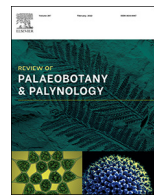




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# Review of Palaeobotany and Palynology

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## Editorial

# Palaeobotanical records from cave environments

## 1. Introduction

Caves have been historically sources of literary and mythological inspiration, settings for geographical, geological, and biological research and, undoubtedly, cornerstones for archaeology and paleontology. This special issue deals with caves as sources of knowledge on past ecosystems, with special attention to pollen, macrofossil, and charcoal analyses.

Palynology of cave sites deserves special attention. Ever since pioneer works (Dimbleby, 1957, 1961a, 1961b, 1962; Girard and Renault-Miskovsky, 1969; Leroi-Gourhan, 1973; Damblon, 1974; Bui-Thi, 1974; Dimbleby and Evans, 1974; Greig and Turner, 1974; Leroi-Gourhan and Renault-Miskovsky, 1977; Bastin, 1978; Dupré, 1979; Scott, 1982; Bryant and Holloway, 1983; Boyer-Klein, 1984; Dimbleby, 1985; O'Rourke and Mead, 1985), followed by the works of Dupré (1985, 1988), Burjachs (1986), Cattani and Renault-Miskovsky (1989), Davis (1990), García Antón and Sáinz Ollero (1991), Carrión (1992a, 1992b), Horowitz (1992), Kelso (1993), García-Antón (1995), Scott (1995), Carrión and Munuera (1997), Carrión et al. (1998), López-García et al. (2002); López Sáez et al. (2003), and González-Sampériz (2004), among others, the palynology of cave sites has been giving rise to controversy. In the beginning, it was not generally accepted, for instance, that cave sediments could contribute in conjunction with archeological inquiry to the reconstruction of prehistoric environments (Bottema, 1975; Bottema and Woldring, 1994; Coûteaux, 1977; Turner and Hannon, 1988; Sánchez-Goñi, 1991, 1994). As pointed out by authors such as Hall (1981), Dimbleby (1985), Hunt (1994), Weinstein-Evron (1994) and Carrión et al. (1999a), skepticism was fed by the possibility of gaps in the pollen sequences due to stratigraphical discontinuities, differential preservation or destruction of palynomorphs, pollen transport by animals causing over-representation of some taxa, and reworking or contamination of sediments by younger pollen.

In the face of these drawbacks, studies were carried out comparing pollen spectra of cave and rock-shelter sediments with pollen rain and vegetation of the cave mouth, and of the wider environment beyond. Pollen-analytical examination of modern surface sediments was aimed at determining the degree of fidelity of pollen assemblages from cave sediments relative to the external vegetation. In this line, some works suggested that the record of present-day sediments from caves might be better than those obtained from artificial pollen traps (Hunt and Coles, 1988; Burney and Burney, 1993; Coles and Gilbertson, 1994; Hunt and Rushworth, 2005). Prieto and Carrión (1999) and Navarro et al. (2000, 2001) studied dust samples from surfaces of several caves differing in location, morphology, size, and position of the entrance. They compared these pollen spectra with (i) those of a mixture of moss polsters and surface sediment from the vicinity of each cavity (local pollen rain) and (ii) samples of surface sediment embracing a range of 20 km around each cave site (regional pollen rain). In order

to ascertain the suitability of caves for pollen analysis, Navarro et al. (2000, 2001) developed a linear regression model, which statistically contrasted internal and external pollen input at the sample level. The model also produced a relationship between pollen percentages of each internal sample and external percentages. The conclusions were that depositional and preservational features of the pollen spectra inside caves are uneven and influenced by the cave morphology, sedimentary types, pollen transport by animals, periodic flooding and human activities. In addition, it is clear that caves with large entrances and isodiametric chambers show fewer problems of alteration in the pollen spectra and will probably have higher pollen influx than caves with smaller entrances.

Other empirical studies have suggested that sediments associated with dry depositional and post-depositional conditions may be reliable materials for environmental reconstruction from pollen analysis in cave sites (Carrión et al., 2009, 2013; Fiacconi and Hunt, 2017). It seems that desiccation is a desirable property as it enhances microfossil preservation and minimizes bioturbation (Davis, 1990; Navarro et al., 2001; Carrión et al., 2009; Lebreton et al., 2010), while episodically or perennially wet cave sediments seem to rarely preserve pollen well. On the other hand, while speleothems were long thought to be unsuitable for pollen preservation (Carrión and Scott, 1999), several studies show their potential, especially if the speleothems lie close to cave openings have been growing in a well-ventilated cave and sometimes under other circumstances as well (Brook et al., 1990; Carrión, 1992a; Burney and Burney, 1993; McGarry and Caseldine, 2004; Sniderman et al., 2016, 2019; Festi et al., 2016; Matley et al., 2020). Furthermore, speleothems up to ca. 600 ka can be accurately dated using the U-Th system (Cheng et al., 2013) while older samples can be dated using the U-Pb system (Woodhead et al., 2010, 2019, 2022). Therefore, pollen records from speleothems can help to chronologically constrain vegetation changes far beyond the radiocarbon limit (Meyer et al., 2009; Sniderman et al., 2016; Luetscher et al., 2021; Honiat et al., 2022).

In a review paper on the taphonomy of cave floors pollen assemblages, Hunt and Fiacconi (2018) concluded that (i) the pollen and spores reaching floors of cave entrances are generally representative of vegetation in the vicinity of the cave; (ii) the representation of anemophilous taxa declines with depth in caves of simple morphology; (iii) the complexity of taphonomic patterns in pollen spectra increases in morphologically-complex cavities and where animals, including humans, have utilized the caves for any purpose; and (iv) taphonomic effects relating to sedimentation or diagenesis may be seen through disproportionate percentages of durable pollen types, with supporting evidence from sedimentological techniques, particularly micromorphology. Hunt and Fiacconi (2018) recommend taphonomic evaluation of the site and selection of sampling sites within areas dominated by relatively simple pollen fallout near the mouths of caves.

We must now admit that the taphonomy of pollen assemblages in caves has not yet been sufficiently developed to make more precise recommendations. Sampling work for pollen is a complex process in which, whenever possible, the palynologist should try to avoid areas with apparent or suspected bioturbation, areas under drip points, or bat or bird colonies, other areas with fallen blocks, and narrow areas at the bottom of the cave. It is also important to replicate the sampling in several correlative stratigraphical sections in order to disentangle vegetation trends from changes in taphonomy. To the extent possible, a brief survey of surface pollen rain should accompany the site's paleoecological record.

The future could perhaps lie in revisiting some ideas that seem more than relevant to the experimental deficit. Advances such as ultraviolet fluorescence microscopy, facilitated by digital image analysis (Hunt et al., 2007), may help assess the stratigraphic integrity of pollen assemblages where mixing is suspected. It seems that, as pollen 'ages' taphonomically, the intensity of fluorescence diminishes and color progresses from blue, through yellow, to orange, red, and finally brown. Recycled material is less bright and can also be identified (Hunt et al., 2007). The palynofacies technique (Hunt and Coles, 1988) can also provide signatures useful for resolving taphonomic uncertainties in the investigation of palaeoecological patterns.

Because of a decreasing number of researchers during the last decades and a clearly insufficient experimental effort, cave palynology continues on its way with the aforementioned pitfalls while trying to provide palaeobotanical and, when possible, palaeoecological records. Generally, uncertainties apart, palynologists now accept cave pollen spectra as evidence of past local vegetation to a variable degree, and on occasions, as representing the regional flora (e.g. Messenger et al., 2011; Burjachs et al., 2012; Revelles et al., 2016). In some regions, the number of studies on palaeofloras and palaeovegetations in caves is considerable, as is the case of the Iberian Peninsula, France, and Italy (Carrión et al., 2013; Edwards et al., 2015). In this region, a number of Quaternary cave paleorecords coincide closely with well-established regional pollen records from lakes and peat bogs, and paleoclimatological inferences from sedimentological, paleontological, and charcoal findings at the wetland sites (Burjachs and Julià, 1994; Carrión et al., 1999a, 2010, 2013; López-Sáez et al., 2007; González-Sampérez et al., 2010; Burjachs et al., 2012), confirming the complementary nature of cave and wetland archives. Finally, it is also remarkable that some palynological records in caves, with good pollen preservation, taxonomic discrimination, and stratigraphical control, have managed to change concepts about the structure and plant diversity of Quaternary paleoecosystems linked to glacial refuges of temperate and Mediterranean woody species (González-Sampérez et al., 2010; Carrión et al., 2003, 2018, 2019a, 2019b; Magri et al., 2017; Camuera et al., 2019; Ochando et al., 2019, 2020a, 2020b, 2020d).

Coprolites and other fossil fecal deposits, sometimes frequent in cave sediments, may exhibit good pollen-analytical properties for paleoenvironmental reconstruction (e.g. Scott, 1987, 1994; Betancourt et al., 1989; Horwitz and Goldberg, 1989; Reinhard and Bryant, 1992; Scott and Cooremans, 1992; Alcover et al., 1999; Carrión et al., 2000, 2001, 2006, 2007, 2008, 2018; Hunt et al., 2001; Pearson and Betancourt, 2002; Scott et al., 2003; González-Sampérez et al., 2003; Yll et al., 2006; Burry et al., 2008; Velázquez et al., 2010, 2015; Martínez-Tosto et al., 2012; Wood et al., 2012, 2021; Gatta et al., 2016; Djamali et al., 2020; Ochando et al., 2020c).

Pollen analysis of bat dung has also shown potential in palaeoecological studies (Bui-Thi and Girard, 2000; Leroy and Simms, 2006; Maher, 2006). The mechanisms of incorporation of pollen grains and spores into bat guano are: (i) direct ingestion of insects that are themselves covered by pollen or whose digestive system contains pollen, (ii) together with fragments of bat skin and hair during grooming, and (iii) dust brought onto guano by air currents. Carrión et al. (2006) showed that pollen analysis of fresh bat guano can reflect local vegetation of the environments surrounding the cavities where bat colonies settle.

In addition, bat guano may be a good tool for obtaining information on entomophilous plants otherwise under-represented in peat bogs and lake sediments.

Experimental work is worth mentioning, especially when applicable beyond temperate and boreal regions. Carrión (2002) investigated the pollen-vegetation relationships in samples from soil surfaces, animal dung of different origin, and sediments in depressions or basins that, in theory, should have pollen spectra that are comparable to those from sedimentary basins elsewhere. Pollen spectra from depressions were very sensitive to long-distance wind and water transport, thus masking the representation of pollen from the surrounding insect-pollinated vegetation. Interestingly, pollen spectra from dung were the excellent analogues of local and regional vegetation and showed the best analytical potential in terms of pollen concentration and taxon diversity. Pollination properties of the species studied indicated they will rarely be found in lake bottoms.

Remarkably, analysis of charcoal from archeological contexts has been developing since the beginning of the second half of the last century. Since carbonization facilitates preservation, anthracology has been one of the most recurrent archeobotanical disciplines. Indeed, the remains of charcoal in sediments of anthropic origin are very frequent. As with palynology, in its beginnings the discipline was not exempted from methodological debates; in this case, pitting the power of paleoecological interpretation against the imperative to limit inference to issues of fuel paleoeconomics (Salisbury and Jane, 1940; Godwin and Tansley, 1941). Paleoecological anthracology had a great development in France through the Montpellier School (Vernet, 1967, 1973; Badal et al., 1994; Chabal, 1997). Many recent works tend to be integrative and avoid the old scholastic biases, so that the paleolandscape is harmonically associated with the paleoethnological (Allué, 2002; Asouti and Austin, 2005; Piqué, 2006; Carrión-Marco et al., 2010; Zapata et al., 2013; Badal and Martínez-Varea, 2018; Uzquiano, 2019; Real et al., 2022).

In this Special Issue, thirteen new cave-based studies, providing interesting palaeoecological, archeological, and pollen-taphonomic information, are presented. The cave infills of Grotta Romanelli in Apulia, Italy, have been sampled for pollen by Ermolli et al. (2022). The site is archeologically renowned for its rich Middle and Upper Paleolithic industries. Pollen analyses have been primarily performed on *Terre rosse*, a lithostratigraphical unit of supposed interstadial age, and secondly, on a more recent *Terre brune* unit, dated to the latest Pleistocene-Early Holocene. The occurrence of *Olea* all throughout the *Terre rosse* suggests this unit belongs to the Last Interglacial (Eemian), during which this species was widespread in the Mediterranean basin. This chronology would involve a change in the stratigraphical interpretation of the beach below the *Terre rosse*. The *Terre brune* deposition may have taken place under steppe landscape conditions. The abundance of several herbs, occasionally found in clusters, suggests intentional introduction by humans (Neanderthals and/or *Homo sapiens*) into the cave. This is the case with *Crithmum maritimum*, *Muscari comosum*, and *Asparagus maritimus/Ornithogalum*, whose taxonomic affinities have been deduced from the local abundance and the high frequency in the fossil pollen record. *Asparagus* could have been consumed in bulbs and young sprouts.

Ruiz-Alonso et al. (2021)'s paper deals with fossil pollen and archeological charcoal of three cave sites from northern Morocco: Kaf Taht-el-Ghar Cave, 8 km southeast from Tetuan, and two sites within the El Khil cave complex, close to Tanger. The Tingitana Peninsula, where the sites are located, is a region relevant to investigate the onset of the Neolithic in a strategic region next to the Strait of Gibraltar. The authors infer the past vegetation of the area as well as the impact of human activities on the landscape. Palynologically, they pay special attention to pollen grains from cultivated species as well as to non-pollen palynomorphs linked to livestock grazing, fire events, and arid phases. The indicator value of such non-pollen palynomorphs as *Pleospora*, *Chaetomium*, *Podospora*, *Sordaria*, and *Gelasinospora*, is

stressed. Charred-wood remains document the exploitation patterns of forest resources by the settlers, as well as their uses of timber. Kaf Taht-el-Ghar displays a long archeological sequence with Paleolithic, Epipaleolithic, Neolithic, and Historic occupations. The pollen sequence documents the depletion of Pleistocene pine and juniper forests during the Epipaleolithic and the associated spread of grasslands while stands of oak remain scattered. Both, the palynological and anthracological records, suggest that the disappearance of *Abies pinsapo*, *Cedrus atlantica*, and *Taxus baccata* was synchronous. Cereal and broad beans (*Vicia faba*) are detected as early as the onset of the Neolithic, in both cave systems. These agricultural activities coincide with the establishment of a cultural landscape in the region, which is basically the result of forest clearance and spread of thermophilous shrublands and olives. Human pressure is also visible through grazing activities.

A combination of pollen, charcoal, and seeds is one of the best approaches to the reconstruction of past environments through cave sediments. To this purpose, Revelles et al. (2022) evaluate the potential of cave and rock-shelters integrating archeobotanical data from several NE Iberian sites, with occupations from the Middle Paleolithic to the Bronze Age. The re-visited pollen records provide information on the vegetation and climate changes during the late Quaternary, although the authors stress the need for considering pollen transport in shaping cave pollen spectra, with emphasis on anthropogenic input of plant materials to the cave sediment. The charcoal records provide information on the local vegetation landscape and data on plant resources exploited by humans. For instance, they show the importance of conifers in Pleistocene sites together with the fact that several taxa underrepresented in pollen studies (i.e. *Laurus nobilis*, *Taxus baccata*, *Juniperus*) were important sources of fuel for past societies. The record of preserved seeds shows the presence of edible wild fruits since the beginning of the sequences, and cultivated and synanthropic plants from the Middle Holocene onwards. In addition, they discuss the importance of fumer deposits to study herding practices, seasonality, and waste management in prehistoric societies (Expósito and Burjachs, 2016; Burguet-Coca et al., 2020).

Integrating results of pollen and plant macrofossil analyses of sediments from two archeological caves in Neuquén Province, Argentina (Epullán Grande and Epullán Chica), Prieto et al. (2021) describe vegetation, climate, and plant-human interactions during the Holocene in northwestern Extra-Andean Patagonia, Argentina. The sites studied lie within the Shrub-grass Steppe, for which paleoecological studies are needed. This is a region where lakes are scarce and usually ephemeral. In their absence, these cave records are able to inform on the Holocene vegetation history of this arid land, and additionally on the relationships between landscape and human occupations. The Early Holocene (ca. 11,400–8500 cal. BP) shows a grass steppe associated with colder and moister conditions than today. Mid-Holocene (ca. 8500–5800 cal. BP) environments are shrubbier, with a plausible increase in temperature and aridity. After ca. 5800 cal. BP, winter precipitation, summer dryness and a greater climate variability between ca. 2500 and 1600 cal. BP, would have promoted an expansion of shrubs over grasses, and the establishment of a shrub-grass steppe resembling modern-day ecosystems. The authors infer paleoclimatic conditions which would differ from other Patagonian areas. This disparity would be more accentuated, however, during the Early and Late Holocene. It seems that hunter-gatherers were present in the study region as soon as at ca. 8000 cal. BP, and their populations expanded after ca. 5800 cal. BP. It seems that northwestern Patagonian caves were firstly exclusively used as burial places. Between ca. 8500 and 5800 cal. BP, they show signs of processing and anthropic deposition of plant macrofossils, including *Larrea nitida*, grasses, and *Austrocaactus* aff. *Bertinii*. Grass, leaves, and twigs were used to prepare the occupational surface. *L. nitida* stems were probably used for firewood due to its content of resins. Interestingly, the use of plants by hunter-gatherers intensified and diversified after 5800 cal. BP. Shrubs such as *Colliguaja integerrima*, some species of Asteraceae, *Mulinum spinosum*, *Schinus* spp., *L. nitida* and *Berberis* sp., as well as a

fragment of charred wood of *Prosopis denudans* and wood, fruits and leaflets of *Geoffroea decorticans*, are shown in the macrofossil records. These species may have been used to prepare settlement surfaces, storage and burials, for fuels, food, and medicinal purposes (especially cacti as flocculants). This study is of great ethnobotanical value, and opens new avenues of research on several plant groups such as Loranthaceae, that occurrence in the pollen record is difficult to interpret.

Ochando et al. (2022) report on the late Pleistocene vegetation in Vale do Lapedo through pollen analysis of coprolites (probably carnivores) from Gravettian levels of Abrigo do Lagar Velho rockshelter. The vegetation between ca. 30 and 27.3 ka cal. BP is a mosaic dominated by *Pinus*, Poaceae, *Erica*, *Artemisia*, *Juniperus*, and *Quercus*. These taxa are accompanied by other broad-leaf trees, Mediterranean woody shrubs and trees, conifers, xerothermophytes, indicators of saline substrates and heliophytes such as *Erica*, Asteroideae, Cistaceae, *Ephedra fragilis*, and *E. distachya*. Mediterranean forests with *Quercus ilex*, *Q. suber*, *Pinus pinaster*, *P. halepensis*, *Olea europea*, *Pistacia lentiscus*, *Myrtus communis*, *Erica arborea*, and a diversity of shrubs, clearly developed in the vicinity, along with potentially riparian taxa such as *Alnus*, *Frangula*, *Fraxinus*, *Ulmus*, and *Salix*. The appearance of a gallery forest near the site is in itself evidence of fresh water availability for humans and hunted animals that frequented the region. These results connect with ongoing debates on the persistence of human populations in the coastal shelves of southwestern Iberia during the Pleistocene (Finlayson and Carrión, 2007; Carrión et al., 2019a).

Velázquez and Burry (2022) provide pollen analyses of Holocene camelid coprolites from Patagonia. Camelids were one of the main resources of hunter-gatherers inhabiting this region. The coprolites were sampled from levels dated between 5900 and 6260 cal. BP in the site Cueva Milodón Norte 1 within the area of the Pueyrredón Lake. Coprolite pollen spectra are characterized by *Nothofagus*, Asteroideae, *Cerastium*, and Poaceae, with relatively high pollen concentrations (24,000–111,000 grains/g). Some taxa are characteristic of the present-day *Nothofagus* forest, including Onagraceae, *Lathyrus* and the fern *Blechnum*. It is concluded that the camelids used both the steppe and the forest in search of food.

Scott et al. (2022b) report on three fossil hyrax dung sites lying along a north to south transect between 21°S and 24°S in southern Africa. The fecal deposits of *Procavia capensis*, so-called hyrax middens, are paleolatrines with characteristics that are particularly interesting for palynology. First, the urine cements the excrement almost simultaneously with its formation. Second, they can be stratified deposits for many thousands or tens of thousands of years and create a very favorable microenvironment for pollen preservation. On the other hand, hyraxes gather and consume a very wide range of plant species. Hence, hyrax dung palynology has been very successful in Quaternary paleovegetation studies (Scott, 1994, 1996; Carrión et al., 1999b; Scott et al., 2004, 2022a; Gil-Romera et al., 2006; Chase et al., 2010, 2012, 2013; Quick et al., 2011). In addition, isotopes obtained from hyrax dung can also inform about paleoclimates, and the potential of new research is expanded through aDNA and other remains such as plant cuticles and insects (Chase et al., 2010).

Scott et al. (2022b)'s paper combine pollen and geochemistry to shed light on the Holocene environmental history of central Namibia, Africa. Poaceae-dominated communities suggest that the early Holocene between ca. 9.6 and 7.7 ka was relatively humid. Thereafter, a series of step-wise changes occurred, including the prominence of different pioneer plant communities of which changes in ratios between grassy and shrub pollen types, suggests moisture oscillations. Increased C4 plants around ca. 4.5 ka indicates the development of a different climatic regime and a subtropical savanna towards the south at c. 24°S. The authors interpret this environmental change as a biotic response to a shift in the rainfall distribution between an early, more even seasonal distribution and the current late Holocene summer rainfall regime.

Basumatary and Tripathi (2021) investigate the preservation of pollen grains, spores and non-pollen palynomorphs on bat guano samples

from Eraaning Cave in Meghalaya, India, and related the pollen spectra with the present-day vegetation of the vicinity. The results are stimulating for future paleoecological research in Meghalaya, a region with an abundance of cave habitats. The pollen in samples of bat guano is a good reflection of the tropical mixed deciduous forest, incorporating anthropogenic pollen indicators (*Areca*, *Psidium*, *Cerealia*, *Melastoma*, *Citrus*), pollen taxa from riparian biotopes and from evergreen plant species from not only local but also extra-local vegetation. This study supports former palynological research on bat guano (Hunt and Rushworth, 2005; Carrión et al., 2006; Batina and Reese, 2011; Feurdean et al., 2011; Marais et al., 2015; Basumatary et al., 2020). Nevertheless, it is worth noticing the importance of establishing the animal vector. In this case, the cavern is home to multiple bat species, mainly *Rhinolophus subbadius*, *R. pusillus*, *R. pearsonii*, and *Miniopterus schreibersii*, all of which are primarily consumers of flying insects (moths, beetles, flies, leaf hoppers, etc.) and other arthropods which feed on fruits, nectar, and flowers, and fishes. This diversity may have promoted a rich pollen assemblage within the bat guano samples.

Mas et al. (2022) contribute to this issue with a thorough study of fossil charcoal from Cova Colomera (Central Pre-Pyrenees, northern Spain), a good archeological model system to explain early herding activities, in this case by Neolithic and Bronze Age human groups. The cave contains fumiers deposits typical of husbandry activities. The authors provide a vegetation sequence and a hypothesis of the processes controlling vegetation changes in connection with climatic variations and anthropogenic disturbance. It is shown that, during the Middle Holocene, the region was dominated by mixed oak forests with other deciduous trees and conifers. These pristine ecosystems survived during the Late Holocene, but showing internal dynamics characterized by the progressive increase of evergreen oaks at the expense of conifers. Herding activities do not appear to have affected substantially the vegetation of these mountains whereas landscape clearing is unrecognizable.

By means of the identification of charcoal and seeds, Carrión-Marco et al. (2022) study the vegetation dynamics of a region of northern Africa during the Pleistocene–Holocene transition, and the beginning of farming. Gueldaman GLD 1 Cave shows the longest archeobotanical sequence available to date for Algeria. In addition, the authors provide information on the use of this cave by human communities during the prehistory. With remarkably fine resolution, they also document the colonization of the site by Cupressaceae, a conifer, at the onset of the Holocene, along with the gradual integration of sclerophyllous angiosperms, especially species of *Pistacia*. The Neolithic phase is dominated by *Olea europaea* accompanied by *Arbutus* and evergreen *Quercus*, among others.

Vidal-Matutano et al. (2022) report charcoal analysis from De Nadale Cave in northeastern Italy. Dated to c. 70 ka BP (MIS 4), this Mousterian site offers a unique opportunity to work on a very poorly documented period of Neanderthal evolution. The anthracological work on De Nadale material shows the abundance of *Picea*, *Larix*, *Pinus sylvestris*, and *Betula*. These findings suggest the existence of a cold and humid climate in the vicinity of the site. It seems that a lowering of the subalpine vegetation belt occurred during this time period. Apart from the paleolandscape reconstruction, the authors have developed experimental research on charcoal preservation, noticing decay prior to charring caused by fungi and insects. This observation is particularly conspicuous for the *Pinus sylvestris* samples where large transverse bore holes in earlywood degraded tracheids are documented. The palaeoecological picture fits into the paleozoological inference including small mammals, and also with the regional reference pollen sequences.

On a more purely experimental ground, Vidal-Matutano et al. (2021) provide an impressive dataset of microscopic decay features in charcoal of *Pinus canariensis*. Hitherto within the Prehispanic Canary Islands, fuel gathering strategies were interpreted as the result of a taxonomic selection based on specific wood physical properties, paying insufficient attention to wood soundness, which could have significantly

weighed on indigenous firewood selection, hearth functions, and supply areas. This work confirms the correlation between the macroscopic and microscopic state of the wood, with a gradual trend from healthy to rotten, according to varying proportions of low to high micromorphological alteration features within each charcoal assemblage. New data are also provided on charcoal vitrification. High frequencies of vitrified pieces within a batch composed of pitch wood with highly degraded sapwood suggest a connection between vitrification and the combustion of high resin contents. This study has biogeographical implications to the history of the *Pinus canariensis* and the role played by humans on its current distribution and its auto- and synecology. This is a pioneering study in Prehispanic context of the Canary Islands contributing to a better understanding of firewood management. Beyond that, it is an empirical approach applicable to charcoal analyses in caves.

Atkins et al. (2022) investigate the preservation quality of Quaternary plant macrofossils of Casuarinaceae, *Astroloma humifusum*, *Banksia marginata*, and *Eucalyptus* species for Robertson Cave, in the World Heritage listed Naracoorte Caves in Australia. Robertson Cave shows a continuous fossil record embracing the period from the Last Glacial Maximum to the present day. With this taphonomical research, the authors demonstrate that fossil preservation is variable among taxa and plant organs, with woody endocarps and fruits being better preserved than leaves and flowers. In some cases (*Eucalyptus* spp.), the age of the sedimentary matrix may be influential on preservation, but this pattern is not general. Thus, *B. marginata* and *A. humifusum* have a high preservation potential, regardless of age. In other cases, fire may have affected the preservation of plant taxa. This study shows the challenges of vegetation reconstruction through macrofossils: preservation and floristic changes may be difficult to disentangle. Either the case, plant macrofossil may provide a taxonomic detail impossible to reach with pollen analysis.

Caves are definitely valuable potential archives of paleoecological information. Here we have brought some significant examples along with a review of the state of the art. However, let's put it this way: "methodologically" we have not reached the ceiling... This means that there are still many aspects of palaeobotanical/palynological research in caves that can be improved. More work could be done to refine the stratigraphic resolution of some records, the taxonomic discrimination of others and, above all, the patterns and processes that configure taphocenoses in caves. If we had to prioritize, apart from research with aDNA, we think that experimental research on the mechanisms of incorporation and preservation of pollen grains, spores, charcoal, and other microfossils, requires urgent and specifically oriented projects.

## 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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