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Late Pleistocene climate induced changes in paleo-vegetation in Borneo: Possible implications to human divergence

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ABSTRACT

The impact of changes in vegetation on ancient human colonization and divergence in Southeast Asia is unclear. Here we present a 40 ky history of vegetation evolution in Borneo, which has been recognized as one of the hubs for early human migration, based on a pollen sequence from the southern South China Sea. Our pollen record shows that the succession of vegetation in Borneo responded to orbital climate changes as well as to the millennial-scale cold events in boreal high-latitudes in the form of upper montane taxa expansion. We find that the altitude structure of vegetation in Borneo changed from a clear altitudinal zonation of upper montane, lower montane, and lowland forests during MIS 3 to one that was dominated by upper montane forests during the last glacial maximum (MIS 2). Five expansions of upper montane forests during the past 40 ky, indicating the decrease of temperature, apparently correspond to five cold events in the northern high latitudes, with a lag of 500–1000 years. To test the influence of the changes in Borneo's vegetation on human distribution we compare our palynological data with archaeological records and the molecular evolution of ancient human genotype in Southeast Asian islands. The expansion of upper montane forests and the accompanying contraction of lowland forests in Borneo during the last glacial maximum and the last deglaciation may have promoted the divergence of human genotype. Our study offers a new perspective on the possible impact of vegetation succession on the colonization of *Homo sapiens* on Southeast Asian islands.

1. Introduction

Borneo is the largest island within the Maritime continent and has been recognized as one of the hubs for early human migration in Southeast Asia (Yew et al., 2018). During the Pleistocene, Borneo was connected to the Southeast Asia islands through the exposed Sunda Shelf and became a corridor of human migration (Bird et al., 2005). During the last glacial maximum (LGM), the sea level dropped by ~120 m (Lambeck et al., 2014), and the Sunda shelf was completely exposed (Voris, 2000). The exposure of the Sunda shelf had major environmental implications to the region (Louys and Roberts, 2020), and a strong impact on the Indo-Pacific hydroclimate and biogeography (DiNezio et al., 2016).

Paleoclimate model simulations show that the exposed Sunda Shelf was covered by savanna in the middle Pleistocene, promoting the spread of modern humans and herbivores in Southeast Asia (Bird et al., 2005; Louys and Turner, 2012). In the late Pleistocene, tropical rainforests replaced the savannah, apparently leading to the expansion of rainforests species and *Homo sapiens*, and the extinction of *Homo erectus* (Louys and Roberts, 2020). These have fully emphasized the key role that vegetation played in the migration and dispersal of ancient humans. Unfortunately, the research on the relationship between ancient humans and vegetation has not received sufficient attention.

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Archives of pollen and spores have long been a particularly useful tool for reconstructing changes in terrestrial vegetation varying from local (peat, pond, small lakes) to regional (large lakes, ocean) (Daniau et al., 2019). The spatial coverage of pollen sequence data covers almost all regions of the earth, including high, low latitudes and altitudes. Terrestrial pollen sequences, however, often suffer from discontinuities, which compromise the cores' chronostratigraphy and consequently impede reliable reconstructions of past vegetation and climate changes. In contrast, marine pollen records benefit from continuous sedimentation and provide information on vegetation changes at a regional scale (Heusser, 1988). In addition to radiocarbon dating, the chronology of marine sequences can be derived from measurements of stable oxygen isotopes of foraminifera for reliable comparison with the marine records (Heusser, 1988; Sánchez Goñi et al., 2018). Thus, marine pollen is very instrumental in reconstructing vegetation on larger areas, especially islands with rugged terrain.

The application of palynological analysis involving ancient humans on Southeast Asian islands has been relatively limited. In Borneo, the pollen sequence comes from the Niah cave and its surrounding strata, which record the vegetation environments of ancient humans (Barker et al., 2007; Hunt et al., 2012). *Homo sapiens* were able to exploit rainforest resources by collecting and processing poisonous plants, hunting wild boars and some arboreal primates to survive in lowland rainforests (Barker et al., 2007). However, due to sediment disturbances, a continuous record of secular changes in vegetation has, thus far, not been reconstructed (Hunt et al., 2012). To date, published marine pollen records from Borneo come mostly from sites near the Sunda Shelf, and therefore are strongly affected by sea-level changes and may not fully represent temporal vegetation changes in Borneo (Sun et al., 2000; Wang et al., 2009). Also, there is a lack of marine pollen records documenting the response of vegetation to millennial climate change and its role in human diversity change. Previous studies have used carbon stable isotopic records in organic markers from cores in the Indo-Pacific warm pool region to reconstruct changes in vegetation composition, and inferred that the regional vegetation is vulnerable to the increases in water stress arising from enhanced seasonality of rainfall (Dubois et al., 2014). In addition, the insect cuticles preserved in cave guano profiles suggest that the vegetation composition of Southeast Asian islands have different temporal evolution (Wurster et al., 2010) and the orbital forcing may be the cause of the difference (Tierney et al., 2012).

Unfortunately, because the Sunda shelf has been gradually submerged since the last deglaciation, no archaeological remains have been preserved, further blocking the exploration of the prehistory of the evolution of *Homo sapiens* in relation to vegetation variation. The application of mitochondrial DNA (mtDNA) in archaeogenetics has been demonstrated to be a valuable method of tracing the origin and dispersal of *Homo sapiens*, especially in the absence of archaeological records (Rabett, 2012). Another advantage of mtDNA is its well-defined molecular clock, which allows estimating more accurately the ages for the different clades (Soares et al., 2009). Combining archaeological genetics with accurate estimates of time and reconstructed vegetation changes can provide new opportunities for exploring the relationship between ancient human evolution and vegetation variation.

In order to highlight the role of vegetation in human migration and divergence, the history of vegetation variations in Borneo based on palynological reconstruction were compared with the divergence time of haplogroup E, the major human genotype in the Southeast Asian islands. Here we assess the relationships between vegetation changes in Borneo and climate variability on different temporal scales and explore their possible influence to human colonization and divergence. This study attempts to find possible motivations for hominin evolution by comparing the paleoclimate variation with changes in the genetic diversity of local *Homo sapiens.*

2. Study area

2.1. Climate and vegetation

The East Asian monsoon dominates the climate in the South China Sea (SCS) and the surrounding areas. The seasonally alternating winter and summer monsoons govern seasonal precipitation and vegetation distribution (Wang and Li, 2009). Currently, the strong northeastern winter monsoon, formed by cooling in the high latitudes of the Eurasian continent, lasts for almost six months (November to April), whereas the weaker southwest summer monsoon, accompanied by an increase in temperature over the continent, lasts for four months (mid-May to mid-September) (Chu and Wang, 2003).

The largely opposite precipitation distribution in the north and south of the SCS, which can be attributed to the north-south migration of the Intertropical Convergence Zone (ITCZ), driven by seasonal reversal monsoon winds (Bischoff and Schneider, 2014). Furthermore, the annual rainfall in south China and the Indochina Peninsula is 1700–2000 mm in the north part of the SCS; approximately 85–90 % of the rainfall falls in the summer monsoon. Annual rainfall in the southern part of the South China Sea is more abundant, with an annual rainfall of 2500–3000 mm in the Malay Peninsula, Sumatra, and Borneo (Liu et al., 2012). Furthermore, the southern part of the SCS does not exhibit a remarkable seasonal variation of rainfall, and the East Asian winter monsoon (EAWM) is observed to prevail in the humid season. On interannual time scale, El Niño-Southern Oscillation (ENSO) events exert the major effect on the hydroclimatology of the SCS (Juneng and Tangang, 2005).

Landmasses surrounding the southern part of the SCS, including the Indochina region, the Malay Peninsula, and islands of Borneo, Sumatra, and the Philippines, are covered with tropical and seasonal rainforests (Fig. 1). Among those, the islands of Borneo, Java, and Sumatra close to the Sunda Shelf are covered with tropical rainforests (Florin, 1963). Lowland rainforests comprised primarily of Dipterocarpaceae, Moraceae, Meliaceae, Sapindaceae, Rubiaceae, and Rutaceae and can be observed at altitudes of lower than 1200 m. Lower montane forests that mainly comprises *Castanopsis*, *Quercus*, Theaceae, Myrtaceae, and Elaeocarpaceae is present from 1200–1500 m, whereas upper montane forests that mainly comprises *Podocarpus*, *Dacrycarpus* and *Dacrydium* can be observed up than 1500 m (Kitayama, 1992; Yuan et al., 2006). In these tropical rainforests, herbs can be seen as a lower layer of the forest (Zhang et al., 2011).

2.2. Distribution of archaeological sites

On Southeast Asian islands, there are mainly 4 confirmed archaeological sites related to *Homo sapiens*, where fossils were found in caves. Famously, the Niah Cave in Borneo has yielded one of the earliest human fossils (relate to human activity range from 46 to 43 ka) (Barker et al., 2007). The earliest evidence (~73 ka) of rainforests occupation by *Homo sapiens* in Sumatra comes from the Lida Ajer cave (Westaway et al., 2017). Skeletal fossils of *Homo sapiens* have also been found in the Moh kiew cave in the Malay Peninsula (~25.8 ka) (Matsumura and Pookajorn, 2005) and the Tabon cave in Palawan (~16.5 ka) (Détroit et al., 2004).

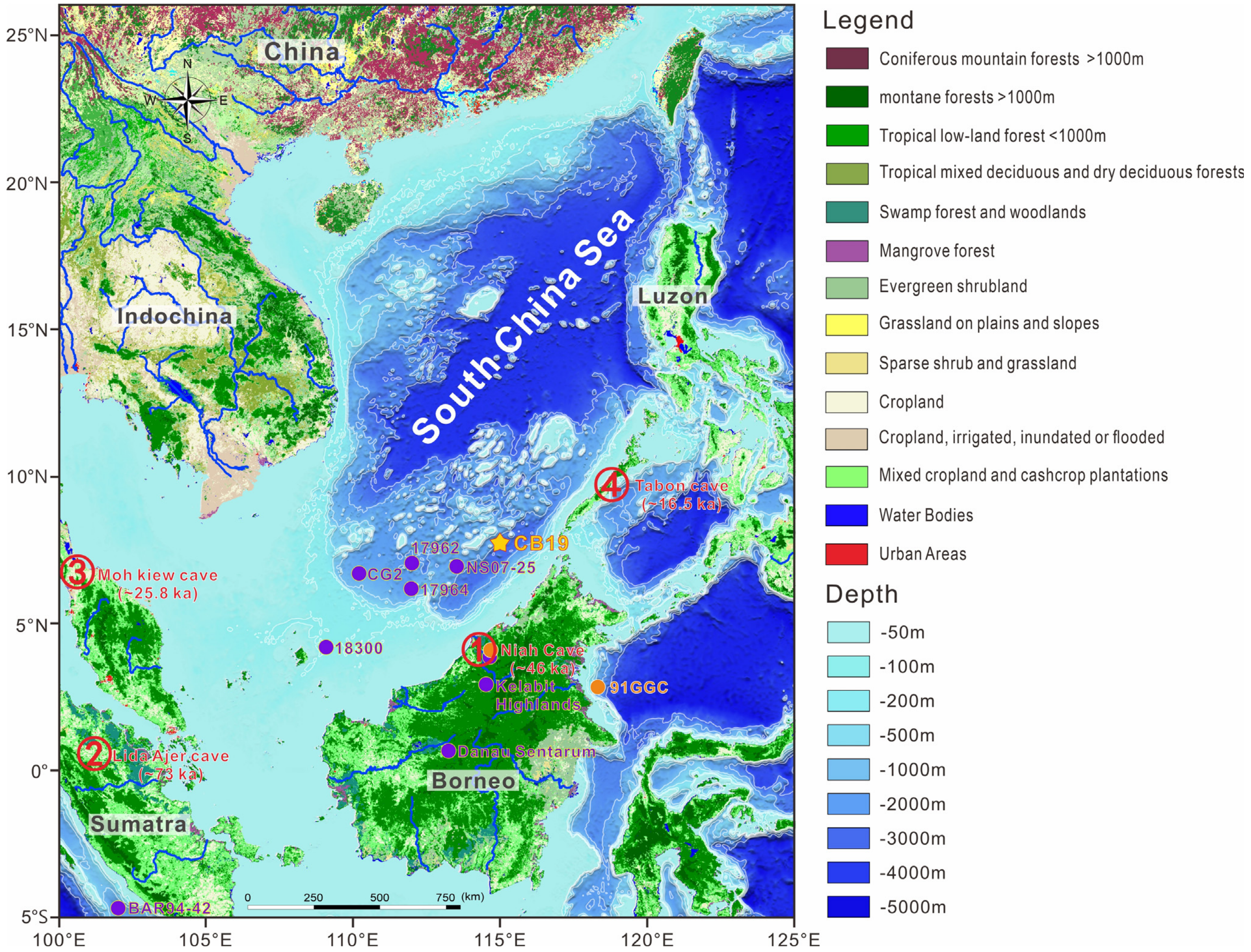

Fig. 1. Map of the vegetation, monsoon, current systems around the South China Sea (SCS), and the location of core CB19. The data on vegetation are taken from Global Land Cover 2000) (Stibig et al., 2007) and from https://forobs.jrc.ec.europa.eu/products/glc2000/glc2000.php. Locations of archaeological sites mentioned in the text also shown: 1. Niah cave in Borneo (Barker et al., 2007); 2. Lida Ajer cave in Sumatra (Westaway et al., 2017); 3. Moh kiew cave in the Malay Peninsula (Matsumura and Pookajorn, 2005); 4. Tabon cave in Palawan (Détroit et al., 2004). Purple dots represent palynological records; Orange dots represent geochemical records. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3. Material and methods

3.1. Material

Gravity core CB19 (114.6°E, 7.7°N, a total length of 342 cm) was recovered during the SCS Survey Cruise with R/V KE XUE YI HAO belonging to the Institute of Oceanology, Chinese Academy of Sciences in 2012. The coring site was located on the continental slope at a water depth of 1798 m, about 230 km from the north coast of Borneo, and could maintain a distance of ~150 km offshore when the LGM sea level drops to −120 m, thus maintaining the marine sedimentary facies. In addition, the core CB19 is closest to Borneo and has a narrow continental shelf compared to other marine pollen site from the southern SCS (Fig. 1), so the CB19 pollen sequence is relatively less affected by sea-level changes. The lithology of core CB19 was divided into four sections without obvious bioturbation: 0–18 cm brown-dark brown silty clay; 18–80 cm light yellow-brown clay; 80–140 cm gray-brown silty clay; 140–342 cm gray clay (Fig. 2). The sediment core was sampled at 2 cm intervals and measured at 4 cm intervals for palynological analysis of 86 sediment samples.

3.2. Chronological framework

The chronostratigraphic framework of core CB19 was established using accelerator mass spectrometry (AMS) ^{14}C-dating method (Table 1). More than 8 mg of well-preserved planktonic foraminifera of seven horizons in core CB19 were picked for AMS ^{14}C dating at the Woods Hole Oceanographic Institute and Beta laboratory, respectively. The seven AMS ^{14}C data were calibrated to calendar years before present (calendar year BP) using the Bayesian age-depth model (Fig. 2). The Bayesian age-depth model implemented in R version 3.6.1 with a Bacon age modeling (Blaauw and Christen, 2011) and the updated age calibration curve of Marine 20 (0–55,000 cal year) (Heaton et al., 2020) without a further adjustment for a regional ^{14}C reservoir age (ΔR = deviation from the average global reservoir age of 400 years). The investigated interval of the studied core has a basal age of 39 ka. In this study, we mainly focused on the lower section of core CB19 sediments spanning from 11 ka to 39 ka (core length from 86 cm to 342 cm; 256 cm long) to determine the vegetation changes on Borneo based on palynological records.

The sedimentation rates (cm/kyr) (named accumulation rate parameter in Bacon software) in core CB19 were also outputted by

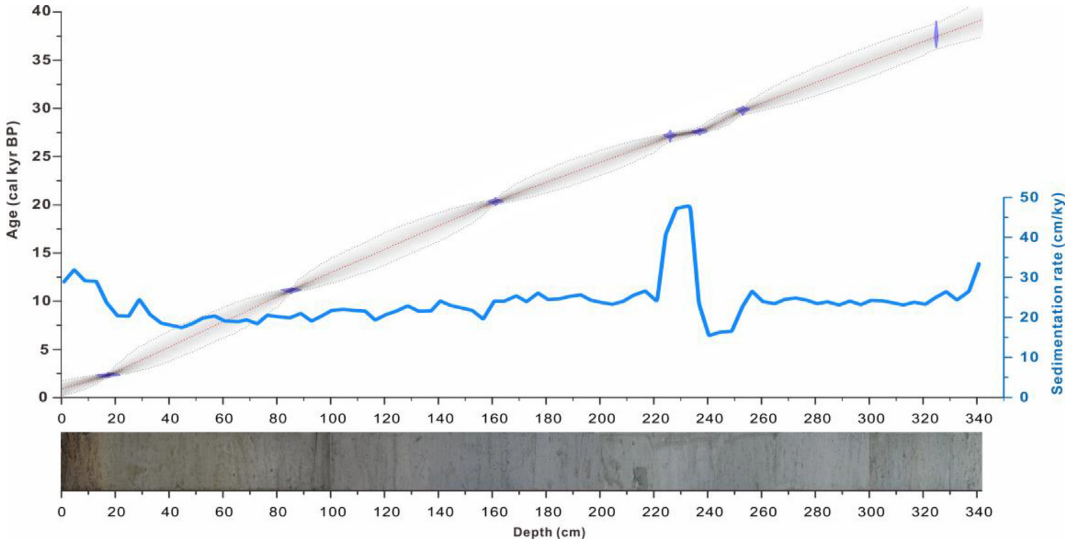

Fig. 2. Age-depth model, sedimentation rate, and core image of core CB19. The age depth relationship was calculated with the Bayesian statistic by using the Bacon age-modeling (Blaauw and Christen, 2011) overlying the distributions of the individual dates (blue). Line curve shows the best model (red line: mean), area between blue lines indicate chronological uncertainties (the model's 95 % probability interval). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
AMS^{14}C and calendar year ages of core CB19 from the Southern South China Sea.

Sample depth (cm)	Foraminifera species	AMS^{14}C age (yr B.P.)	Calendar age (cal yr B.P.)
16–18	Mixed planktonic foraminifera	3060 ± 20	2819 (2751–2894)
84–86	*Neogloboquadrina dutertrei*	10480 ± 30	11079 (10967–11190)
160–162	*Neogloboquadrina dutertrei*	17890 ± 50	20617 (20433–20800)
224–228	Mixed planktonic foraminifera	24100 ± 140	27531 (27305–27757)
236–238	*Neogloboquadrina dutertrei*	24550 ± 80	27811 (27642–27980)
252–254	*Neogloboquadrina dutertrei*	26740 ± 100	30297 (29884–30709)
322–328	Mixed planktonic foraminifera	34000 ± 450	37398 (36283–38513)

the R script Bacon software (Blaauw and Christen, 2011). The maximum sedimentation rate was observed during 27–28 ka with an average of 48 cm/ky, and the minimum value was observed during 28.5–29.5 ka with an average of 16 cm/ky. The average sedimentation rate for the core CB19 was 24 cm/ky.

3.3. Palynological analysis

All samples were prepared in the Key Laboratory of Marine Geology and Environment, Institute of Oceanology, Chinese Academy of Sciences. A Lycopodium tablet containing 20,848 ± 3457 spores (Lund University, Batch No. 1031) was added to each sample before the chemical treatments were conducted to calculate the pollen concentration (grains/g). Hydrochloric and hydrofluoric acids were used to remove carbonates and silicates, and then the residues were sieved over a 10 μm mesh screen in an ultrasonic water bath to remove the impurities. Pollen grains and spores were counted under a Leica DMLB2 light microscope. Usually, at least 300 terrestrial palynomorphs were counted for each sample. Trees, herbs, and fern spores were included in the pollen sum and pollen taxa, and relative abundance were calculated on this basis. The TILIA 2.0 and CorelDraw 18.0 software programs were used to plot pollen diagrams. Additionally, pollen zones were based on the results of constrained cluster analysis (CONISS) (Grimm, 1987).

3.4. Acquisition of records of ancient human colonization and genotype divergence

In this study, we use archaeological and human molecular biology records to reconstruct the colonization history and genotype divergence of ancient humans in this region. Archaeological records are mainly from caves on the Southeast Asian islands. Furthermore, the divergence data of human genotypes are mainly derived from maternally inherited mtDNA. The coding of mtDNA from the genetic heritage of modern populations is a powerful tool for tracing the origins and dispersal of *Homo sapiens* in the Late Pleistocene (Rabett, 2012). The use of mtDNA in archaeogenetics can make use of molecular clock to estimate the age of different clades, which is helpful to determine the factors causing the changes in the human gene pool (Soares et al., 2009). By consulting the human genome studies that overlap our study area, we selected the most common and most diverse native island Southeast Asia haplogroup E among the numerous mtDNA haplogroups as an important comparative study object. Haplogroup E likely evolved from haplogroup M9, ~35,000 years ago (Soares et al., 2008) and was almost entirely restricted to eastern Sundaland for evolution in situ, resulting in a particularly clear and highly informative distribution (Hill et al., 2007). Therefore, haplogroup E is important for the investigation of the features of human prehistory in this region. Its coalescence age is estimated to be ~27.4 ka, and its branches are

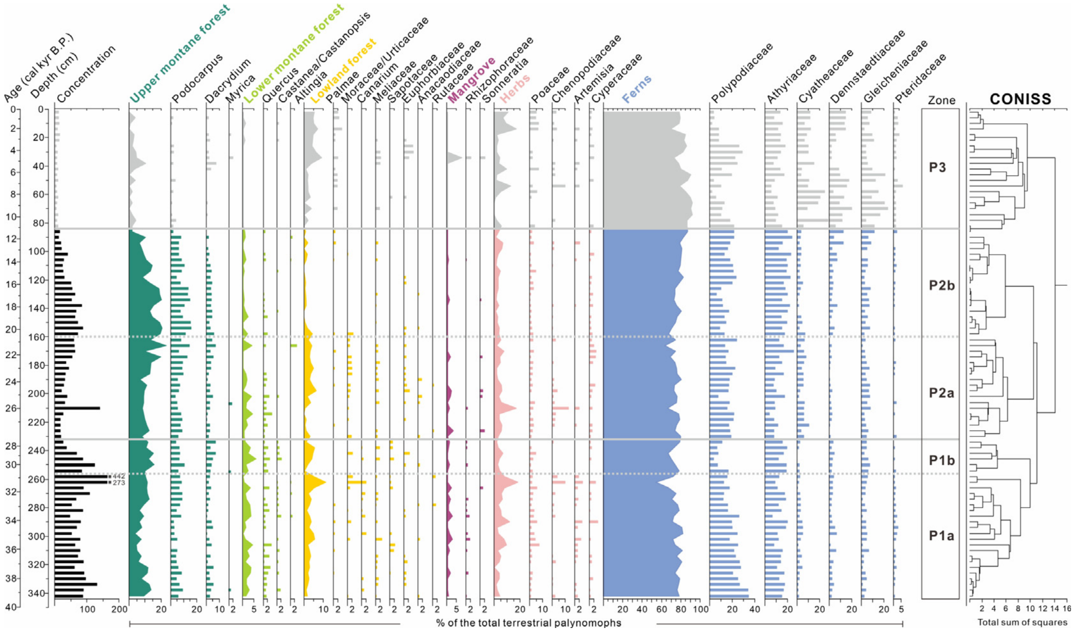

Fig. 3. Pollen percentages of selected taxa from core CB19 Pollen assemblage zones were derived by CONISS (Grimm, 1987).

estimated to be 14 ka for E1 and 9.9 ka for E2. These are subdivided into sub-plates with specific regional characteristics: E1a and E1b, E2a and E2b.

4. Results

According to palynological studies from surface sediment samples, sediment pollen in the southeastern SCS was mainly from the adjacent Borneo and was dispersed by high-gradient rivers (Luo et al., 2016; Sun et al., 1999). Also, considering the sea level drop of 120 m during the LGM, the distance between the core site of CB19 and the Borneo is much smaller than its distance from the broad Sunda shelf in the west (Fig. 1). Consequently, it is most reasonable to infer that the pollen sequence of core CB19 mainly records the vegetation changes in Borneo.

In total 116 palynomorphs, including 58 arboreal taxa, 27 herbs, and 31 fern spores, were identified. Unfortunately, due to the low concentration of pollen, the sediments in the upper layer (0–84 cm) of the core CB19, did not yield the quantity of palynomorphs in accordance with the statistical standards (300 grains), so the samples could not be used for analysis, and marked with gray to show the difference (Fig. 3).

4.1. Palynological zonation results

Several taxa groups were obtained based on the different ecological characteristics (Bush et al., 2011; Wang et al., 2009). The tropical upper montane forests group mainly included *Podocarpus*, *Dacrydium*, and *Myrica* pollen, whereas the tropical lower montane forests group included *Quercus*, *Castanea/Castanopsis*, and *Altingia*. Furthermore, the tropical lowland rainforests group included *Palmae*, Moraceae/Urticaceae, *Canarium*, Meliaceae, Sapotaceae, Euphorbiaceae, Anacardiaceae, and Rutaceae. The mangroves were *Rhizophora* and *Sonneratia*, the herb taxa were Poaceae, Chenopodiaceae, *Artemisia*, and Cyperaceae, and the ferns included Polypodiaceae, Athyriaceae, Cyatheaceae, Dennstaedtiaceae, Gleicheniaceae, and Pteridaceae (Fig. 4). *Pinus* can be considered to be an exotic taxon in the tropics (Moss et al., 2005; Poliakova et al., 2014). Therefore, *Pinus* is regarded as a separate taxonomic unit in this study.

Finally, the pollen diagram can be divided into 3 zones based on the results of the depth-constrained cluster analysis obtained via the sum-of-squares method using CONISS for TILIA and the pollen percentages of major taxa. The two zones at the bottom were further divided into subzone to facilitate interpretation (Fig. 3).

4.1.1. Subzone P1a (342-258 cm, 39–30.6 ka)

The pollen of trees in this zone is dominated by upper montane forests (~8.3 %), mainly composed of *Podocarpus* and *Dacrydium*, whereas lowland forest reaches maximum values of ~3.5 %, mainly consisting of Moraceae/Urticaceae, Meliaceae, and Sapotaceae. Mangrove pollen frequently presents in this zone compared to the later zone. Among the herbaceous plants, Poaceae has the highest content, with an average of 2.4 %. Polypodiaceae (~21 %) and Athyriaceae (~14 %) are the dominant spores amongst Cyatheaceae, Dennstaedtiaceae, Gleicheniaceae, and Pteridaceae that participate in low values. The pollen concentration in this zone is relatively high with an average of 104 grains/g.

4.1.2. Subzone P1b (258-234 cm, 30.6–27.5 ka)

High abundance of upper montane forests (~12 %) mark the pollen assemblages. *Podocarpus* is stable at a high value, while the percentage of *Dacrydium* steadily increases. The tropical lower montane forests and lowland rainforests change synchronously, both of them declined rapidly in the latter half zone. Herbs percentage shows a considerable drop (3 %), only Poaceae (~2.2 %) remains relatively stable. Pteridophyte spore remains stable, as the increase of Athyriaceae (~17 %) compensates for the decrease of Polypodiaceae (8 %). Pollen concentration is considerably dropped, with an average of 71 grains/g.

4.1.3. Subzone P2a (234-162 cm, 27.5–20.6 ka)

The most prominent characteristic of this zone is the abrupt increase trend of upper montane taxa, reaching a maximum

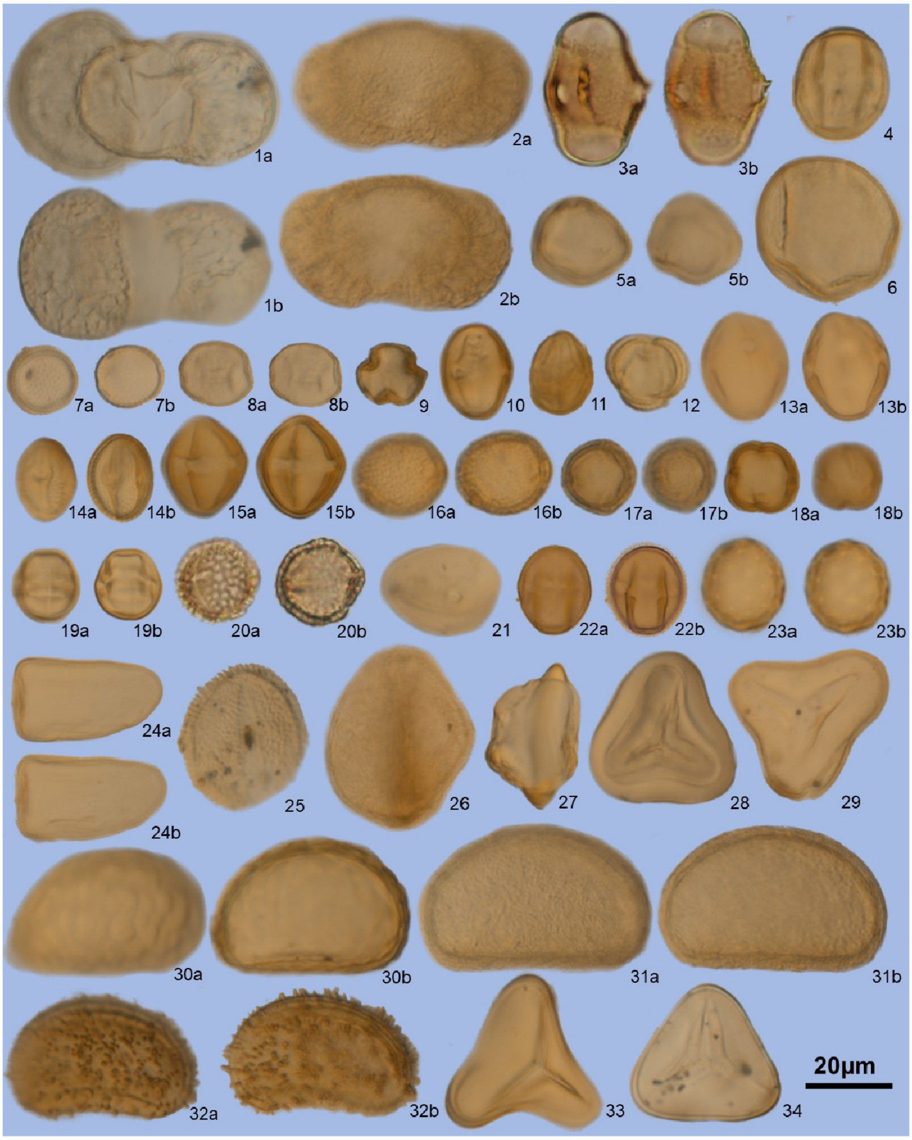

Fig. 4. Representative photographs of palynological grains from the core CB19. Scale bar = 20 μm. 1: *Podocarpus*; 2: *Dacrydium*; 3: *Sonneratia*; 4,6: *Quercus*; 5: *Myrica*; 7–8: Moraceae/Urticaceae; 9–10: Euphorbiaceae; 11,22: *Castanea/Castanopsis*; 12: *Artemisia*; 13–14: Meliaceae; 15,19: Rhizophoraceae; 16–17: Anacardiaceae; 18: Sapotaceae; 20: Rutaceae; 21: Poaceae; 23: Chenopodiaceae; 24: Cyperaceae; 25–26: Palmae; 27–28: Pteridaceae; 29: Dennstaedtiaceae; 30–31: Polypodiaceae; 32: Athyriaceae; 33: Cyatheaceae; 34: Gleicheniaceae.

abundance of 22 %, compared to 8 % at the beginning of this zone. *Dacrydium*, one of the main components of upper montane taxa, reaches maximum values of 7.2 %. The lowland rainforests increase in the latter part of the zone, and mainly contribute by Moraceae/Urticaceae, Meliaceae, and Euphorbiaceae. On the contrary, the content of lower montane taxa represented by *Quercus* declines gradually. Mangrove pollen appeared more frequently than in the previous zone. Chenopodiaceae rises sharply peaking at 12 % at the top of this zone, while a continuous curve of Poaceae (~2 %) is noticed. The abundance of fern spores in this zone maintains a high level. The pollen concentration (41 grains/g) displays a moderate increase except for one layer.

4.1.4. Subzone P2b (162-86 cm, 20.6–11 ka)

Overall, the pollen assemblages are characterized by a major decline of upper montane forests (mainly *Podocarpus*) at the beginning of the zone whereas they present two abrupt increases thereafter. The abundance of lower montane and lowland taxa exhibits a pronounced decrease, with *Canarium* and Rutaceae missing in this zone. Herbaceous groups are relatively stable, mainly composed of Poaceae and Cyperaceae. Polypodiaceae, Dennstaedtiaceae, and Gleicheniaceae, as the main representatives of pteridophytes, display a gradual increase. The average pollen concentration is 16 grains/g.

4.1.5. Zone P3 (86-0 cm, 11–0 ka)

The most prominent characteristic of this zone is the dominance of fern spores, reaching the maximum abundance of 98 %, and oscillating decline thereafter. The upper montane and lower montane forest taxa exhibit a pronounced decrease, *Dacrydium* has a small peak enhancement in the latter half zone, while the lower montane taxa have almost disappeared. Mangrove pollen only presents in one layer. The herbaceous vegetation represented by Poaceae increased significantly in the latter part, reaching the highest value (6.8 %) in this column. The pollen concentration drops to the lowest in the whole profile.

5. Discussions

Human migration in this region was likely related to the type and distribution of vegetation. During the middle Pleistocene, the exposed Sunda shelf was covered with savannas, which was conducive to human and megafauna migrations. But when the vegetation shifted to tropical lowland rainforests, the dense forests not only blocked hominid migration, but may even lead to the extinction of hominids (*Homo erectus*). After ancient humans colonized tropical islands, the impact of vegetation changes on human survival remains unclear especially in the context of climate change. Below we discuss the relationships between vegetation changes in northern Borneo as reflected in our reconstructed pollen record from the southern part of the South China Sea, and climate variability during the past 40,000 years.

5.1. Vegetation history and climatic implications

Based on the temporal variations of pollen assemblage characteristics in core CB19, the vegetation evolution in Borneo can be divided into two stages, which are roughly coincident with marine isotope stages, MIS 3 and MIS 2.

5.1.1. Vegetation during the MIS 3 in the northeast Borneo (P1)

The pollen assemblages of P1 (Fig. 3; 39–27.5 ka) demonstrate the stable altitudinal sequences of forest in the northeast Borneo for this interval, except for the upper montane taxa increased in zone P1b and the beginning of P1a. The vertical pattern of the forest, from high altitude to low altitude, followed by upper montane, lower montane, and lowland forests, resembles the modern transect analysis in Mount Kinabalu (Kitayama, 1992). Although the taxa of upper montane forests decline slightly in the middle of zone P1a, it still dominates the forest taxa, reflecting cool temperatures. Pollen records at Kelabit Highlands in Borneo suggest that during 47–30 ka, the upper-montane taxa were much more abundant than during the Holocene, indicating significantly colder in temperature (Jones et al., 2014). Zone P1b and the beginning of P1a display fluctuation of vegetation, which is characterized by the increase in the upper montane forest species of *Podocarpus* and *Dacrydium*, thus indicating a decrease in temperature. In palynology records from exposure in the Niah cave, *Podocarpus* makes up over half the pollen at 40 ka, suggesting the vegetation zones shifted downward by ~1400 m (Hunt et al., 2012). As discussed below, these rapid changes in vegetation may be the response to the cold events at high latitudes in the northern hemisphere. It is noteworthy that during the P1b interval, the upper montane forest increased simultaneously with lowland and lower montane forests, which may be related to the decrease of sea level (Fig. 3). Because the sea level dropped rapidly around 30 ka (Lambeck et al., 2014), the continental shelf was exposed, providing space for the settlement of lowland rainforest. Then, the rapid decrease of lowland and low montane groups suggested that the effect of temperature decrease on the distribution of vegetation exceeded the living space expansion.

The abundance of fern spores at the P1 interval, with a slight downward trend (the most obvious in Polypodiaceae), but still maintains a high content, suggesting humid conditions in Borneo at MIS 3. Similar fern content is also documented in other nearby marine pollen records during the same period, indicating a strong summer monsoon (Luo et al., 2019). Pollen and spore grains in humid tropical areas are mostly river-borne (Dupont and Wyputta, 2003), and the relatively high pollen concentration in P1 during this period may indicate higher river runoff. A latitudinal transect of speleothem oxygen isotope records shows that atmospheric convection in the heart of the Maritime continent region was reduced from ~40 ka, but remained wet at late MIS 3 (Krause et al., 2019). The stable carbon isotope composition of ancient cave guano profiles from caves on peninsular Malaysia, Palawan, and Borneo suggest the rainforest was maintained on the tropical islands during late MIS 3, supporting the humid environment of the Maritime continent area (Wurster et al., 2010).

In general, except for the changes in the vegetation pattern related to the two abrupt cold climate events, during MIS 3 the vertical structure of vegetation in northern Borneo was stable, with low temperature but higher humidity.

5.1.2. Vegetation response to the MIS 2 climate deterioration (P2)

Compared with zone P1, the most prominent features of the pollen assemblage in the middle of zone P2 (Fig. 3; 23–18 ka, LGM) are the expansion of upper montane forests and the collapse of lower montane and lowland forests in northern Borneo, suggesting a further drop in temperature. The substantial contraction of *Quercus*, the main representative of lower montane taxa, along with the decrease of other lowland components, notably Moraceae/Urticaceae, Meliaceae, and Euphorbiaceae, signal the collapse of lower montane and lowland forest at low and medium elevations. Furthermore, the pronounced enhancement of *Podocarpus* and *Dacrydium*, reveals the replacement in lower altitude vegetation in Borneo with upper montane forest, suggesting a significant drop in temperature. This variation of pollen spectra synthesis is in accordance not only with the pollen assemblages of highlands in Borneo (Jones et al., 2014) but also with marine pollen records from the southern SCS (Luo et al., 2019; Sun et al., 2000). The expansion of upper montane forests has been documented in many pollen archives across Southeast Asia (Maloney and McCormac, 1995; Stuijts et al., 1988), and is mostly associated with the LGM (van der Kaars and Dam, 1997).

In contrast to the dramatic change of arboreal pollen during MIS 2, herbs remained at a low level, indicating that the climate change inadequately generated more open vegetation in northern Borneo. The high Pteridophyte content in this period also indicates that the precipitation did not decrease significantly. Other pollen records on land and offshore of Borneo suggest that the decline in precipitation was insufficient to open the forest canopy, therefore the rainforest vegetation persisted on Borneo during the LGM (Anshari et al., 2004; Luo et al., 2019). However, records of other tropical islands during the same interval suggest the expansion of open vegetation associated with the decline of precipitation. The results of the stable isotopic composition of vascular plant fatty acids from a core on the coast of Sumba indicate an expansion of C4 herbs during the LGM (Dubois et al., 2014). The stable carbon isotope records exhibited a substantial forest contraction during the LGM on both peninsular Malaysia and Palawan (Wurster et al., 2010), reflecting the decline in precipitation. Nevertheless, the paleoclimate proxies from the Borneo showed a consistent relatively humid climate during the LGM (Carolin et al., 2013; Dubois et al., 2014; Partin et al., 2007; Wurster et al., 2010). Meanwhile, most modeling studies show Borneo and most of the exposed Sunda Shelf were covered by rainforest during the LGM (Cannon et al., 2009; Prentice et al., 2011; Raes et al., 2014), which was confirmed by palynological records from offshore Borneo (Wang et al., 2009; Yang et al., 2020). The difference in the temporal evolution of paleoclimate data at different has been attributed to the variable modulation of the seasonal precipitation cycle in each region by orbital forcing (Tierney et al., 2012). In addition, tropical rainforests in Southeast Asia, as the ecologically sensitive areas, amplify their response to climate change, and are highly sensitive to changes in temperature and cloudiness, whereas they are less sensitive to precipitation (Seddon et al., 2016).

Interestingly, there is a mismatch between the LGM cooling from Borneo (7–9 °C) (Hunt et al., 2012) and the southern SCS (4 °C) (Zhao et al., 2006). This mismatch is due to the steeper temperature lapse rate in the tropics during the LGM (Loomis et al., 2017). During the last glacial period, a steeper lapse rate makes vegetation in the tropics more susceptible to temperature changes, especially in the montane areas, as cooling is amplified with increasing elevation. Moreover, the mean SST in the tropics strongly influences the lapse rate (Soden and Held, 2006), especially in the tropical western Pacific (Loomis et al., 2017). This suggests that small decreases in SST may trigger larger cooling at higher elevations and the corresponding expansion of upper montane vegetation.

In the late period of zone P2 (18–11 ka), the content of fern spores gradually increased along with the decrease of upper montane taxa, implying that the climate changed to warmer and wetter during the last deglacial compared with LGM. Meanwhile, the decline of mangrove pollen, especially in P2b, indicates the rapid rise of sea level during the deglaciation, which could have destroyed mangrove habitats. In addition, the presence of two abrupt high value of upper montane taxa at the end of P2 may indicate two abrupt re-cooling events during the last deglacial warming, correlating with the Heinrich event (Heinrich, 1988), recorded in several sites from the southern SCS (Luo et al., 2019; Yang et al., 2020). With the rapid increase in sea level during the last glacial period, the replacement of lower altitudes forest by upper montane taxa could have been more severe than that during the LGM. It should be pointed out that our study uses a 10 μm mesh screen, which may miss smaller pollen grain (such as *Ficus*), thereby overestimating the degree of compression in lowland forest.

Overall, the climate deterioration in MIS 2 causes the instability of the vegetation pattern. During the LGM, the lower montane and lowland forests were mostly replaced by upper montane forests. The two abrupt increases of upper montane taxa at the end of P2b, likely reflect the response to the northern high latitude cold events, leading to further expansion of the upper montane forest during the last deglacial warming.

5.2. Responses of upper montane group to cold events at northern high latitudes

During the late Pleistocene, there were five times of vegetation expansion of upper montane taxa represented by *Podocarpus* and *Dacrydium*, which recorded the rapid oscillation of environmental conditions in the southern South China Sea. As mentioned above, the upper montane forest in Borneo up to 1500 m, mainly composed of gymnosperms such as *Podocarpus* and *Dacrydium* (Bush et al., 2011). These upper montane taxa usually indicate relatively cold environmental conditions (Jones et al., 2014; Turney et al., 2006; van der Kaars et al., 2010), and can migrate to lower altitude when the climate becomes colder (Hunt et al., 2012; van der Kaars et al., 2000, 2012).

The high content of repeated upper montane pollen in core CB19 apparently corresponds to Heinrich events (H0 – H4) indicated by the Greenland ice core oxygen isotope data (Rasmussen et al., 2006; Stuiver and Grootes, 2000). During the cold stadials, the relative content of pollen in the upper montane forest increased by 6–12 %, indicating that the vegetation response to the millennial-scale climate cooling in the southern SCS is represented by the downward expansion of upper montane elements with *Podocarpus* and *Dacrydium* as the main components (Fig. 5). Pollen records from the Niah cave in Borneo show that during the stadial, the elevation of vegetation zones was depressed by up to 1400 m relative to their modern positions, indicating a decrease in temperature of 7–9 °C compared with present (Hunt et al., 2012). In Sumatra, the expansion of *Dacrydium* and *Vaccinium* during the glacial stage reflects the characteristics of lower temperature and a more arid environment (Maloney, 1995). The marine pollen diagram from the Core 17964 in the southern South China Sea, showing alternating predominance between upper montane forest and lowland rain forest, is possibly attributable to Heinrich events (Sun and Li, 1999). These cold events reported in tropical marine records (Fraser et al., 2014; Jian et al., 2020; Zhao et al., 2006) have also been recorded on land in other tropical regions. Pollen sequences in southern Brazil (Ledru et al., 2009) and Central Africa (Bonnefille and Riollet, 1988) also record the rapid evolution of vegetation at the millennial-scale, marked by the increase of *Podocarpus*. In addition, tropical vegetation responds significantly to cold events (e.g. Heinrich events) but not to warming events (e.g. D-O warming events), implying that tropical vegetation tends to maintain the impact of cold events and improving the resolution of cold events (Harrison and Sanchez Goñi, 2010). As a cooling index, *Podocarpus* shows a wide range of expansions during millennial-scale cooling periods, which reflect the rapid response of vegetation to climate change. The results of these pollen data also indicate that the relative content of the upper montane components (dominated by *Podocarpus*) can be used as an effective indicator of climate change in the tropical region on a millennial-scale.

Marine records in the tropical region also document an abrupt drop in sea surface temperature (SST), which was smaller than that on land due to a possible steeper mean atmospheric lapse rate at that time (De Deckker et al., 2003; Loomis et al., 2017). UK'37 derived sea surface temperature (SST) records from the western equatorial Pacific, including the southern SCS (Zhao et al., 2006), the Western Pacific warm pool (Fraser et al., 2014; Jian et al., 2020), and from the western tropical Atlantic (Jaeschke et al., 2007; Rama-Corredor et al., 2015), exhibit millennial-scale SST variations. These records show that during the cold events at high latitudes in the northern hemisphere, SST in the tropics decreases correspondingly.

It is important to note that there is a lower abundance interval in the generally high content of upper montane taxa during the LGM (P2b), presenting in two peaks. This upward retracement of upper montane forest in the Borneo around 20 ka is probably caused by a slight increase in SST (Zhao et al., 2006). As SST in the tropics strongly impacts on the lapse rate (Soden and Held, 2006), and the lapse rate is particularly sensitive to SST changes in the tropical Western Pacific (Loomis et al., 2017). A shoaling of the Lapse rate caused by a slight SST increase will then amplify the warming in the high-altitude areas. Thus, an increase in SST around 20 ka would lead to an upward contraction of the upper montane rainforest.

In addition, records from the tropical western Pacific, suggest that regional convection likely decreased coeval with Heinrich events (Carolin et al., 2013; Partin et al., 2007; Russell et al., 2014). However, a latitudinal transect of atmospheric convection and precipitation records across the Marine continent shows that the latitudinal response to millennial-scale climate forcing decreases toward the western equatorial Pacific, where Borneo is located (Krause et al., 2019). This also enabled Borneo to maintain the tropical rainforests during the last glacial period compared with other tropical islands (Raes et al., 2014; Wurster et al., 2010). Moreover, tropical rainforests in Southeast Asia are strongly sensitive to changes in temperature and cloudiness, and less sensitive to precipitation (Seddon et al., 2016). These indicate that rainfall decline in response to the Heinrich event is not capable of changing vegetation in Borneo compared with the decrease in temperature.

By comparing with the Greenland ice core record, we find that the peak of upper montane pollen recorded by core CB19 lags by 500–1000 years the ice core record, indicating that it takes roughly millennium for upper montane vegetation to expand downward. It should be noted that the sparse dating controls and dating uncertainties may contribute partly to the lag time interval. In tropical

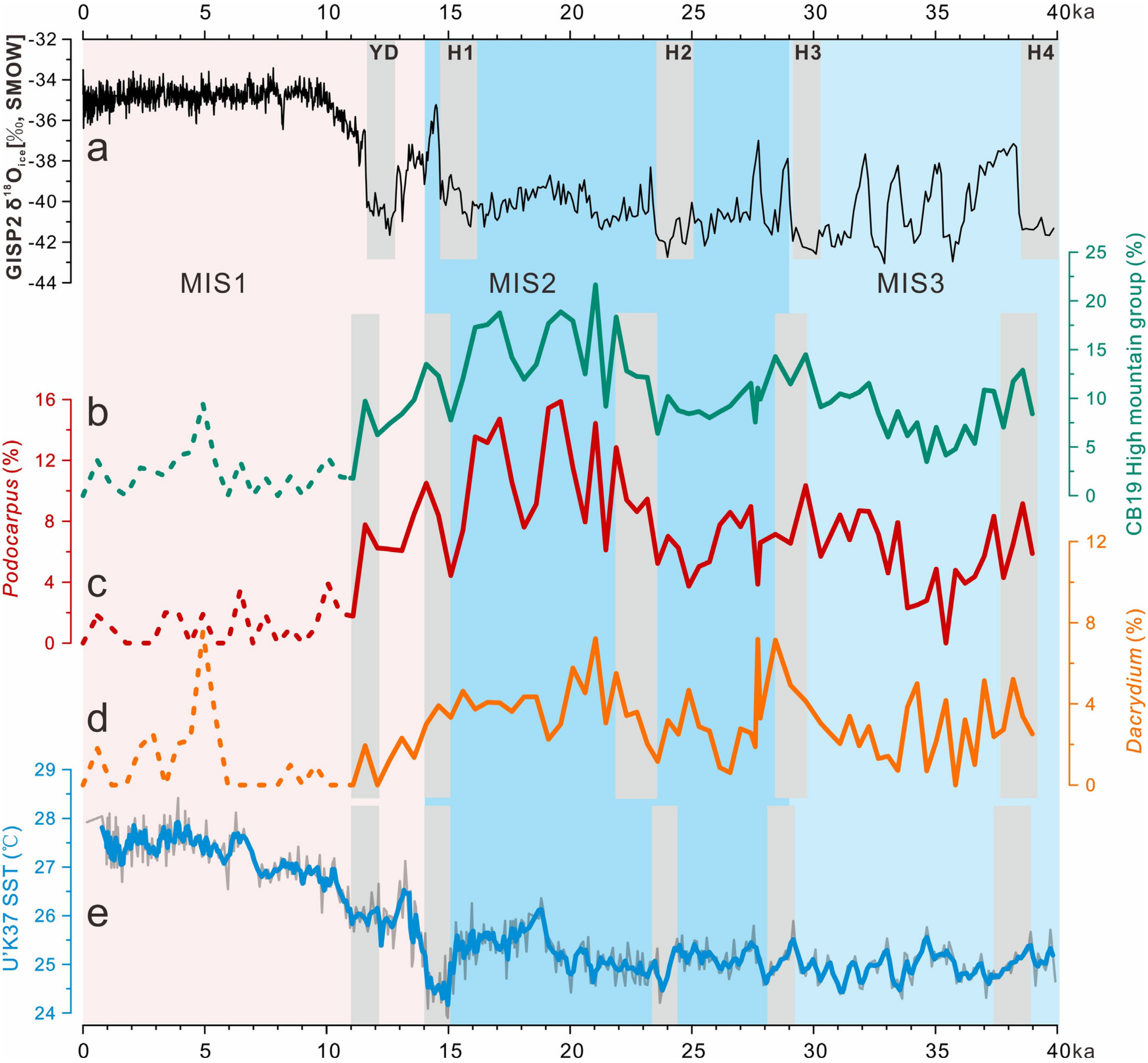

Fig. 5. Comparison of cold event proxy records in core CB19 with other climate records. a GISP2 $\delta^{18}O_{ice}$ (Rasmussen et al., 2006; Stuiver and Grootes, 2000); b Upper montane group abundance of core CB19 (this study); c *Podocarpus* pollen abundance of core CB19 (this study); d *Dacrydium* pollen abundance of core CB19 (this study). e UK'37SST record of core MD97-2151 in the southern SCS (Zhao et al., 2006). Vertical gray bars indicate the YD and Hinrich events H1 to H4. The shades of pink, blue and light blue represent MIS, MIS2 and MIS3, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

South America, Lynch's Crater Deposit records suggest that the response time of vegetation to climate change is ~1 ky (Muller et al., 2008). Furthermore, the pollen data from a varve sediment core in Lake Suigetsu in Japan suggests that the onset of the cold reversal interval lagged that of the North Atlantic by several centuries (Nakagawa et al., 2005).

5.3. The coupling of vegetation succession to Homo sapiens genotype diversity

The use of mtDNA in archaeogenetics has proven to be a powerful tool for effectively tracing the origin and spread of *Homo sapiens* through the genetic heritage of modern populations, especially in the absence of an archaeological record (Rabett, 2012). The high-resolution mtDNA evidence from Europe has revealed that climate change during the LGM had an important impact on human genetic diversity in western Europe (Pereira et al., 2005; Torroni et al., 2001). This severe climatic stage drove modern human contraction to southern refuges (Posth et al., 2016), causing humans to experience genetic bottlenecks and population declines (Stewart et al., 2010; Willis et al., 2004). The sea level rise caused by global warming during the last deglaciation had an equally profound effect on the modern humans who settled in Southeast Asia (Hill et al., 2007; Karafet et al., 2010). By plotting the sequence of mtDNA genomes from autochthonous haplogroups, it was found that rapid coastal transformation and resulting land-loss probably shaped much of the genetic structure of Southeast Asian islands (Hill et al., 2007; Soares et al., 2008, 2011). Thus, combining climate change with archaeogenetics will provide a rarely explored perspective for investigating human prehistory.

During the Late Pleistocene, the most active period of hominin dispersal, the Southeast Asia islands, as the hub area for ancient human expansion (Yew et al., 2018), not only experienced drastic changes in sea level, but the type and distribution of vegetation on them have also fluctuated dramatically (Cannon et al., 2009). During this period, the savannah retreated on Sundaland and was replaced by a highly stratified closed-canopy rainforest. The expansion of the rainforest led to the disappearance of the land corridor between Asia, Indonesia, and Borneo, but also altered the original fauna and even induced the extinction of *Homo erectus* (Louys and Roberts, 2020). *Homo sapiens* with unique adaptability and plasticity can adapt to the rainforest environment and migrate to the lowland rainforests of Southeast Asia during the Late Pleistocene (Louys and Roberts, 2020). This is reflected in the archaeological sites of *Homo sapiens* in Southeast Asia, which are all related to the existence of tropical lowland forests (Barker et al., 2007; Westaway et al., 2017). Records from Sri Lanka show that *Homo sapiens* fully adapted to the closed rain forest (Roberts et al., 2017). Archaeological archives from Niah Cave in Borneo suggest that *Homo sapiens* used rainforest resources by collecting and processing poisonous plants, hunting wild boars and some arboreal primates, to survive in the lowland rainforest (Barker et al., 2007). In Sumatra, records show that the history of *Homo sapiens* using rainforest resources has been pushed forward to 73 ka (Westaway et al., 2017). This suggests that the settlement of *Homo sapiens* in Southeast Asia could not be dissociated from the adaptation to the rainforest environment and the utilization of rainforest resources. Unfortunately, there is scarce research on the relationship between the prehistory of hominin and vegetation changes.

Haplogroup E, an important component of mtDNA diversity in the Southeast Asia islands (Hill et al., 2007), probably evolved within the descendants of the first settlers (they arrived carrying haplogroup M at ~50 ka) of Sundaland (Macaulay et al., 2005). This haplogroup likely evolved from haplogroup M9, ~35,000 years ago (Soares et al., 2008) and was almost entirely restricted to eastern Sundaland for evolution in situ, resulting in a particularly clear and highly informative distribution (Hill et al., 2007). Furthermore, all subclades of haplogroup E are present in Borneo, which suggests that the location of mutations arose for haplogroup E is most likely to be in the vicinity of northeast Sundaland (Soares et al., 2008). Therefore, haplogroup E is important for the investigation of the features of human prehistory in this region.

According to the study of the mtDNA molecular clock, the divergence time of haplogroup E is 27.4 ka (Soares et al., 2009). In addition to haplogroup E, other mtDNA haplogroups (haplogroup F1a and haplogroup B4a) settled in Southeast Asian islands also diverged at approximately a similar time (Hill et al., 2007; Soares et al., 2009, 2011), possibly leading to a decline in population size. Although the age estimates of haplogroup E divergence present large confidence intervals, it is unlikely that haplogroup E diverged later than the onset of the last deglaciation, since all of the age estimates of clades are in the last deglaciation (Soares et al., 2009). In addition, the phylogeographic inferences from haplogroups and populations survey suggest that climate change may have had an important impact on the human diversity in the Southeast Asian islands and led to an overall population decline during the LGM (Karafet et al., 2010; Pope and Terrell, 2008). Therefore, the most plausible interval for the divergence of haplogroup E is during the LGM.

In this period, the transition from relatively warm MIS 3 to cold MIS 2, the pollen sequence of core CB19 clearly shows a major shift in the vegetation of Borneo, with an expansion of the upper montane forest and a rapid contraction of the lower montane and lowland forests. Similar observations are commonly found in other Southeast Asian islands' pollen records (Hunt et al., 2012; Jones et al., 2014). The biodiversity and animal community structure of tropical rain forests show that with increasing altitudes, the species richness decreases (Willig and Presley, 2016), and also the production of energy and protein decreases significantly (Dwyer, 1983). Therefore, compared with lowland rainforests, upper montane rainforests offer more limited living resources for *Homo sapiens*. In addition, there is an absence of archaeological evidence from Southeast Asia that *Homo sapiens* occupied the upper montane forest areas during the LGM (Barker et al., 2007; Summerhayes et al., 2010; Westaway et al., 2017). We suggest the expansion of Borneo's upper montane forest during LGM may have restricted the living habitat (lowland rainforest) of the *Homo sapiens*, which may increase the survival pressure on them and may lead to a decrease in the population size. This hypothesis is supported by population change trends in Southeast and East Asia inferred from cumulative bayesian skyline plots of mtDNA diversity in Southeast & East Asia, with a clear decrease in population size around 30 ka (Karmin et al., 2015) (Fig. 6).

It is worth noting that during this period, the global sea level has dropped significantly, which is conducive to the expansion of lowland rain forests in the exposed continental shelf area (Cannon et al., 2009). The pollen spectra of CB19 also show the simultaneous increase of lowland and lower montane rainforest (Fig. 3). However, the subsequent rapid decline of lowland and lower montane groups and the stable high abundance of upper montane forest define the altitude distribution structure of Borneo vegetation in the MIS 2 (Fig. 6 d3). It may reasonably infer that the expansion of upper montane forest to low altitudes deprived the habitat of hominin and shaped the hominin diversity in the region. During the same period, European mtDNA haplogroups V and H possessed similar responses to climate change (Pereira et al., 2005; Torroni et al., 2001). The severe glacial climate propelled early Europeans carrying these haplogroups into southern refuges and altered the composition of human genetic diversity in Western Europe (Posth et al., 2016).

Similar climatic influences on human haplogroup diversity also occurred during the last deglaciation. Several studies have shown that sea-level rise may have profoundly altered the genetic structure of Southeast Asian islands and are the main driving force shaping modern human diversity in the region (Hill et al., 2007; Karafet et al., 2010; Soares et al., 2008, 2011). Sea level rise during the last deglacial halved the land area of Sundaland and doubled the coastline (Bird et al., 2005). In addition, there were two large-scale melt-water pulses during the sea level rise during the last deglaciation (Lambeck et al., 2014), which may have a catastrophic impact on the human population (Pope and Terrell, 2008; Soares et al., 2008). Rapid sea-level rise triggered largely autochthonous dispersals (Soares et al., 2016), and may have promoted the development of sailing technology (Soares et al., 2008).

Here, we want to highlight the contribution of vegetation change to hominin genetic divergence during rapid sea level rise. The comparison revealed that haplogroup E1 and E2 corresponded to lagged vegetation responses to H1 and Younger Dryas (YD) cold events, respectively, in terms of the timing of divergence during the last deglaciation. During the same period, there were two rapid sea level rises due to melt-water pulses, namely MWP-1a and MWP-1b (Lambeck et al., 2014). The rise of sea level destroyed the original low-altitude vegetation, and the downward replacement of upper montane forest caused by the cold events may have combined to increase the pressure on *Homo sapiens* to obtain living resources. It could be inferred that climate-induced changes in vegetation may have influenced the evolution of the modern human gene pool along with sea level changes.

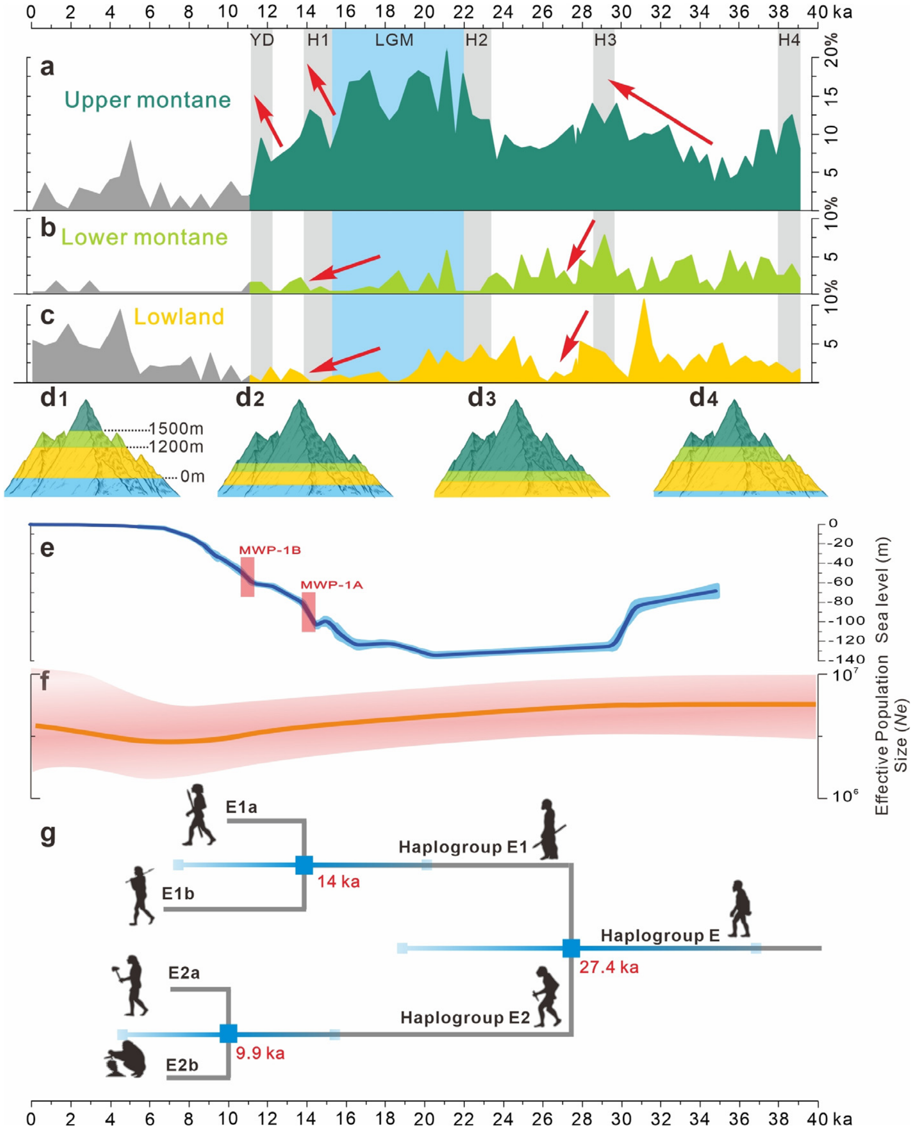

Fig. 6. Comparison of main tropical rainforest groups in core CB19 and haplogroup E phylogeny. an Upper montane taxa abundance of core CB19 (this study); b Lower montane taxa abundance of core CB19 (this study); c Lowland taxa abundance of core CB19 (this study); d Schematic diagram of the vertical structure of Borneo vegetation: d_1 Modern; d_2 The last deglaciation; d_3 The LGM; d_4 MIS 3; e Ice-volume equivalent sea-level (Lambeck et al., 2014); f Bayesian skyline plots of mtDNA in Southeast & East Asia (Karmin et al., 2015); g Simplified mtDNA Haplogroup phylogeny modified from Soares et al. (2009). Age estimates are marked at the nodes. Bars on nodes represent the confidence intervals.

6. Conclusions

The dynamics of vegetation succession in northern Borneo since 40 ka has been reconstructed by the analysis of pollen and spore assemblages in core CB19. The pollen sequence reveals that the vegetation structure of Borneo changed significantly in the late Pleistocene. Compared with the stable vegetation structure of MIS 3, the upper montane forest expanded and compressed the living space of lower montane and lowland forests during MIS 2. These broad temporal patterns of the pollen sequence are also interrupted by five millennial-scale events of high abundance of upper montane forest taxa, which correspond to 5 cold events in the northern high latitudes. The high value of upper montane pollen lags the cold event marked by $\delta^{18}O_{ice}$ by 500−1000 years.

From the comparison of the temporal variations in abundance of upper montane group and haplogroup E phylogeny, we found that the divergence of *Homo sapiens* genotypes is closely related to the vertical migration of vegetation in Borneo. During the LGM, *Homo sapiens*' habitat (lowland rainforest) was under intense pressure from the expansion of the upper montane forest, which also shrank the resources available for *Homo sapiens*, possibly leading to the divergence of haplogroup E. Rapid sea-level rise during the last deglacial period would have been catastrophic for *Homo sapiens*, and the simultaneous occurrence of a lagged vegetation response (lowland rainforest contraction) corresponding to H1 and YD cold events may have enhanced this effect. Our results highlight the impact that climate-induced changes in vegetation can have on the evolution of the modern human gene pool, either alone or in conjunction with sea-level changes.

Author contribution

Yanli Lei, Tiegang Li, and Zhimin Jian conceived of the presented idea and directed the project. Zaibao Yang compiled the data and wrote the paper. Yair Rosenthal directed the writing and helped shape the research and analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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