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A long record of environmental change from bat guano deposits in Makangit Cave, Palawan, Philippines

Michael I. Bird[1], Ella M. Boobyer[1], Charlotte Bryant[2], Helen A. Lewis[3], Victor Paz[4] and W. Edryd Stephens[1]

[1] School of Geography & Geosciences, University of St Andrews, St Andrews Fife KY16 9AL, Scotland, UK. E-mail: michael.bird@st-andrews.ac.uk

[2] NERC Radiocarbon Laboratory, Scottish Enterprise Technology Park, Rankine Avenue, East Kilbride, Glasgow G75 0QF, Scotland, UK.

[3] Institute of Archaeology, University of Oxford, 36 Beaumont Street, Oxford OX2 6LB, UK.

[4] Archaeological Studies Program, Palma Hall Basement, University of the Philippines, Diliman, Quezon City 1101.

ABSTRACT: We present the first record of Holocene and Pleistocene environmental change derived from the chemical and stable-isotope composition of a tropical cave guano sequence from Makangit Cave in northern Palawan (Philippines). The 180 cm sequence of guano, derived predominantly from insectivorous bats and birds, consists of two distinct units. An upper section of reddish-brown oxidised guano to 110 cm was deposited since the mid-Holocene while a lower section of black, reduced guano was deposited through the Last Glacial Maximum (LGM) to >30 000 BP. Carbon-isotope ($\delta^{13}C$) values in guano deposited during the LGM are as high as $-13{\cdot}5$‰ indicating that a C_4-dominated grassland existed in the area around the cave at this time. Guano $\delta^{13}C$ values of -25‰ to -28‰ suggest that this open vegetation was replaced by C_3-dominated closed tropical forest, similar to that of the present, by the mid-Holocene. The results suggest that the climate of northern Palawan was substantially drier at the LGM than is currently the case.

KEY WORDS: carbon-isotope, Holocene, palaeoenvironment, Quaternary, radiocarbon, Sundaland

Palawan is the westernmost island of the Philippines and represents a 'stepping stone' for the dispersal of flora, fauna and humans between the ancient continent of Sundaland to the southwest (comprising much of Malaysia and Indonesia exposed as a single contiguous landmass by lowered sea level during periods of Quaternary glaciation) and the many islands of the Philippine archipelago to the east (Fig. 1). The island occupies an ambiguous geographic and biogeographic position. It is neither 'continental' nor truly 'oceanic' and while Wallace (1860) grouped Palawan with Sundaland and the Philippines into a single biogeographic province, Huxley (1868) grouped Palawan with Sundaland and identified the rest of the Philippine archipelago as a separate biogeographically distinct region with closer affinities to Wallacea.

Prior to recent anthropogenic clearance, most of Palawan was covered by tropical forests. However, its position towards the northern modern latitudinal limit of humid tropical forests means that changes in climate to cooler and drier conditions, such as are thought to have characterised the last glacial maximum (LGM; 18 000 BP), could potentially have led to the replacement of tropical forest by more open vegetation types across much of the island. The palaeoenvironmental and biogeographic history of Palawan over the Quaternary is likely to have been determined by both changing sea level, and hence changing distance to adjacent land masses and continentality, and also by changes in climate leading to potentially large changes in the ecosystems available for exploitation by fauna and humans on the island. Despite the position of Palawan in a region likely to have undergone potentially large changes in environment in the past, there are currently few studies that document terrestrial environmental change on the island, partly due to a paucity of suitable 'traditional' records for palaeoenvironmental reconstruction, such as lakes or swamps.

The existence of numerous limestone caves on the island, many containing thick and ancient deposits of bird and bat guano, does suggest the possibility that long records of environmental change might be obtainable from the guano. Cave guano accumulates from the detritus of bats and birds that roost in large numbers in many tropical caves (note: this is not the lithified phosphatic guano of tropical islands). Guano is carbon- and nitrogen-rich material initially composed of uric acid (birds) or urea (bats) along with the excreted residue of the digestive process, including a large quantity of undigested insect exoskeletal material. In some caves, insect exoskeletons build up a loose 'drift' of fresh guano on the floor of the cave and this layer is home to many detritivores, resulting in its intense bioturbation. Fresh guano in this layer is rapidly degraded (over months) and a fine, earthy residue, containing few macroscopic organic remains, accumulates at the base of the bioturbated fresh material. Over millennia, deposits of guano several metres thick may build up on the cave floor.

Such deposits represent a major and, as yet, completely untapped source of tropical palaeoenvironmental information, although there has been some research on the organic geochemistry of the guano at Carlsbad Cavern in the US (Des Marais *et al.* 1980) and the mineralogy and mechanisms of guano, bone and ash diagenesis in cave archaeological sites around the Mediterranean (e.g. Schiegl *et al.* 1996; Karkanus *et al.* 2002; Weiner *et al.* 2002; Shahack-Gross *et al.* 2004).

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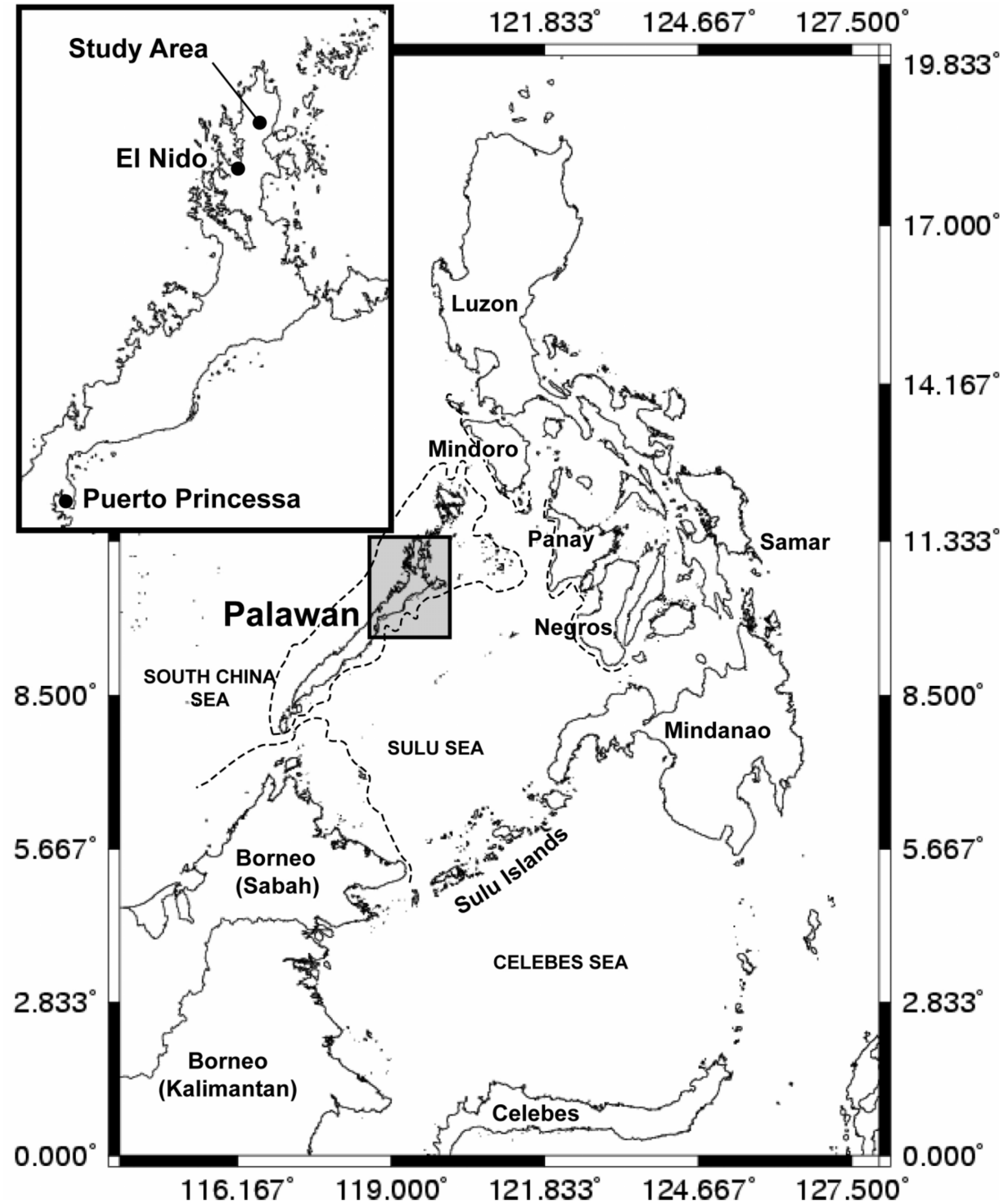

Figure 1 Map showing the location of Palawan, with inset showing the study area in northern Palawan. Dashed line indicates approximate position of the 120m isobath, defining the extent of Greater Palawan and surrounding land masses at the Last Glacial Maximum.

The vast majority of bats and birds that roost in large colonies in tropical caves are insectivorous, and the food chain sustaining the bat and bird population leads ultimately back to the local vegetation. As a result, changes in the stable carbon-isotope ($\delta^{13}C$) composition of a sedimentary sequence of guano can be used to reconstruct past changes in vegetation around the caves. This is because in tropical forests, all plants use the C_3 photosynthetic pathway, with $\delta^{13}C$ controlled largely by the canopy density and water stress. Denser canopies and lower water stress lead to low $\delta^{13}C$ values ($< -27‰$), less dense canopies and higher water stress lead to higher $\delta^{13}C$ values (up to ca. $-25‰$). As rainfall decreases in amount and increases in seasonality, forests give way to more open vegetation characterised by variable proportions of grasses that utilise the C4 pathway, with $\delta^{13}C$ values up to $-12‰$ (see Bird & Pousai 1997 for a review). The $\delta^{15}N$ composition of the guano should provide information on the trophic level at which the guano-producing cave population is feeding (e.g. Hobson & Clark 1992), with a frugivorous population producing guano with a lower $\delta^{15}N$ composition than that of an insectivorous population. In addition, changes in the inorganic elemental composition down through an accumulation of guano should also be interpretable in terms of changing balances between guano accumulation and degradation.

Thus, the parallel analysis of several proxies should enable long, regionally integrated records of past environmental change to be developed from tropical cave guano. This paper represents the first attempt to obtain such a record, and presents the first long record of terrestrial environmental change from Palawan.

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1. Background

1.1. Palaeogeography of Palawan

'Greater Palawan', comprising the main island of Palawan and several smaller islands of the Calamaines Group to the north and east (the largest being Busuanga), represents a single micro-continent rifted from Eurasia around at around 32 Ma. This detached block of dominantly Palaeozoic rocks rafted southeast as sea-floor spreading led to the opening of the modern South China Sea. The northern end of Greater Palawan became an emergent oceanic island at between 5 Ma and 10 Ma, as the micro-continent collided with the northern continental margin of Sundaland. Subsequent deformation led to the uplift of modern Palawan Island above sea-level (Hall 1998, 2001). Palawan Island is divided in the centre by the Sabang Thrust with Carboniferous to Permian metamorphic units and Cretaceous to Eocene sediments north of the thrust, and sedimentary units and ophiolites to the south.

The area of Greater Palawan exposed above sea-level has fluctuated dramatically since the onset of glacial/interglacial Milankovitch cycles during the Quaternary. During interglacial periods of high sea-level, such as today, the main island of Palawan is reduced to a long thin body of land with other scattered smaller islands emergent to the southwest and northeast (e.g. Voris 2000). In detail, the shape and size of emergent areas on greater Palawan are likely to have changed considerably during interglacial periods, due both to ongoing uplift of the area and hydro-isostatic effects of changing water loading in the seas surrounding Palawan (Lambeck & Chappell 2001; Lambeck *et al.* 2002). Maeda *et al.* (2004) mapped widespread wave-cut notches in limestones on the coast of Palawan up to 3 m above modern sea-level and dating from the mid-Holocene; whilst notches dating to the last interglacial ($\sim$120 ka) are now up to 7 m above modern mean sea-level, indicating that some tectonic uplift has occurred since the last interglacial, although the effect of this uplift on the distribution of land and sea has likely been minimal. This suggests that Palawan may have been substantially smaller in the relatively recent past, due to flooding of low-lying coastal areas; but owing to the mountainous spine that runs down the centre of the island, it is unlikely that the main island was fragmented into several smaller islands during the Quaternary.

During glacial periods sea-level was substantially lower than today, and at the last glacial maximum, for example, eustatic sea-level was reduced by $\sim$130 m (Lambeck *et al.* 2002). It is clear that this lowering of sea-level connected the interglacial islands of Greater Palawan into a single landmass, and it is also clear that sea-level has never been low enough to connect greater Palawan to the islands of the main Philippine archipelago.

However, it remains unclear whether greater Palawan has ever been connected by a land bridge to Borneo. Relative sea-level is determined both by global changes in ocean water volume and by local responses to both changes in water loading and tectonism; and therefore, for example, LGM sea-level was only 116 m below modern sea-level on the Sunda Shelf to the west of Palawan (Hanebuth *et al.* 2000). The maximum depth through the Balabac Straits that separate Palawan from Borneo is 145 m, making it unlikely that a connection existed during the LGM, but Rohling *et al.* (1998) have suggested that ice volumes during the glacial period centred on 450 ka may have been $\sim$15% greater than at the LGM and greater than at any time during the last 3 Ma (Lambeck *et al.* 2002). Thus it is possible that a tenuous land bridge may have connected Palawan and Borneo at least once during the Quaternary.

1.2. Biogeography, palaeoenvironment and archaeology of Palawan

Greater Palawan is currently considered a single ecoregion (Wikramanayake *et al.* 2001), with vegetation dominated by lowland evergreen dipterocarp rainforest. The eastern half of the main island is in a rainshadow and hence vegetation grades to moist semi-deciduous forests; specialised forest types occur on limestone and ultramafic substrates and close to the coasts.

Consistent with the location of Palawan, between the continent of Sundaland and the oceanic islands of the Philippines, the fauna of Palawan contains elements drawn from both. A recent survey suggests the main island of Palawan contains 58 species of mammal, of which 13 are endemic to Palawan. Twelve of the endemic mammals are non-volant and have their closest relatives on the sunda shelf, and of the total non-volant fauna, 92% are derived from the Sundaland region (Esselstyn *et al.* 2004). Greater Palawan is also home to 16 endemic species of birds (Peterson *et al.* 2000).

The high proportion of fauna derived from Sundaland is suggestive of a land bridge in the past, although the absence of large carnivores and primates from the Holocene fossil record of Palawan suggests that if any connection ever existed, it was not recent (Reis & Garong 2001). Genetic studies of the *Cyrtandra* (Gesneriaceae – herbs, shrubs and lianas) from the region suggest a recent dispersal into Palawan from Sundaland, imprinted on a more ancient connection to the flora of the other islands of the Philippines (Atkins *et al.* 2001).

There is currently limited terrestrial information on palaeoenvironmental change from terrestrial sites on Palawan; however it is possible to draw some conclusions as to the likely trajectory of past environmental change from palaeoclimate records derived from marine sediment cores in the region. Rosenthal *et al.* (2003) presented a high resolution record from the Sulu Sea, southeast of Palawan, which suggests that temperatures during the LGM were $2{\cdot}3 \pm 0{\cdot}5\,°C$ cooler, rising to approximately modern levels by the beginning of the Holocene; while Stott *et al.* (2002) suggest that rainfall in the region was decreased through the development of persistent 'super-ENSO' conditions (millennial patterns in the El Niño Southern Oscillation) during the LGM. Depending on the magnitude of rainfall reduction on Palawan, it is reasonable to expect a contraction in moist rainforest area on Palawan and expansion of vegetation types adapted to lower or more seasonal rainfall at the LGM, and this is also suggested by most modelling studies of vegetation change at the LGM (see Bird *et al.* 2005 for a review). Some support for a contraction in rainforest area in the region is provided by Meijaard (2003) who found that whilst forest-dependent faunal species occur on the main island of Palawan, several of the smaller islands of Greater Palawan do not contain any forest-dependent species. One explanation for this observation is that these islands were not forested at the time at which they were separated from greater Palawan by post-glacial sea-level rise.

Fox (1970) found pig and deer remains in his Late Palaeolithic flake assemblages at Tabon Cave, Quezon (central Palawan), and in a shell midden at Guri Cave; deer are thought to have become extinct on Palawan after c. 4000 years ago and to be related to an extant species found on the Calamianes Islands just to the north, though this has not been confirmed. Fox lists Bornean and West Malayan mammals found on Palawan and the Calamianes, but not known in the rest of Philippines – e.g. scaly anteater, slow porcupine, mongoose, 'skunk' – and suggests their presence would be consistent with a land bridge connection to Borneo at some time.

The earliest known human occupation of the island comes from Tabon Cave, where modern human specimens have been dated to 16 500 ± 2000 yr BP (U-series, human frontal bone previously estimated at c. 22 000 yr BP from charcoal), 31 000 ± 8000 yr BP (U-series, human mandible), and 47 000 ± 11 000 yr BP (U-series, human tibia) (Fox 1970; Dizon 2003). Tabon Cave also produced a series of Palaeolithic lithic assemblages, with radiocarbon dates on associated charcoal ranging from 9250 ± 250 yr BP to 30 500 ± 1100 yr BP (Fox 1970). Many caves appear to contain occupation and cooking deposits dating from around 12–15 000 yr BP through to at least 7000 years ago (Fox 1970; Szabó & Swete-Kelly 2002; Lewis *et al*. 2006); the occupation model suggests long term sporadic (and possibly seasonal) use of caves for occupation in the Later Palaeolithic.

Fox (1970) suggested on the basis of changing archaeological evidence that the Tabon Cave itself was abandoned for occupation around 8000–7000 years ago; he related this to rising sea-levels during the Holocene, suggesting that people who were focused on forest and estuarine resources moved further inland once the coast began to approach the caves in the area. He further supported this idea by the lack of marine remains found in caves in the central Palawan region predating 7000 years ago, and their frequency after this (except at Tabon Cave itself, which produced no marine shells). This suggestion may also be supported by sedimentary evidence suggesting beach development near Tabon Cave in Fox's later deposits (H. Lewis, unpublished data); future work to be carried out in 2006 should clarify this. Fox's model may also be supported by recent work at Ille Cave (1 km from the current study area), where a large shell midden with Late Palaeolithic dates shows fresh-water and/or estuarine resources. Marine shells appear in the later (undated, but probably Neolithic or Metal Age) burials overlying this deposit. Later deposits in the caves in the central and northern Palawan area are mainly cemetery deposits (jar burial cemeteries dominate). These cemeteries appear similar to others found on Borneo, as well as on other neighbouring Philippine Islands (Fox 1970).

2. Study area and sampling

Makangit Caves (11°11.969′N; 119°30.037′E – Fig. 1) lie northeast of El Nido, in Barangay New Ibajay, close to the northern tip of the main island of Palawan, in an isolated graphitic marble karst massif about 500 m in diameter. The local vegetation consists of carbonate-adapted forest species on karst areas, with the intervening alluvial plains of the Dewil River covered with a mix of open paddy fields, lowland semi-deciduous forest and bamboo thicket. Evidence for extended human occupation of currently unknown maximum antiquity has been found at Ille Cave, in another Karst tower 500 m from Makangit, and a lithic workshop and fossil deer bones have been located with the Makangit massif itself (Szabó & Swete Kelly 2002; Teodosio *et al*. unpublished data).

The massif is honeycombed with passages and chambers inhabited by a mix of insectivorous bats (*Hipposideros* spp.), frugivorous bats (*Eonycteris* spp.) and swiftlets (*Collocalia* spp.). Considerable guano mining has occurred in the more accessible locations, but an undisturbed cavern was located in the upper reaches of a narrow passage 4 m wide by 3 m high, which serves as a fly-way for bats and birds living deeper in the cave system and is not subject to either water flow or mass movement from higher deposits. The passage is currently inhabited by insectivorous bats and the floor of the cave is thinly covered by a mix of insect carapaces and fresh bat droppings.

A pit 2 m in depth was excavated through the accumulated guano that now forms a flat floor to the passage. Beneath a 1-cm-layer of modern, undecomposed guano, a gypsiferous upper layer was present from 1–3 cm, displaying some evidence of infilled burrows 1 cm wide and 3 cm deep. From 3–102 cm the guano was earthy, diffusely banded and reddish-brown, with common gypsiferous nodules <0·5 cm in diameter and distinct gypsiferous bands at 17 cm, 50 cm and 80 cm. A transitional boundary occurs between 102 cm and 112 cm, with the guano becoming progressively darker in colour and displaying a silvery sheen due to the presence of fine gypsum crystals distributed throughout the guano matrix. The lower boundary of this transitional unit is irregular and represents a redox front separating drier, oxidised guano above and black, wet, reduced guano containing little or no gypsum below. Reduced black guano, with no discernible sedimentary structures, continues from 112 cm to the base of the profile at 200 cm, where it grades into degraded and phosphatised marble bedrock after 180 cm (Fig. 2).

After excavating to bedrock, the exposed profile was sampled at 3 cm intervals, adjusted where necessary to ensure that sample intervals did not cross stratigraphic boundaries. Approximately 100 g of guano were sampled per increment and sealed in a plastic Ziploc bag, and modern, undecomposed samples of both bat and bird guano were collected from the cave and other caves in the immediate region. Upon return to the laboratory all samples were kept in a cold store at 4°C until sub-sampling for analysis.

3. Experimental methods

In the laboratory, each sample was mixed and ~10 g of guano was taken for further analysis. This was weighed, dried at 60°C overnight and re-weighed to allow calculation of water content before being crushed in a mortar and pestle. An aliquot was mixed 1:1 with water and pH determined on the resulting slurry.

No carbonate was present in any samples, so organic carbon and nitrogen content and stable isotope composition was determined on 1–2 mg aliquots of raw crushed material using a Costech elemental analyser fitted with a zero-blank autosampler coupled to a Finnegan Delta Plus-XL mass spectrometer operated in continuous flow mode (EA–IRM–MS). Stable-isotope results are reported as per mil (‰) deviations from the V-PDB standard for carbon ($\delta^{13}C$) and air for nitrogen ($\delta^{15}N$), with a reproducibility of better than ±0·1‰ for internal standards.

Initial analysis of bulk samples yielded unrealistically high $\delta^{13}C$ values in samples towards the base of the profile. X-ray diffraction of these samples revealed the presence of lithogenic graphite in these samples, derived from weathering of the marble walls of the chamber, with a $\delta^{13}C$ value of −2·5 ± 0·5‰. Accordingly, a weighed aliquot of every sample was heated overnight in a muffle furnace at 400°C for five hours to remove accessible organic carbon from the sample. The carbon content and $\delta^{13}C$ of an aliquot of the ashed residue was determined, and used to calculate the carbon content and $\delta^{13}C$ of pure guano and graphite in the sample by mass balance. The $\delta^{13}C$ value of the ashed residue and the observation that some nitrogen remained in the sample suggested that the ashing process did not completely remove all guano-derived carbon from some samples, possibly due to the physical protection of organic carbon by authigenic mineral phases. Therefore, the pure graphite content was calculated by mass balance using the $\delta^{13}C$ value of the ashed residue to infer the amount of guano-derived carbon left in the sample, assuming a graphite $\delta^{13}C$ value of −2·5‰.

The inorganic chemistry of selected pulverised and pelletised samples was determined by X-ray fluorescence (XRF)

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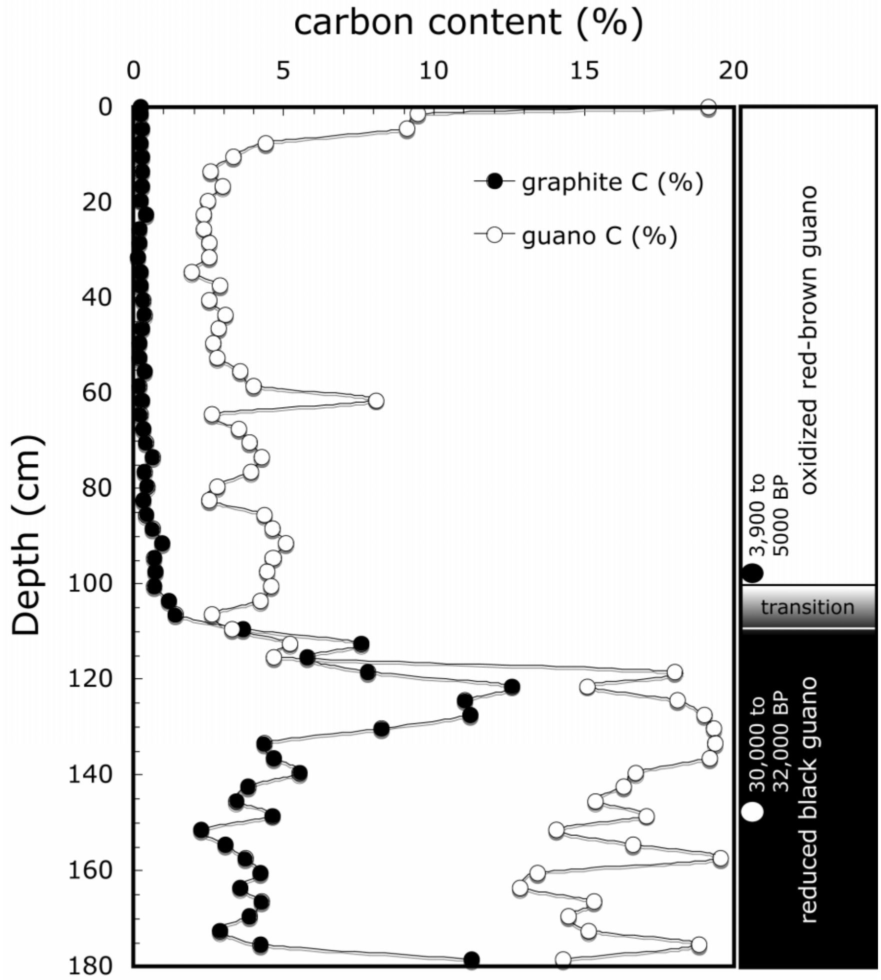

Figure 2 Guano and graphite carbon contents from 0–180 cm in the Makangit Cave section. Stratigraphy and position of available radiocarbon dates on the profile also shown (see text for explanation).

spectrometry using polarised X-ray beams with source, sample and detector in a Cartesian geometric arrangement in order to minimise scattering of primary X-rays by the organic-rich matrix of the guano. This technique has been applied to trace element analysis in plant material and shown to be accurate and precise over six orders of magnitude of concentration (Stephens & Calder 2004).

Samples for radiocarbon dating were first extracted with 2:1 HPLC grade dicholomethane:methanol to remove lipids (Folch *et al*. 1957). The extraction residue for each sample was then digested in 2 M HCl (80°C; 8 hours), washed free from mineral acid with distilled water, and then digested in 1 M KOH (80°C; 2 hours). The digestion was repeated using distilled water until no further humic material was extracted. The residue was rinsed free of alkali, digested in 1 M HCl (80°C; 2 hours) then rinsed free of acid, dried and homogenised. The total carbon in a known weight of the pre-treated sample was recovered as CO_2 by heating with CuO in a sealed quartz tube. The gas was converted to graphite by Fe/Zn reduction, and the radiocarbon activity of the resultant graphite measured by accelerator mass spectrometry at the NERC Radiocarbon Laboratory, East Kilbride. Analysis of a known 'radiocarbon-dead' guano sample from Niah Cave (Borneo) using the above pre-treatment protocol, yielded a radiocarbon activity indistinguishable from the usual process blank for the laboratory. As the samples chosen for dating from Makangit Cave were found to contain lithogenic graphite (as discussed above), a mass balance approach was used to calculate a maximum correction to the dates for this contamination, assuming that the lithogenic graphite contained no radiocarbon.

4. Results

The uppermost samples from the profile have carbon (Fig. 2) and nitrogen (Fig. 3) contents similar to modern guano from the area (Table 1), but these decline rapidly over the upper 20 cm to ~5% carbon and ~4% nitrogen. From 20 cm to 110 cm carbon content increases slightly while nitrogen content continues to decrease so that the C/N ratio of the guano increases from 1 to 2 over the interval. Beneath 110 cm, carbon content rises dramatically to 15–20% while nitrogen increases to 5–6%.

The amount of graphite in the guano is low (<0·5%) at the top of the profile and increases slowly with depth to 110 cm, with a peak in abundance of ~12·6% at 120–125 cm. The $\delta^{13}C$ value of the lithogenic graphite at the base of the profile is −2‰ to −3‰, but the $\delta^{13}C$ value of the carbon measured as graphite is more variable, tending to decrease as the abundance of graphite decreases (Fig. 4). This decrease is due to a small proportion of guano in most samples being protected by occlusion in authigenic mineral phases, such as gypsum and hence was not removed by the thermal oxidation used to quantify the graphite content of the samples (discussed above).

The $\delta^{13}C$ value of the guano is similar to that of modern samples at the surface (−25·2‰; Fig. 4) but decreases to

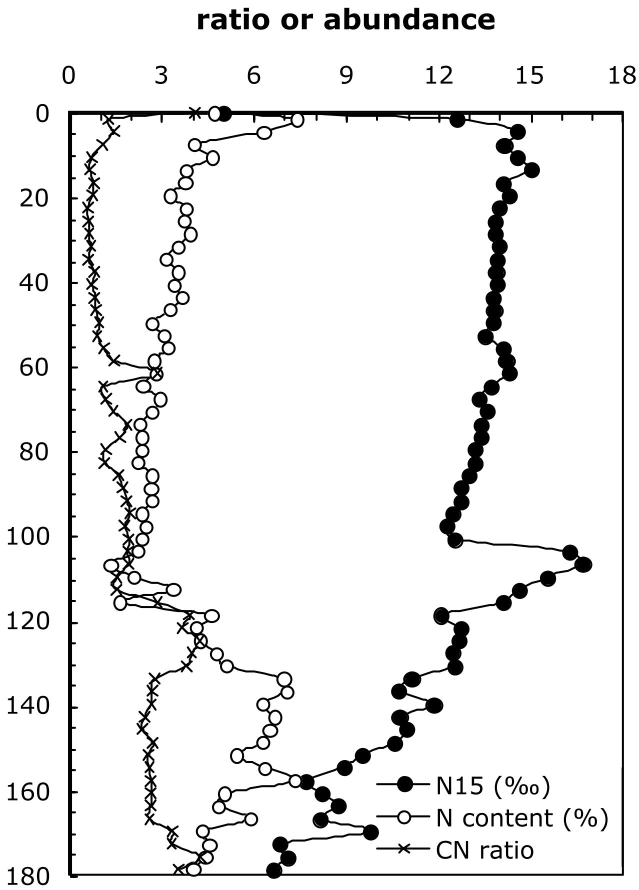

Figure 3 Nitrogen content and nitrogen-isotope composition, and C/N ratio of guano the Makangit Cave section. C/N ratio has been corrected for the presence of graphitic carbon in the samples.

− 27·5‰ at 20 cm, varying between these values to 110 cm. Beneath 110 cm, $\delta^{13}C$ value of the guano increases dramatically to as high as − 13·7‰ at 118 cm before decreasing to − 24‰ at 160 cm and then increasing to values around − 20‰ at the base of the profile. The $\delta^{15}N$ value of the guano increases dramatically by 8‰ to values of + 14·5 in the upper 10 cm of the profile, thereafter declining gradually and irregularly to values of + 7‰ at the base of the profile (Fig. 3).

Individual elements in the profile generally exhibit one of three trends through the profile. Those elements, such as Zr and Si that are likely to be of minerogenic origin and also likely to be immobile after deposition, tend to show the same pattern as graphite content, with low values in the upper part of the profile, increasing rapidly below 110 cm to a peak around 120 cm depth and remaining comparatively high to the bottom of the profile (Fig. 5). In contrast, Ca and S are high in the upper parts of the profile but decrease rapidly below 120 cm and remain low to the base of the profile (Fig. 5). Nutrient elements such as P and K do not exhibit any dramatic variations through the profile (Fig. 6). Most metals tend to follow a similar trend to immobile elements, with low concentrations in the upper parts of the profile, rising gradually as depth increases, then rising suddenly below 120 cm with concentrations remaining high to the base of the profile (Fig. 6).

Two radiocarbon dates were obtained from the profile as listed in Table 2. An apparent age of 5019 ± 33 yrs BP was obtained from the base of the oxidised guano at 96–99 cm, and an apparent age of 31 900 ± 1250 yrs BP was obtained from the middle of the reduced guano interval at 147–150 cm depth.

5. Discussion

5.1. Stratigraphy and chronology

Interpretation of the environmental record encoded in cave guano is dependent on an understanding of how these processes operate and how these may have changed over time. Interpretation is also dependent on the stratigraphic integrity of the guano sequence being maintained over time. In this case, there is evidence of shallow burrows up to 3 cm in depth in the uppermost part of the sequence, indicating that some bioturbation of the deposit has occurred. However, the maintenance of discrete, undisturbed layers in the oxidised upper half of the deposit, and the preservation of large, coherent elemental and isotopic variations over comparatively narrow depth intervals throughout the sequence suggests that the effects of bioturbation on the stratigraphic integrity of the sequence have been minimal.

The chronology of the deposit is only constrained by two radiocarbon dates and the interpretation of the dates is complicated by the fact that the samples contain a component of lithogenic graphite weathered from the marble cave walls. This graphite is radiocarbon-dead, and hence the raw radiocarbon dates must be adjusted to allow for the dilution of the radiocarbon activity by radiocarbon-dead graphite. The raw and corrected data is presented in Table 2 and the actual age of each of the dated samples is likely to lie between the raw and corrected ages. The dates are in stratigraphic order, with the 96–99 cm interval deposited in the mid-Holocene (∼ 3900–5000 BP) and the 147–150 cm interval deposited prior to the LGM (∼ 30 000–33 000 BP). These dates suggest an order of magnitude change in apparent accumulation rate from 0·015–0·02 mm/yr prior to the mid-Holocene to 0·2–0·25 mm/yr since the mid-Holocene.

Changes in the elemental and mineralogical composition through the sequence provide strong and considerably more detailed support for changes in apparent accumulation rate over the time period represented by the sequence. Some components of guano, in particular Ca and in this case also graphite, derive primarily from weathering in the immediate environment. Other elements, such as Si, Zr and Ti, are derived both from local weathering, and from mineral particles present in the guano, or blown into the chamber as dust from outside the cave. The development of a sequence of cave guano is dependent primarily on the balance between the inputs (in turn dependent on the number of individuals inhabiting the cave) and the loss of material through microbial metabolism in the case of organic material and a range of dissolution/remobilisation processes in the case of both organic and inorganic components.

Figure 5 shows variations through the sequence in graphite, Si and Zr abundance, all of which are primarily cave-derived, and immobile after deposition. This means that they can be interpreted as a record of accumulation rate, with high abundance indicating low guano accumulation rate and vice versa. Variations in all three components are strikingly coherent, and suggest that guano has been accumulating very rapidly since the mid-Holocene, but this was preceded by a period between 30 000 BP and the mid-Holocene when apparent accumulation rate was considerably slower. At around 120 cm depth, here interpreted to represent the LGM, apparent accumulation rate was up to 50 times lower than in the late Holocene. Prior to the LGM, and for an indeterminate time prior to 30 000 BP, apparent accumulation rates were faster than during the LGM, but still ∼ 10 times slower than in the Late Holocene.

A large number of other elements are primarily imported with the guano. These elements include mineral nutrients such as P and K and most metals. These are usually only present in

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Table 1 Carbon and nitrogen abundance and stable isotope composition for modern, undecomposed, bird and bat guano from Makangit Cave and other caves within a 1 km radius

Sample	$\delta^{13}C$	±	$\delta^{15}N$	±	%C	±	%N	±	CN	±
Modern bird-4	−25·09	0·02	8·09	0·07	35·65	0·15	11·41	0·12	3·13	0·05
Modern bat-6	−26·65	0·12	10·83	0·20	30·68	0·87	9·25	0·21	3·32	0·06
Modern bird-2	−26·42	0·14	10·50	0·03	29·93	0·38	10·42	0·31	2·88	0·12
Modern bird-1	−25·29	0·06	7·06	0·07	33·38	1·31	7·74	0·24	4·31	0·04
Surface-1	−25·71		10·59		17·10		7·62		2·24	
Surface-2	−26·33	0·04	11·31	0·17	23·96	0·08	9·71	0·06	2·47	0·01
Surface-3	−25·16	0·12	7·36	0·17	26·88	1·18	5·26	0·33	5·12	0·10
Surface-4	−26·33		10·04		29·91		10·57		2·83	
Surface-5	−25·58		11·07		22·75		9·33		2·44	
Mean (±1 s)	−25·84	0·60	9·65	1·67	27·80	5·76	9·03	1·88	3·19	0·95

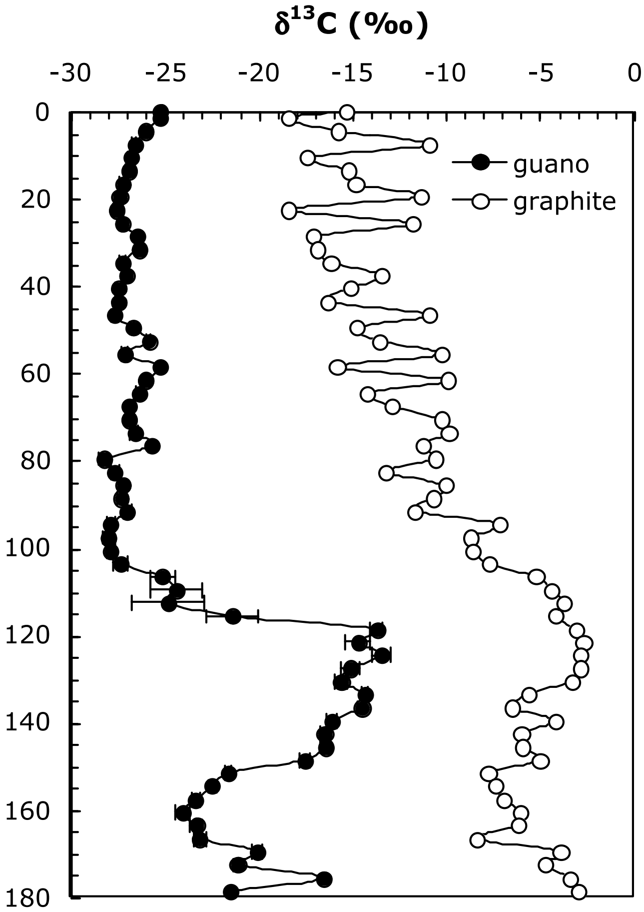

Figure 4 Carbon-isotope composition of the guano section in Makangit Cave, corrected for the presence of lithogenic carbon assuming an error of ±5% on graphite content and ±0·5‰ on graphite carbon-isotope composition. Also shown is the carbon-isotope composition of the graphitic residue following ashing at 400°C.

low abundance in the cave wallrock, but transition metals in particular are efficiently excreted by most organisms (e.g. Dauwe *et al.* 2000) and nutrients in excess of those required for metabolism are also excreted. Most of these elements follow a similar trend to the immobile elements and are greatly enriched over their natural abundance in guano (up to 0·9% Cu and 0·18% Cr for example). This indicates considerable residual enrichment of these elements through microbial remineralisation of organic matter in the lower part of the profile but detailed interpretation is hampered by the possibility of post-depositional mobility for many of these elements.

The most striking exceptions to the above trends are provided by Ca and S, which are low towards the base of the profile in the reduced guano and high from 110 cm to the surface in the oxidised guano. These elements are key to interpreting the change in apparent accumulation rate that coincides with the change from reducing to oxidising conditions that occurs between 100 cm and 120 cm. Sulphur, for example is 50 times more abundant in the oxidised upper profile than in the lower profile. This is because under reducing conditions, sulphur delivered to the profile surface in guano is not oxidised and can be leached as sulphide from the system, or volatilised and lost as H_2S. The sulphur that remains is likely to be present in base metal sulphide minerals.

Once conditions at the guano surface became oxidising, sulphur became oxidised to sulphate and immediately immobilised as gypsum through reaction with Ca-rich cave waters. Thus, while considerable loss of organic matter from the guano through microbial metabolism has occurred continuously, leading to significant enrichment of a wide range of minor and trace elements in the reduced lower part of the profile, the volume reduction associated with the loss of organic matter (and sulphur) has been offset in the oxidised upper part of the profile by the formation of gypsum. The observation that the lower half of the profile is strongly reduced provides some reassurance that although apparent accumulation rate was low, the stratigraphic integrity of the sequence has not been destroyed by bioturbation, as anoxia at the guano surface would have prevented burrowing by higher organisms.

The cause of the change from reducing to oxidising conditions in the guano is most likely the result of the guano accumulating to an elevation where saturation of the profile was no longer possible, possibly facilitated by an increase in the delivery rate of guano to the site as the resident population of bats and birds increased in the post-glacial period. As the site is located on a fly-way to other roosts in the cave, it is unlikely that guano deposition ever halted completely, even if the actual chamber itself was not occupied, unless the cave system was completely abandoned. In summary, the guano deposit at Makangit cave appears to have high stratigraphic integrity, even when accumulation rates were low, and hence is suitable for the reconstruction of palaeoenvironmental conditions near the cave. The record appears to cover a period from >30 000 BP to the present, with a comparatively narrow anoxic glacial and post-glacial section and a greatly expanded, oxidised post mid-Holocene section.

5.2. Palaeoenvironmental reconstruction

As the stratigraphy of the guano profile is relatively undisturbed, the stable-isotope composition of organic matter in the

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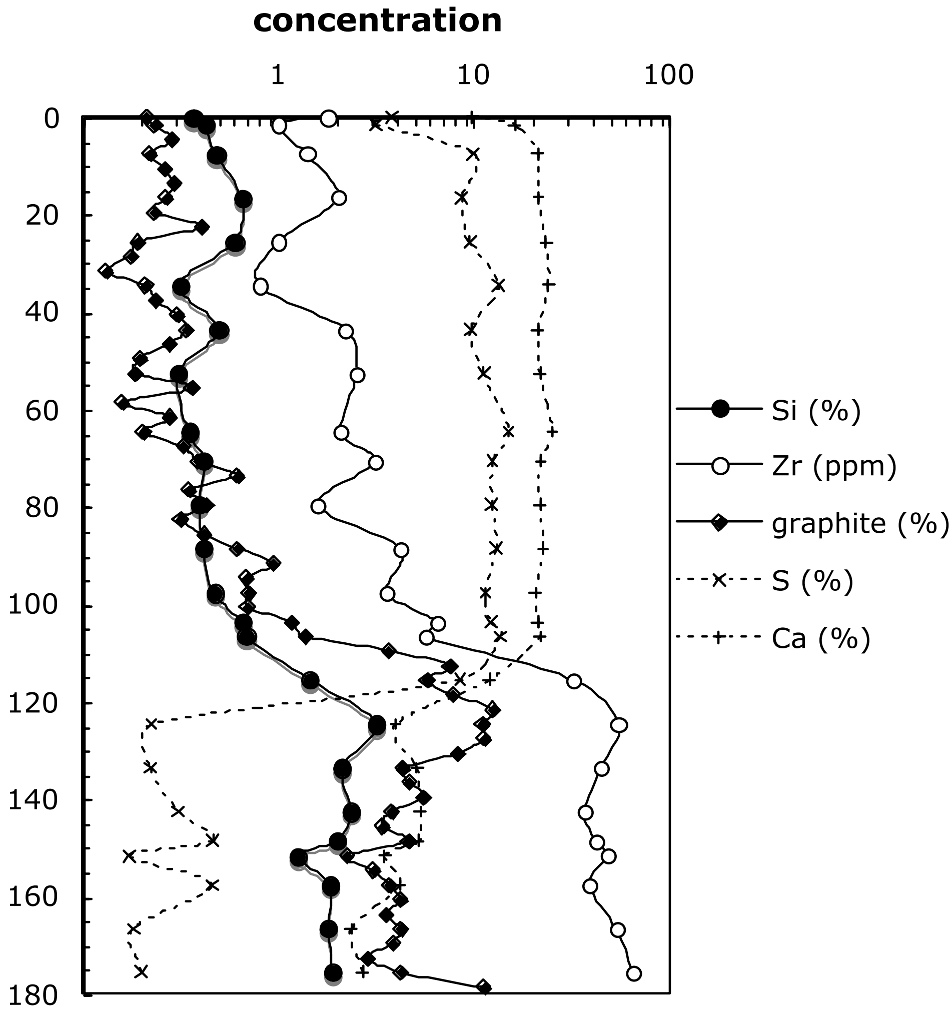

Figure 5 Abundance of components considered lithogenic and immobile (graphite, Si, Zr) as well as Ca and S, the major components of gypsum in the oxidised upper section of the guano section at Makangit Cave.

guano can be used to infer vegetation, and by implication climate, changes in the area surrounding the cave over the last >30 000 years. However, as the organic matter has undergone considerable decomposition and loss through microbial re-processing and remineralisation, it is important to assess the potential impact of post-depositional processes on the isotopic composition of the guano. It is not possible to unequivocally demonstrate that there has been no change in isotopic composition, but the evidence suggests that, at least for carbon, the impact has been small.

The guano at the top of the profile has a $\delta^{13}C$ value of −25·2‰, within the range of modern values from guano from the area, but this value decreases to values of −27·5‰ in the top 20 cm (Fig. 4). This may indicate that the effect of early diagenesis is to decrease $\delta^{13}C$ values by ~2‰. However, prior to recent clearance, the vegetation was closed forest and the value at 20 cm is consistent with closed forest. Therefore the later rise in $\delta^{13}C$ value would be wholly consistent with local clearance for agriculture, which would increase the proportion of area colonised by C_4 species, and hence the $\delta^{13}C$ value of guano in the cave. Thus, while some effect of diagenesis on the $\delta^{13}C$ value of the ancient guano cannot be ruled out, it is likely to be small (<2‰) in the context of the large range of values observed down the profile.

The $\delta^{15}N$ variations down the profile do suggest a significant impact of early diagenesis (Fig. 3). Whilst the $\delta^{15}N$ values are within the modern range at the top of the profile, they increase rapidly and immediately by 7‰, to values between +12‰ and +15‰ which is well outside the range observed in modern guano samples from the area. Whilst it is conceivable that bird and bat populations were feeding at a higher trophic level prior to large-scale human disturbance in the area, it is more likely that the $\delta^{15}N$ values are significantly affected by fractionation associated with microbial production of ammonia (e.g. Pyatt 2003). This suggests that the $\delta^{15}N$ values of the guano are not useful for detailed environmental reconstruction, but the generally high values are nevertheless broadly consistent with the cave being occupied dominantly by an insectivorous population of bats and birds throughout the interval of guano deposition. The low pH of the guano throughout the sequence and particularly in the lower parts where values are 3·5 to 5·5, also suggests a dominantly insectivorous population, as Shahack-Gross *et al.* (2004) found that the pH of the guano of insectivorous bats was significantly lower than either fruit-eating bats or pigeons.

The $\delta^{13}C$ values of the guano vary between −25‰ and −28‰ over the period from mid-Holocene to the present, consistent with closed and periodically drier forest, with a possible minor C_4 component in the region surrounding the cave (Fig. 4). Over the comparatively narrow interval between 100 cm and 120 cm, $\delta^{13}C$ values increase dramatically to between −13‰ and −15‰. The maximum $\delta^{13}C$ values are coincident with the peak in graphite, Si and Zr abundances, indicating low accumulation rates, as discussed above. Coupled with the available radiocarbon dating evidence, the data suggests that this interval is likely to represent the LGM. The $\delta^{13}C$ values indicate the dominance of C_4 plants, suggesting a grassland, or very sparsely treed savanna, was established

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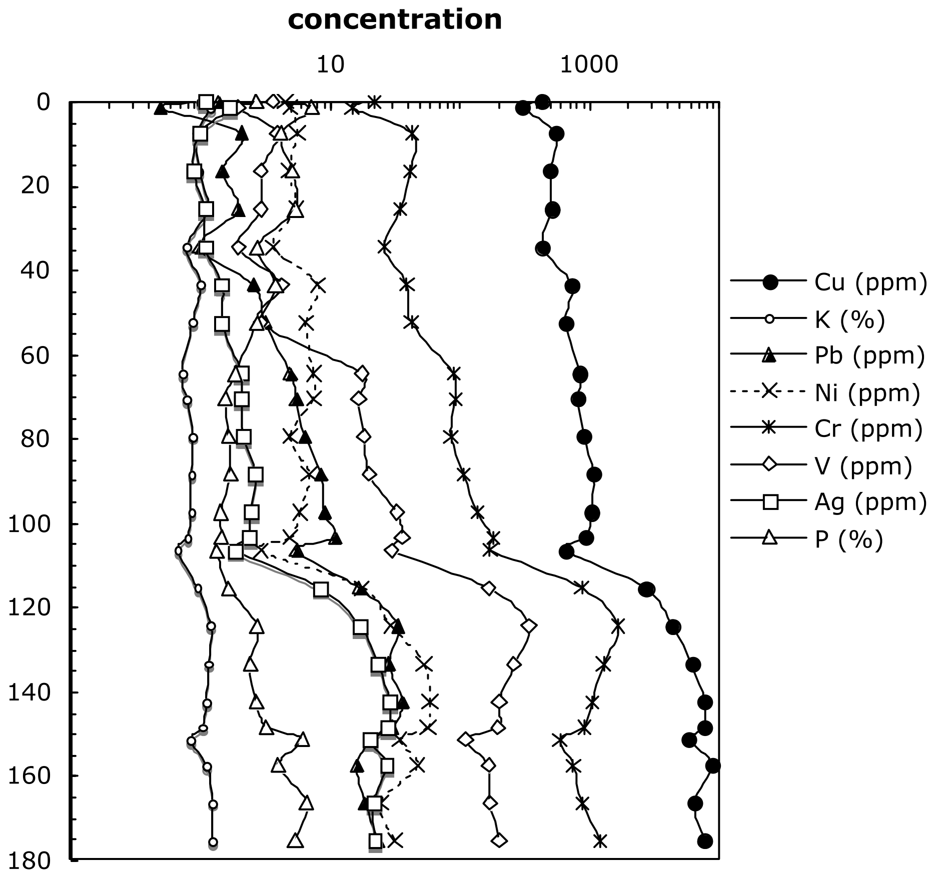

Figure 6 Abundance of inorganic nutrient elements (P and K) and selected base metals (Cu, Pb, Ag, Cr, V, Ni) in the guano section at Makangit Cave.

Table 2 Radiocarbon dates obtained on samples from the guano profile at Makangit Cave. The sample identifier is the depth interval from which the sample was collected. % graphite is the percentage of total carbon in the sample that is derived from graphite. Raw dates are presented in uncalibrated years BP (± 1 SD); corrected dates have been calculated as described in the text

Sample	AMS number	$\delta^{13}C$	Raw age (BP)	Graphite (%)	Corrected age (BP)
96–99 cm	SUERC-6530	− 26·9	5019 ± 33	13·3	3870
147–150 cm	SUERC-6531	− 10·8	31900 ± 1250	20·8	29990

around the cave during the LGM. This in turn suggests a dramatic decrease in rainfall in the region, consistent with the inferences of some previous studies (Heaney 1991; Bird *et al.* 2005). Unfortunately, the interval representing the immediate post-glacial and early Holocene is represented only by a narrow thickness of guano, making it impossible to determine whether forest re-establishment rapidly followed the LGM, or was delayed until early to mid-Holocene times.

Prior to the LGM, at some time around and preceding 30 000 BP, the vegetation contained a higher proportion of C_3 plants, but $\delta^{13}C$ values of − 20‰ to − 23‰ suggest that variably wooded savanna with grassy understorey was maintained at the site over the rest of the interval represented by the profile. At Tabon Cave, Fox (1970) reported a thick travertine layer found across the cave floor, bracketed by charcoal dates of >21 000 and 23 200 ± 1000 yr BP, interpreted as indicating locally wet conditions in the cave during this time. It is possible that this event may be related to the period of wetter conditions indicated by the lower $\delta^{13}C$ values in the guano sequence between 150 cm and 170 cm, although further dating will be required to accurately constrain the timing of the event.

6. Conclusion

The preservation of stratigraphic features and coherent trends in the elemental, isotopic and mineralogical composition in the guano sequence at Makangit Cave suggests that the material is suitable for use in the generation of proxy records of palaeoenvironmental change. The similarity of trends through the profile in graphite abundance and immobile element abundance suggests that these can be used to infer accumulations rates; and whilst the nitrogen isotope composition of the guano may have been substantially modified by microbial processes, the carbon-isotope composition of the guano is not substantially modified and can therefore be used to infer vegetation, and hence climate in the cave area at the time the guano was deposited.

Graphite abundance, immobile element abundance (Zr, Si) and the available radiocarbon dates for the profile suggest there have been large changes in the rate of guano accumulation. From prior to 30 000 BP, accumulation rates in the currently saturated, reduced guano were low, and decreased still further into the LGM. At some time following the LGM,

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accumulation rates increased dramatically, related to a change to oxidising conditions at the guano surface which allowed the formation and preservation of gypsum in the profile. At the LGM, $\delta^{13}C$ values of up to $-13{\cdot}5‰$ indicate that the vegetation around the cave was dominated by C_4 plants, suggestive of a grassland or sparsely wooded savanna. Prior to the LGM, a mixed C_3/C_4 savanna vegetation type is indicated by $\delta^{13}C$ values between $-20‰$ and $-23‰$, but the antiquity of the base of the sequence remains to be determined.

By the mid-Holocene, C_3-dominated closed forest ($\delta^{13}C$ value of $-25‰$ to $-28‰$) was established around the cave and remained until the present. Unfortunately, the details of the transition from LGM grassland to Holocene forest are poorly resolved and the site will be re-visited in 2006 to obtain a higher resolution record of this interval, in order to establish in detail the timing of forest establishment at the site.

The conclusion that the region was covered by grassland or sparsely wooded savanna at the LGM has significant implications for climate change in the region. The results suggest that the area was substantially drier at the LGM than at present, consistent with the results of some other studies (Stott *et al.* 2002), and lending weight to the hypothesis that the entire region, including Sundaland, may have been substantially drier at several times during the last glacial period, including the LGM (Heaney 1991; Bird *et al.* 2005), leading to widespread forest contraction and commensurate expansion of open savanna vegetation. This in turn would have impacted on the resources available to support the dispersal of humans and fauna through the region at the critical times of lowered sea-level, when land bridges were available to facilitate dispersal.

The observation that forest-dependent species do occur in the modern fauna of Palawan (Meijaard 2003) indicates that forest was continuously present on Palawan, but the results of this study suggest that either it was restricted to refugia at the LGM, or to more southerly parts of the island. The absence of forest-dependent species from several of the smaller islands of Greater Palawan to the north of the main island (Meijaard 2003) suggests that forest may have disappeared from a large area of at least northern Greater Palawan during the LGM. In a local archaeological context, evidence for the abandonment of occupation at Tabon Cave around 7000 BP, attributed to sea-level rise by Fox (1970), may therefore be, at least partly, a response to the post-glacial expansion of forest on Palawan.

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