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Cave surface pollen and the palynological potential of karstic cave sediments in palaeoecology

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Abstract

Palynological results are presented of surface cave sediments from six caves of southeastern Spain, which differ in location, morphology, size, orientation and number of entrances. The results address several issues of pollen taphonomy in a cave environment. Modern sediments from caves contain pollen assemblages that may reflect local and regional vegetation even better than those obtained in the exterior environment. Cave geometry is an important factor affecting the quality of pollen spectra registered inside the cavity. Generally, the highest concentrations of palynomorphs are observed in the cave entrance and in sediments associated to dry depositional conditions. Speleothems and wet carbonated sediments, and those obtained from wall and rear areas often contain altered pollen spectra. Biotically transported taxa can help to provide palaeoecological information. The depositional context is extremely complex and caution should be taken in palaeoecological reconstruction. Therefore, uniform rules for sampling strategy should not be applied to all cave sediments. © 2001 Published by Elsevier Science B.V.

Keywords: Taphonomy; palynology; palaeoecology; Spain; caves

1. Introduction

Cave sediments are important sources of palaeoenvironmental information in arid lands, where conventional deposits for pollen and macrofossil analysis are scarce (Davis, 1990; Horowitz, 1992). Cave palynology has great potential provided that it is based on several pollen sequences to give a coherent palaeoclimatological reconstruction (Carrión et al., 1999). Admittedly, scepticism arises on account of the absence of a firm experimental background for cave palynology (Turner and Hannon, 1988). Hitherto, most experimental studies have been conducted to determine the airborne pollen influx by using Cour filters (Burjachs, 1988), UFH filters (Loublier, 1974), modified Tauber traps (Burney and Burney, 1993), Petri dishes (Bui-Thi-Mai, 1974), and microscope slides coated in petroleum jelly (Van Campo and Leroi-Gourhan, 1956; Coles and Gilbertson, 1994). Overall, these studies suggest that airborne pollen can provide a reliable proxy of the external pollen rain (Burney and Burney, 1993). However, airborne pollen is only part of the actual pollen input in cave depositional environment, biotic transport is also a major source of organic remains in

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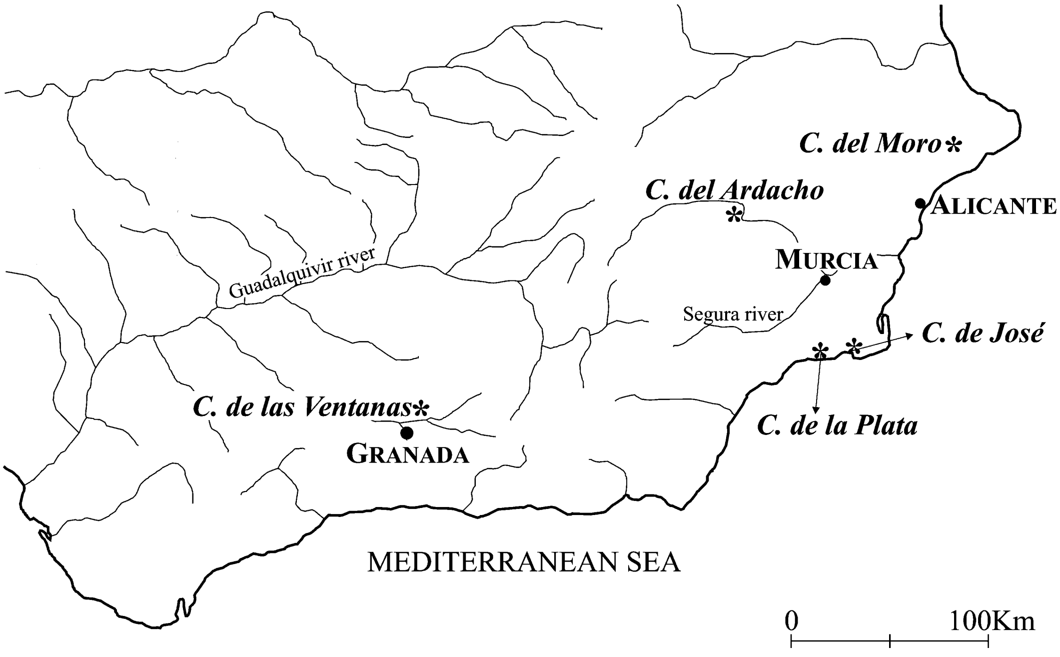


Fig. 1. Location of studied caves in southeastern Spain.

caves (Davis, 1990), and faecal materials may even contain reliable pollen spectra in terms of landscape reconstruction (Scott and Cooremans, 1992). In addition, streams entering cave systems and percolating water infiltrating through bedrock can be sources of pollen (Coles, 1988; Coles et al., 1989; Davis, 1990), especially in karstic cavities. The pollen record of surface sediments from two caves in southeastern Spain, both adjacent but different in morphology and sedimentary features was presented by Navarro et al. (2000) in a preliminary report. Pollen assemblages from these caves reflected the vegetation of both local and regional catchment areas. However, there were differences in reliability of the pollen spectra in relation to cave geometry, sediment humidity, and sample situation across the cave surface (Navarro et al., 2000). In order to contrast previous findings and construct a more robust picture of the pollen incorporation and pollen spectra reliability in cave systems, here we report results from four new caves based on the same sampling strategy. Future efforts will be devoted to assess the weight of post-depositional processes in shaping pollen spectra from cave sites.

2. Setting and description of the caves

The caves described below lie in southeastern Spain and differ in location, morphology, size, entrance orientation, and number of openings (Fig. 1). This region has been selected because, on account of its contrasting physiography, it represents an excellent model system to address palaeoecological issues, and because of its abundance of karstic caves, many of which have been unexplored or relatively little altered by man.

2.1. Cueva de las Ventanas (1040 m asl, 37°24′54″N, 03°25′17″W, Píñar, Granada) (Fig. 2)

A main chamber facing north and ca. 60 m deep, which lies beyond a narrow passage connecting with a second chamber and other secondary cavities. Floor sediment generally wet as a result of internal karst activity including dripping and superficial water movement.

2.2. Cueva del Moro I and Cueva del Moro II (843 m asl, 38°46′28″N, 00°31′07″W, Agres, Alicante) (Fig. 3)

Two caves belonging to the same karstic system,

Table 1
Internal samples from studied caves

	Sample no.	Sample type
Cueva del Moro I	20,21,23,28,29,31,33,34,36	Dry floor sediment
	37,38,39,42	Wet floor sediment
	22,24,26,27,30,32,41,43	Speleothem
	25	Bat guano
Cueva del Moro II	1,2,3,4,6,7,8,9,10,11,12,13,14,15,16,18	Dry floor sediment
	5	Speleothem
	17	Spider's web
Cueva de José	7,12,15,16,17,18,19,21,25,26,27	Dry floor sediment
	4,6,8,10,22,23,24	Dry sediment with dung (*)
	9,13,28,29,30	Dry organic sediment (**)
	1	Wet floor sediment
	14	Wet sediment with dung (*)
	11	Bird guano
Cueva de la Plata	1,2,4,8,9,10,14,16	Dry floor sediment
	5,6	Dry sediment with bat guano (*)
	11	Moss polster
	12	Speleothem
Cueva del Ardacho	4,8,11,16,17,18,19,21,24	Dry floor sediment
	6,12,20	Dry sediment with dung (*)
	3,6	Dry organic sediment (**)
	7,14,15	Dry sediment with spider's web (***)
	13	Wet floor sediment
	5	Bat guano
	1,2,23	Spider's web

connected at ca. 60 m depth and with their mouths orientated northwest and separated by ca. 15 m. Cueva del Moro I is 60 m deep, has two entrances and three chambers with "sac" cavities. Cueva del Moro II is 20 m deep, and has a single entrance and two chambers connected by three narrow passages. Karst activity is nowadays almost absent in Moro II but still perceptible in Moro I, where parts of the floor receives moisture from dripping water that forms carbonate crusts. In general, however, the floor sediment is dry and uncompacted (Navarro et al., 2000).

2.3. Cueva de José (400 m asl, 37°35′05″N, 01°09′08″W, Mazarrón, Murcia) (Fig. 4)

Simple "sac" cavity consisting of a single chamber ca. 17 m deep, 14 m wide, 4 m tall, circular in cross-section. It has a single circular entrance, facing northwest. The cave ceiling is 4–5 m high and shows no stalactites. The floor is mantled with fine and dry sediments containing abundant goat and boar faeces. Fallen blocks are common and sediments appear to have been removed in some parts of the cave (Prieto and Carrión, 1999).

2.4. Cueva de la Plata (116 m asl, 37°35′22″N, 01°12′55″W, Mazarrón, Murcia) (Fig. 5)

This cavity is southwest-facing with three entrances, and two openings on the upper part, and one on the floor level. The entrances are connected with a narrow passage leading to the main chamber, which is narrowed reaching 30 m deep. Dry sediment prevails throughout the cave surface.

2.5. Cueva del Ardacho (825 m asl, 38°20′30″N, 02°01′36″W, Férez, Albacete) (Fig. 6)

The outside cavity with multiple entrances leads

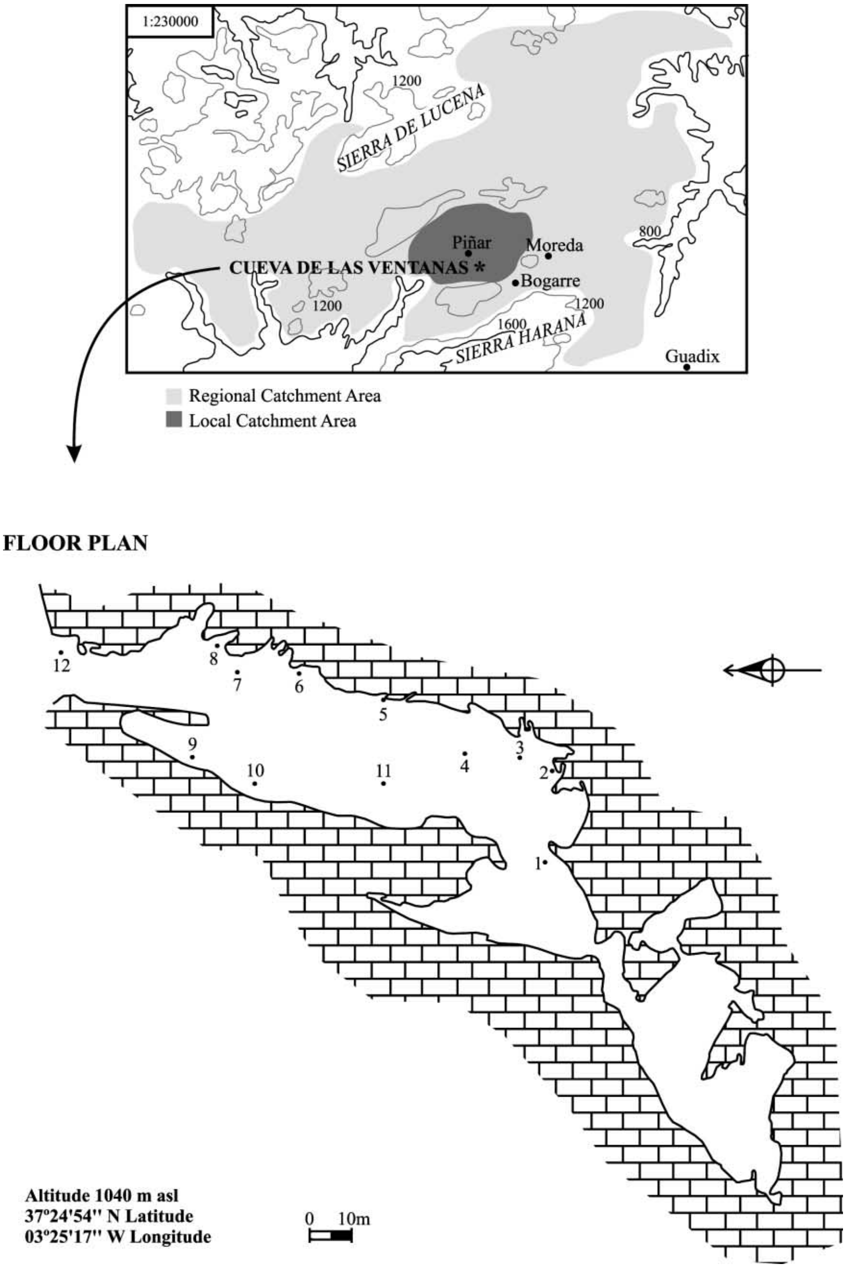
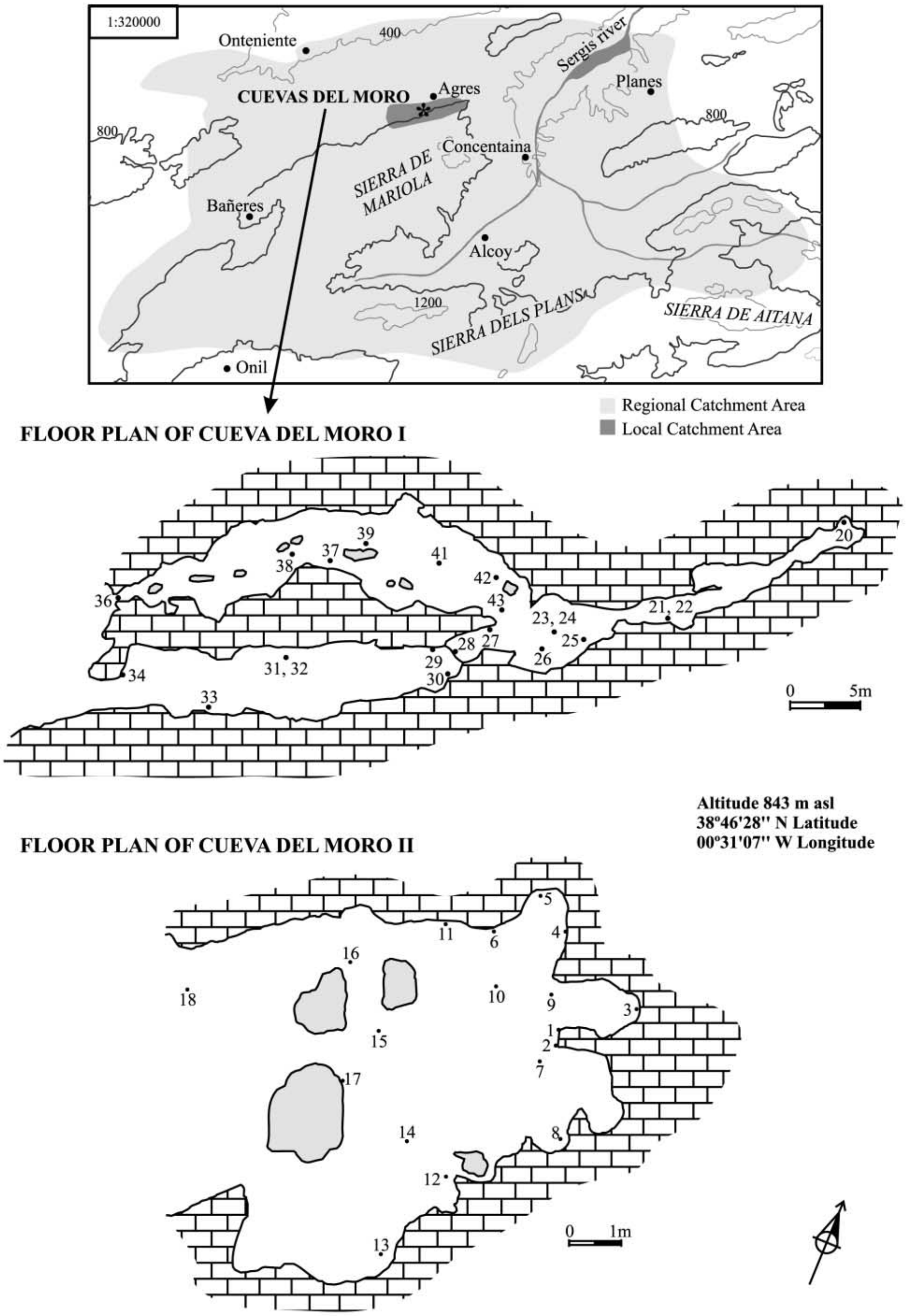


Fig. 2. Location and longitudinal section of Cueva de las Ventanas with location of pollen samples.

to the main chamber (II), and further to the smallest cell (III), and a wider chamber (I). The whole cave is ca. 30 m deep and faces northwest. Relatively dry sediment prevails throughout the cave surface.

3. Materials and methods

As in previous report by Navarro et al. (2000) in Cuevas del Moro, samples in Cueva de las Ventanas, Cueva de José, Cueva del Ardacho, and Cueva de la


FLOOR PLAN OF CUEVA DEL MORO I

FLOOR PLAN OF CUEVA DEL MORO II

Altitude 843 m asl
38°46'28'' N Latitude
00°31'07'' W Longitude

Fig. 3. Location and longitudinal sections of Cueva del Moro I and Cueva del Moro II with location of pollen samples.

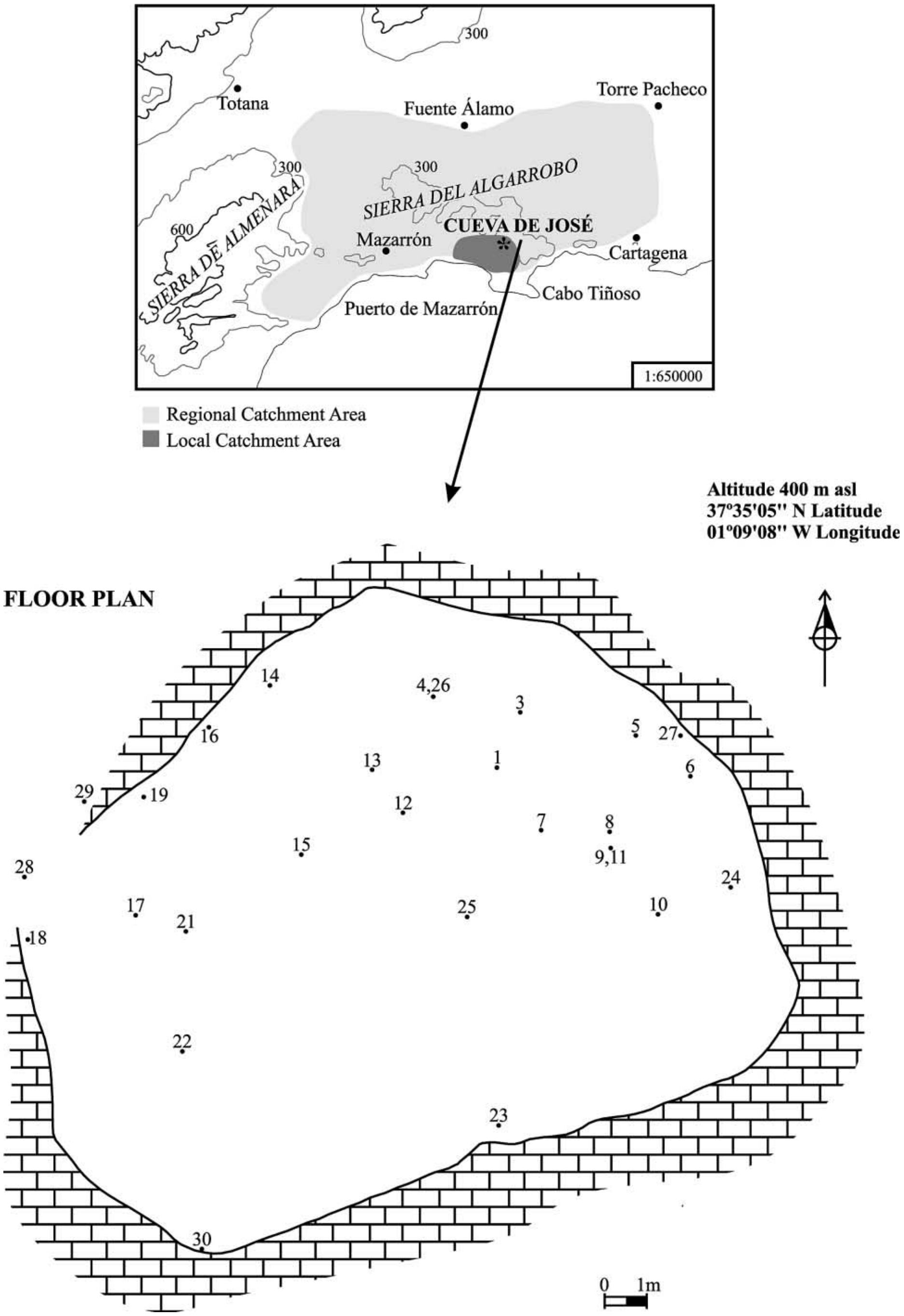


Fig. 4. Location and longitudinal section of Cueva de José with location of pollen samples.

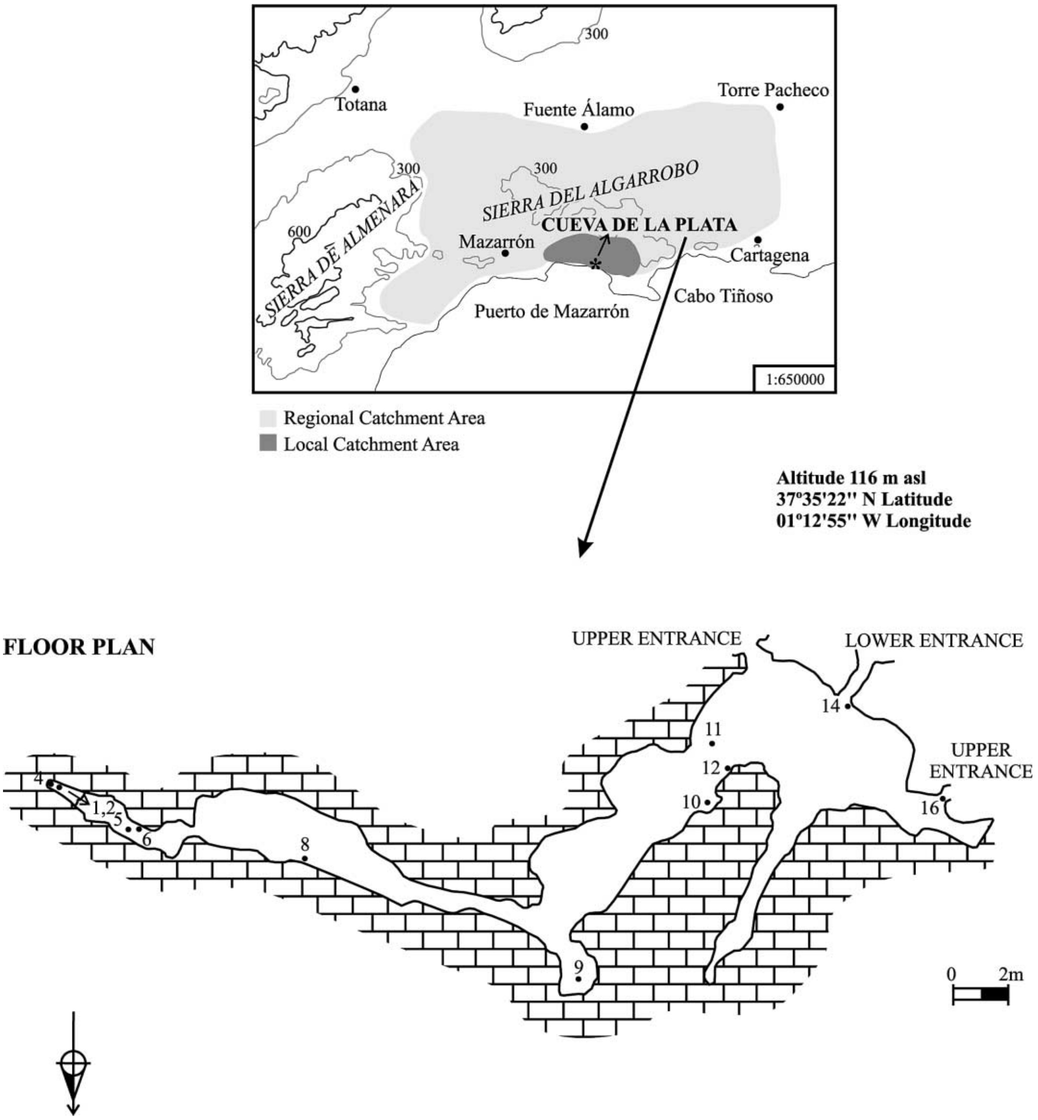


Fig. 5. Location and longitudinal section of Cueva de la Plata with location of pollen samples.

Plata, consisted mainly of floor sediment, but also speleothems, moss polsters, spider's webs, and animals's faeces (Table 1). Modern sediment samples were collected from throughout the surface by means of a spatula and avoiding foot print and disturbed areas. Laboratory treatment (5–15 g per sample) followed Girard and Renault-Miskovsky (1969). *Lycopodium clavatum* spore tablets of a known concentration were added in order to calculate pollen concentration per gram of dry sediment. In addition, a mixture of moss polsters and surface sediments from the cave surroundings and from 20 km around the sites were collected as control of local and regional pollen rain respectively (exterior surface). These local and regional catchment areas are shown in Figs. 2–6. Percentage pollen diagrams of selected taxa were plotted using Tilia and Tilia Graph programs (Grimm, 1991). Pollen types were grouped in two conventional categories according to prevailing pollination of their producing plant taxa: anemophilous

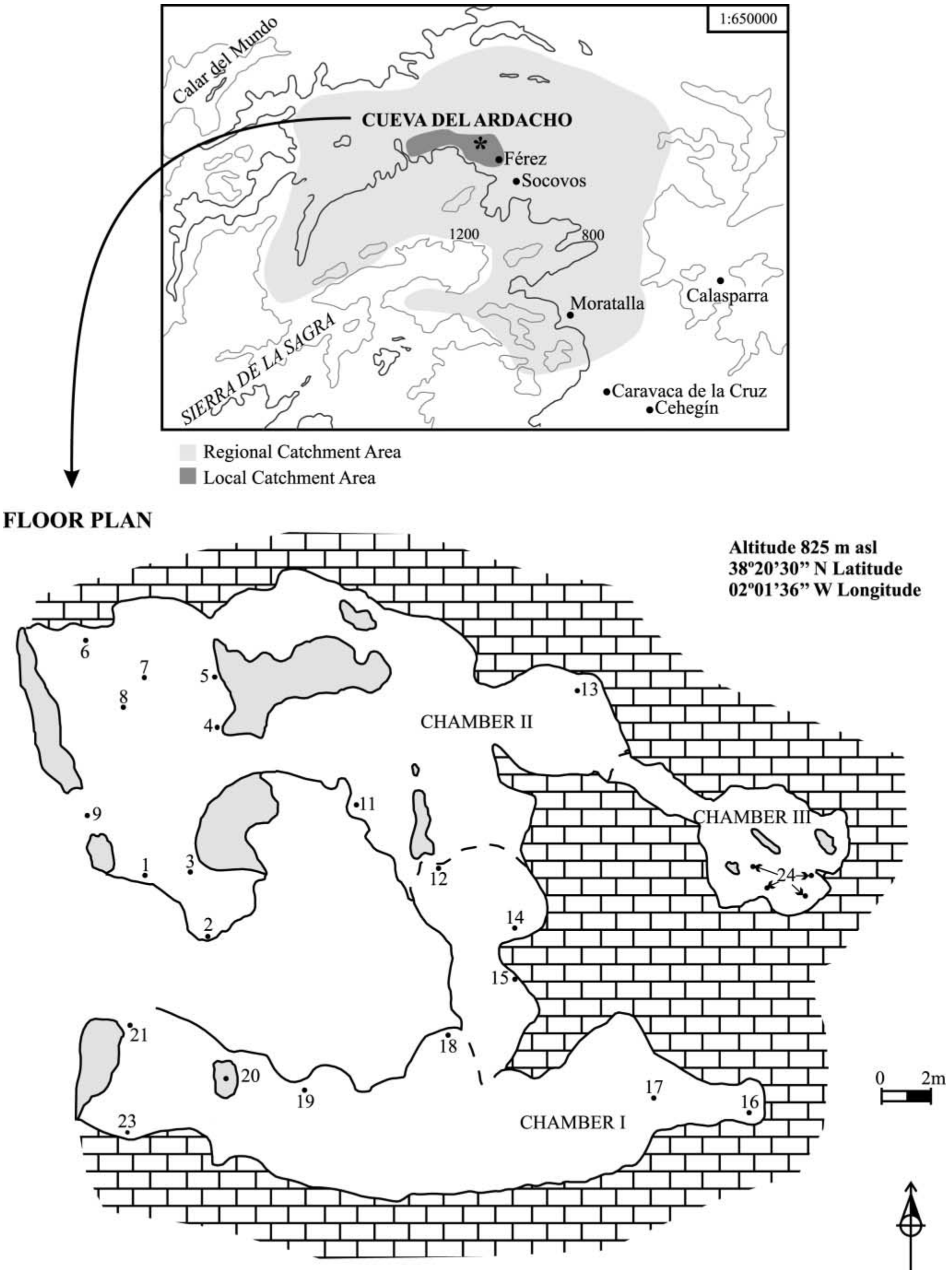


Fig. 6. Location and longitudinal section of Cueva del Ardacho with location of pollen samples.

and zoophilous (Table 2). Spearman correlation coefficients were used for comparison of variables and a linear regression model was applied to contrast internal and external pollen spectra (Navarro et al., 2000).

In addition, pollen deposition inside and outside the cave was compared with estimates of the abundance of the main taxa in the catchment vegetation. This estimation was obtained from phytosociological

Table 2
Pollen types and adopted classification of main pollination for their producing plant taxa (Z = zoophilous, A = anemophilous)

Allium t.	Z	*Ephedra nebrodensis*	A	*Pinus pinaster*	A
Alnus	A	*Erodium t.*	Z	*Pistacia lentiscus t.*	A
Anagallis arvensis t.	Z	*Eryngium t.*	Z	*Plantago*	A
Anchusa azurea t.	Z	*Euphorbia*	Z	*Plumbaginaceae*	Z
Anthyllis t.	Z	Fabaceae	Z	Poaceae	A
Antirrhinum t.	Z	*Ficus*	Z	*Polygala*	Z
Apiaceae	Z	*Fraxinus ornus t.*	Z	*Polygonaceae*	Z
Arctostaphylos uva-ursi t.	Z	*Fumana thymifolia t.*	Z	*Polygonum aviculare t.*	Z
Arisarum	Z	*Fumaria*	Z	*Populus*	A
Asparagus t.	Z	Genisteae	Z	Portulacaceae	Z
Asphodelus cerasiferus	Z	Geraniaceae	Z	Primulaceae	Z
Asphodelus fistulosus	Z	*Gladiolus t.*	Z	*Prunus*	Z
Asteroideae	Z	*Hedera helix*	Z	*Psoralea*	Z
Bellis t.	Z	*Helianthemum croceum t.*	Z	*Quercus faginea t.*	A
Betula	A	*Hypecoum*	Z	*Quercus ilex-coccifera t.*	A
Blackstonia perfoliata	Z	*Hypericum t.*	Z	Ranunculaceae	Z
Boraginaceae	Z	Iridaceae	Z	*Reseda*	Z
Brassicaceae	Z	*Juglans*	A	*Rhamnus*	A
Buglossoides t.	Z	*Juncus*	A	Rosaceae	Z
Bupleurum	Z	Lamiaceae 3-colpate	Z	Rubiaceae	Z
Calicotome	Z	Lamiaceae 6-colpate	Z	*Rubus t.*	Z
Campanula	Z	*Lathyrus t.*	Z	*Rumex crispus t.*	A
Capparis spinosa	Z	*Lavandula t.*	Z	*Ruta*	Z
Caryophyllaceae	Z	Liliaceae	Z	*Salix*	Z
Castanea	A	*Linum*	Z	*Sambucus t.*	Z
Casuarina	A	*Lithodora*	Z	*Sanguisorba ancistroides*	A
Cedrus	A	*Lotus t.*	Z	*Sarcocapnos*	Z
Centaurea	Z	*Lycium*	Z	*Scabiosa t.*	Z
Centaurium t.	Z	*Lygeum*	A	*Schinus molle*	Z
Centranthus t.	Z	*Lysimachia t.*	Z	Scrophulariaceae	Z
Cephalantera	Z	Malvaceae	Z	*Sideritis*	Z
Ceratonia siliqua t.	Z	*Marrubium*	Z	*Smilax*	Z
Cerealia	A	*Maytenus*	Z	Solanaceae	Z
Chaenorrhinum t.	Z	*Medicago hispida t.*	Z	*Solanum*	Z
Chamaerops humilis	A	*Mercurialis*	A	*Spergula arvensis*	Z
Chenopodiaceae	A	*Myosotis t.*	Z	*Tamarix*	Z
Cichorioideae	Z	*Myrtus*	Z	*Taxus*	A
Cistaceae	Z	*Neatostema t.*	Z	*Thalictrum*	Z
Cistus t.	Z	*Nerium oleander*	Z	Thymelaeaceae	Z
Cistus clusii-albidus t.	Z	*Nicotiana*	Z	*Trifolium t.*	Z
Cistus salviifolius t.	Z	*Nonea t.*	Z	*Typha angustifolia*	A
Convolvulus	Z	*Olea*	A	*Ulex parviflorus t.*	Z
Coris monspeliensis	Z	*Ononis t.*	Z	*Ulmus*	A
Coronilla t.	Z	*Opuntia*	Z	Urticaceae	A
Corylus	A	Orchidaceae	Z	*Valeriana*	Z
Crassulaceae	Z	*Osyris*	Z	*Valerianella*	Z
Cupressaceae	A	*Oxalis*	Z	*Verbascum t.*	Z
Cyperaceae	A	*Papaver*	Z	*Viburnum tinus t.*	Z
Digitalis	Z	*Parietaria t.*	A	*Viola*	Z
Dipsacaceae	Z	*Paronychia t.*	Z	*Withania*	Z
Dorycnium pentaphyllum	Z	*Periploca*	Z	*Xanthium*	A
Ecballium	Z	*Phillyrea*	Z	*Zygophyllum*	Z
Ephedra fragilis	A	*Pinus*	A		

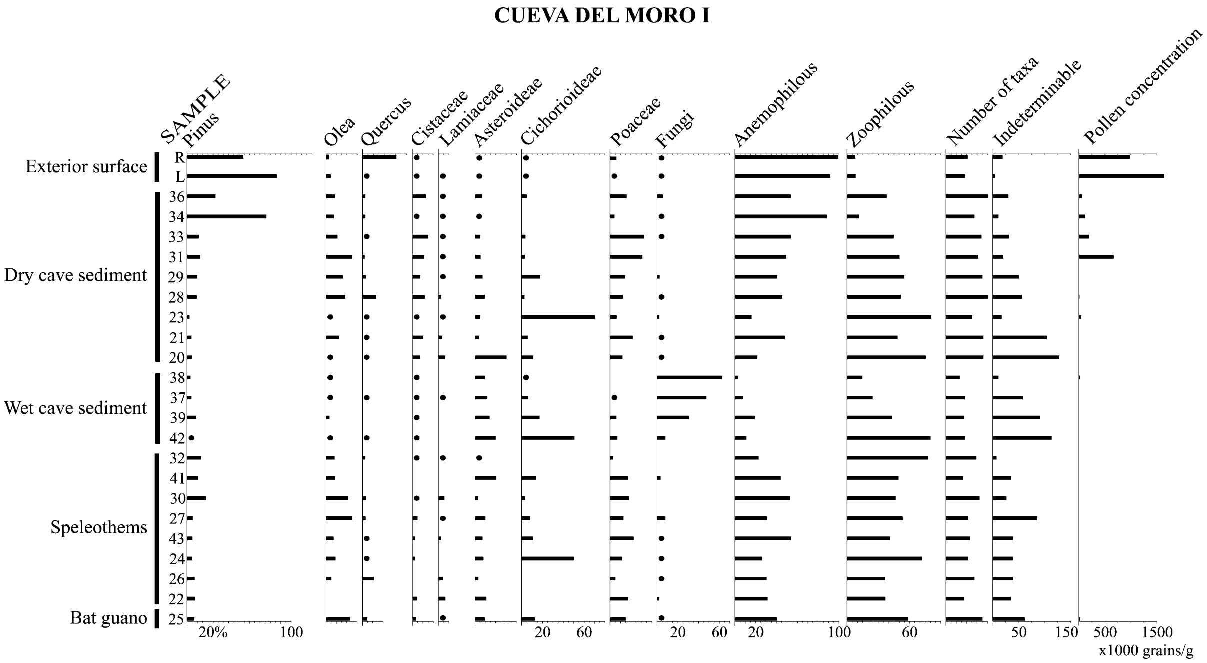


Fig. 7. Pollen diagram of selected taxa from Cueva del Moro I. Samples grouped according to sediment types and ordered according to distance from the entrance.

tables of each cave zone (Costa et al., 1982; Peris, 1983; de la Torre, 1988,1991; Stübing et al., 1989 for Cueva Moro I and II; Alcaraz and Garre, 1987; Alcaraz and de la Torre, 1988; Alcaraz et al., 1989, 1991 for Cueva de José and Cueva de la Plata; and Peinado and Martínez-Parras, 1985; Alcaraz and Sánchez-Gómez, 1988; Sánchez-Gómez, 1990 for Cueva del Ardacho).

4. Results

4.1. Cueva de las Ventanas

No pollen diagram is shown in this case because all samples showed only few grains of Asteraceae and abundant spores of Sordariaceae and other fungi. Plausibly, the nutrient-rich conditions—as a consequence of the presence of dung—in combination with the high humidity may have had a positive effect on the occurrence of bacteria, which could have been responsible for the degradation of pollen.

4.2. Cueva del Moro I (Tables 3 and 4, Fig. 7) (Navarro et al., 2000)

Most samples yielded sufficient well-preserved pollen. Seventy palynomorph types were identified. Pollen spectra variation is too some degree related to the sediment type. Asteraceae, fungal spores, and indeterminable pollen are dominant in wet sediments (Fig. 7). Dry sediments show higher pollen-taxon diversity, and a relatively constant pattern of Poaceae dominance, with important contributions of Cistaceae, Asteraceae, *Quercus*, *Olea*, and *Pinus*. Speleothem samples show variable percentages with occasionally high Cichorioideae, *Olea*, Poaceae, and Asteroideae. Bat guano is dominated by *Olea*, Asteraceae, and Poaceae. The number of taxa drops below 25 in most wet sediment and speleothem samples and pollen concentration varies along the entrance (71,241 grains/g in samples 36–126,414 grains/g in sample 34) remaining, with the exception of samples 31 and 33, below 100,000 grains/g (Table 3). Speleothem and wet sediment samples showed considerably lower pollen concentration values.

Table 3
Number of taxa and pollen concentration at Cueva del Moro I

Samples		Number of taxa	Concentration (grains/g)
Dry floor sediment	20	36	15,368
	21	36	6767
	23	25	40,359
	28	40	14,207
	29	35	5315
	31	31	792,040
	33	34	249,067
	34	27	126,414
	36	40	71,241
Wet floor sediment	37	18	14,472
	38	13	14,904
	39	17	11,533
	42	18	15,398
Speleothem	22	17	223
	24	21	5806
	26	27	761
	27	21	679
	30	32	542
	32	29	3572
	41	16	107
	43	23	261
Bat guano	25	35	26,906
Local	–	18	760,217
Regional	–	20	767,262

Zoophilous taxa increase towards the rear of the cave, and anemophilous taxa abound more in the entrance (Fig. 7). This pattern is visible in the pollen diagrams, and is suggested by a significant positive correlation detected between zoophilous taxa and distance to the entrance and a negative one between anemophilous taxa and distance to the entrance (Table 4). The existence of entrance-rear gradients was formerly suggested by Van Campo and Leroi-Gourhan (1956); Loublier (1974); Bui-Thi-Mai (1974); Bottema (1975); Leroi-Gourhan and Renault-Miskovsky (1977), and Coles and Gilbertson (1994). There are also positive correlations between indeterminable pollen and distance to the entrance, and between indeterminable pollen and Cichorioideae. These correlations suggest that differential preservation can occur relatively rapidly in cave systems and that high Cichorioideae percentages may eventually be linked to that phenomenon.

Table 4
Spearman correlation coefficients for a set of variables from Cueva del Moro I (level of significance* = 0.05; level of significance** = 0.01)

Variables	Coefficients
Distance to the entrance—Anemophilous	−0.401*
Distance to the entrance—Zoophilous	+0.521**
Distance to the entrance—*Pinus*	−0.552**
Distance to the entrance—Pollen concentration	−0.385*
Distance to the entrance—Indeterminable	+0.558**
Cichorioideae—Indeterminable	+0.493**

4.3. Cueva del Moro II (Tables 5 and 6, Fig. 8) (Navarro et al., 2000)

Pollen spectra show lesser spatial variation throughout cave surface than those in Moro I. 97 pollen types were identified. The dominant pollen taxa are *Pinus*, *Quercus*, and Poaceae. *Pinus* shows a negative gradient towards the rear of the cave, while

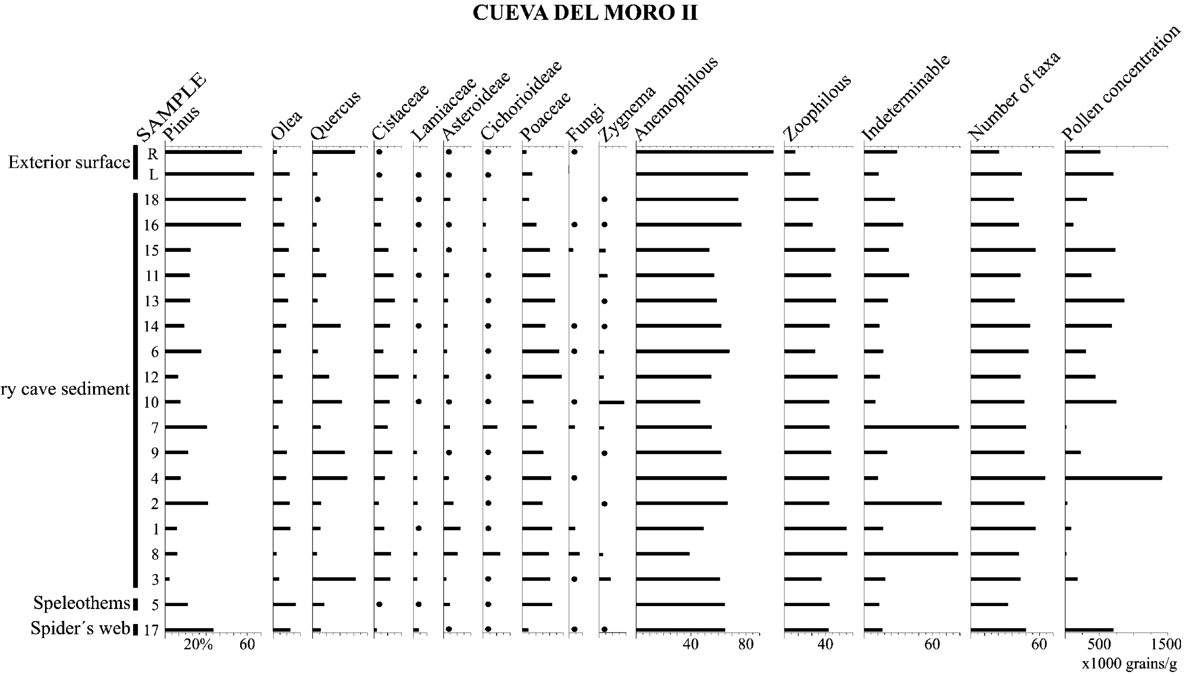


Fig. 8. Pollen diagram of selected taxa from Cueva del Moro II. Samples grouped according to sediment types and ordered according to distance from the entrance.

Table 5
Number of taxa and pollen concentration at Cueva del Moro II

Samples		Number of taxa	Concentration (grains/g)
Dry floor sediment	1	47	95,781
	2	39	43,806
	3	36	206,384
	4	54	1,554,631
	6	42	341,52
	7	40	24,773
	8	35	28,109
	9	39	262,429
	10	39	805,903
	11	36	506,172
	12	36	495,300
	13	32	1,008,333
	14	43	750,500
	15	47	861,787
	16	35	147,221
	18	31	381,830
Speleothem	5	27	1515
Spider’s web	17	40	794,287
Local	–	37	774,308
Regional	–	20	767,262

Table 6
Spearman correlation coefficients for a set of variables from Cueva del Moro II (level of significance* = 0.05; level of significance** = 0.01)

Variables	Coefficients
Distance to the entrance—Anemophilous	−0.425*
Distance to the entrance—Zoophilous	+0.417*
Distance to the entrance—*Pinus*	−0.715**
Distance to the entrance—Pollen concentration	−0.506*
Cichorioideae—Indeterminable	+0.525*

Poaceae and *Olea* increase (Fig. 8). By comparison with Cueva del Moro I, this cavity shows pollen spectra with lower percentages of fungal spores, and higher numbers of taxa and pollen concentration. The number of palynomorph types is relatively high in all samples (27–47), showing low variation throughout the cave and pollen concentration varying greatly between samples (Table 5). There is a general dominance of anemophilous taxa inside the cave, and these decrease slightly with distance to the entrance while zoophilous taxa increase towards the rear of the cave, as confirmed by Spearman correlation coefficients (Table 6). There is negative correlation between pollen concentration and distance to the entrance, and positive correlation between indeterminable pollen and Cichorioideae, which suggests again differential pollen preservation at some parts of the cave.

4.4. Cueva de José (Tables 7 and 8, Fig. 9) (Prieto and Carrión, 1999)

The pollen diagram shows relatively homogeneous pollen spectra, which is probably linked to the isodiametric morphology of the cavity, such as observed in Cueva del Moro II (Fig. 8). A total of 127 palynological types were identified. All types occurring in external pollen spectra do repeat in the cave sediment (Fig. 9). Bird guano sample (11) shows slightly higher number of taxa than external samples. This sample also shows abundant indeterminable pollen. Asteraceae shows low spatial variability, being slightly more abundant in wet sediment samples (1 and 14). A relatively high number of pollen taxa (35–77), and high pollen concentration are noticed in most samples, particularly those collected from dry sediment

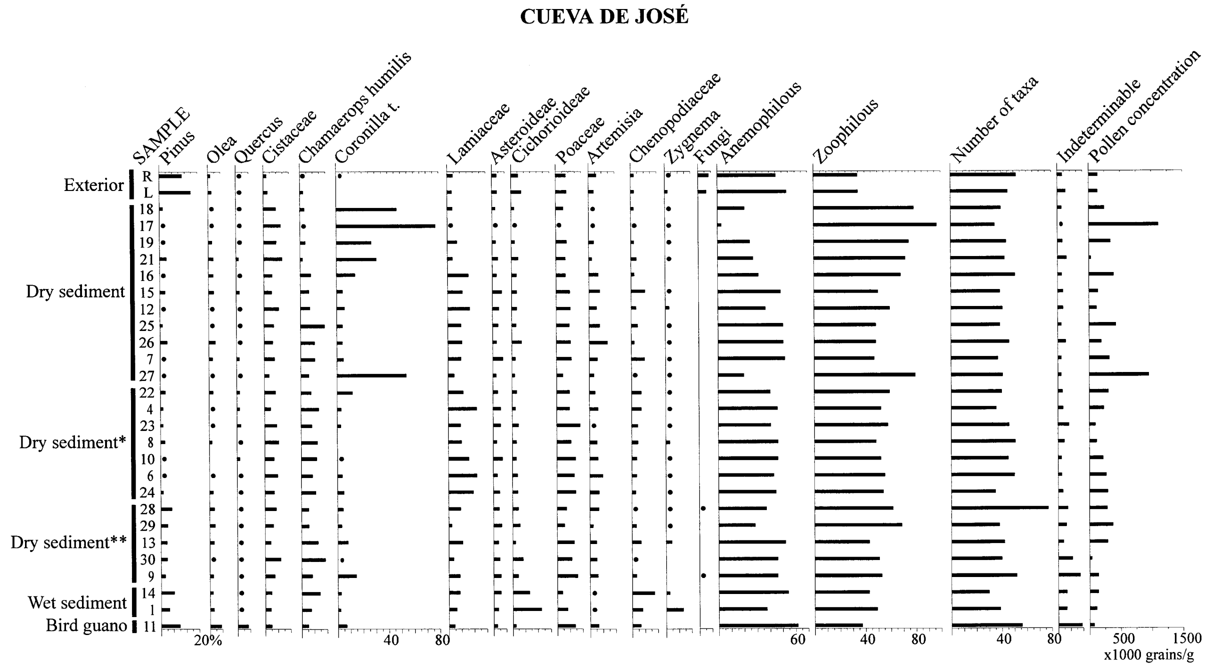


Fig. 9. Pollen diagram of selected taxa from Cueva de José. Samples grouped according to sediment types and ordered according to distance from the entrance.

Table 7
Number of taxa and pollen concentration at Cueva de José

Samples		Number of taxa	Concentration (grains/g)
Dry floor sediment	7	37	326,414
	12	41	124,208
	15	39	149,546
	16	51	396,317
	17	35	1,116,044
	18	40	246,310
	19	44	344,780
	21	43	33,156
	25	39	427,743
	26	46	195,789
	27	41	955,824
Dry sediment with decomposed dung	4	36	234,648
	6	50	274,728
	8	51	118,535
	10	45	224,281
	22	40	304,175
	23	46	100,304
	24	35	296,796
Dry organic sediment	9	52	141,574
	13	42	292,503
	28	77	286,151
	29	38	373,476
	30	40	42,154
Wet floor sediment	1	39	119,099
Wet sediment with dung	14	30	145,009
Bird guano	11	56	74,651
Local	–	45	141,316
Regional	–	52	145,156

(samples 17 and 27) (Table 7). There is dominance of zoophilous taxa inside the cave, especially close to the entrance, which is confirmed by Spearman correlation (Table 8).

Table 8
Spearman correlation coefficients for a set of variables from Cueva de José (level of significance* = 0.05; level of significance** = 0.01)

Variables	Coefficients
Distance to the entrance—Anemophilous	+0.387*
Distance to the entrance—Zoophilous	−0.397*
Distance to the entrance—Poaceae	+0.65**
Cichorioideae—Pollen concentration	−0.409*

4.5. Cueva de la Plata (Tables 9 and 10, Fig. 10)

One hundred and eighteen pollen types have been identified. *Pinus*, Cistaceae, Lamiaceae, and *Olea* dominate the pollen spectra (Fig. 10). *Pinus* decreases towards the deepest part of the cavity, while *Olea* and Lamiaceae are more abundant. Fungal spores show relatively high percentages inside and outside the cave. In general, zoophilous taxa are dominant in the cave pollen spectra, with the highest percentage in speleothem sample (12). This sample, located close to the entrance, also shows the highest number of taxa and pollen concentration (Table 9). Previous works on speleothems also showed the potential of entrance facies (Brook et al., 1990; Carrión, 1992a; Burney

CUEVA DE LA PLATA

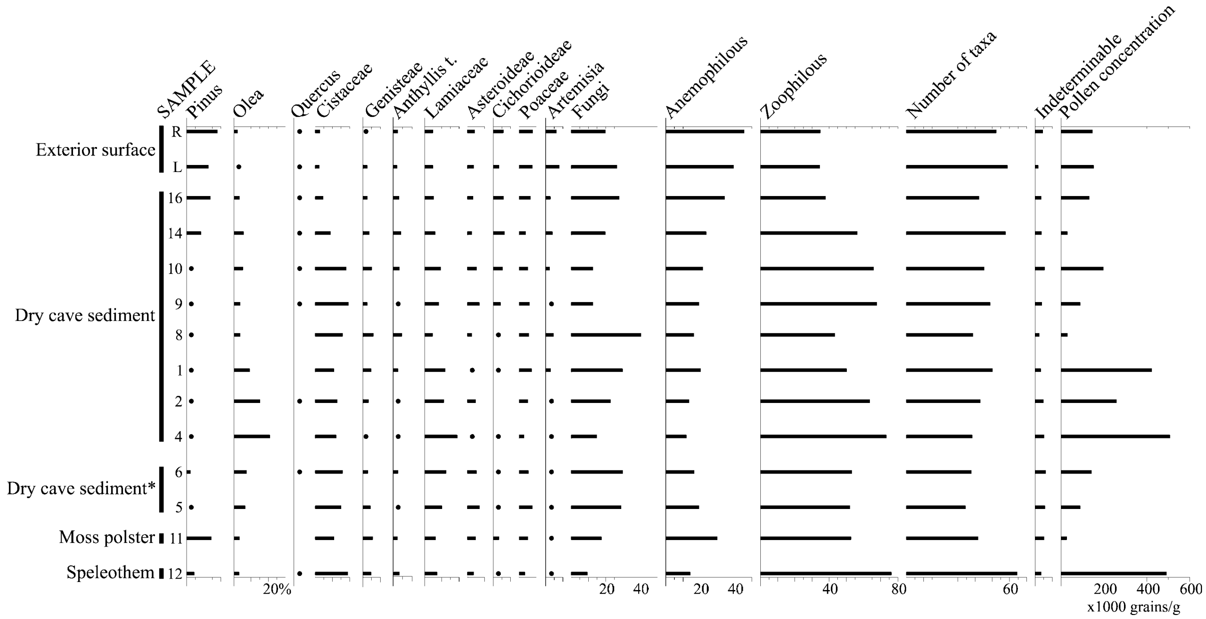


Fig. 10. Pollen diagram of selected taxa from Cueva de la Plata. Samples grouped according to sediment types and ordered according to distance from the entrance.

Table 9
Number of taxa and pollen concentration at Cueva de la Plata

Samples		Number of taxa	Concentration (grains/g)
Dry floor sediment	16	42	94,478
	14	58	23,514
	10	45	172,381
	9	49	78,687
	8	39	17,997
	1	50	301,219
	2	43	202,663
	4	38	434,880
Dry sediment with bat guano	6	38	101,519
	5	34	66,180
Moss polster	11	42	20,563
Speleothem	12	64	353,276
Local	–	59	112,959
Regional	–	52	117,113

Table 10
Spearman correlation coefficients for a set of variables from Cueva de la Plata (level of significance* = 0.05; level of significance** = 0.01)

Variables	Coefficients
Distance to the entrance—Anemophilous	−0.729**
Distance to the entrance—*Pinus*	−0.687**
Distance to the entrance—Pollen concentration	−0.557*
Distance to the entrance—Indeterminable	+0.497*
Cichorioideae—Pollen concentration	−0.503*

and Burney, 1993; Scott, 1995). Spearman correlation shows negative entrance-to-rear gradient for *Pinus*, and positive for indeterminable pollen (Table 10). It is therefore likely that post-depositional degradation processes affected significantly sediment at the rear of the cave.

4.6. Cueva del Ardacho (Tables 11 and 12, Fig. 11)

All types represented in local and regional pollen rain are present in the cave sediment, 94 in total. The pollen diagram shows a general dominance of anemophilous taxa in both internal and external samples, although these decrease towards the rear of the cave (Fig. 11). *Pinus* exhibits a negative gradient with increasing distance to the entrance, although it reaches relatively prominent values in several internal samples (i.e. sample 14). There is sharp variation in particular taxa percentages throughout the cave surface, as for Lamiaceae, Cupressaceae or Poaceae. Behind this pattern, there might be some influence of the complex cave morphology that includes narrow and long chambers and passages, and multiple entrances. The number of taxa is relatively high and shows little spatial variation (25–41) (Table 11). Pollen concentration is relatively high and it can be even higher inside than outside the cave. Spearman coefficients assess the negative influence of the distance to the entrance for pollen concentration (Table 12). There is again a positive relationship between Cichorioideae and indeterminable pollen inside the cave.

4.7. Assessing external vegetation through cave pollen spectra

Linear regression as applied to each cavity supports the hypothesis that pollen spectra from cave sediment reflects local and regional vegetation. As regard percentages, explained variability from floor sediment samples surpassed 80% (Table 13). Comparing cave pollen percentages with external pollen rain and

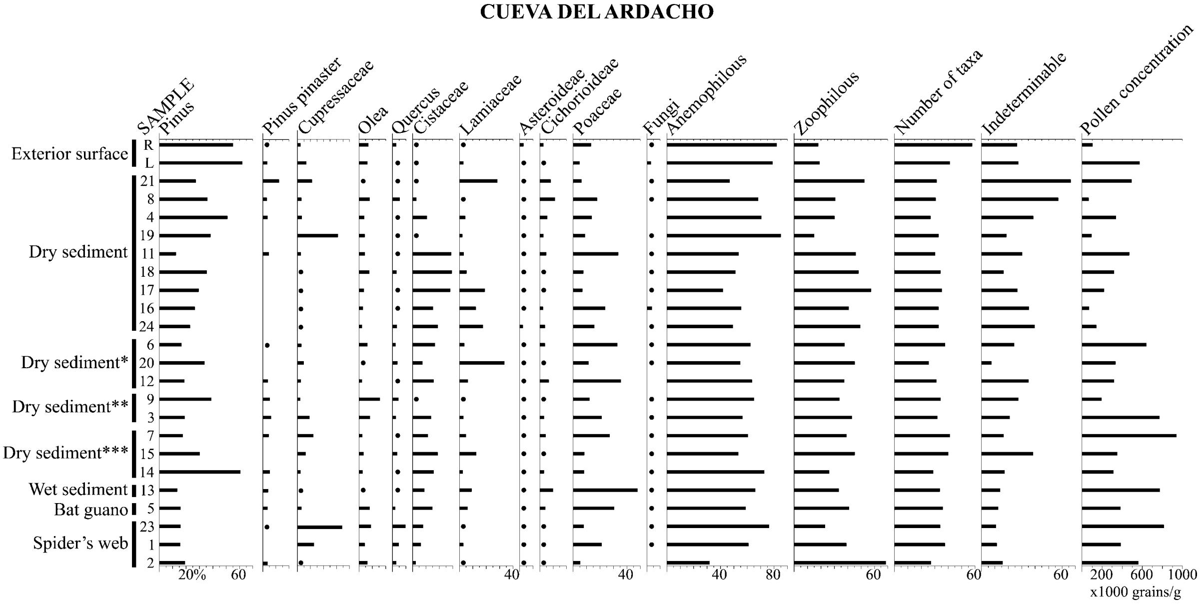


Fig. 11. Pollen diagram of selected taxa from Cueva del Ardacho. Samples grouped according to sediment types and ordered according to distance from the entrance.

Table 11
Number of taxa and pollen concentration at Cueva del Ardacho

Samples		Number of taxa	Concentration (grains/g)
Dry floor sediment	21	31	488,682
	8	30	67,611
	4	27	343,079
	19	33	90,203
	11	30	465,691
	18	34	314,474
	17	36	217,791
	16	33	65,522
	24	33	143,776
Dry sediment with dung	6	37	633,864
	20	25	330,960
	12	31	316,507
Dry organic sediment	9	34	196,913
	3	32	766,313
Dry sediment with spider's web	7	41	936,847
	15	40	349,612
	14	29	313,530
Wet floor sediment	13	34	776,430
Bat guano	5	36	379,597
Spider's web	23	34	810,868
	1	37	376,826
	2	27	559,461
Local	–	41	569,492
Regional	–	58	101,090

vegetation cover values obtained from phytosociological tables, we often observe over-representation of Lamiaceae, *Olea*, Cistaceae, Asteraceae, and Poaceae, and under-representation of *Pinus* inside the cavity compared to the external pollen rain. But it is also clear that cave sediment may provide a better reflection of present-day vegetation than the exterior pollen rain does (Fig. 12). However, this ability may also come from the very fact that cave sediment incorporates pollen types that customarily are not recorded in natural or artificial traps for airborne pollen. Interestingly, cave sediment might correct the bias produced by the abundant production and almost universal dispersal of pollen from wind-pollinated taxa.

Table 12
Spearman correlation coefficients for a set of variables from Cueva del Ardacho (level of significance* = 0.05; level of significance** = 0.01)

Variables	Coefficients
Distance to the entrance—Pollen concentration	−0.405*
Cichorioideae—Indeterminable	+0.414*

Table 13
Linear regression analysis

Cave	ExpVar (%)	
	Local	Regional
Cueva del Moro I	100.0	98.8
Cueva del Moro II	99.9	99.8
Cueva de José	93.7	91.6
Cueva de la Plata	82.6	92.4
Cueva del Ardacho	99.9	99.5

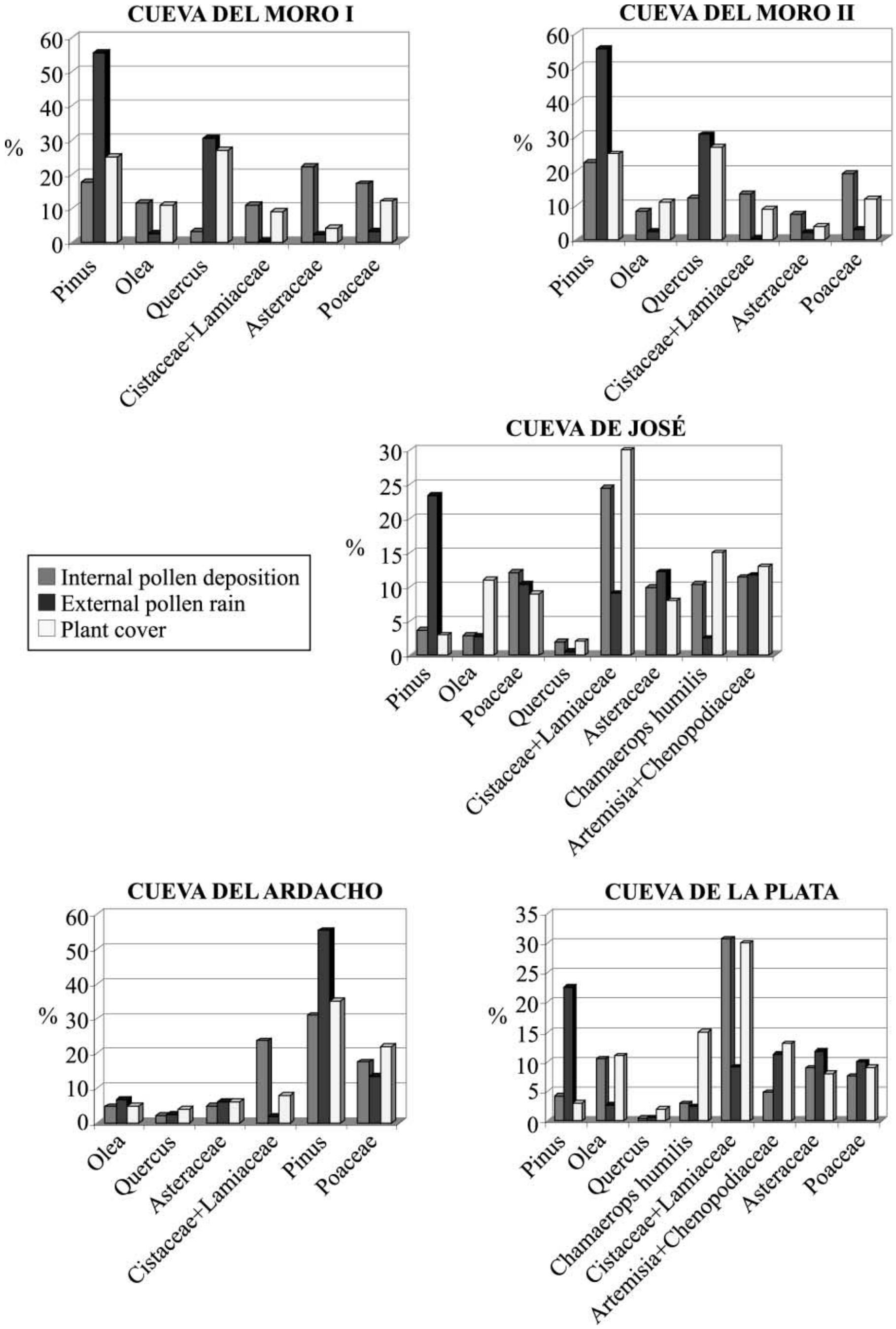


Fig. 12. Percentage comparison between average plant cover, external pollen rain and internal pollen deposition.

5. Discussion

Pollen concentration varied greatly between caves and samples, being sometimes higher inside than outside the cave. An exception is Cueva del Moro I, where pollen concentration attained very low values (mean of 64,361 grains/g), probably due to pollen decay during dry–wet cycles. Evidence from Cueva de las Ventanas, and spatial changes in pollen concentration throughout vertical sections of other caves such as Beneito (Carrión and Munuera, 1997) and Carihuela (Carrión et al., 1998) support this hypothesis and remark the value of aridity for preservation of biotic remains in cave environment (Davis, 1990).

Pollen preservation was generally reasonable. Cueva del Moro I, which showed relatively humid sediment, showed the highest values of indeterminable pollen, while Cueva de José and Cueva de la Plata, which sediments were deposited under greater aridity, showed very low percentages of indeterminable. Dry sediment shows little spatial variation in its pollen spectra, generally high pollen concentration, and good representation of the external vegetation. In contrast, wet sediment and wall samples, as well as those samples taken from dripping areas, often showed biased pollen spectra with low pollen concentration values, high percentages of non-pollen microfossils such as fungal spores, and raised percentage and concentration values of Cichorioideae pollen. Speleothem samples showed the poorest pollen spectra in terms of pollen sum, pollen concentration, and microscope discrimination, although they are potentially useful especially when located nearby the entrance. Dung or dung-containing samples showed high percentages of zoophilous taxa, but they proved to be useful to correct the bias associated to pollen rain in regions with entomophilous-dominated vegetation types.

Cave morphology is demonstrated to play an important role in pollen deposition in cave sediments, as postulated before by O'Rourke (1985); Burney and Burney (1993). All caves, excepting Cueva de José, showed a negative grade for pollen concentration with increasing distance to the entrance. In general, the highest pollen concentrations were recorded in entrance areas, and the lowest at the rear of the caves. It is worth mentioning that caves with isodiametric morphology and short length (Cueva de José, Cueva del Moro II) are better for pollen analysis because they show more homogeneous pollen spectra throughout the cave surface. Caves with narrow and long chambers may register high percentages of indeterminable pollen and Cichorioideae grains and undesirably low values of pollen concentration (Cueva del Ardacho, Cueva del Moro I, Cueva de la Plata).

All the caves, with the exception of Cueva de José, produced a relatively low pollen deposition for anemophilous taxa, and a higher representation for zoophilous taxa. Pollen introduced in the cave through biotic transport (in form of faeces, on paws and fur, on bedding or food materials, etc.) is abundant at the deepest part of the cave, (Burney and Burney, 1993; Diot, 1991). Samples from the rear of the cave are often biased by apparently animal-transported pollen such as Lamiaceae, Cistaceae, Asteraceae, but also by Poaceae which, although anemophilous pollen, can be transported by animals into the cave. Cueva de José is somewhat an exception, showing a dominance of zoophilous taxa close to the cave entrance and anemophilous taxa at the rear of the cave. However, this cave is situated in the context of vegetation dominated by entomophilous flora.

The highest percentages of Cichorioideae were recorded from wet and carbonate impregnated sediments. At Cueva del Ardacho and Cueva del Moro I and II, a significant positive relationship was found between Cichorioideae and indeterminable pollen, which suggests degradation of pollen assemblages. Selective transport has been stressed previously by Bottema (1975) and Coûteaux (1977), but, beyond doubt, this phenomenon has been over-generalised. In fact, this correlation was not detected at Cueva de la Plata and Cueva de José, which showed excellent analytical potential at their largely dry floor sediment. Furthermore, there are palaeoecological records with acceptable pollen preservation and abundance of Asteraceae pollen, especially in Pleistocene beds (Carrión, 1992b). Differential preservation cannot be the only reason to explain high incidence of Asteraceae pollen in cave sediments. The possibility that the morphology of Asteraceae pollen play a role in the transport cannot be discarded.

6. Concluding remarks

We have addressed several issues of pollen taphonomy in cave environment. The depositional context is extremely complex and caution should be taken at providing detailed rules for sampling strategy and palaeoecological reconstruction. Increasing the palaeo-database in semi-arid regions is urgent, so the need arises for studies directed towards understanding post-depositional processes.

Cave geometry is an important factor affecting the quality of pollen spectra registered inside the cavity. Caves in which the dominant type of pollen transfer from the external environment is airborne will often show a decrease in pollen deposition with increasing distance into the cave. Generally, in these cases, the highest concentrations of pollen and spores are observed in the cave entrance areas, and the lowest at the rear of the cave. But this is not a universal rule. Sometimes, when biotic or aquatic pollen transfer is dominant, pollen deposition increases toward the rear of caves.

Sediments associated with dry depositional conditions are the most reliable materials for environmental reconstruction from pollen analysis in cave sites. In contrast, speleothems and wet or carbonated sediment samples have been demonstrated to be less suitable for pollen analysis, often containing altered pollen spectra and low concentration. The potential may still exist if the speleothems lie close to the cave openings.

Dung and other organic remains are often an important source of pollen, notwithstanding that they may produce biased pollen spectra with over-representation of animal-transported pollen types. Biotic transport into the cave, mainly represented by animal faeces, nesting materials, food, etc., should not be systematically considered a problem for pollen analysis, but sometimes a help to record in the cave taxa with a high palaeoecological indicator value.

Sediments from caves contain pollen assemblages that may reflect the vegetation from local and regional catchment areas. Globally considered, pollen spectra inside caves are similar to those obtained in the exterior environment. They can even represent the external vegetation which actually grows outside the cave better than those from external sediment samples. This is especially true in areas with an entomophilous-dominated flora.

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