Pollen taphonomy of cave sediments: what does the pollen record in caves tell us about external environments and how do we assess its reliability?

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Abstract

Cave sediments may contain important long-term records of past environments and human activity. Pollen provides key evidence, since it disperses widely and is relatively durable. We still know relatively little about the dispersal of pollen into caves, and its preservation within cave sediments, compared with our relatively detailed knowledge of pollen taphonomy in other sedimentary environments. Pollen taphonomy in caves is dependent on a variety of transport pathways and seems to be very contingent on local circumstance. The airfall component of cave pollen assemblages often seems comparable with airfall spectra in the landscape outside the cave, but bees, birds and bats may transport considerable quantities of pollen into caves, and the entrance-flora may also be significant. Cave sediments are rarely waterlogged and pollen within them can be subject tomicrobial and chemical degradation. Sedimentation in caves is often episodic, with episodes of storage and deposition, sometimes redeposition of sediment, which means that biostratinomic, preservational, factors become very significant. Comparison with sequences outside caves is difficult because few caves are found in landscapes where there are comparable pollen records from lakes and bogs. Here we review the factors affecting cave pollen taphonomy and hence the reliability of palynological analysis of sediments from caves, with suggestions for future investigation.

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1. Introduction

Cave sediment sequences often accumulated over hundreds of thousands of years (e.g. Bouzouggar et al. 2007; Douka et al. 2014; McFarlane & Lundberg 2005). They contain important sedimentary evidence for environmental change plus archaeological and palaeobiological materials indicating cultural practises and environmental change – including lithics, animal bones, mollusc shell, eggshell, pollen, plant macro-remainssuch as seeds and charcoal (e.g. McBurney, 1967; Bailey & Woodward 1997; Barker 2012, 2016; Bouzouggar et al. 2007). With multidisciplinary study of cave sequences, we can piece together a relatively rounded understanding of the sequence of human activity and its changing environmental context.

Pollen assemblages are, *in potentia*, a key line of evidence in the study of cave sequences. Pollen assemblages from non-cave depositional environments such as bogs and lakes are used widely to infer past environments (Faegri & Iversen 1975; Faegri et al. 1989; Moore et al. 1991). Pollen thus provides a potential link between the cave and its wider landscape context, because pollen grains and spores, which are produced by plants living in the landscape outside the cave, are known to disperse widely by both wind, insect and vertebrate vectors (Englund 1993; Nason et al. 1996; Hunt & Rushworth 2005; Jha et al. 2010; Šikoparija et al. 2013). This dispersal may take pollen into caves where they may be preserved by being buried in accreting sediments. Although pollen has been used in an increasing number of cave investigations (e.g. Schutrumpf 1939; Derville & Firtion 1951; Welten 1954, 1956; Van Campo & Leroi-Gourhan 1956; Anderson 1955; Donner & Kurten 1958; Martin 1961; Bryant 1974; Leroi-Gourhan 1975; Gale & Hunt 1985; Gale et al. 1993; Carrion et al. 2001; Caseldine et al. 2008; Djamali et al. 2011; Festi et al. 2016; Gatta et al 2016; Hunt et al. 2016; Linstadter et al. 2016), our knowledge of the how representative of outside environments cave pollen assemblages might be is still fairly insubstantial, relative to our understanding of taphonomic processes in bogs and lakes, which are often the preferred environments for pollen research in regions where they exist. This matters because without a robust understanding of taphonomy it is not completely clear how much of the pollen signal reflects environmental events in the world outside the cave, and how much reflects taphonomic processes, in any given case. This paper therefore reviews the state of the art in cave pollen taphonomy, identifies wide-scale trends and patterns and suggests research directions for the future.

2. The concept(s) of Taphonomy

The term ‘taphonomy’ was coined by Efremov (1940). It is the science of the route by which living organisms become fossilised (Behrensmayer & Kidwell 1985). Pollen taphonomy can be conceptualised as the processes of necrolysis (by which organic materials such as pollen grains are generated and dispersed), biostratinomy (in which they are transported, deposited and buried) and diagenesis (in which buried materials come into equilibrium with the burial environment after deposition). Thus, pollen taphonomy includes a sequence of necrolytic processes through which pollen grains are generated in the male organs of plants, and dispersed by vectors such as insects, birds, mammals, wind and water. Then follow biostratinomic processes, firstly of transport in the environment by these and other vectors, then deposition, burial and preservation resulting from a variety of sedimentary and diagenetic processes (Fig. 1).

FIG 1 ABOUT HERE

2. Necrolysis: Pollen dispersal

In nature, plants produce pollen and disperse it to other plants (in most cases: there are a few self-pollinators) as part of their reproductive cycle. Dispersal is generally either by wind (anemophilous pollen such as pine, oak and grass) or by animal vectors such as bees, flies or beetles (entomophilous pollen such as that of the daisy family [Asteraceae]) bats and birds (zoophilous pollen such as the mangrove *Sonneratia*), although a few taxa, such as the marine eel-grasses, have pollen grains without preservable exines that disperse in water.

3. Biostratinomy

Pollen can be dispersed into caves by the vectors utilised by the plants (wind, insects, bats and birds in particular), but it may also enter caves by indirect means, carried by secondary vectors or processes after original deposition in the landscape. A variety of transport pathways, very contingent on local circumstance, are known from studies of pollen taphonomy in caves (e.g. Van Campo & Leroi-Gourhan, 1956; Dimbleby 1985; Burney & Burney, 1993; Coles & Gilbertson, 1994; Prieto & Carrión, 1999; Navarro Camacho et al., 2000; Navarro et al., 2001; Navarro et al., 2002; Hunt & Rushworth, 2005; Simpson & Hunt, 2009; de Porras et al., 2011). These biostratinomic processes are usually regarded as a linear sequence, but pollen grains are durable enough and some cave environments sufficiently dynamic geomorphologically that recycling can occur. This means that sediments and their contained pollen can be eroded and redeposited (Hunt et al. 2015) on more than one occasion in the history of a pollen grain.

Biostratinomic processes include:

3.1 Direct fallout from the cave entrance flora.

At Creswell Crags, in caves such as C7 and Dog Hole Cave, spores derived from the cave-entrance fern flora comprised between a 25 and 40% of the annual palynological fallout (Coles & Gilbertson 1994). This phenomenon seems to be most marked in small humid caves subject to little human activity, with luxuriant cave-mouth vegetation. It is less marked in larger caves, and in caves where the cave-mouth flora is restricted at Creswell (Coles & Gilbertson 1994).In the wet tropical forest zone, fern spores, derived mostly from the entrance flora are between 20 and 40% of the total annual fallout in the very large cave-mouth of the Great Cave of Niah (Hunt et al. in press). The contribution of the entrance flora seems less marked or absent in arid-zone caves where the entrance flora is sparse or absent and other vectors and processes predominate (e.g. Weinstein 1987; Simpson 2016).

3.2 By aeolian transport from more distant vegetation.

This may be either from pollen dispersal by parent plants or from the resuspension and transport by wind of previously-deposited material. Airfall of pollen in caves after aeolian dispersal and transport from parent plants is very widely reported (e.g. Derville & Firtion 1954; van Campo & Leroi-Gourhan 1956; Weinstein 1987; Coles & Gilbertson 1994; Navarro et al. 2001; Hunt & Rushworth 2005; de Porras et al. 2011; Fiacconi & Hunt 2015, 2016). The airfall component of cave pollen assemblages is often closely comparable with airfall spectra in the landscape close outside the cave (e.g. Coles & Gilbertson 1993; Hunt & Rushworth 2005; de Porras et al. 2011; Fiacconi & Hunt 2016). Total pollen accumulation figures from airfall, when measured, tend to be remarkably low in caves, generally at least one order of magnitude lower than accumulation rates outside the caves concerned (Table 1). In general, the proportion of anemophilous pollen as a percentage of total pollen accumulation in the entrance zone of caves is comparable with that accumulating close outside the cave (e.g. Coles & Gilbertson 1994; Hunt & Rushworth 2005; De Porras et al. 2011; Fiacconi & Hunt 2016). In many sac-like caves, the percentage of anemophilous pollen generally declines away from the cave mouth, particularly in caves that are narrow for their length (van Campo & Leroi-Gourhan 1956; Coles & Gilbertson 1994; de Porras et al. 2011; Fiacconi & Hunt 2016, Fig.2). Other patterns may occur in more geomorphologically-complex systems (van Campo & Leroi-Gourhan 1956; Fiacconi & Hunt 2016) or where transport of pollen by vertebrates predominates (e.g. Navarro et al. 2001; de Porras 2011). Resuspension and aeolian transport of previously-deposited material is rarely reported, mostly from cold-stage sediments of loessic origin in what are today temperate-zone caves (e.g. Coles & Hunt 1985; Gale & Hunt 1985).

FIG 2 ABOUT HERE

TABLE 1 ABOUT HERE

3.3 In drip water from the land surface above, and in sinking streams from more distant catchments.

Drip water sometimes contains large amounts of pollen (e.g. Genty et al. 2001; Simpson 2016) but this is not always the case. No pollen was found in drip water in cave C7 at Creswell Crags (Coles and Gilbertson 1994) or in caves in mesic forest in New York State (Burney & Piggott Burney 1993), while drip waters analysed by Fiacconi & Hunt (2016) at Shanidar Cave contained very little or no pollen. There may be a filtering effect in biologically-active and relatively organic-rich epikarst zones, as at Creswell and in New York State. On the other hand, moss growing on seeps at Caf Sidar contained heterogeneous assemblages interpreted by Fiacconi & Hunt (2016) as largely generated by parent-plants growing close to the inlets to the conduits leading to these seeps. Peterson (1976) demonstrated the transport of pollen through streamways up to 0.8 km into the vadose Mammoth Cave system in Kentucky. The pollen became increasingly degraded as it passed down the streamway channel, but Peterson (1976) argued that the pollen load in the streamway reflected closely the vegetation in the catchment of the sinking stream. Lycopodium spores were used as tracers in karst groundwater before the advent of dye-tracing (e.g. Atkinson 1968) thus indicating that palynomorphs may be transported several kilometres underground in phreatic systems. It must be noted that river waters sometimes contain rather taphonomically-biased assemblages (e.g. Hunt 1987) and alluvial sediments outside caves often contain assemblages showing a strong taphonomic imprint (e.g. Fall 1987; Hunt 1987), so care must be taken in interpreting pollen from waterlain sediments in caves.

3.4 Within debris/mud flows and surface wash entering the cave.

A considerable proportion of sediments in many caves in the temperate zone originate from mud- and debris flows and these sediments are not uncommon even in tropical caves (e.g. Gilbertson et al. 2005). To our knowledge, no-one has sampled an active mass movement within a cave for palynology. Recycled palynomorphs were found in a mudflow deposit in a Swiss cave (Welten 1954) and pollen was found in mudflow deposits in the Great Cave of Niah, where consistent assemblages within the mudflow unit suggest that materials had been homogenised by the mudflow processes

(Hunt et al. 2012). It is likely that mass-movement deposits elsewhere in caves will also contain pollen. Similarly, we are not aware of taphonomic studies of the pollen load in sheet-wash or rill flows entering caves. Simpson (2016) has sampled Holocene deposits resulting from these mechanisms at the Haua Fteah, Libya and they do not seem to be distinguishable palynologically from near-contemporary deposits resulting from other processes.

3.5 By vertebrates.

Transport by vertebrates is very locally-contingent because the spatial distribution of animal behaviour in caves appears to be very highly patterned, for instance by roosting and denning behaviour (Fig 3). Among others, Scott (1987), Carrión et al. (2001), González-Seampériz et al. (2003) and Djamali (2011) suggest that hyaena coprolites from caves contain pollen indicative of the general vegetation around the cave. A similar case has been argued for coprolites of giant ground sloths in North American caves (Martin et al. 1961; Thompson et al. 1980), rat droppings in a Libyan cave (Gale et al. 1993) and for sheep droppings (de Porras et al. 2011). This is likely to be the case also for other taxa (e.g. Ingram 1969). Among the vertebrates, birds and bats which roost within the cave may be very significant as vectors of pollen e.g. Hunt & Rushworth (2005) recorded an influx of up to 1427 pollen grains per cm^2 per year below swiftlet nests at Niah. This is not always the case, however, as pigeons at Shanidar appear to import little pollen in their droppings (Fiacconi & Hunt 2016). Ground-living animals such as foxes, badgers, porcupines and rodents may be significant importers of pollen (Bramwell et al. 1984, Diot 1991; Burney & Piggott Burney 1993; de Porras et al. 2015).

FIGURE 3 ABOUT HERE

Another source of pollen within the organic deposits is represented by rodent middens, including those made by packrats, hyrax and other species. Packrats (*Neotoma*) are small rodents, with twenty one species present in different habitats from Canada to Nicaragua (Betancourt et al., 1990). These animals collect vegetal material in an area up to 50 m from their dens, and this is cemented together by urine and preserved as a midden. Packrat middens are interesting because of their content of plant macrofossils and pollen grains and they can also be dated using the radiocarbon method. In dry caves, they can be preserved for thousands of years (Thompson and Anderson, 2000). The provenance of the plants used in construction is local but the pollen can be both from local and regional sources and the contribution of the two different sources is still poorly understood. Issues with the use of packrat middens in vegetational reconstruction are often related to the taphonomic processes of their formation and to post-depositional episodes such as erosion, rockfalls and collapse into crevices, which can produce a relocation of the middens in the stratigraphy (Wells, 1976). Hall & Risking (2010) note that *Juniperus* pollen can be over-represented in packrat middens because the animals gather and eat the male cones.

Hyraxes (*Procavia capensis*) also produce middens. Carrión et al. (1999a) presented a palynological record from a hyrax midden from South Africa, explaining that these middens are different from the ones of other species as *Neotoma* or *Petromus typicus* (Dassie Rat) as they constitute a stratigraphically coherent section. It has been demonstrated that the pollen found in these middens may not be strongly influenced by animal diet and it can produce a good representation of the surrounding vegetation as there is a close correspondence between the pollen composition in the samples and the composition of the vegetation in the area. Likewise, de Porras et al. (2015) showed that rodent middens in Chile contained pollen assemblages representative of the local vegetation.

A special case particularly notable in Mediterranean countries, North Africa and the Middle East are *fumier* deposits – thick, layered accumulations of dung and ash from partially-burnt dung resulting from domesticates such as sheep, goats and cattle stalled within caves. These contain pollen (e.g. Esposito & Burjachs 2016) which has been brought into the cave in gut contents (guano, dung), and on fur and feet. Pollen assemblages often reflect the vegetation where the animals have grazed, rather than that growing immediately around the cave (Fig. 4).

FIGURE 4 ABOUT HERE

3.6 By invertebrates.

Several groups of insects nest in caves – bees and wasps particularly. Bees nesting in caves are known to accumulate pollen, particularly entomophilous taxa such as Asteraceae and Lactucae (Bottema 1975). In general, in the surface sediments of sac-shaped caves not subject to major vertebrate activity, entomophilous pollen rises in percentage terms towards the rear of the cave (Fiacconi & Hunt 2016). Solitary wasps sometimes line their nest-burrows with polleniferous mud, collected outside the cave (Hunt & Rushworth 2005).

3.7 On or by people.

People bring pollen into caves in numerous ways. Pollen can be introduced on feet, skin, hair and clothing. Vegetation carried into a cave for animal fodder, bedding or food may carry pollen with it and in particular inflorescences brought into the cave for food, medicine, ornament or ritual may contain pollen (e.g. Leroi-Gourhan 1975; Hunt et al. 2012). Pollen may be introduced on the fur or in the gut contents of animals brought into the cave for food (Coles et al. 1989). Caves have also been used as latrines and pollen may be contained in human coprolites (e.g. Bryant 1974; Schoenwetter 1974; Rhode 2003; Dean 2006; Hunt et al. 2011). It has been noted that surface sediments of caves frequented by people may contain higher concentrations of pollen than sediments in those caves where people are rarely present (van Campo & Leroi-Gourhan 1956), but this is not always the case – the surface sediments of Shanidar Cave (which receives thousands of tourists per year) required a heavy liquid step to produce countable assemblages, but this was not required for other caves in the same region which are rarely, if ever, visited (Fiacconi & Hunt 2016).

3.8 Overview

The above discussion suggests that evaluation of the pattern of pollen accumulation in caves before excavation starts is a very worthwhile investment of time and resources since it is likely to identify sampling localities where pollen accumulation approximates to areas outside the cave. In general, the research cited suggests that areas close to the cave mouth are likely to provide samples with less marked taphonomic bias than those in the rear of the cave (Fig. 3). Pollen dispersed by wind is also likely to be more abundant in this entrance-zone than it will be toward the rear of the cave. Areas beneath bat and bird roosts and drips should be avoided if possible.

4. Sedimentation in caves and diagenetic factors

Issues relating to pollen deterioration on archaeological sites, including caves, are discussed by Bryant & Hall (1993). Since cave sediments are rarely waterlogged, degradation of organic matter, including pollen, is likely to happen at times. The saturation of cave sediments by ammonia, which happens in some guano-rich tropical caves, seems however to lead to very well-preserved pollen, as at Niah Cave (Hunt et al. 2016). On the other hand, experimental studies and field experience both suggest that episodic wetting and drying of cave sediments and some forms of human activity such as burning both lead to extremely poor pollen preservation (Campbell 1991; Bryant & Hall 1993; Navarro et al. 2001).

While cave surface sediments often contain pollen assemblages very similar to those accumulating outside caves, there are reasons to suspect that some subfossil assemblages from caves have acquired a strong taphonomic imprint. In particular, pollen of durable taxa – Lactucae, *Pinus*, fern spores, *Tilia* are sometimes more common in cave sediments than is ecologically likely (e.g. Bramwell et al. 1984; Bottema 1975). This 'over-representation' is perhaps more likely to reflect preferential destruction of less durable taxa within the cave sediments rather than biostratinomic factors. It has been known for many years (e.g. Havinga, 1984) that not all pollen grains are equally durable to decay processes. Further, it is becoming apparent that the type of degradation is also important, with microbial activity seeming to lead to different results than attack by oxidising chemicals (e.g. Hopkins 2010; Marquer et al. 2010; although see Lebreton et al. 2010). This is possible in caves where lime-rich environments are conducive to microbial activity (Bryant & Hall 1993), although pollen in stalagmites is often well-preserved (Burney & Piggott Burney 1993; Caseldine et al. 2008).

Sedimentation in caves is often episodic (Gale & Hunt 1985) with sediment storage, erosion and redeposition sometimes very frequent but can be identified only by high resolution dating (Hunt et al. 2015). In this situation, biostratinomic, preservational, factors become very significant since erosion and resedimentation of pollen will provide opportunities for repeated microbial and oxidative breakdown of pollen grains. Identifying the products of these biostratinomic and preservational factors becomes critical in deciphering the pollen record. Episodes of very slow sedimentation may lead to extremely high pollen concentrations and 'telescoped' assemblages where whole interglacials are represented by no more than 10 cm of sediment accretion (Hunt & Gale 1986). Episodes of non-deposition can be recognised by sudden changes in pollen assemblages and displacements in age-depth curves (Hunt et al. 2015, 2016). At present, the observation of ecologically-incoherent assemblages or assemblages rich in durable taxa seem the best indicators of taphonomic complexity as a result of erosion and re-sedimentation.

5. Paired and comparative studies

Cave pollen records come from karst areas where lakes or bogs to provide comparisons are infrequent and where there may not be available well-dated sediments for comparative studies (e.g. Caseldine et al. 2008). A few studies have been done where cave sequences are located close to non-cave sites which have also been sampled for pollen, for instance the Younger Dryas and Early Holocene sequence at Kirkhead Cave, UK (Gale & Hunt 1985) shows very similar assemblages to nearby lacustrine sequences (Oldfield 1963), except that high fern spores reflect the cave-entrance flora. Similarly, there are parallels between swamp, cave and hyrax dung deposits in later Holocene deposits in the Karoo, South Africa (Scott et al. 2005). Finally, a recent article by Iriarte-Chiapusso et al. (2016) reconstructed the Cantrabrian Gravettian by comparing the data recorded by caves, used so far for the palaeoenvironmental reconstruction of this period, with new data becoming available from open air sites in the region. In this case, they argued that data from open-air sites helped to improve the biased picture based on the information from caves. Further paired studies are highly desirable to demonstrate the robustness of cave pollen records.

Where multidisciplinary investigations have been carried out, we may evaluate the reliability of pollen assemblages through comparison with other indicators of palaeoenvironmental change. There are, of course, issues relating to what we ‘see’ with any given class of indicator, both in terms of resolution and reach. The resolution of pollen data can be quite fine-grained in circumstances where distinctive plant taxa are close to their ecological tolerances. Oxygen isotopes of stalagmites, may, however have finer resolution, with errors of less than a degree Celsius, but some groups, such as the mammals, generally enable recognition of only rather broad habitat categories. In terms of reach, pollen reflects vegetation usually within a few tens to hundreds of metres from a cave, sometimes closer (Weinstein 1983; Coles & Gilbertson 1994; de Porras et al. 2011) so is typically greater than, for instance molluscs, which typically occupy very small home ranges. Nevertheless, in general changes in pollen assemblages will be accompanied by changes in other indicators. This can be seen, for instance at La Riera, Spain (Strauss et al. 1981), where the beginning of the Holocene is indicated by pollen, mammals and land snails, and at Carihuela Cave (Spain) where the pollen record parallels the sediment and micromammal sequence (Carrion et al. 1999).

6. Conclusions

Pollen in cave sediments can provide important evidence for the palaeoecology of karst regions where other types of site may be very sparse. The pollen record in caves is particularly important because of the great chronological depth of many cave sequences, and because the pollen record in caves may be closely related to archaeological evidence for human activity and to evidence provided by other palaeoecological and sedimentary indicators. Pollen may provide direct evidence for some patterns of human behaviour, such as the import of inflorescences into caves but is most important in providing high-resolution palaeoenvironmental recontstruction.

Reliability is perhaps difficult to quantify with certainty, but studies in a variety of biomes in caves with simple morphology have shown that in general the pollen and spores reaching floors of cave entrances are representative of vegetation in the immediate environs of the cave. The representation of anemophilous taxa then declines towards the rear of simple caves in a fairly predictable way. There are exceptions to these patterns in more geomorphologically-complex caves and where vertebrates (including people) using the cave as a latrine or activity area are eating or gathering vegetation some distance away from the cave. Guano and similar materials will generally be visible to sedimentological or geochemical investigations, however, so the pollen associated with materials of this sort can be treated as potentially unrepresentative of local vegetation. Other taphonomic effects relating to sedimentation or diagenesis may be indicated through the assemblages themselves and particularly through disproportionate percentages of durable taxa, with supporting evidence from sedimentological techniques, particularly micromorphology. Many issues relating to taphonomy can be avoided, or at least minimised, by taphonomic evaluation of the site and selection of sampling sites within areas dominated by relatively simple pollen fallout near the mouth of the cave. Given these constraints, pollen from caves can indeed be said to be reliable.

Further systematic investigations are still needed of pollen taphonomy in complex cave systems, of some of the less well-understood sedimentary mechanisms such as mudflows, and of pollen degradation in cave environments. It would also be highly desirable if high-quality inside-outside paired studies took place, where cave pollen records were compared to sequences from nearby localities such as lakes or bogs.

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CAPTIONS TO FIGURES

Figure 1. Sketch of taphonomic pathway from vegetation outside caves to the subfossil pollen assemblages in cave deposits

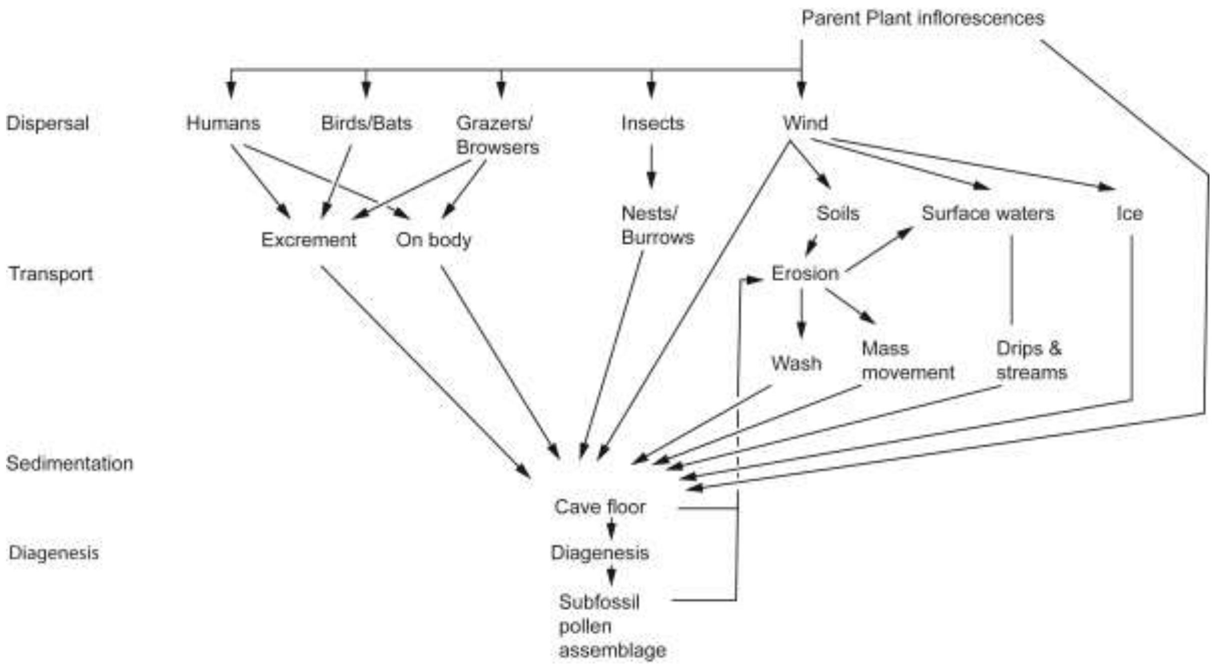


Figure 2. Plot of differences in the % anemophilous pollen between the front and the rear of the cave against cave geometry (as summarised by the cave length/breadth ratio) from sac-like caves in Kurdish Iraq. This shows that the proportion of anemophilous pollen declines most markedly from the front to the rear of caves which are long relative to their breadth (r2=0.7572). Data from the

Cueva del Moro I and II from Navarro et al. (2001) is plotted to show that a similar pattern may hold in Spanish caves, but this is not included in the calculation of the trendline.

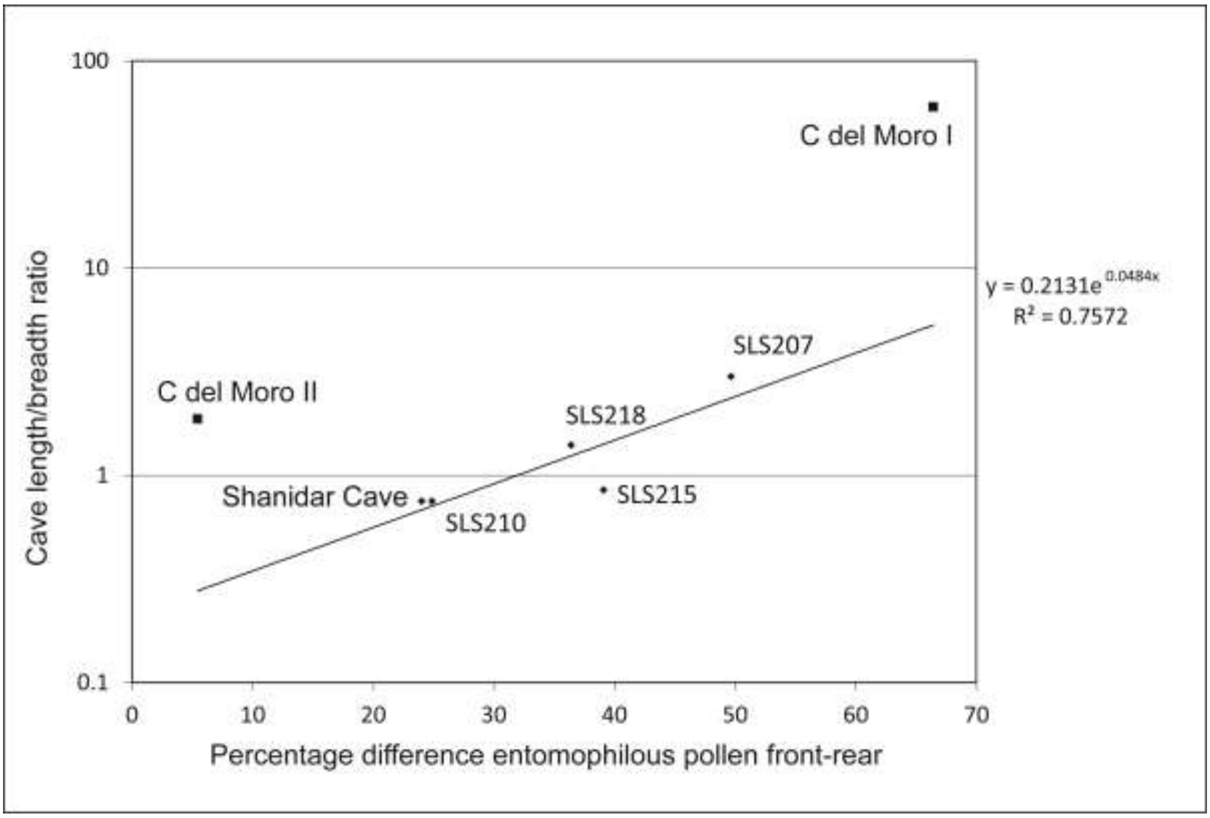


Figure 3. Pollen taphonomic summary for the Great Cave of Niah (data from Hunt & Rushworth 2005; Hunt et al. 2016). Mangrove and riverine taxa is disproportionally represented in the pollen accumulating under the nesting zone, where it arrives mostly in guano, reflecting the feeding behaviour of the bats and swiftlets over coastal and riverine vegetation communities. ‘Hell Trench’ – the area from which stratigraphic pollen work (Hunt et al. 2016) was done in the cave – lies in the front of the airfall zone, in the topographic low between the entrance talus/flowstone rampart and the guano mound which dominates the rear of the cave.

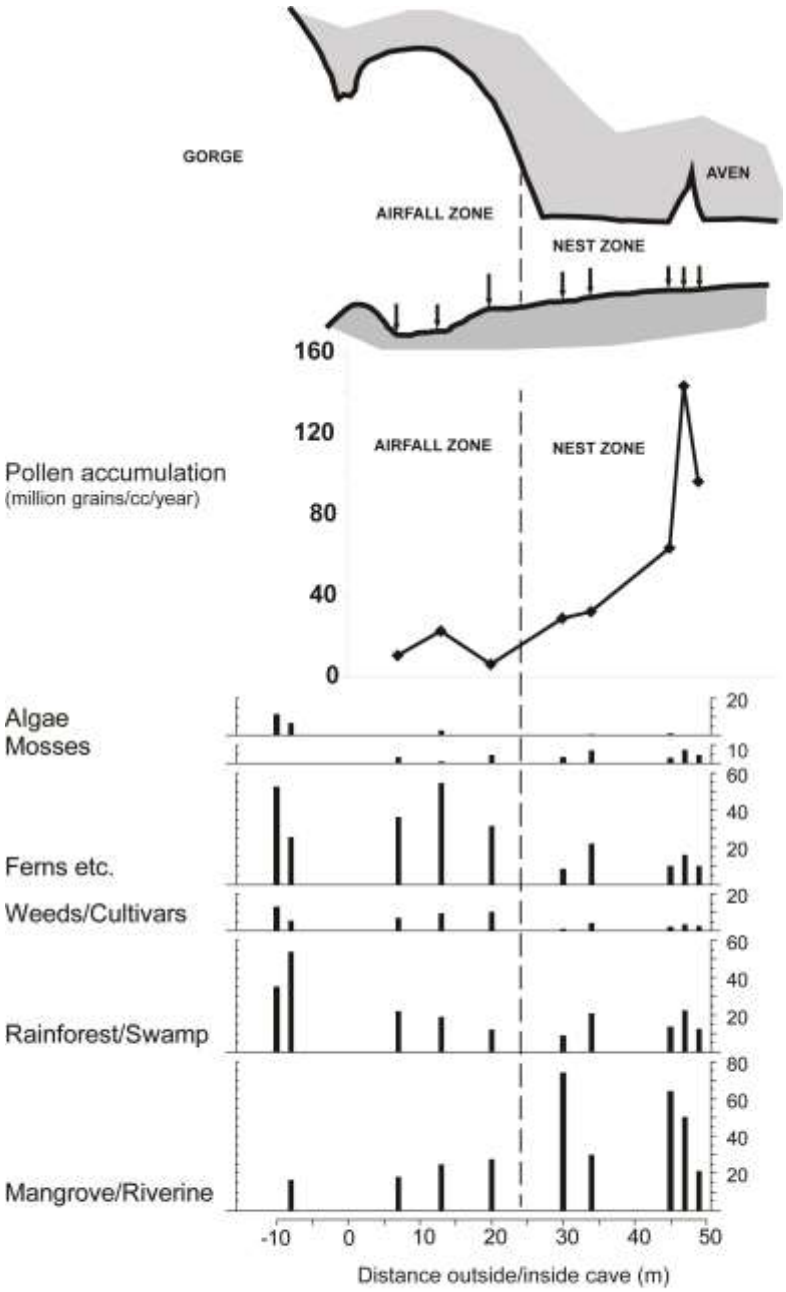
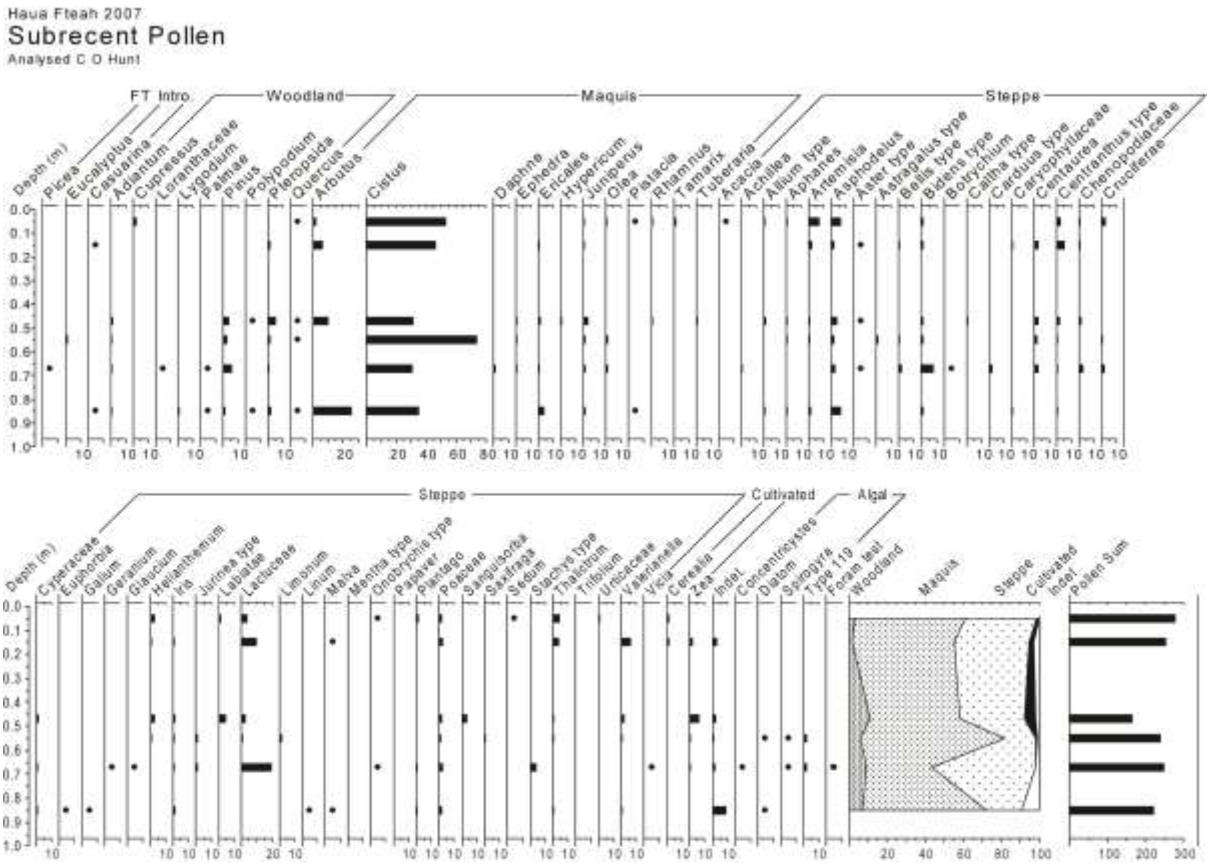


Figure 4. At the Haua Fteah, Libya, subrecent *fumier* deposits are dominated by *Cistus* and *Arbutus*, reflecting sheep, goats and cattle grazing in wadis where vegetation is dominated by these maquis species, several km away from the cave. Pollen traps and sticky slides suggest that the local airfall pollen is dominated by Juniperus and Poaceae (Simpson & Hunt 2009; Simpson 2016).



CAPTIONS TO TABLES

Table 1: Airfall pollen accumulation rates in caves compared with pollen influx figures outside the same caves

Vegetation type	Cave pollen influx: pollen grains per cm^2 per year	External pollen influx: pollen grains per cm^2 per year	Author
Temperate woodland, shrubs and herbaceous vegetation	84-488	7800	Coles & Gilbertson (1994)
Mesic temperate forest	61-1685	8605-48200	Burney & Piggott Burney (1993)
Herb-rich steppe with some trees	4-6	n/a	Fiacconi & Hunt (in press)
Wet lowland tropical forest	62-225	n/a	Hunt & Rushworth (2005)