence of refugia (Lokop, MRT, Bukit Lawang, Suaq in northern Sumatra, Siberut and Danum in Sabah). As forward selection in the RDA showed that no environmental variable was significant, we ran a principal component analysis (PCA) of these sites and plotted the resulting ordination diagram.

The other lowland sites were then added to the matrix and an RDA was used again to assess the importance of the environmental variables. Again, no environmental variable was significant. We therefore ran another PCA of the combined data to see where they fell in the final ordination diagram.

## RESULTS

In total, 187 species of termite have been collected in transects in south-east Asia. Of these, 57 are not yet

formally described (F. J. Gathorne-Hardy unpubl. data). These morphospecies tend to be rare, often only collected once and are frequently missing one of the castes, so a full description is often impossible.

No endemic species was found on Siberut. Most species are found in most parts of the region, as are functional taxonomic units and clades (Table 4).

The ordination diagram from the PCA of putative refugia and savannah sites (Fig. 2) shows that the putative savannah sites clump together and the refugia sites lie in a different area. When refugium is added to the matrix as an environmental variable, it is significant ( $P = 0.003$ ).

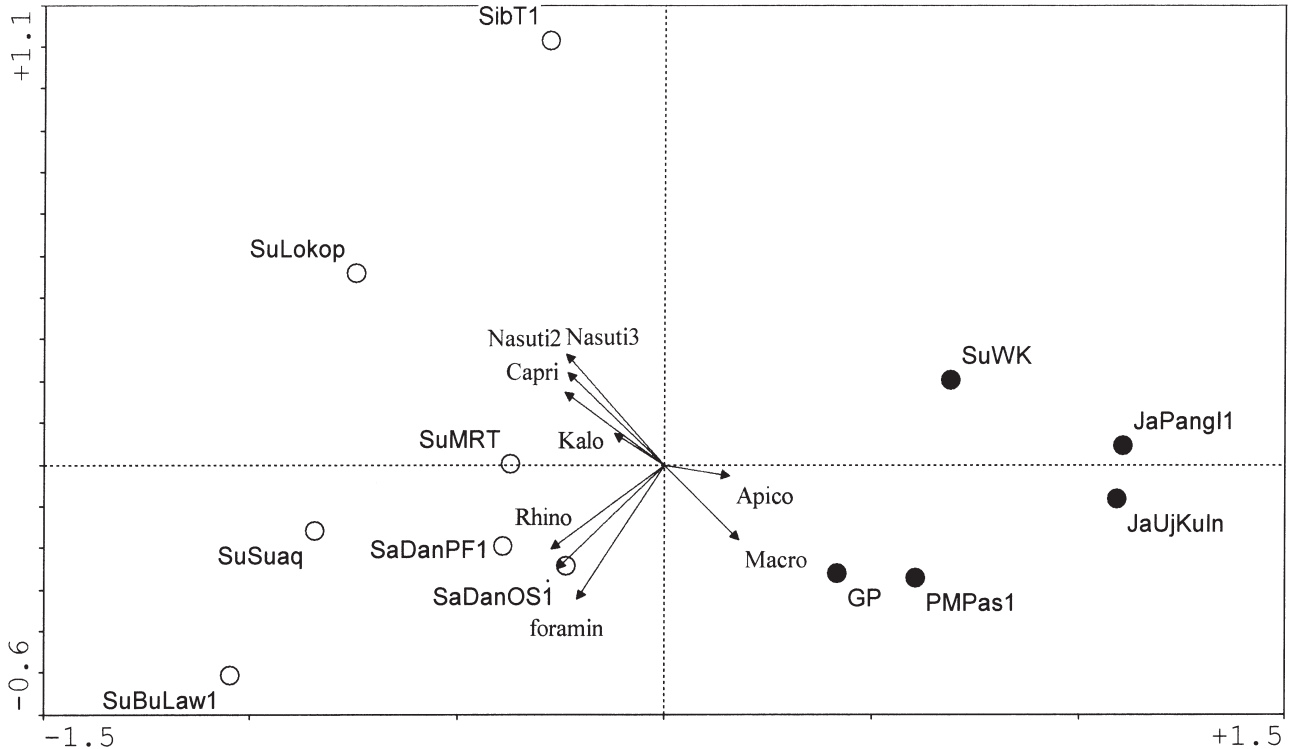
When the other, unknown refugium status sites were added to the data matrix, the ordination diagram of the PCA (Fig. 3) showed that the Thai sites seemed to cluster with the putative savannah sites, and Tabalong, Barito Ulu, Bukit Barisan and Jambi sites seemed to cluster with the putative refugia sites.

We tested to see whether sites formed separate clumps due to their refugium status by coding refugium status as an environmental variable. Coding sites that

**Table 4.** Number of hits in each transect of each functional taxonomic group. Kalo, Kalotermitidae; Rhino, Rhinotermitidae; Macro, Macrotermitinae; Foramin, *Foraminitermes* group; Ami, *Amitermes* group; Capri, *Termes/Capritermes* group; Apico, Apicotermitinae; Nasuti2, Group II Nasutitermitinae; Nasuti3, Group III Nasutitermitinae

Site	Functional taxonomic group								
	Kalo	Rhino	Macro	Foramin	Ami	Capro	Apico	Nasuti2	Nasuti3
ThKhSo	2	4	13	0	5	6	0	14	0
ThDoSuFP	0	1	11	0	16	4	6	0	0
ThDoSuB	0	0	17	0	11	5	5	1	0
ThKhYa	1	5	17	0	2	10	0	6	1
PMPas1	0	7	34	1	3	15	1	4	4
SaDanOS1	1	13	13.5	0.5	13	31	0	8.5	3
SaDanPF1	0.5	8	9	1.5	14.5	40	1	5.5	5
BU1ry	0	23	8	0	5	28	0	17	12
BU2ndry	0	15	11	5	6	20	0	19	11
GP	0	7	3	1	6	14	0	0	0
Tabysf	0	16	24	0	19	32	0	11	3
Tabosf	0	9	15	0	16	33	2	1	1
SuKet500	0	4	12	0	0	7	0	26	7
SuSuaq	0	17	16	2	10	32	0	19	11
SuMRT	0	13	16	0	15	20	0	15	10
SuBuLaw1	0.5	13.5	3.5	3.5	15.5	23	0	29.5	6.5
SuLokop	2	11	3	1	9	25	0	41	9
SuJaPF	0	10	11	0	14	53	0	12	6
SuJaLogF	0	9	9	0	19	39	0	1	10
SuWK	0	3	4	0	3	11	2	12	0
BBar	0	7	28	0	10	45	0	26	3
SibT1	0	5	3	0	2	42	0	20.5	12.5
JaUjKuIn	0	4	38	0	0	8	1	2	3
JaPangI1	0.5	0.5	20.5	0	1	3	0	6.5	0





**Figure 2.** Ordination diagram showing PCA of functional taxonomic groups of termites from putative refugia and non-refugia. ● putative non-refugia, ○ putative refugia. Kalo, Kalotermitidae; Rhino, Rhinotermitidae; Macro, Macrotermitinae; Ami, *Amitermes* group; Foramin, *Foraminitermes* group; Apico, Apicotermitinae; Capri, *Termes/Capritermes* group; Nasuti2, Group II Nasutitermitinae; Nasuti3, Group III Nasutitermitinae.

clustered close to putative refugia were coded as refugia in the partial PCA, and those close to putative savannah as savannah). We then changed the coding of one site, so that a proposed refugium site was coded as a savannah site, ran an RDA and forward selection provided us with an  $F$ -value for refugium. We then changed the coding of another site, this time a proposed savannah site. Again we ran an RDA and extracted the  $F$ -value. This continued until refugium status was no longer a significant environmental variable. The resulting  $F$ -values from the RDA analysis were plotted and formed a bell-curve, with no changes of refugium status having the highest value, demonstrating that the perceived difference in the two clusters is real.

Macrotermitinae are found in all sites but are more abundant in savannah sites. Soil-feeding termites are also found in all sites but are more abundant in refugia sites (Table 4 and Fig. 3).

## DISCUSSION

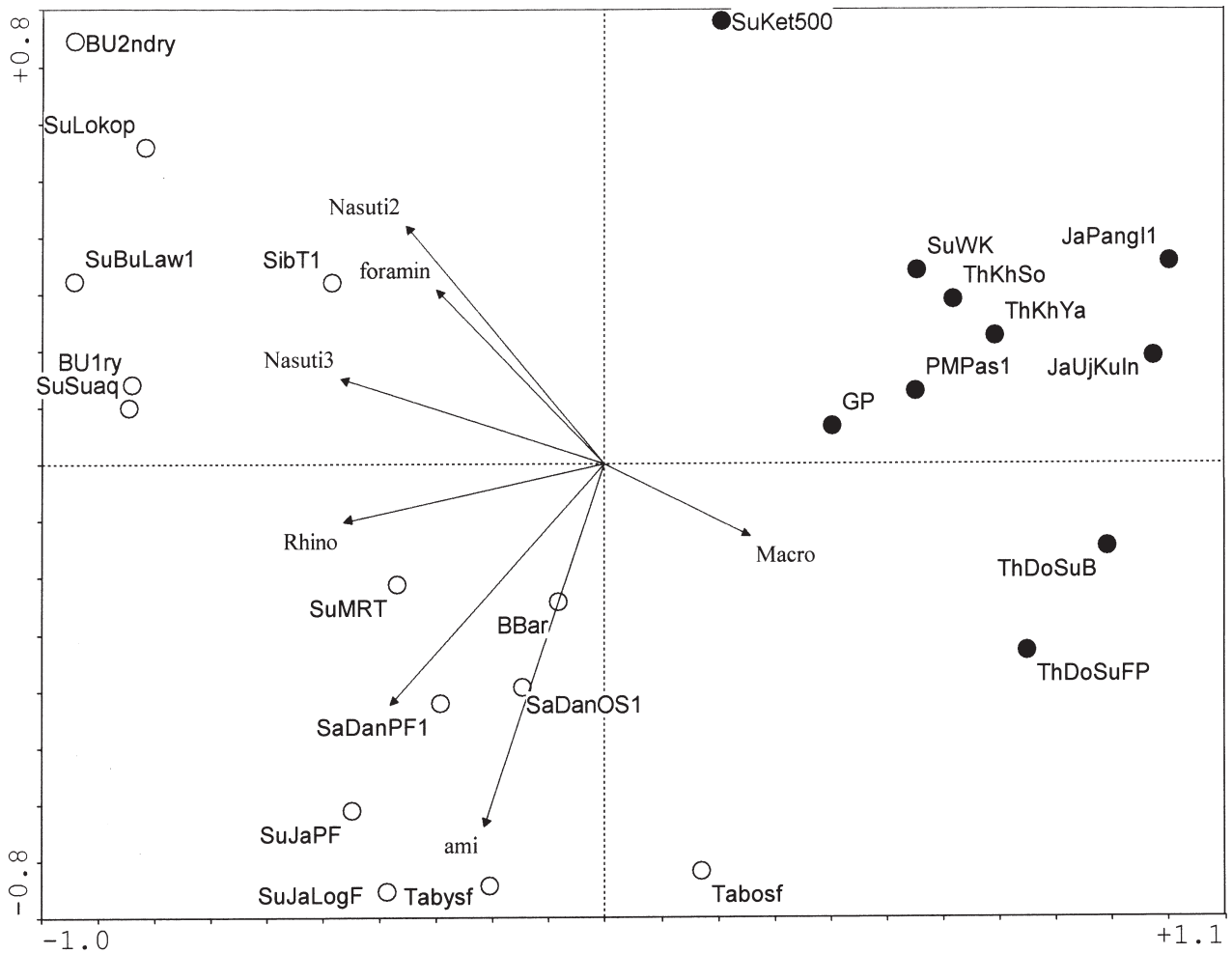
### HISTORICAL FACTORS REVEALED

The PCA in Figure 3 shows that the putative savannah sites have a different termite composition from

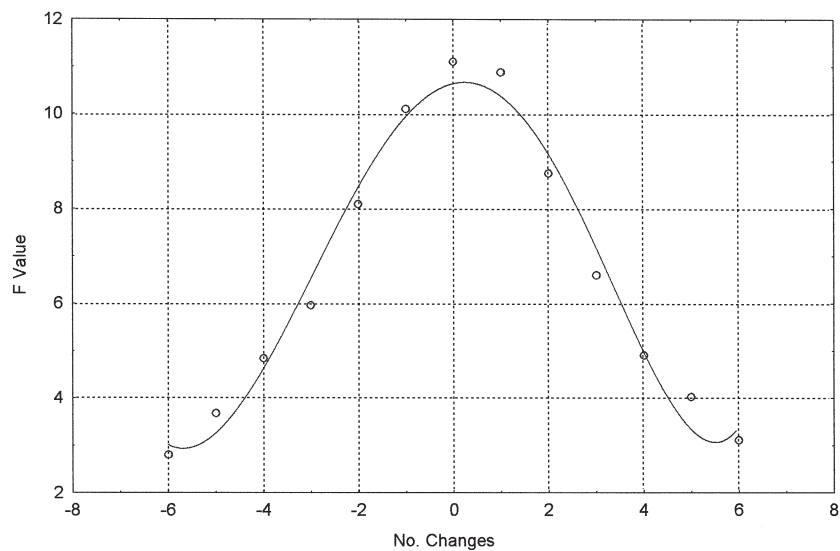
the refugia sites. No modern environmental variable is significant, and we have demonstrated that the separation of the refugia and savannah sites is real. Therefore, it is probable that termite composition can reflect history and is different in prehistoric savannah sites from prehistoric refugia.

We propose that the unknown refugium status sites that cluster around known savannah sites were probably savannah during the LGM, and that those that cluster around refugia were also refugia during the LGM.

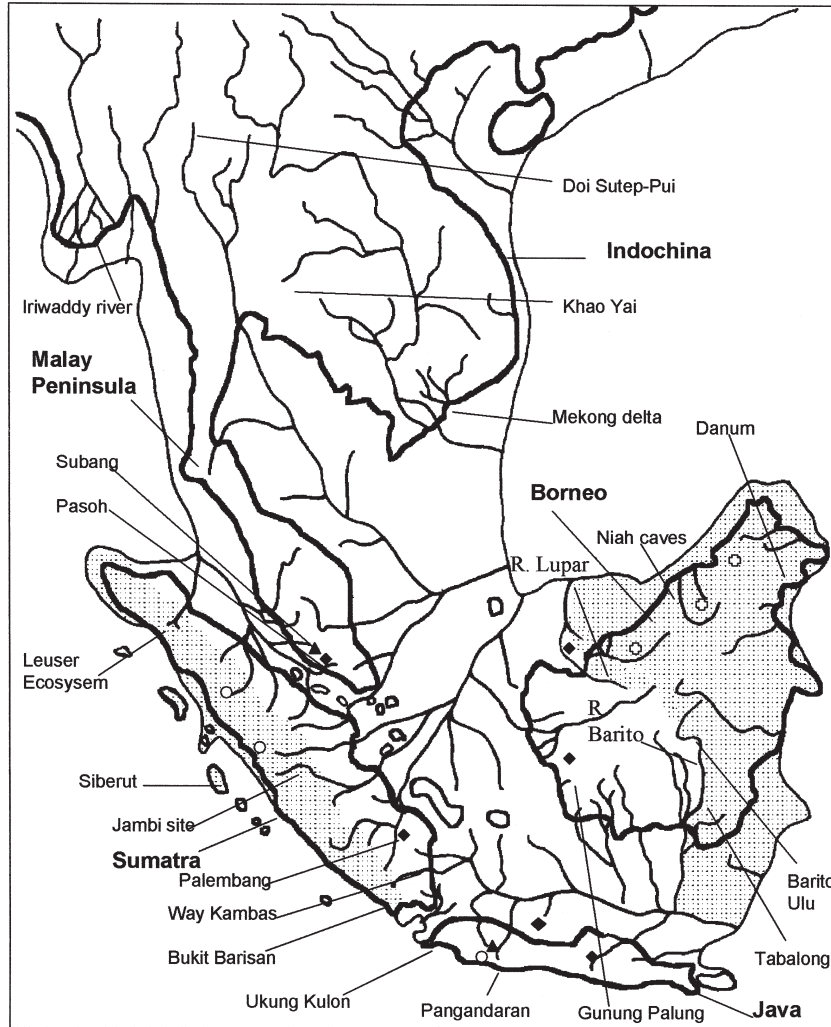
Although our findings are indications only, and need additional palynological and geological work to provide confirmation, we have now a broader-based picture of the effects of glacial climate change on the rainforests of south-east Asia. During the ice ages when the climate became more seasonal, rainforest refugia existed in the Mentawai islands, most of the north of Sumatra and at the base of the Barisan Mountains. Northern Sarawak, Brunei, Sabah and eastern Kalimantan up to the Barito river were also refugia. Thailand, the Malay Peninsula, south-east Sumatra, western Borneo (west of the Barito and Lupar rivers), and Java were severely affected by Pleistocene



**Figure 3.** Ordination diagram showing PCA of functional taxonomic groups of termites from all sites. ● putative non-refugia, ○ putative refugia. Kalo, Kalotermitidae; Rhino, Rhinotermitidae; Macro, Macrotermitinae; Ami, *Amitermes* group; Foramin, *Foraminitermes* group; Apico, Apicotermitinae; Capri, *Termes/Capritermes* group; Nasuti2, Group II Nasutitermitinae; Nasuti3, Group III Nasutitermitinae.



**Figure 4.** Bell curve showing *F*-value against number of changes in refugium status. This shows that when there are no changes the *F*-value is highest.



**Figure 5.** Map of Sundaland at LGM showing rivers, probable rainforest refugia and savannah areas. Heavy lines = modern coastline; light lines = coastline at 120 m below present sea level / modern and palaeo-river courses (from Voris, 2000); stippled area = probable rainforest refugia during LGM (limits uncertain); white area = savannah areas during LGM (limits uncertain and river valleys probably forested). Termite sampling sites: ▲ palynological evidence indicating savannah during LGM; ◆ geological evidence indicating savannah during the Pleistocene; ○ palynological evidence indicating continuing rainforest; ◻ interriverian dipterocarp endemism indicating continuing rainforest.

drought. These areas were probably all vegetated by savannah, or wooded (with *Pinus* or deciduous trees) savannah (Medway, 1972; Cranbrook, 2000; Morley, 2000). The savannah probably spread out onto most of the exposed Sunda shelf.

Most termite species are found both in refuge and savannah areas (Tho, 1992). It is therefore probable that small, local refugia, such as sheltered riverbanks, etc., existed throughout the region. The large river valleys of the exposed shelf were probably wet enough to provide an environment suitable for rainforest organisms.

We have used a combination of all works on the

Pleistocene in south-east Asia to draw a map, illustrating the possible extent of glacial rainforest contraction during the LGM (Fig. 5).

EXCEPTION TO THE MODEL

The Ketambe 500 m site, although geographically in the middle of the northern Sumatran refugium, clumps together with the savannah sites in the second ordination diagram. It is thought that the Alas valley was dammed by volcanic debris from the Toba eruption of 74 kya, forming a lake. The water level slowly decreased as the dam was eroded, and it is thought

that the Ketambe 500 m site was exposed ~10 kya (van Schaik & Mirmanto, 1985). It is interesting to note that although it was not a savannah, but was flooded, Ketambe shows a similar termite composition to the Pleistocene savannah sites.

#### THE REFUGIA IN CONTEXT: A REGIONAL HISTORY

It is probable that south-east Asia has been populated by termites since the late Cretaceous or early Palaeocene, for Kalotermitidae and Rhinotermitidae are extremely good colonisers (Gathorne-Hardy *et al.*, 2000b) and are not rainforest dependant. Most of the south-east Asian soil-feeding termites (*Termes/Capritermes* group, *Labritermes* and *Apicotermitinae*) are thought to be descended from Gondwanan ancestors, and probably rafted from Africa on the Indian plate (Eggleton, 2000; Davies, 2001). The soil-feeding Nasutitermitinae probably evolved from wood-feeding nasutes, that had rafted and island-hopped over the Pacific from South America (Davies, 2001; Eggleton & Davies, in press).

It appears that the first land connection between India and Asia appeared in the Oligocene (Najman *et al.*, 2001). This, coupled with a perhumid lowland climate in Burma and Assam, allowed Gondwanan rainforest organisms to colonize mainland Asia (Morley, 2000). Rainforest was rare in south-east Asia during the Oligocene and Early Miocene, as the climate was predominantly seasonal and dry. The climate changed to a perhumid one in the Mid-Miocene, and rainforest colonized the region (Morley, 2000). Termites probably followed the forest to south-east Asia and colonized all forested areas. From the early until the late Miocene south-east Asia was effectively a single lowland (apart from the Bornean highlands) land mass (Hall, 1998). The region remained as a single rainforested block until the late Miocene-early Pliocene (Muller, 1972; Morley, 2000). A few periods of heightened Gramineae pollen have been found, but not enough to indicate a large area of Savannah (Muller, 1972).

Speciation of soil-feeding termites is thought to require a large area of lowland rainforest that is stable for a long time (Davies, 2001). These requirements were met during the Miocene in south-east Asia when they applied for 10–15 Myr. It is probable that the endemic south-east Asian soil-feeding termites (both the Termitinae and Nasutitermitinae) speciated during the Miocene.

Uplift of the Tibetan plateau and the Himalayas in the late Miocene/early Pliocene strengthened the monsoon system (Ruddiman & Kutzbach, 1990; An, 2000). This probably increased seasonality in Indochina and Java (there is evidence of savannah vegetation from Mio-Pliocene deposits in the Iriwaddy

delta and Pliocene Java (Morley, 2000)), reducing the size of the rainforest block.

The Mentawai islands emerged in the Pliocene (Samuel *et al.*, 1997) and probably became isolated 3 or 4 Mya (Chatterjee, 2001; F. J. Gathorne-Hardy & W. Harcourt-Smith, unpubl. data). That non-dispersive species (such as *Pseudocapritermes orientalis* and *Malaysiitermes spinocephalus*) are identical in every taxonomic character to those at Danum, 2000 km away and that no endemic termite species was found on Siberut, demonstrates the extremely slow rate of termite speciation.

With the advent of Quaternary glaciations, savannah formed in large parts of south-east Asia, driving rainforest obligates to the refugia identified above. The large rivers draining the Sunda shelf probably provided refugia along their banks. Savannah organisms, such as mastodons, stegodonts, elephants, antelopes, hippopotami and oxen proliferated, as did *Homo erectus* (Whitten, Soeriaatmadja & Suraya, 1996; Cranbrook, 2000). During interglacials, the sea rose, the rainforest returned and the savannah animals were constrained to Indochina and a few patches of Java. Each of the glacial episodes probably showed a similar pattern.

It is probable that the rainforest refugia are centres of speciation, not because of their fragmentation and subsequent isolation from each other, but because of their long-term stability, allowing fragile organisms (such as soil-feeding termites) to persist. The recognition of the refugia sites and the recovery from prehistoric disturbance is still not complete, this highlights the long-term fragility of the rainforest ecosystem and the importance of conserving prehistoric refugia as modern rainforest refugia.

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