Quaternary International 761 (2026) 110186

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Influences of seasonal prey availability and anthropogenic landscape on small-vertebrate based palaeoecological reconstructions: a case study from the mid-late Holocene transition at El Mirador cave (Sierra de Atapuerca, Spain)

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ARTICLE INFO

Keywords:
Predation
Seasonality
Landscape anthropization
Small vertebrates
Palaeoecological reconstruction
Herpetofauna

ABSTRACT

Birds of prey and carnivorous mammals are among the primary accumulating agents of faunal remains, mainly isolated bones and teeth in the karst sediment sites. The microvertebrate remains from their feces and pellets tend to be usually dispersed in the sediment at El Mirador cave (Atapuerca, Spain). Although, twenty small accumulations have been recovered in the Chalcolithic (MIR5) and Bronze Age (MIR4) levels. These accumulations contain an extraordinary number of bone remains of amphibians and reptiles, together with small-mammals and birds. Previous taphonomic study done on the most significant accumulation from MIR4 identified it as a pellet produced by a medium-large owl. Here we describe for the first time the whole sample of pellets recovered from El Mirador cave, describing their faunal content and analysing their similarities by means of statistical analyses. Important variations are evidenced, concerning the taxonomic composition and the number of prey species between different pellets in MIR4, which are put in relation with the owl hunting seasonality and the reproductive cycles of herpetofauna. This study permits to contrast between different hypotheses concerning the seasonality and Holocene anthropization of the landscape, and finally to infer how these possible biases (such as seasonality, predation, ethology, phenology and the annual activity of prey species) can affect palaeoenvironmental and palaeoclimatic reconstructions (Habitat Weighting and Mutual Ecogeographic Range methods). The palaeoenvironmental reconstructions using the different seasonal associations indicates changes in the distribution of primary habitats, with increased wet areas between late winter and mid-spring and increased aridity between mid-spring and summer. Palaeoclimatic reconstructions did not reveal significant differences concerning annual or monthly temperatures. The unique faunistic composition of these accumulations is interpreted as a collateral effect of the human impact during the Chalcolithic-Bronze Age transition in Atapuerca area, which forced owls to hunt on less optimal but more seasonally abundant preys.

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https://doi.org/10.1016/j.quaint.2026.110186
Received 9 September 2025; Received in revised form 8 February 2026; Accepted 19 February 2026

1. Introduction

In recent years, the use of Quaternary microvertebrate assemblages for palaeoenvironmental and palaeoclimatic reconstructions has received considerable attention in the literature with the introduction of innovative methods of past reconstructions such as the Mutual Ecogeographic Range and Habitat Weighting methods (e.g., Evans et al., 1981; Andrews, 2006; Blain, 2009; Blain et al., 2008, 2009, 2016; López-García et al., 2011). These methods use current small-vertebrate concurrences to estimate temperature and rainfall data and to determine the primary landscape environments surrounding the studied sites through actualistic data on the species that are present in the fossil assemblages. However, modern literature about the diets of birds of prey indicate that their composition varies with the seasons and over the years, according to seasonal-annual cycles and/or due to environmental changes (Pérez-Mellado, 1978; Zerunian et al., 1982; Donázar, 1989; Lara, 1995; García and Cervera, 2001; Saada et al., 2024). Studies on the effects of predation, prey cycling, and time averaging on relative abundance in small-mammal accumulations by avian raptors suggest that the effect of time averaging on relative abundances of different species is negligible for assemblages accumulated over more than 140 years (Terry, 2008). All these data suggest the existence of possible interpretation biases in the archaeological and paleontological record from disaggregated coprocoenotic remains, when such remains were accumulated over shorter periods of time, including the under-representation or absence of some taxa and the over-representation of others.

These biases could lead to alterations in reconstructions of the past and the degrees of confidence and accuracy that can be ascribed to them, especially in assemblages made up of few specimens. They can also particularly affect Holocene archaeological sites with very marked stratigraphy containing successive chronocultural periods in defined levels representing chronologically short phases. These short-time levels are therefore more likely to be biased since the contributions are attributed to a briefer period of time.

Birds expel bone remains and other undigested organic materials after initial digestion in a tightly-packed mass called *pellet* (Mikkola, 1995). Their complete conservation is exceedingly rare in the paleontological and archaeological record, although pellets are occasionally accumulated in large taphocenoses of small bones (De Cupere et al., 2009). In most cases, the faunal remains from pellets appear dispersed inside the sediment, affected by pre-depositional and post-depositional taphonomic processes that promote disintegration, such as weathering, trampling and water streams (Andrews, 1990; Fernández-Jalvo and Andrews, 2003, 2016; García-Morato et al., 2019). This disaggregation effect can be seen in most Quaternary sites, where the microvertebrate remains (or some of them) were said to be contributed by birds of prey (Accipitriformes, Falconiformes and Strigiformes). Moreover, coprocoenotic remains are mostly dispersed in the sediment together with remains from other sources, which minimises the biases that predator contributions can sometimes give rise to in the interpretations of past environments and climates.

At El Mirador cave (Burgos, Spain), twenty concentrated accumulations containing faunal remains with a significant abundance of herpetofauna were recovered from levels MIR4 and MIR5, dated to the Chalcolithic and to the Bronze Age (Vergès et al., 2016, 2022) (Fig. 1). To determine their origin, a taphonomic analysis was performed on the largest accumulation (MIR5-P21-n4). The results identified the accumulation as an avian pellet produced by a category 2 predator for herpetological remains (equivalent to category predator 3 for small-mammals remains), probably the tawny owl *Strix aluco* and mostly the eagle owl *Bubo bubo*, which was preserved intact due to the special conditions of the cave during the Chalcolithic period, when it was used as a burial space (Bisbal-Chinesta et al., 2020). Later, a subsequent study based on the remains of small-mammals from these same levels also proposed *B. bubo* as the main agent of coprocoenotic accumulation (García-Morato et al., 2023). Additionally, the quantitative taxonomic composition of this pellet points to the seasonal predation of *Hyla* gr. *Hyla arborea* (*Hyla molleri*) during a period in which this tree frog would have been abundant in the wet and temperate landscape around the cave (Bisbal-Chinesta et al., 2020).

Fig. 1. Pictures of two accumulations of small-vertebrate remains identified as avian pellets from El Mirador cave (Burgos, Spain), in situ. **A:** MIR5-P21-n7, from the central test pit. **B**: MIR204-S34-n5, from the northern section.

The aim of this paper is to explore the seasonal variations and its effects on palaeoenvironmental and palaeoclimatic reconstructions, by the study of the exceptional preservation of individualised small-vertebrate accumulations at El Mirador cave interpreted as owl pellets. The data derived from this study are compared with those yielded by the small-mammal associations and archaeobotanical remains from El Mirador cave, thus allowing to examine the implications for landscape alterations in relation with Holocene environmental and climatic changes and/or the human impact (López-García, 2008; Cabanes et al., 2009; Bañuls-Cardona et al., 2013, 2017a, 2017b; Euba et al., 2016; Expósito et al., 2017, 2022; Bisbal-Chinesta et al., 2020; Bañuls-Cardona and Bisbal-Chinesta, 2022; García-Morato et al., 2023; Domínguez-García et al., 2024).

2. El Mirador cave and the 4.2 ka BP Bond event

El Mirador cave (*cueva de El Mirador* in Spanish) is located on the slopes of the southern tip of the Sierra de Atapuerca, within the municipality of Ibeas de Juarros, and it is part of the Atapuerca karst system. It is located at 42° 20′ 58″ N and 03° 30′ 33″ W and it rises to 1033 m.a.s.l. over the middle basin of the Arlanzón River. The cave is currently 23 m wide by 4 m high and 15 m deep and is configured as an open shelter due to the collapse of the vault (Vergès et al., 2002). The vegetation of the surrounding areas is characterised by cereal croplands and by mixed open Mediterranean continental forests of *Quercus ilex* subsps. *rotundifolia* and *ballota* and *Quercus faginea*, together with communities of *Quercus pyrenaica* on the fluvial terraces and siliceous soils, as well as signs of Atlantic-Eurosiberian influences in the presence of *Erica vagans* and *Calluna vulgaris* (Rodríguez et al., 2016).

Between 1999 and 2008, the archaeological work focused on a 6 m^2 test pit located in the central area of the western half of the cave, where a large Holocene succession was found, consisting of 24 differentiated archaeological levels: MIR1 and MIR2 are mixed layers altered by animal burrows and modern anthropogenic actions; MIR3 is partially disturbed, with mixed remains from the Middle to Late Bronze Age; MIR4 is a substantial level from the Middle Bronze Age, which is the result of the use of the cave as a livestock pen and includes at its base a secondary burial of cannibalised human bones from the Early Bronze Age that were buried during the Middle Bronze Age (Cáceres et al., 2007; Vergès et al., 2016); MIR5 is a thin level with scarce anthropogenic contributions, but it is rich in small-vertebrate remains (Vergès et al., 2002). The remaining Holocene levels (MIR6–MIR24) are assigned to the Neolithic and are mostly made up of livestock pen waste, mainly *fumiers*, with the Late Neolithic represented at the top of the sequence (including MIR6) (Angelucci et al., 2009; Vergès, 2022; Vergès et al., 2016, 2022).

New dating obtained from the rodent bones contained in pellet MIR5-P21-n4 (Beta-521985: 4530–4417 cal BP; Table 1) indicates that it is contemporaneous with the Chalcolithic collective burial in MIR203 (4880–4480 cal BP and 4550–4390 cal BP) in the northern section of the cave (sector 200) (Gómez-Sánchez et al., 2014; Ceperuelo et al., 2014, 2015; Lozano et al., 2015; Vergès et al., 2016, 2022). The sedimentation in MIR5 is attributed to exclusively natural processes and occurred very slowly, around 0.1 mm/year, in contrast to the 4-5 mm/year of the levels MIR11 to MIR16, caused by the anthropic activity of the *fumiers* (Vergès et al., 2008). This low sedimentation rate has been associated with the interruption of anthropogenic contributions during MIR5 (Vergès et al., 2002), proof of little to no human activity in the cave during the deposition of the sediments, as the pellets would have been rapidly disintegrated by trampling or other actions associated with human occupation. In western sector 100, another individual burial of a young man from the Middle Bronze Age (MIR106) was found on a ledge of the karst wall, dated 3670–3470 cal BP (Vergès et al., 2016). This burial is contemporaneous with the base of MIR4 (3730–3530 cal BP) (Vergès et al., 2002, 2016, 2022).

The regional climatic context in which both MIR4 and MIR5 are framed was affected by the 4.2 ka BP Bond event, which although it occurred on a global scale, varied greatly in its climatic expression at the local and regional level (Magny et al., 2009, 2013; Bini et al., 2019). Controversy persists as to whether the 4.2 ka BP Bond event is a unique long cooling and drying interval (Cullen et al., 2000; Drysdale et al., 2006; Dixit et al., 2014), or a consecutive succession of dry/wet events (Magny et al., 2009; Railsback et al., 2018). Different palaeohydrological and palaeomarine proxies suggest an arid phase in the southern central Mediterranean between 4500 and 4000 BP, while the northern regions experienced increased humidity north of 40° latitude (Magny et al., 2013). An isotopic study of speleothems from central Italy and their comparison with central Mediterranean records of between 4300 and 3800 BP again points to regional differences, with drier conditions in the central and southern areas of the Italian Peninsula but no significant changes in temperatures, while the northern zones and the Alps tended towards a colder and wetter climate. In this same study, an increase in aridity was associated with a decrease in precipitation during the summer, which would have led to summer drought (Zanchetta et al., 2016).

The results of another multiproxy study in the Mediterranean Basin suggest a drier seasonality at the regional level for the same period, both in winter and summer, although in some areas the conditions remained as or even more humid (Bini et al., 2019). At a local level, these increments in aridity may have been related to torrential rain events, which would have increased erosion (Cartier et al., 2019; Bini et al., 2019). Regional pollen research in the central Mediterranean zone depicts the regionalisation of climate and vegetation cover changes as of the 4.2 ka BP Bond event according to latitude: the northern regions (43°–45°) underwent a very slight decrease in precipitation, though the plant composition remained unchanged; in the central area (39°–43°), there was both a decrease in precipitation and a decrease in tree pollen, though this pattern is imprecise in some sequences; while in the southern regions (36°–39°), there was a very marked decrease in tree pollen as well as marked human impact. The increase in aridity in the southern regions is due to the influence of the north African climate, which is characterised by high pressure resulting in limited rainfall (Di Rita and Magri, 2019).

The data available for the Iberian Peninsula also point to great variation at the regional level. A peninsular macro study showed an increasing trend towards aridity due to a decrease in winter rainfall from 6000 to 3000 cal BP, which was aggravated during the 4.2 ka BP Bond event by the severe increase in summer drought. At the same time, the area experienced a drop in winter temperatures between 4400 and 4000 cal BP (Schirrmacher et al., 2020). Other hydrographic evidence for the western Mediterranean suggests a cooling phase between 4300 and 3800 cal BP, with two consecutive cold events in the sea surface temperature of Alboran Sea during the 4.2 ka BP Bond event (Català et al., 2019). Regional variability, therefore, is repeated on the Iberian Peninsula, with the southern and eastern Mediterranean regions

Table 1

Datings from the upper levels of the central test pit sequence, El Mirador cave (Burgos, Spain). The calibration of radiocarbon age to calendar years is based on the High Probability Density Range Method (HPD): Intcal'13 curve (Ramsey, 2009; Reimer et al., 2013).

Level	Material	Identification	Laboratory number	Conventional radiocarbon age BP	2σ calibrated BC	2σ calibrated BP	$^{13}C/^{12}C$ ratio
MIR4 (roof)	Charcoal	*Quercus* sp. evergreen	Beta-154894	3040 ± 40	1440 - 1120	3390 - 3070	−23.9‰
MIR4 (base)	Charcoal	*Quercus* sp. deciduous	Beta-153366	3400 ± 40	1780 - 1580	3730 - 3530	−23.8‰
MIR106	Human bone	*Homo sapiens*	Beta-296226	3340 ± 30	1720 - 1520	3670 - 3470	−19.4‰
MIR4 (pit)	Human bone	*Homo sapiens*	Beta-153366	3670 ± 40	2060 - 1820	4010 - 3770	−19.3‰
MIR4 (pit)	Human bone	*Homo sapiens*	Beta-182042	3830 ± 40	2270 - 1990	4220 - 3940	−18.8‰
MIR4 (pit)	Human bone	*Homo sapiens*	Beta-182041	3900 ± 40	2380 - 2100	4330 - 4050	−19.2‰
MIR5 (MIR5-P21-n4 pellet)	**Rodent bone**	**Rodentia indet.**	**Beta-521985**	**4010 ± 30**	**2581–2468**	**4530–4417**	**−22.4‰**
MIR203	Human bone	*Homo sapiens*	Beta-296225	4000 ± 30	2600 - 2440	4550 - 4390	−18.9‰
MIR203	Human bone	*Homo sapiens*	Beta-296227	4220 ± 30	2930 - 2530	4880 - 4480	−18.7‰
MIR6	Charcoal	*Quercus* sp. evergreen	Beta-153367	4780 ± 40	3680 - 3400	5630 - 5350	−23.5‰

undergoing more abrupt changes during this climate event, and the northern areas of Eurosiberian and Atlantic influence remaining more stable (Lillios et al., 2016).

In El Mirador cave, the effects of the 4.2 ka BP Bond event have been identified in the increased aridity in MIR5 and the lowermost part at the base of MIR4 (between 4530 cal BP to 3730 cal BP), according to the palynological record (Expósito et al., 2017, 2022). Plant macro-remains and palynological studies indicate that, from the early Neolithic through to the Bronze Age, the surrounding environment consisted of a mosaic landscape featuring mixed woodlands dominated by pines (*Pinus* sp.) and oaks (*Quercus* sp.). These wooded areas coexisted with more open zones, likely used for agriculture and for grazing livestock (Rodríguez et al., 2016; Expósito et al., 2017, 2022). Throughout the Holocene, significant landscape modifications occurred, most prominently a steady reduction in forest coverage density (Rodríguez et al., 2016; Expósito et al., 2017, 2022; Bañuls-Cardona et al., 2017a). These environmental shifts are primarily associated with growing human impact, although periods of increased aridity are linked to climatic changes (Rodríguez et al., 2016; Expósito et al., 2017, 2022). Linked to the 4.2 ka BP Bond event, in MIR5 and the lowermost part of MIR4 the deciduous oak species, mesophilous plants and hygrophilous riparian taxa decreased, as well as fall the diversity of trees and shrubs is also noted, even including those taxa linked to anthropization and livestock pressure, such as cereal crops and nitrophilous vegetation (Expósito et al., 2017, 2022). In addition, the low presence of post-depositional taphonomic evidence of manganese coatings and carbonate crusts over the bone remains supports an arid phase, both being associated with dry conditions. These alterations appear more frequently in lowermost MIR4 compared to MIR5, suggesting that MIR4 experienced slightly more humid environmental conditions than MIR5 (García-Morato et al., 2023).

3. Material and methods

3.1. Sampling

During the 2000 excavation campaign in El Mirador cave, twenty accumulations were identified containing subfossil microvertebrate remains from the lowest layer of level MIR4 and from level MIR5 in grids P21, P22, Q20, and Q21 of the central test pit (Table 2). All these taphocenoses had an elongated and rounded original shape, totally or partially preserved at the time of their discovery (Fig. 2). They were isolated, their locations recorded and then removed from the excavation surface. Except for MIR4-P21-n264, which has been preserved for further studies, their content was subsequently isolated in the Micropaleontology laboratory of the Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA) through screening with a running-water washing system and decreasing mesh sizes (5 mm, 2 mm and 0.5 mm). They were identified taxonomically using a trinocular stereomicroscope (Euromex NexiusZoom NZ1903-S, 0.67-4.5, WF 10x/22 mm, with digital camera Euromex CMEX-5 with CMOS 5 Mp sensor). A total of 7482 bone elements were counted.

Table 2
List of the accumulations of small-vertebrate remains identified as avian pellets from MIR4 and MIR5 levels and their stratigraphic positions inside El Mirador Cave (Burgos, Spain). Note that the irregularity of the ground causes that some MIR5 pellets to be in higher positions compared to other MIR4 pellets.

Accumulation	Level	Square	Number	Location		
				X.	Y.	Z.
MIR4-Q21-n227	MIR4	Q21	227	63	19	1275
MIR4-Q21-n228	MIR4	Q21	228	63	23	1274
MIR4-Q21-n231	MIR4	Q21	231	58	29	1282
MIR4-Q21-n233	MIR4	Q21	233	58	5	1283
MIR4-Q21-n234	MIR4	Q21	234	60	30	1282
MIR4-Q21-n235	MIR4	Q21	235	47	30	1281
MIR4-P21-n243	MIR4	P21	243	87	25	1267
MIR4-Q21-n245	MIR4	Q21	245	29	32	1286
MIR4-P21-n246	MIR4	P21	246	38	25	1269
MIR4-P21-n252	MIR4	P21	252	81	69	1274
MIR4-Q20-n261	MIR4	Q20	261	24	90	1285
MIR4-Q20-n262	MIR4	Q20	262	28	93	1287
MIR4-P21-n264	MIR4	P21	264	30	15	1275
MIR4-P21-n267	MIR4	P21	267	59	10	1272
MIR4-P22-n380	MIR4	P22	380	51	76	1278
MIR5-P22-n1	MIR5	P22	1	29	10	1273
MIR5-P22-n2	MIR5	P22	2	50	41	1278
MIR5-P21-n4	MIR5	P21	4	25	38	1284
MIR5-P21-n7	MIR5	P21	7	94	48	1285
MIR5-P22-n13	MIR5	P22	13	38	5	1287

3.2. Taxonomic identification

The anatomical elements were used to identify the herpetofauna: the parasphenoids, frontals, humeri and the vertebrae for caudates (Buckley and Sanchiz, 2012; Gleed-Owen, 1998; Ratnikov, 2015); frontoparietals, squamosals, scapulae, humeri, vertebrae and ilia for anurans (Bailon, 1999; Blain and Arribas, 2017); the cranial bones and vertebrae for non-ophidian squamates (Barahona, 1996; Barahona and Barbadillo, 1997; Gleed-Owen, 1998; Blain, 2009; Caputo, 2004); and the vertebrae for snakes (Szyndlar, 1984). For small-mammals, the first lower molar was used during the species-level taxonomic identification for the Arvicolinae, and isolated teeth for *Apodemus* (Chaline, 1972; Cuenca-Bescós et al., 1997, 2008) and for *Sorex* (Reumer, 1984; Cuenca-Bescós et al., 2008). The number of identified specimens (NISP) and minimum number of individuals (MNI) were calculated using laterality, zoning and completeness. In the case of Arvicolinae remains, non-diagnostic elements at the species level (e.g., molars other than m1, as well as cranial and postcranial elements) recovered from the same avian pellet as diagnostic remains allowing taxonomic assignment to a species or higher taxonomic level were considered to belong to a single individual. This procedure was applied to avoid artificial inflation of the MNI, while still taking into account laterality, zoning and completeness criteria.

Modern specimens from the reference collections of the Museo Nacional de Ciencias Naturales of Madrid (MNCN-CSIC), Muséum National d'Histoire Naturelle of Paris and the Micropaleontology Laboratory of the IPHES-CERCA were used as comparison material. Taxonomic nomenclature is based on the Standard List of the Spanish Herpetological Association (*Asociación Herpetológica Española*), published by Sánchez-Vialas et al. (2024).

3.3. Statistical analysis

Two data matrices were created to study the differences in the faunistic composition of the pellets and to infer possible trends in predation for each level (MIR4 and MIR5) (Supplementary Material 1 and 2). The different pellets are shown in the columns, and the taxa are shown in the rows along with their minimum number of individuals (MNI). Unlike other analyses based on presence/absence, in this case, the quantitative values of individuals by species in the data matrices are maintained. The aim is to infer percentage variations in representativeness (NMI) and not only proximity relationships by taxonomic composition.

In addition, some normalizations have been applied in order to reduce dispersion and facilitate interpretation. Lacertidae indet. (small), Lacertidae indet. (medium-sized) and *Vipera* sp. (*Vipera aspis/seoanei*) are included because they respond to different habitat contexts and have environmental significance despite the lack of their taxonomic definition. Due to the impossibility of determining most of the small-mammals in the sample to the species level, all the identified arvicoline voles (Arvicolinae indet., *Microtus* sp., *Microtus agrestis*, *Microtus arvalis* and *Microtus* (*Terricola*) *duodecimcostatus*) were grouped in the clade Arvicolinae (subfamily). However, Bufonidae indet. was not added because

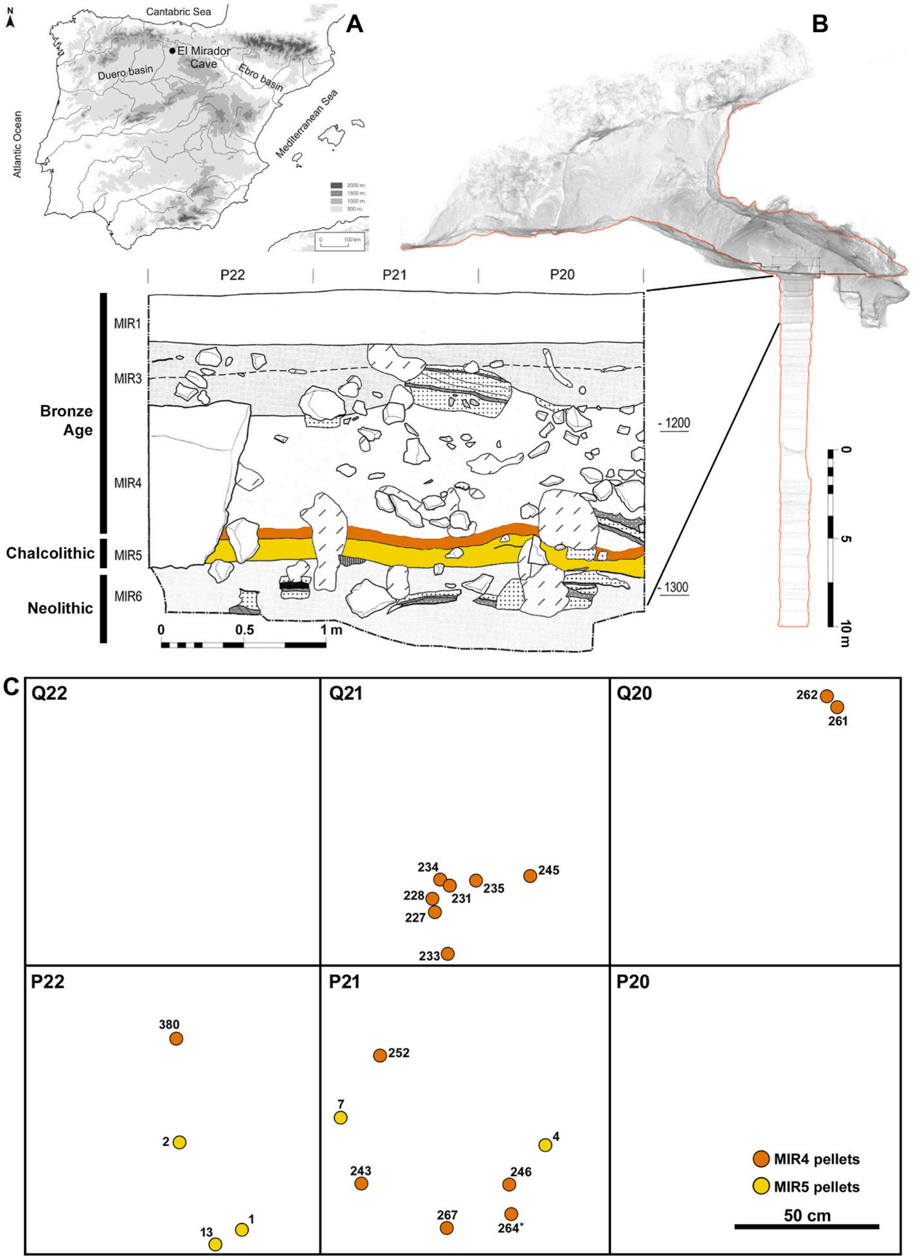

Fig. 2. El Mirador cave from Sierra de Atapuerca (Burgos, Spain). **A:** Location of El Mirador cave in the Iberian Peninsula; **B:** N-S section of the cave with the test pit and stratigraphic profile from the Late Neolithic-Bronze Age south section of the test pit, showing the stratigraphical position of the accumulations (orange: MIR4; yellow: MIR5); **C:** Horizontal projection of the accumulations of small-vertebrate remains identified as avian pellets from the basis of MIR4 and MIR5 levels in the grids of the central test pit sequence. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

it can correspond to two species with different ecological requirements (*Bufo spinosus* and *Epidalea calamita*).

A correspondence analysis (CA) was used on the data matrices (Greenacre, 2010). CA is the recommended method for comparing assemblages (assigned to column) and the taxa they include (assigned to rows) in an equivalent way. The primary objective in this paper is to delineate proximity relationships among the various taxa documented in the owl pellets, grouping them more closely based on the degree of their concurrence. Taxa with higher concurrence are positioned closer together, while more atypical taxa are positioned eccentrically relative to the rest of the sample. Similarly, the pellet associations are organized following this pattern, structured according to the frequency of concurrences within their composition. The Paleontological Statistics program (PAST, version 4.03) was used for all statistical analyses (Hammer et al., 2001).

3.4. *Palaeoenvironmental reconstruction*

We used the habitat weighting method (Evans et al., 1981; Andrews, 2006; adapted by Blain et al., 2008 for herpetofauna) for the palaeoenvironmental reconstruction. This method employs a percentage distribution in five different habitats preferentially occupied by each identified species, calculated based on the MNI per taxon (Table 3).

The five habitats included are: *Open Dry*: environments with little vegetation or vegetation of low height and subject to seasonal changes in humidity, especially during the summer drought; *Open Humid*: wet areas with low perennial and dense vegetation that remains wet throughout the year; *Woodland*: environments with greater plant cover reaching comparatively greater heights, from medium shrublands to closed forests, including the margins of these areas; *Rocky*: open environments with low or scarce vegetation, poor substrate and an abundance of

Table 3
Habitat weighting values for the herpetofauna and small-mammal species from the pellets of MIR4 and MIR5, El Mirador cave (Burgos, Spain).

Species	Common name	Open Dry	Open Humid	Woodland	Rocky	Water Edge
Lissotriton helveticus	Palmate newt		0.2			0.8
Triturus marmoratus	Marbled newt		0.4	0.2		0.4
Alytes obstetricans	Common midwife toad		0.6	0.2		0.2
Pelobates cultripes	European spadefoot toad	0.8				0.2
Hyla molleri (*Hyla* gr. *Hyla arborea*)	Iberian tree frog		0.5	0.2		0.3
Bufo spinosus (*Bufo* gr. *Bufo bufo*)	Spiny common toad	0.1	0.3	0.4		0.2
Epidalea calamita	Natterjack toad	0.65			0.25	0.1
Rana temporaria	Common brown frog		0.4	0.4		0.2
Anguis fragilis	Slowworm		0.25	0.75		
Chalcides striatus	Western three-toed skink		0.4	0.3	0.3	
Lacerta bilineata	Western green lizard		0.5	0.4	0.1	
Timon lepidus	Ocellated lizard	0.5			0.5	
Coronella austriaca	Smooth snake		0.5	0.25	0.25	
Vipera aspis/seoanei	Viper		0.25	0.5	0.25	
Microtus agrestis	Field vole		0.5	0.5		
Microtus arvalis	Common vole	0.5		0.5		
Microtus (Terricola) duodecimcostatus	Mediterranean pine vole		0.25	0.5	0.25	
Apodemus sylvaticus	Wood mouse			1		
Sorex araneus	Common Eurasian shrew		0.5	0.5		

emerged rock and stones; *Water Edge*: aquatic and peri-aquatic environments, permanent or temporary bodies of water and their immediate surrounding areas, with hydrophilic and hygrophilous vegetation.

The percentage data for each species are provided in Blain et al. (2008, 2010, 2011a, 2011b, 2013) and López-García et al. (2011) for herpetofauna, and López-García et al. (2011) for small-mammals. For *Lacerta bilineata*, without a previous record, new parameters were created based on Ortiz-Santaliestra et al. (2011), Masó and Pijoan (2011) and Gosá and Rubio (2015).

3.5. Palaeoclimatic reconstruction

The palaeoclimatic reconstruction is based on the mutual ecogeographic range method (MER), which quantifies rainfall and temperatures and, from these, the different bioclimatic indices using the concurrence of microvertebrate species from the same level (Blain, 2009; Blain et al., 2009, 2016). For this purpose, the locations on the Iberian Peninsula where the same species currently live are identified as appearing in concurrence at the same level of the archaeological record, using the geographical division into 10 × 10 km UTM squares. In order to avoid distortions in the results, the grids affected by disturbing factors, such as the industrial anthropization of the landscape or an extreme difference in elevation from that of the El Mirador site, were excluded.

The main distribution atlases of herpetofauna and mammals in the Iberian Peninsula were used for the MER (Palomo et al., 2007; AHE, 2025) in conjunction with the climatic parameters of the weather stations located in the grids where the current concurrences are located (Climatic-Data.org). As current reference sample, we used the climate data obtained between 1982 and 2012 in Ibeas de Juarros, the closest town to El Mirador cave (2.2 km, west). The data obtained were the mean annual temperature (MAT), mean monthly temperature and precipitation for each month of the year, and the mean annual precipitation (MAP), thus representing a total of 26 parameters.

4. Results

4.1. Small-vertebrate content from the MIR4 and MIR5 pellets

A total of 14 accumulations of small-vertebrate remans identified as avian pellets from MIR4 and five from MIR5 have been documented, which include 7482 identified bone specimens (NISP) and a minimum number of individuals (MNI) of 350 (Fig. 3, Tables 4 and 5). The faunal remains are distributed in at least 20 different taxa with generic or specific level adscription. These are the caudates *Lissotriton helveticus* (431 NISP, 34 MNI) and *Triturus marmoratus* (156 NISP, 15 MNI); and the anurans *Alytes obstetricans* (5 NISP, 2 MNI), *Pelobates cultripes* (21 NISP, 6 MNI), *Hyla* gr. *Hyla arborea* (2877 NISP, 136 MNI), *Epidalea calamita* (28 NISP, 6 MNI), *Bufo* gr. *B. bufo* (31 NISP, 5 MNI), and *Rana temporaria* (163 NISP, 15 MNI). Reptiles include the squamates *Anguis fragilis* (186 NISP, 12 MNI), *Chalcides striatus* (1241 NISP, 42 MNI), *Lacerta* cf. *bilineata* (127 NISP, 7 MNI), *Timon lepidus* (16 NISP, 4 MNI), *Coronella austriaca* (115 NISP, 6 MNI), and *Vipera* sp. (*Vipera aspis/seoanei*) (3 NISP, 1 MNI). In addition, at least one undetermined snake and nine Lacertidae individuals could not be identified more precisely due to a lack of diagnostic criteria. These are small (3 MNI) and medium-sized (6 MNI) lizards, which may correspond to both adult and juvenile individuals of one or more species. The sample also includes remains of indeterminate newts (4 NISP), indeterminate anurans (36 NISP), indeterminate toads (6 NISP) and indeterminate lacertilians (1438 NISP).

The mammals are represented by rodents and insectivores. The only insectivore (Eulipotyphla) identified is the red toothed shrew *Sorex araneus* (1 NISP, 1 MNI), determined by means of a single first left upper molar from MIR4-P21-n252 (Fig. 3AI). The most prevalent clade is Rodentia, especially the species of arvicoline (Cricetidae) voles, *Microtus agrestis* (7 NISP, 4 MNI), *Microtus arvalis* (5 NISP, 4 MNI), and *Microtus* (*Terricola*) *duodecimcostatus* (5 NISP, 3 MNI), but also the murid *Apodemus sylvaticus* (36 NISP, 6 MNI). However, a high number of remains could not be determined beyond the subfamily level (Arvicolinae indet., 221 NISP) or order level (Rodentia indet., 275 NISP) owing to the lack of diagnostic characters. After excluding remains attributable to individuals already identified at the species level based on diagnostic elements in the same avian pellet, the MNI was estimated at 24 for indeterminate arvicolines and 3 for indeterminate rodents (Tables 4 and 5).

Likewise, the presence of indeterminate birds (3 NISP, 2 MNI) has been documented in the pellets through an indeterminate Galliformes right tarsometatarsus from MIR4-Q21-n245 (Fig. 3.AC.1-2) and an indeterminate Passeriformes right carpometacarpus and phalange bones from MIR4-P22-n380 (Fig. 3AD 1-2).

There are differences in the species number and the representation percentages of each taxon between the pellet assemblages of MIR4 and MIR5. One of the most notable of these differences is the higher percentage of *Hyla* gr. *H. arborea* in MIR5, where this tree frog represents 66.33% of the association, when compared to MIR4 (7.65%). In contrast, other taxa are more abundant in MIR4, such as newts, skinks and voles. The number of species remains stable at both levels with a

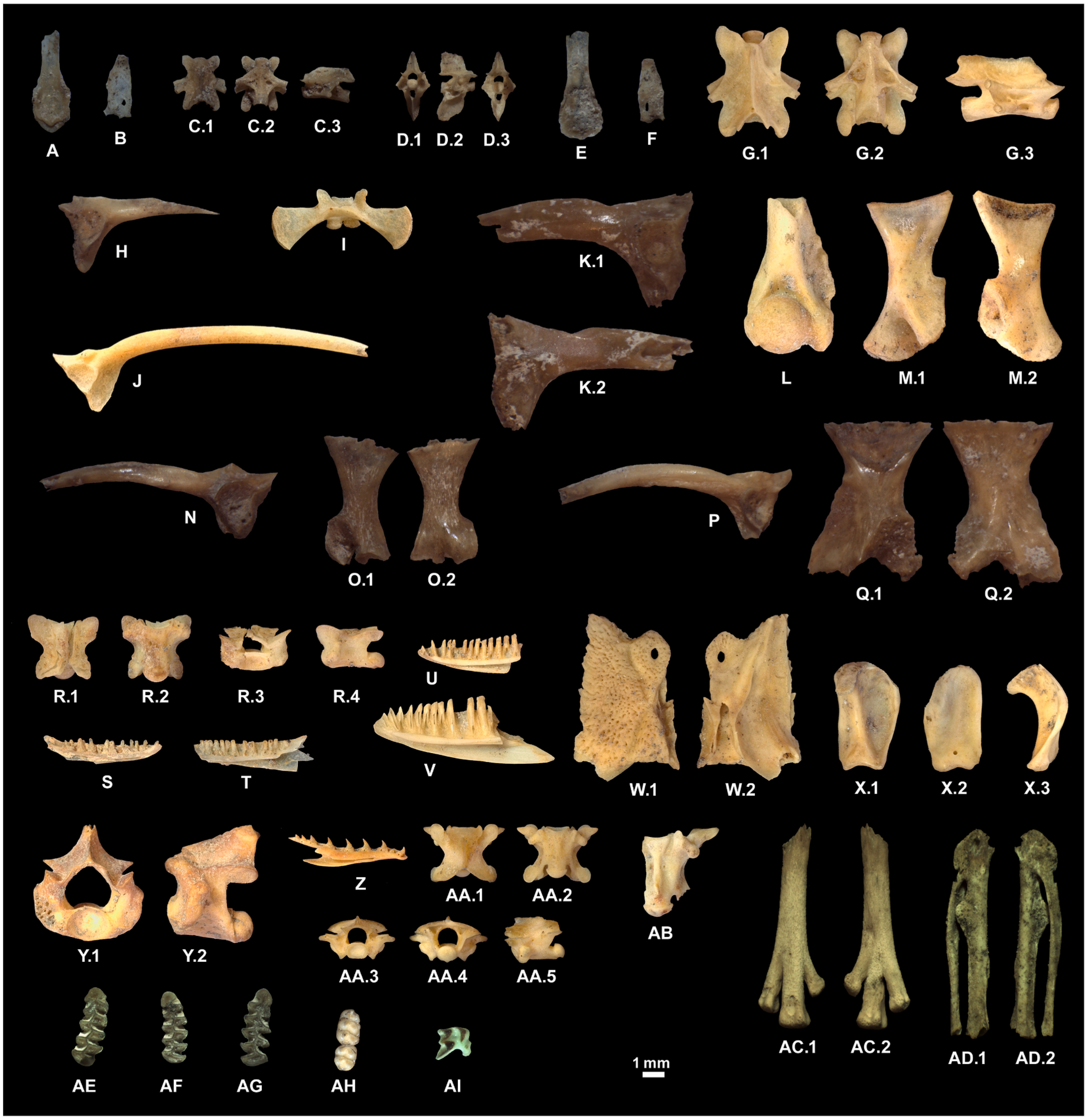

Fig. 3. Small-vertebrates from the accumulations of small-vertebrate remains identified as avian pellets of MIR4 and MIR5 levels, El Mirador cave (Burgos, Spain) represented for purpose of comparison at same scale. **A-D:** *Lissotriton helveticus*, **A:** parasphenoid, dorsal view, **B:** right orbitosphenoid, medial view, **C:** trunk vertebra, dorsal (C.1), ventral (C.2) and lateral (C.3) views, **D:** caudal vertebra, anterior (D.1), lateral (D.2) and posterior (D.3) views (MIR4-Q20-n262); **E-G:** *Triturus marmoratus*, **E:** parasphenoid, dorsal view, **F:** left orbitosphenoid, medial view (MIR4-Q20-n262), **G:** trunk vertebra, dorsal (G.1), ventral (G.2) and right lateral (G.3) views (MIR5-P21-n4); **H:** *Alytes obstetricans*, right ilium, lateral view (MIR5-P21-n7); **I-J:** *Hyla* gr. *H. arborea*, **I:** sacral vertebra, dorsal view, **J:** right ilium, lateral view (MIR5-P21-n4); **K:** *Pelobates cultripes*, left ilium, lateral (K.1) and medial (K.2) views (MIR5-P21-n7); **L-M:** *Rana temporaria*, **L:** right humerus, ventral view, **M:** right scapula, ventral (M.1) and dorsal (M.2) views (MIR5-P21-n4); **N-O:** *Epidalea calamita*, **N:** left ilium, lateral view, **O:** right scapula, dorsal (O.1) and ventral (O.2) views (MIR4-Q21-n233), **P-Q:** *Bufo* gr. *B. bufo*, **P:** left ilium, lateral view, **Q:** left scapula, dorsal (Q.1) and ventral (Q.2) views (MIR5-P21-n7); **R:** *Anguis fragilis*, trunk vertebra, dorsal (R.1), ventral (R.2), lateral (R.3) and anterior (R.4) views (MIR5-P21-n4); **S-T:** *Chalcides striatus*, **S:** left dentary, medial view; **T:** right dentary, medial view (MIR5-P21-n4); **U:** Lacertidae indet. (small size), right dentary, medial view (MIR5-P21-n4); **V-X:** *Lacerta* cf. *bilineata*, **V:** right dentary, medial view; **W:** parietal, dorsal (W.1) and ventral (W.2) views; **X:** quadrate, anterodorsal (X.1), posterodorsal (X.2) and lateral (X.3) views (MIR5-P21-n4); **Y:** *Timon* cf. *lepidus*, cervical vertebra, anterior (Y.1) and left lateral (Y.2) views (MIR5-P21-n4); **Z-AA:** *Coronella austriaca*, **Z:** left dentary, medial view (MIR5-P21-n4); **AA:** trunk vertebra, dorsal (AA.1), ventral (AA.2), anterior (AA.3), posterior (AA.4) and left lateral (AA.5) views (MIR5-P21-n4); **AB:** *Vipera* sp., trunk vertebra, ventral view (MIR5-P21-n4); **AC:** Galliformes indet.; right tarsometatarsus, dorsal (AC.1) and ventral (AC.2) views (MIR4-Q21-n245), **AD:** Passeriformes indet., right carpometacarpus, dorsal (AD.1) and ventral (AD.2) views (MIR4-P22-n380); **AE:** *Microtus agrestis*, first left lower molar, occlusal view (MIR4-P21-n246); **AF:** *Microtus arvalis*, first left lower molar, occlusal view (MIR4-P21-n246); **AG:** *Microtus* (*Terricola*) *duodecimcostatus*, first right lower molar, occlusal view (MIR5-P22-n1); **AH:** *Apodemus sylvaticus*, first and second right lower molars, occlusal view (MIR4-P21-n246); **AI:** *Sorex araneus*, first left upper molar, occlusal view (MIR4-P21-n252).

total of 17-18 different identified taxa, of which 15 coincide in both MIR4 and MIR5. MIR5 presents a greater number of herpetofauna species, with the midwife toad *A. obstetricans* and the snake *Vipera* sp. (*V. aspis/seoanei*), while the field vole *M. agrestis* and common shrew *S. araneus* appear in the MIR4 pellets. However, the apparent absence of *M. agrestis* in MIR5 may be linked to the problematic identification of the Arvicolinae remains due to the absence of diagnostic elements.

Table 4
Distribution of small-vertebrates according to the minimum number of individuals (MNI) by pellets from MIR4, El Mirador cave (Burgos, Spain).

TAXA	MIR4Q21 227		MIR4Q21 228		MIR4Q21 231		MIR4Q21 233		MIR4Q21 234		MIR4Q21 235		MIR4P21 243		MIR4Q21 245		MIR4P21 246		MIR4P21 252		MIR4Q20 261		MIR4Q20 262		MIR4P21 267		MIR4P22 380	
	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI
Salamandridae indet.																					2							
Lissotriton helveticus	2	1	5	2							1	1					6	1	118	8	120	5	167	12	1	1		
Triturus marmoratus																			20	2	49	3	39	3	6	2		
Anura indet.							5						9								3				9			
Pelobates cultripes							3	1			2	1																
Hyla gr. *arborea*	3	2							1	1					4	1	1	1	6	1	21	3	29	2	8	1	1	1
Bufonidae indet.			3	1																					1	1		
Epidalea calamita			1	1	1	1	13	2					12	1														
Bufo gr. *bufo*																					1	1						
Rana temporaria											1	1									56	5	58	6				
Lacertilia indet.	49		153		572		9		58		333		181		3				33						2		45	
Anguis fragilis			23	1	4	1			9	1			73	2					1	1							22	1
Chalcides striatus	73	5	173	6	388	12	10	1	37	2	456	7			45	2			6	1			3	1	10	1	11	1
Lacertidae indet. (small size)															1	1												
Lacertidae indet. (medium size)	2	1	4	2																	1	1	2	1			1	1
Lacerta cf. *bilineata*													27	1					1	1								
Timon lepidus									3	1	10	1																
Ophidia indet.																			1	1								
Coronella austriaca			1	1													1	1							1	1		
Galliformes indet.															1	1												
Passeriformes indet.																											2	1
Rodentia indet.	16		1		1						15	1	8	2	131				2		7		1		1			
Arvicolinae indet.	1	1	4	1	1	1									12	1	144	8	2		2		17	2	1	1		
Microtus sp.																												
Microtus agrestis																	6	3	1	1								
Microtus arvalis																	3	2			1	1						
Microtus (Terricola) duodecimcostatus															1	1												
Apodemus sylvaticus															2	1	32	3										
Sorex araneus																			1	1								
TOTAL	146	10	368	15	967	15	40	4	108	5	818	12	310	6	200	8	193	19	192	17	263	19	316	27	40	8	82	5

Table 5
Distribution of small-vertebrates according to the minimum number of individuals (MNI) by pellets from MIR5, El Mirador cave (Burgos, Spain).

TAXA	MIR5 P22 1		MIR5 P22 2		MIR5 P21 4		MIR5 P21 7		MIR5 P22 13	
	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI	NISP	NMI
Salamandridae indet.			2							
Lissotriton helveticus	2	1	8	1			1	1		
Triturus marmoratus	3	1	3	1	36	3				
Anura indet.	2						8			
Alytes obstetricans			3	1			2	1		
Pelobates cultripes			4	1			12	3		
Hyla gr. *arborea*	12	2	767	33	1706	66	11	1	307	21
Bufonidae indet.	2									
Epidalea calamita	1	1								
Bufo gr. *bufo*							29	3	1	1
Rana temporaria			26	2	22	1				
Lacertilia indet.										
Anguis fragilis	17	2	3	1	12	1	22	1		
Chalcides striatus	13	1	14	1	2	1				
Lacertidae indet. (small size)			2	1	24	1				
Lacerta cf. *bilineata*	3	1	3	1	93	3				
Timon lepidus			1	1	2	1				
Coronella austriaca	2	1			110	2				
Vipera sp. (*aspis/seoanei*)					3	1				
Rodentia indet.	62		5		16		2		7	
Arvicolinae indet.	26	3	2	1			4	1	5	1
Microtus sp.					8	3				
Microtus arvalis									1	1
Microtus (*Terricola*) *duodecimcostatus*	4	2								
Apodemus sylvaticus			1	1	1	1				
TOTAL	149	15	844	46	2035	84	91	11	321	24

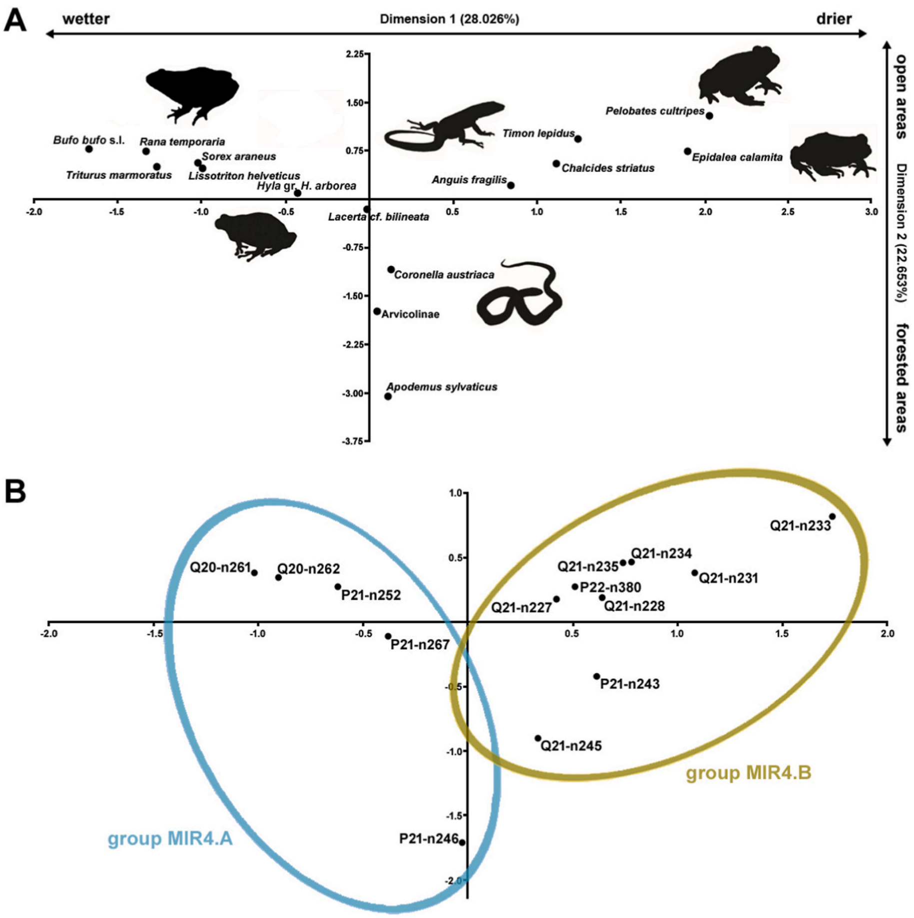

Fig. 4. Graphic representation of correspondence analyses of the taxa (A) and pellet assemblages (B) from MIR4, El Mirador cave (Burgos, Spain).

4.2. Taxonomic comparison between pellets

4.2.1. MIR4

In the correspondence analysis of species from MIR4, the horizontal axis is interpreted in a left-right direction from higher to lower moisture, while the vertical axis shows differences in a top-bottom direction from open to forested areas (Fig. 4A). This results in a graphic representation of the species with the formation of three large groups: one located in the upper left quadrant, made up of the aquatic or highly hygrophilous species *L. helveticus*, *T. marmoratus, Bufo* gr. *B. bufo* (*B. spinosus*), *R. temporaria* and *S. araneus*; another one in the upper right quadrant made up of species with preferences for sunny and open habitats, *A. fragilis*, *C. striatus*, *T. lepidus*, *E. calamita* and *P. cultripes*, with an internal organisation that follows the criterion of the horizontal axis (wet-dry); and a third group located in the bottom half comprised of species with preferences for environments with a greater plant cover than those of the second group: *Hyla* gr. *H. arborea*, *Lacerta* cf. *bilineata*, *C. austriaca*, the arvicoline voles and *A. sylvaticus* (Fig. 4A).

The graphic representation of the correspondence analysis for the MIR4 pellets is organised differently, but retains the same dynamics in which the taxa with higher representation values determine the position and the groups are formed by habitat preferences (Fig. 4B). The first group (MIR4.A) is made up of the pellets in which hygrophilous taxa predominate and, more specifically, have a marked presence of *T. marmoratus* and *L. helveticus*. The second group (MIR4.B) includes pellets primarily made up of species with preferences for open lands and with heliophilous tendencies, with *C. striatus* as the dominant species, and to a lesser extent *E. calamita* and *A. fragilis* share the presence of *A. sylvaticus*, considered a marker of forest environments, in concurrence with a high number of arvicolines (*M. agrestis*, *M. arvalis* and *M.* (*T.*) *duodecimcostatus*) (Fig. 4B).

4.2.2. MIR5

The results for MIR5 are different due to the exceptional predominance of *Hyla* gr. *H. arborea* over the rest of taxa and the relatively low number of pellets preserved at this level. Both factors generate a large bias that hinders the paleoecological interpretation of the axes of the correspondence analysis, regardless of the abundance of tree frogs (Fig. 5A-B).

In its graphic representation, this appears as a large accumulation of the taxa in a group monopolised by *Hyla* gr. *H. arborea*, in which this anuran represents between 71.74 and 87.50% of the MNI. The remaining taxa appear in more eccentric positions, marked by *E. calamita* and *B. spinosus* together with *P. cultripes*, respectively (Fig. 5A-B). The distant position of both bufonid species could indicate a wet-dry trend on the vertical axis, but the position of the rest of the species and their scarce record do not support this hypothesis.

4.3. Palaeoenvironmental reconstructions

The habitat weighting method, both in MIR4 and MIR5, suggests a preference for open environment, primarily made up of open humid habitats (31.71% in MIR4, 44.62% in MIR5) and to a lesser extent rocky (10.82% in MIR4, 9.02% in MIR5) and open dry habitats (5.32% in MIR4, 11.41% in MIR5). The presence of woodland environments was also detected, which include medium scrublands to forest formations (26.29% in MIR4, 23.79% in MIR5), together with aquatic and peri-aquatic areas (25.86% in MIR4, 26.04% in MIR5), such as rivers or ponds with riverside vegetation (Fig. 6). These habitat distribution percentages are consistent with the faunal composition identified and predominance of hygrophilous taxa over the comparatively more thermo-xerophilic.

Diachronically, the environmental differences detected between MIR4 and MIR5 are the increase in open dry areas, woodlands and rocky habitats, and the decrease in open humid areas (Fig. 6). However, the

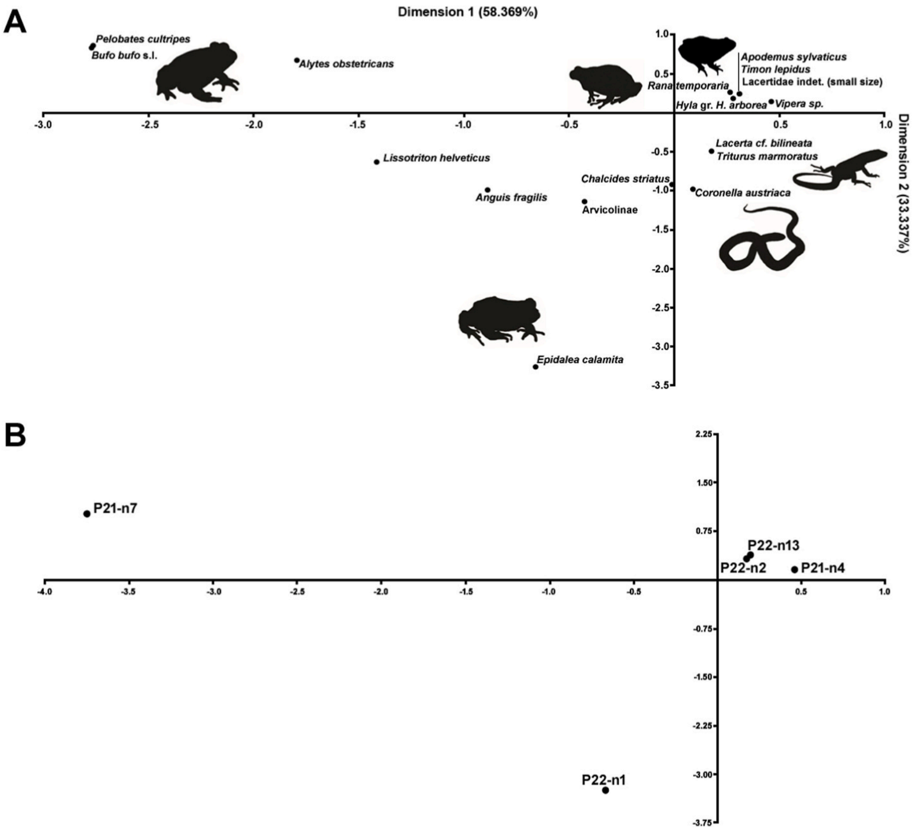

Fig. 5. Graphic representation of correspondence analyses of the taxa (**A**) and pellet assemblages (**B**) from MIR5, El Mirador cave (Burgos, Spain).

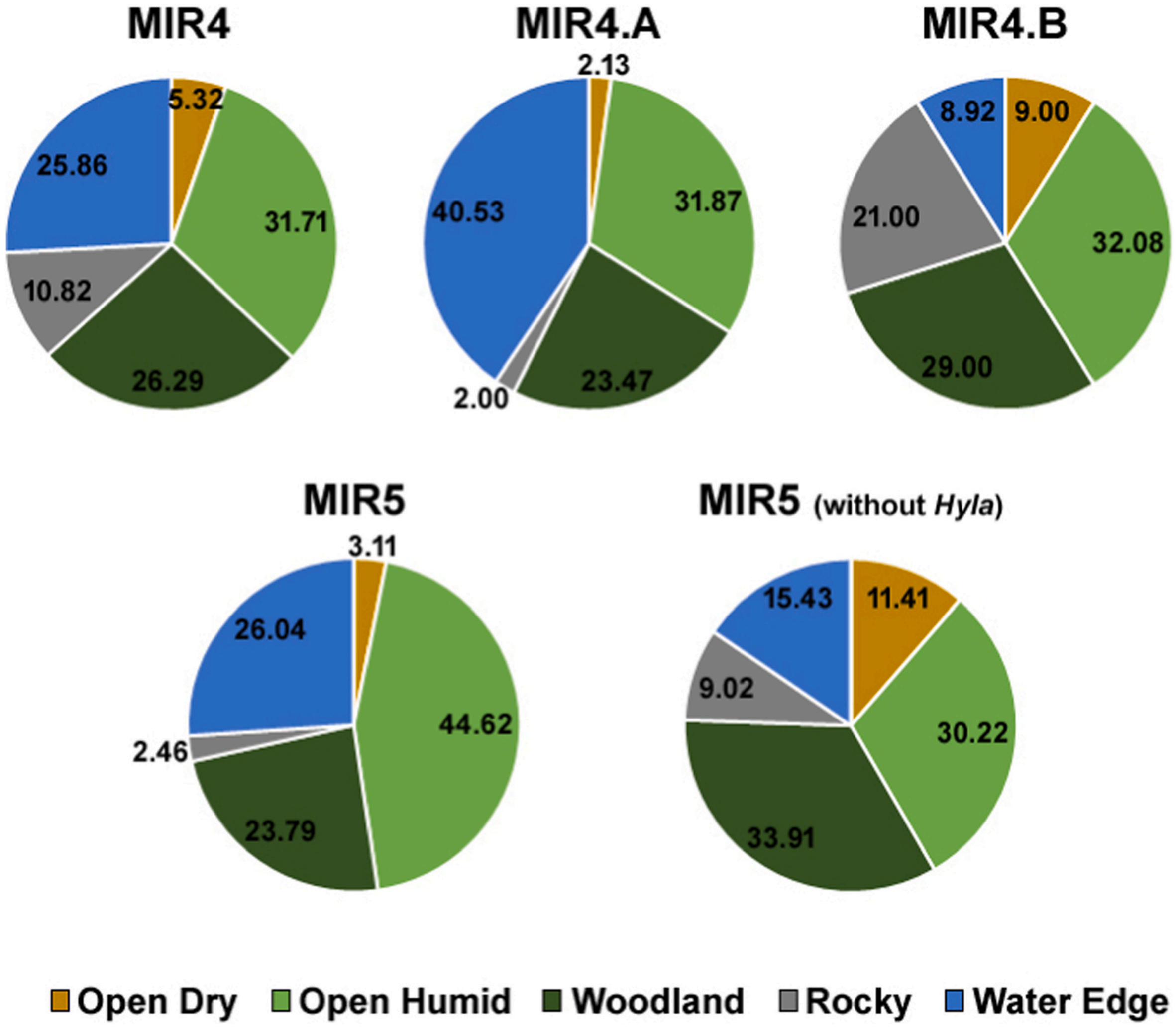

Fig. 6. Palaeoenvironmental reconstructions based on the Habitat Weighting method for MIR4 and MIR5 pellets, El Mirador cave (Burgos, Spain). The values are in percentages (%).

representation of aquatic environment habitats in the two levels is quite similar. This is due primarily to the over-representation of *Hyla* gr. *H. arborea* in MIR5 (66.33%), a typical anuran of wet environments and water pond areas, which is represented in much lower percentages in MIR4 (7.65%). Furthermore, MIR4 contains a higher representation of taxa typical of comparatively rockier and drier areas, such as *E. calamita* and *C. striatus.*

When statistically separating the pellets in MIR4 into two groups (Fig. 4A), the first group, MIR4.A, corresponds to the pellets indicating, through habitat weighting analyses, high percentages of open humid and aquatic environments and low percentages of open dry and rocky habitats; whereas the situation is reversed in the second group (MIR4.B), with high percentages of open dry and rocky environments to the detriment of open wet and aquatic areas. On the other hand, woodland environments are relatively similar in both groups. Removing the over-represented *Hyla* gr. *H. arborea* results in a percentage increase in all habitats to the detriment of open humid environments, although the scenario is similar to previous ones (Fig. 6).

4.4. Palaeoclimatic reconstructions

4.4.1. MIR4 vs. MIR5

The geographical distributions of all species present in the pellets of MIR4 and MIR5 coincide in at least one 10 × 10 km UTM square, except in the case of *S. araneus* (MIR4 and MIR4.A). The shrew *S. araneus* is a species of Eurosiberian requirements that currently has a widespread geographical distribution covering most of western Eurasia but is restricted to the eastern Pyrenees on the Iberian Peninsula and the northern Pyrenees in southwestern France, with no connection to other European populations (López-Fuster et al., 1999; Shchipanov and Pavlova, 2016). This isolation is attributed to the progressive retraction of its range due to the climate warming of the Holocene and particularly to the increasing competitive pressure of *Sorex coronatus*, which has recently expanded from southwestern France (López-Fuster, 2007a; Mackiewicz et al., 2017). The current geographical range of *S. araneus* on the Iberian Peninsula does not correspond to its potential range due to the mutual exclusion of *S. coronatus* (López-Fuster, 2007b). Therefore, *S. araneus* was removed from the analyses for MIR4 because its distribution is biased by a competing species. With this exclusion, the overlaps for both MIR5 and MIR4 are identical and correspond to a single UTM square (30T-TN63), which corresponds to the area between the towns of Soutu y Amíu, Las Oumañas and Espinosa de la Ribeira in the southern areas of Baxa Oumaña and Ḷḷuna d'Abaxu shires and the central-northern part of the province of Llión-León (Fig. 7).

The climate data obtained for MIR4 and MIR5 (Table 6) through the mutual ecogeographic range method suggest an MAT of 9.8 °C, i.e. slightly lower than the current value (−0.3 °C), mainly due to lower mean temperatures during the summer months and early autumn and slightly lower during the rest of the year (Table 6). The range of atmospheric temperature throughout the year was 15.6 °C, between the

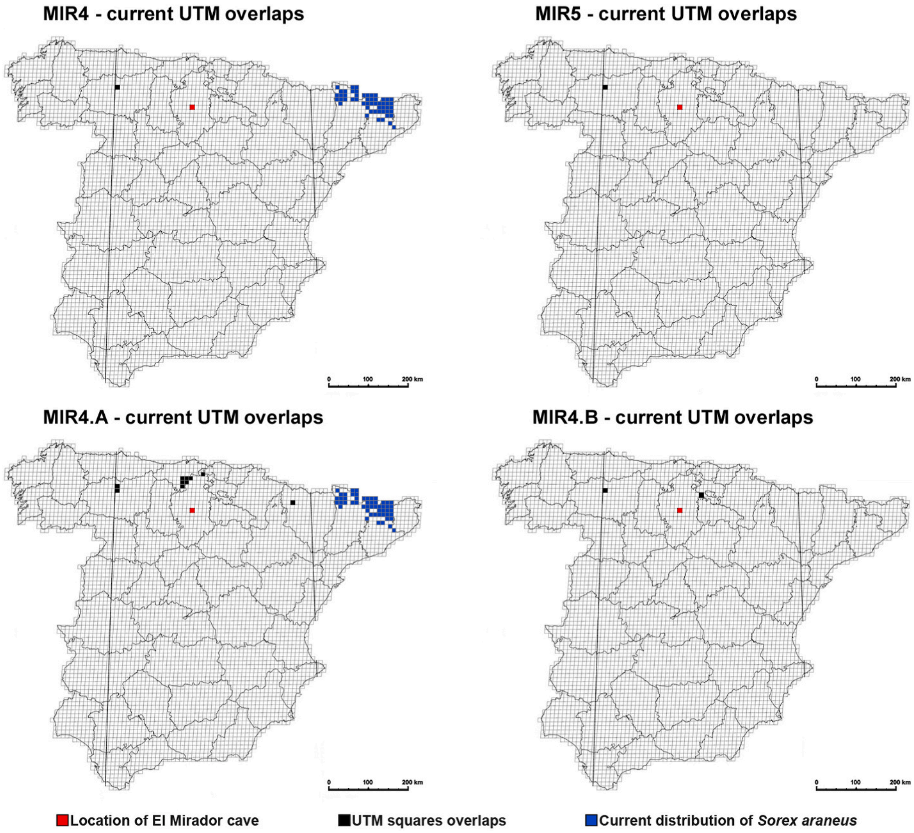

Fig. 7. Overlaps based on a 10 × 10 km UTM grid of the herpetofaunal and small-mammal species present in the pellets from MIR4 and MIR5, El Mirador cave (Burgos, Spain). In black the UTM squares used for MER, in red the location of Atapuerca, in blue the current distribution of the shrew *Sorex araneus* (adapted from López-Fuster, 2007a). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 6
Palaeoclimatic parameters according to the overlaps obtained by Mutual Ecogeographic Range method through the faunal associations from the pellets of MIR4 and MIR5, El Mirador cave (Burgos, Spain).

Temperature (in °C)	MAT	J	F	M	A	M	J	J	A	S	O	N	D
Current	10.1	2.6	3.8	6.5	8.2	11.5	15.4	18.6	18.7	15.9	11	6.2	3.3
MIR4	9.8	2.3	3.7	6.3	8.0	11.2	15.4	17.9	17.9	15.1	10.5	6.0	3.2
SD	-	-	-	-	-	-	-	-	-	-	-	-	-
MIR4.A	10.5	3.8	4.7	7.1	8.6	11.6	15.3	17.8	17.9	15.6	11.5	7.4	4.9
SD	1.1	1.6	1.3	1.3	1.1	0.9	0.7	0.6	0.7	0.9	1.2	1.4	1.6
MIR4.B	11.1	3.9	5.2	7.8	9.3	12.5	16.3	18.8	18.9	16.4	12	7.4	4.8
SD	1.8	2.3	2.1	2.1	1.8	1.8	1.3	1.3	1.4	1.8	2.1	2.0	2.2
MIR5	9.8	2.3	3.7	6.3	8.0	11.2	15.4	17.9	17.9	15.1	10.5	6.0	3.2
SD	-	-	-	-	-	-	-	-	-	-	-	-	-
Precipitation (in mm)	**MAP**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Current	594	50	46	44	57	64	50	30	31	47	51	63	61
MIR4	721	59	62	37	65	64	49	33	39	56	77	94	86
SD	-	-	-	-	-	-	-	-	-	-	-	-	-
MIR4.A	827	72	66	59	74	72	59	40	49	67	80	95	94
SD	84.2	11.8	9.5	11.5	6.8	6	6.4	3.7	6	9.3	8.4	9.8	13.5
MIR4.B	735	64	62	45	64	66	54	34	41	61	74	85	85
SD	17.7	7.1	0.0	11.3	1.4	2.4	7.1	1.4	2.8	6.4	4.2	13.4	2.1
MIR5	721	59	62	37	65	64	49	33	39	56	77	94	86
SD	-	-	-	-	-	-	-	-	-	-	-	-	-

warmest months (July and August, 17.9 °C) and the coldest month (January, 2.3 °C). In contrast, the differences in MAP are more significant, calculated at 721 mm for MIR4 and MIR5, i.e. 127 mm higher than at present (594 mm). In general, the rainfall regime is mostly regular, with low differences in rainfall during most of the year, like today, but with higher rainfall after the summer. There was a dry period during July and August, with monthly rainfall of less than 40 mm. Precipitation increased during autumn and winter, reaching its peak in mid-autumn (94 mm) (Table 6).

4.4.2. *MIR4.A vs. MIR4.B*

The palaeoclimatic data for MIR4.A and MIR4.B were analysed to explore the effects that the groups identified by means of the correspondence analyses may have had on palaeoclimatic reconstructions. For MIR4.A, the number of overlaps in 10 × 10 km UTM squares is ten, because of the assemblage of Eurosiberian and generalist species. In

MIR4.B, it was reduced to two squares because of the assemblage of Eurosiberian and Mediterranean species (Fig. 7).

An MAT of 10.5 °C was obtained for MIR4.A and 11.1 °C for MIR4.B, higher than both the current MAT and that estimated for MIR4. The mean monthly temperatures are higher for MIR4.A, especially during autumn and winter (Table 6 and Fig. 8).

The MAP in MIR4.A is higher than in MIR4, with 827 mm (+106 mm), despite the same rainfall distribution throughout the year. The MAP in MIR4.B is similar to that of MIR4, 735 mm (+14 mm) (Table 6 and Fig. 8). However, due to the low number of concurrences, the standard deviation is very high, mostly in the case of MIR4.B. MIR4 and MIR5 have no standard deviation because only one concurrence was obtained (Table 6).

5. Discussion

The comparative study of the 19 pellets of MIR4 (14 pellets) and MIR5 (5 pellets), suggests the existence of variations in the taxonomic composition and number of individuals, at least for MIR4. The pellets from MIR5, however, include a sample biased by the overabundance of *Hyla*. gr. *H. arborea*. Correspondence analyses have separated the MIR4 pellets into two different groups. The first group (MIR4.A) is primarily made up of amphibians, in which hydro-hygrophilous species with generalist and/or Eurosiberian requirements predominate. Reptiles and heliophilous species prevail in the second group (MIR4.B), but Mediterranean, Eurosiberian and generalist species are also associated with it. The palaeoenvironmental reconstruction points to a mostly humid environment, but with variations between higher humidity (MIR4.A and MIR5) to relatively drier conditions (MIR4.B). For all samples, the palaeoenvironmental data indicate a climate similar to today's, but with more rainfall.

The peculiarities of this record and its interpretation in terms of seasonality are discussed below. The possible effects of biases that may be introduced in the paleoenvironmental and palaeoclimatic reconstructions will also be examined.

5.1. Seasonality of the pellet depositions

The faunal associations documented in MIR4 and MIR5 are characterised by their extraordinarily unique species assemblage in the Late Quaternary record (Bisbal-Chinesta and Blain, 2018). Excluding the case of *S. araneus*, the only UTM square on the Iberian Peninsula in which the same species of herpetofauna and small-mammals are currently found is a small area on the southern slopes of the Cantabrian Mountains, in the province of León, where the Omaña highlands converge with the valley of the Luna river (Palomo et al., 2007; AHE, 2025) (Fig. 7). This faunal association is unusual due to the combined record of typically Mediterranean species, such as *T. lepidus*, with other typically Eurosiberian species, such as *R. temporaria*. Even more special is the concurrence of the anurans *P. cultripes* and *R. temporaria*, which in the northern Iberian Peninsula only occurs in seven 10 × 10 km UTM squares between Galicia and Navarra. In the northeast Iberian Peninsula, they concur in 24 UTM squares in northern and central Catalonia (AHE, 2025). The virtual line drawn by the above-mentioned squares coincides with the boundary between the two main macrobioclimates of the Iberian area: the Mediterranean macrobioclimate and the temperate macrobioclimate with an Atlantic-Eurosiberian influence (López Fernández et al., 2008). This pattern is consistent with the environmental and climatic requirements of the species documented in MIR4 and MIR5.

The correspondence analyses have shown the existence of two groups of pellets within MIR4 based on the presence of distinct species and differences in the number of individuals. This is not the case for MIR5, which is monopolised by *Hyla* gr. *H. arborea*. The comparison of the pellets from MIR4 by means of species concurrences and according to the ethology, phenology and annual activity of the species that currently inhabit the Burgos region (Diego-Rasilla and Ortiz-Santaliestra, 2009; Ortiz-Santaliestra et al., 2011) would identify both groups (MIR4.A and MIR4.B) as the product of two different

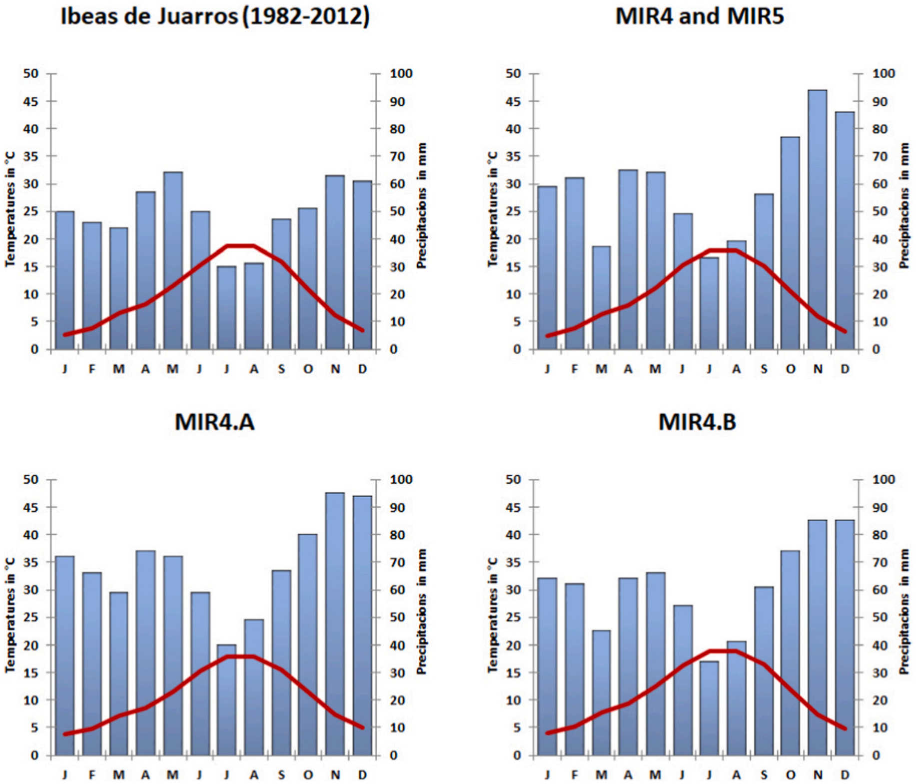

Fig. 8. Climographs of the palaeoclimatic parameters according to the overlaps obtained by Mutual Ecogeographic Range method through the faunal associations from the accumulations considered as pellets of MIR4 and MIR5, El Mirador cave (Burgos, Spain).

seasonal periods, but contiguous in time.

The group dominated by newts, frogs and toads as opposed to squamates (58 amphibians vs. 10 squamates) would suggest a period in the year with an abundance of active amphibians, possibly related to the beginning of the breeding season. The breeding season today on the northern Iberian Peninsula begins with the early rainfalls at the end of winter or the beginning of spring, between February and March (García-París et al., 2004; Diego-Rasilla and Luengo, 2007; Diego-Rasilla and Ortiz-Santaliestra, 2009). Meanwhile, the group in which squamates predominate over amphibians (48 squamates vs. 18 amphibians) suggests a later period of the year, coinciding with the beginning of squamate activity brought about by the increasing temperatures and higher insolation starting in April and May and possibly extending to the summer (Ortiz-Santaliestra et al., 2011) (Fig. 4A). This is consistent with the presence in MIR4.B of thermophilic and Mediterranean species, such as *P. cultripes*, *E. calamita*, *T. lepidus* and *M.* (*T.*) *duodecimcostatus*, which are absent in MIR4.A. In addition, the presence of arvicoline voles in MIR4.A is consistent with a deposition event during the spring and summer months, when the peak activity of these rodents outside their underground burrows occurs due to the growth of vegetation cover after the winter recess (Brügger et al., 2010).

In contrast, the MIR5 pellets suggest another seasonal scenario, owing to the predominant presence of *Hyla* gr. *H. arborea* over all other taxa, as well as the relatively low number of pellets preserved in this level. MIR5 can be interpreted as part of a season-related assemblage, formed during a time when *Hyla* gr. *H. arborea* would have been found in great abundance in the areas surrounding cave. The most plausible scenario is that the deposition event occurred during the reproduction period of *Hyla molleri* (the endemic species of *Hyla* gr. *H. arborea*), i.e. between April and May, when large agglomerations of adult individuals congregate at water points (Lizana et al., 1989; Diego-Rasilla and Ortiz-Santaliestra, 2009), as also previously proposed for the largest pellet MIR5-P21-n4 (Bisbal-Chinesta et al., 2020). The presence of thermophilic species in the MIR5 assemblage, which start their annual activity later than the generalist and Eurosiberian species, is consistent with the proposed period.

5.2. Habitat selection by the predator in the palaeoenvironmental reconstruction

The Holocene palynological record of El Mirador cave generally depicts a mosaic landscape made up of different plant communities comprising mixed forests of *Pinus*, deciduous and evergreen *Quercus*, *Corylus*, *Fagus* and *Juglans*, with swathes of *Cistus* or *Helianthemum* in the clearings formed in the interior, along with riparian communities or riparian forests of *Salix*, *Ulmus* and *Alnus,* accompanied by hydrophilic taxa such as Cyperaceae, *Typha-Sparganium* and *Myriophyllum* in rivers or other nearby water bodies. The surrounding grasslands were represented by Poaceae and other grasses such as *Asphodelus*, Asteraceae, Apiaceae, *Artemisia*, Amaranthaceae, *Plantago* spp., Ranunculaceae and Urticaceae. The complex was intermittently accompanied by cereal crops and other species related to livestock activities, which become increasingly distinct as the Holocene advances to the Bronze Age with the growing anthropogenic landscape (Rodríguez et al., 2016; Expósito et al., 2017, 2022).

Palynological studies of MIR4 and MIR5, however, show evidence of a possible increase in environmental aridity: the percentage of tree pollen from *Pinus* increases drastically, while riparian taxa, mesophilous plants and deciduous *Quercus* disappear or are minimally present in these levels. In turn, the taxonomic diversity of trees, shrubs and herbs decreases, including among taxa linked to anthropization and livestock pressure (Expósito et al., 2017, 2022). These archaeobotanical data are different from those yielded using the habitat weighting method to analyse the pellets, especially about environmental aridity/humidity.

Although normally used for palaeoenvironmental reconstruction based on microvertebrate assemblages, habitat weighting results may also reflect in some way the accumulating agent's selection among the different available habitats around its nest. This is clearer in this case because our fossil assemblages come from non-dispersed pellets that have not mixed with other contributing agents, such as in situ mortality, etc. From this perspective, habitat variability in palaeoenvironmental reconstructions can be attributed to seasonal deposition for the different pellet groups. Based on seasonality, the habitat selection for MIR4 and MIR5 is interpreted within three different seasonal ranges (Fig. 9):

1. The pellets from MIR4.A, attributed to late winter-early spring, with a predominance of hydro-hygrophilous taxa, may suggest preferential habitat selection towards wet meadows and peri-aquatic environments. Rocky areas and dry open environments are not well documented.
2. The pellets from MIR5, attributed to mid-spring in accordance with the timing of the reproduction period of tree frog *Hyla* gr. *H. arborea* (*H. molleri*). The habitat selection is similar to MIR4.A pellets, towards open humid and water habitats.
3. The pellets from MIR4.B, attributed to late spring and/or summer, made up mainly of heliophilous species associated with open habitats and Mediterranean and thermophilic species. The habitat selection results show an increase in open dry environments and rocky habitats and a decrease in wet grasslands and peri-aquatic environments, although humid habitats are still the predator's primary habitat selection.

From an environmental point of view, the changes in the percentages of representation in habitat selection by the predators in MIR4 and MIR5 are consistent with the evolution of plant communities and environmental humidity during the period between late winter and summer, with a dryness beginning in late spring that reaches its maximum in summer (García-Mijangos, 1997; Alejandre et al., 2006; Loidi et al., 2011). Accumulated precipitations during the winter and low temperatures cause high environmental humidity that is maintained as a result of the rainfall between April and May, despite higher springtime temperatures. After this period, aridity increases due to the decrease in summer rainfall and higher atmospheric temperatures, which gives rise to greater evaporation (Table 6 and Fig. 8). This also correlates with the reproductive cycles of the herpetofauna, especially amphibians that require an aquatic larval phase (García-París and Anura, 2004), because they are associated with conditions of continued environmental humidity and the existence of water sources. MIR4.A exhibits the highest percentages of habitats directly associated with high humidity, wet meadows and peri-aquatic environments. In contrast, in MIR4.B the drier environments increase in percentage, with more open dry and rocky habitats at the expense of the wet habitat. The percentages in MIR5, despite coming from an older level, are consistent with the scenario proposed in MIR4. The seasonality in MIR5 can be interpreted as an intermediate phase between MIR4.A and MIR4.B, a wet spring period prior to the increase in environmental dryness.

The predators' habitat selection suggests the existence of a varied environment around the cave for MIR4 and MIR5, which is mostly consistent with the archaeobotanical data for the Holocene sequence of El Mirador cave, but with considerable differences concerning aridity and anthropogenic impact (Cabanes et al., 2009; Allué and Euba, 2008; Vergès et al., 2016; Euba et al., 2016; Rodríguez et al., 2016; Expósito et al., 2017, 2022; Cano-Cano et al., 2022). Palynological studies of levels MIR4 and MIR5, however, point to a possible increase in environmental aridity: the percentage of *Pinus* tree pollen increases drastically, while riparian taxa, mesophilous plants and deciduous *Quercus* disappear or are only minimally present in these levels. In turn, the taxonomic diversity of trees and shrubs decreases, including those taxa linked to anthropization and livestock pressure (Expósito et al., 2017, 2022). The anthracological sequence which is formed by selected wood from the surroundings used mainly as fuel and fodder indicates a decrease of humid taxa such as *Corylus*, *Fraxinus*, *Sambucus* and

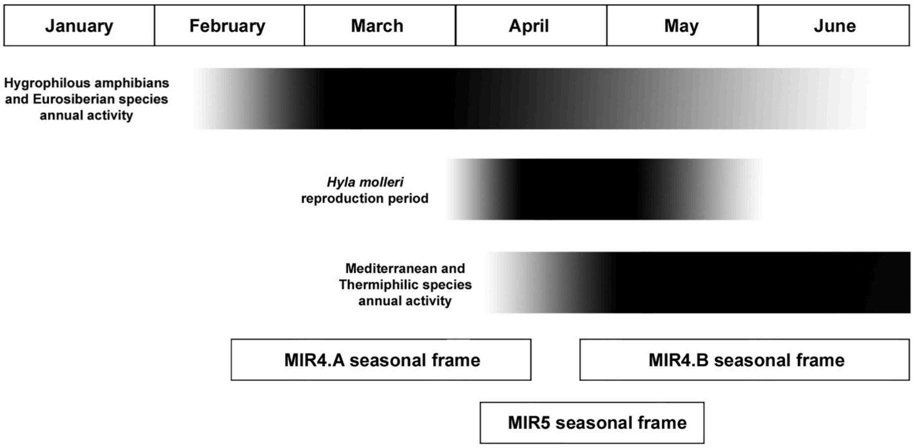

Fig. 9. Proposed seasonal periods for the herpetofauna represented in the avian pellets from MIR4 and MIR5, El Mirador cave (Burgos, Spain).

deciduous *Quercus* between MIR10 and MIR6 and an increase of evergreen *Quercus*. However, in MIR 4 these taxa increase together with the appearance of forest disturbance such as Fabaceae. This would indicate the presence of active water sources nearby the site (Expósito et al., 2022).

This phenomenon of the predominance of *Pinus* among the tree pollen evidence together with its substitution by the evergreen *Quercus* is a generally observed throughout the Iberian Peninsula and is associated with increased human impact on plant communities (Carrión et al., 2010). Similar data suggesting a relationship between increased aridity in vegetation and greater anthropization of the landscape have come from other regions of the western Mediterranean (Magny et al., 2002; Pérez-Díaz et al., 2016; Ramos-Román et al., 2018; Moreno-de las Heras et al., 2018). The palynological record shows a trend towards greater aridity in the El Mirador cave sequence for level MIR5 and the bottom of MIR4, with a chronological interval between 5300 and 3540 cal BP (Expósito et al., 2017, 2022) and is linked, at least in the El Mirador cave sequence, to the regional equivalent of the 4.2 ka event (4100–3950 cal BP) (Magny et al., 2002, 2009).

5.3. Predator diet and human impact

The diet of the predators in the MIR4 and MIR5 pellets clearly displays a preference for herpetofauna species. The main groups represented in the pellets are amphibians (MIR4: 40.13%; MIR5: 80.55%), with some reptiles (MIR4: 38.85%; MIR5: 11.67%) and small-mammals (MIR4: 19.75%; MIR5: 7.78%) in the background, along with the testimonial presence of birds in MIR4 (1.27%).

The published studies on the diet of the two species proposed as possible sources of the accumulation, the eagle-owl *B. bubo* (Hiraldo et al., 1975; Pérez-Mellado, 1978; Vericad et al., 1976; Andrews, 1990; Mikkola, 1995; Serrano, 1998; Sándor and Ionescu, 2009; Obuch and Karaska, 2010; Penteriani and Delgado, 2016) and tawny owl *S. aluco* (Uttendörfer, 1952; Nores, 1980; Alegre et al., 1989; Mikkola, 1995; Villarán, 2000; Romanowsky and Żmihorski, 2009) indicate that their diets mainly comprise mammals, and birds and/or insects, with little or very little herpetofauna. However, amphibians may occasionally represent more than 40% of preys, especially in European populations of *B. bubo* (Hagen, 1950; Frey and Walter, 1986). The maximum percentage of amphibians among the preys of *S. aluco* is lower, with exceptional highs approaching 10% (Uttendörfer, 1952; Mikkola, 1995; Romanowsky and Żmihorski, 2009). The presence of amphibians in the pellets of El Mirador cave exceeds these percentages with very high values, 40.13% in MIR4 and 80.55% in MIR5. What is more unusual is the high presence of reptiles, which reach a maximum of 38.85% in MIR4 and a lower percentage in MIR5 of 11.67% due to the high percentage of *Hyla* gr. *H. arborea* in the pellets from this level. In the literature, the maximum percentage of reptiles among *B. bubo* preys is 28% in eastern Europe (Penteriani and Delgado, 2019). This high representation of reptiles, mostly diurnal species, led us to postulate that *B. bubo* was the accumulating agent of these pellets, in accordance with previous taphonomic studies (Bisbal-Chinesta et al., 2020; García-Morato et al., 2023), as it is a mostly nocturnal and crepuscular species that is also active during the day, unlike *S. aluco* which is much more exclusively nocturnal (Mikkola, 1995; Sunde et al., 2003; Penteriani and Delgado, 2019).

The existence of seasonal variation in diet has been unequivocally documented in nocturnal raptors on the Iberian Peninsula, including the eagle-owl (Pérez-Mellado, 1978; Zerunian et al., 1982; Donázar, 1989; Lara, 1995; García and Cervera, 2001; Andrews and Fernández-Jalvo, 2018). Studies on the composition of the *B. bubo* diet in northern Slovakia have found seasonal predation preferences during spring for the rodents *M. arvalis* and *Arvicola amphibius* and for the frog *R. temporaria*, following the annual cycles of these preys (Obuch and Karaska, 2010). This same study also states that the high representation of frogs (27.90%) and small rodents (51.10%) is due to the growing anthropogenic impact in the prospected area in recent decades consisting of the expansion of extensive agriculture to the detriment of forests, which has decreased biodiversity and the spectrum of available prey for *B. bubo* (Obuch and Karaska, 2010). This phenomenon has been observed in other raptors, such as *Tyto alba* (barn owl), which showed changes in the composition of its diet between 1974 and 1994 in Great Britain: a decrease in the abundance and diversity of its prey and an increase in its dependence on a lower number of species – changes that were associated with new agricultural practices (Love et al., 2000).

In the Mediterranean region, there is also evidence of changes in the diet of the eagle-owl caused by anthropogenic impacts. In Wadi Al Makhrour (Palestine), an increase in population of the invasive black rat *Rattus rattus* to the detriment of native species was linked to the growing anthropization of the landscape (urbanisation) and to the adaptation of the diet of the eagle-owl for new environments, with low biodiversity and variety of preys (Amr et al., 2016). In the Middle Valley of the Ebro River (north-eastern Spain), *B. bubo* presents regional differences in its diet associated with the presence of the European rabbit *Oryctolagus cuniculus*: a reduced number of rabbits correlates with a higher diversity of preys (Serrano, 1998). The same study links the regional rarity of *O. cuniculus* with rabbit haemorrhagic disease (RHD), an infectious disease caused by the calicivirus *Lagovirus* and spread by humans worldwide (Abrantes et al., 2012). This can therefore be considered another human impact.

The palaeoclimatic and palaeoenvironmental conditions suggested by the palynological record for MIR4 and MIR5 diverge from the results yielded by the analysis of the pellet groups. The low representation of plant species associated with water and wet environments contrasts with the high representation of aquatic and semi-aquatic amphibians and with the humid habitats that the accumulating agent would have selected, as well as with the higher reconstructed rainfall for both levels. Although the scale is different, the content of pellets can record the environmental conditions around the cave (2.3 km^2 for an adult *B. bubo*, according to Penteriani et al., 2015), while pollen analyses document changes undergone at a macro/regional level. Therefore, it is possible that the two dynamics are related, and not opposing. Palynological and anthracological studies have pointed to increasing anthropogenic impact on the landscape around the cave from the bottom to the top of the sequence, reaching a maximum at MIR4, beside anthracological record for MIR4 indicates an increase of *Corylus*, *Fraxinus* and *Sambucus* which have water requirements and could be growing nearby local water sources (Euba et al., 2016; Expósito et al., 2017, 2022). The eagle-owl *B. bubo*, the potential accumulating agent of the pellets from El Mirador, is known to be a generalist predator that is highly adaptable to environmental alterations and able to modify its diet to adjust to anthropogenic changes in the landscape (Obuch and Karaska, 2010; Abrantes et al., 2012; Amr et al., 2016; Penteriani and Delgado, 2019). Therefore, the human impact on the landscape is a plausible hypothesis to explain the differences observed between the palaeobotanical data and the exceptional diet of the predator.

As referred to earlier, adult eagle-owls have an average vital territory of 2.3 km^2 around their nests (Penteriani et al., 2015). Applied to the El Mirador cave, this would cover the southern part of the Sierra de Atapuerca and the river terraces formed by the Chorruela brook in its southern part. Outside of this theoretical radius, but nevertheless very nearby, there is the cave of Portalón de Cueva Mayor, the other main human habitat site in Sierra de Atapuerca during the Holocene, which was also inhabited during the Chalcolithic and Bronze Age (Carretero et al., 2008). During the Chalcolithic and Early Bronze Age, El Mirador cave was used as a burial site (Vergès et al., 2016, 2022), which would have made it possible for owls to settle inside the cave in an environment undisturbed by human activities. In contrast, pronounced human impact on the surrounding territory could explain the predator's exceptional diet, which has no parallel in the contemporary literature on European birds of prey. Anthropization gave rise to the degradation of plant communities in the owl's hunting area and possibly to a decrease in available prey (such as rabbits). There are evidences of human consumption of *Oryctolagus cuniculus* at El Mirador cave, including evidence of human consumption of carnivorous mammals: foxes, wild cats and badgers (Martín et al., 2014, 2022). The owl would have preyed on herpetofauna, an abundant resource in the environment but outside the food interest of local human communities. This predilection would generate discordance between the predominant habitat documented by the content of the pellets and the archaeobotanical data, since the predator would have focused on the wet areas where its alternative preys congregated due to its vital requirements: water points and wet meadows. Moreover, this would have occurred coinciding with the 4.2 ka BP Bond event, which would have further reduced the presence of wet and water areas in the landscape, forcing aquatic and hygrophilous species to concentrate in fewer sites.

Despite the results of palynological analyses, the continued presence of wet habitats around the cave as suggested by the composition of the pellets is supported by the pollen of some hydro-hygrophilous species (e.g., Cyperaceae, *Typha-Sparganium*, *Salix*, *Alnus*, *Corylus*) and by anthracological data (*Corylus*, *Fraxinus*, *Sambucus*) from El Mirador cave. In addition to the burnt coals recovered from MIR4 that point to a degradation of the forest cover due to the increased variability of shrub taxa, the presence of deciduous *Quercus*, *Fraxinus* and *Sambucus* suggest the presence of humid environments (Allué and Euba, 2008; Euba et al., 2016; Rodríguez et al., 2016; Expósito et al., 2022). Furthermore, *Cornus*, *Corylus avellana*, *Fagus sylvatica* and *Salix* have been found at the base of MIR4, in the same stratigraphic horizon as the pellets (Allué and Euba, 2008; Cabanes et al., 2009). Whilst some of the plant material may have originated from a region distant from the cave and not from the surrounding area, the presence of these plants is associated with humid environments and/or temperate climates and is consistent with the palaeoclimatic data (Table 6 and Fig. 8).

Approximately 5000 years ago, in the Late Neolithic and Chalcolithic periods, the North Castilian Plateau and the Duero Valley were mainly inhabited by small groups of farmers with cereal agriculture and transhumant livestock, which cultivated the river terraces assisted by draught animals (Fabián, 2006; Carmona-Ballestero, 2013, 2014; Carmona-Ballestero et al., 2013; Delibes de Castro et al., 2015; Blanco-González et al., 2018). These characteristics are reproduced in El Mirador cave, where a mixed economy of agriculture and livestock has been documented, presumably carried out on the set of river terraces formed by the river Arlanzón and its tributary brooks to the south of the cave (Vergès et al., 2018). Even at El Mirador cave some evidence points to the use of bovines as work animals, as documented by the presence of osteopathologies associated with traction in MIR4 (Martín, 2015). Anthropogenic impact is also evident in the pollen sequences of the northern Meseta and other areas near the Sierra de Atapuerca. For example, a sequence from Espinosa de Cerrato (Palencia) shows two major landscape changes of anthropogenic origin: the first dated at c. 4500 BP, with a decrease in the evergreen *Quercus* forests, followed by another between c. 3000 and 2000 BP affecting the *Pinus* forests. The change ends at c. 1500 BP, when the remaining coniferous forests were replaced by a mostly shrub and cereal crop landscape (Franco et al., 2001).

To the east of Atapuerca, in the northern mountains of the Iberian System (Sierra de la Demanda, Sierra de Neila and Sierra de Urbión), palynological data reveal a correlation between prehistoric grazing in these high mountain areas and the expansion of the *Fagus* forests that occurred from c. 5900 to 4200 cal BP, which made possible their spread as a result of the opening up of new spaces (López-Merino et al., 2008). Likewise, this increase in *Fagus* was concurrent with the percentage increase in the presence of *Betula*, Ericaceae and other anthropogenic indicators that benefitted from previous deforestation (López-Merino et al., 2008). The increase in the anthropogenic impact on the landscape in the northern Atlantic-Cantabrian boundary occurred later. In the nearby pollen sequence of Zalama (Basque Country), anthropogenic impact also occurred later (from c. 3400 BP) and resulted in an increase in *Fagus* to the detriment of *Corylus* and deciduous *Quercus*, and the appearance of taxa associated with fire and overgrazing such as *Chaetomium* sp. and *Asphodelus albus* (Pérez-Díaz et al., 2016). All these data testify to the capacity of human communities to alter the landscape through anthropization, generating changes in the record of the past, regardless of the climatic context.

Finally, the hypothesis of greater anthropization of the landscape around El Mirador cave is consistent with the evidence provided by the small-mammal remains (Bañuls-Cardona and López-García, 2016; Bañuls-Cardona et al., 2013, 2017a, 2017b). The small-mammal assemblages of MIR4 and MIR5 are made up of the insectivores *Crocidura russula* and *Sorex araneus-coronatus*, and by the rodents *M. arvalis*, *M. agrestis*, *M.* (*T.*) *duodecimcostatus* and *A. sylvaticus* (Bañuls-Cardona et al., 2017a, 2017b). The main difference between the two assemblages is the presence of *Eliomys quercinus* in MIR4, which is absent in MIR5 (Bañuls-Cardona et al., 2013, 2017a). These assemblages suggest an increase in open spaces to the detriment of forested areas during the transition from the Chalcolithic to the Bronze Age, without significant changes in precipitation or temperature. In contrast, the percentage of synanthropic species (*C. russula*, *M. arvalis*, *M.* (*T.*) *duodecimcostatus* and *E. quercinus*) is high in both levels and in MIR4 it reaches the highest value in the entire sequence (Bañuls-Cardona et al., 2017b). In parallel, MIR4 has yielded evidence of increased open dry environments, which also reach their peak in the level, and a slight increase in wooded areas, although the growth of both of these types of environments resulted in diminished wet meadows in comparison with MIR5 (Bañuls-Cardona et al., 2017a).

The authors link these data to the increasing anthropogenic landscape, which would have reached its peak during the Bronze Age, as represented by MIR4 (Bañuls-Cardona et al., 2017a, 2017b) and other localities with studies of small-vertebrates such as El Mirón cave in Cantabria (Cuenca-Bescós et al., 2008, 2009). Therefore, increased human impact that would have led to the degradation of plant communities can be successfully synchronised with palynological and anthracological data. All these proxies support the hypothesis that the high degree of human impact on the landscape and its effect on environments and preys are a plausible cause for the singular diet of the predators.

5.4. *Seasonality and biases in environmental reconstruction*

The hypothesis that the samples taken from the pellets recovered in MIR4 and MIR5 were affected by seasonality opens the discussion about the possible biases that may occur in palaeoclimatic and palaeoenvironmental reconstructions undertaken using the MER and habitat weighting methods. The exceptional conditions inside the El Mirador cave during the burial phases of the Chalcolithic and the Bronze Age allowed the pellets to be preserved intact (Vergès et al., 2002, 2016). These very unusual and relatively recent coprocoenotic accumulations in much more common conditions would have disintegrated in the sediment along with the small-vertebrate remains contributed by other sources, such as in situ mortality. Therefore, the possible seasonal effects would have been weakened by the rest of the small-vertebrate sample, minimising the biases produced in the palaeoenvironmental and palaeoclimatic reconstructions.

El Mirador cave has provided an interesting record of small-mammals that has been used in both palaeoclimatic and palaeoenvironmental studies (Bañuls-Cardona et al., 2017a, 2017b; Galán et al., 2023; García-Morato et al., 2023; Domínguez-García et al., 2024), which serve as a reference and a point of discussion in relation to the data provided by the pellets (Table 7). Nevertheless, various clarifications should be made before comparing the two records.

The first difference between them is the time frame. The pellets were generated in predation events of few hours or days, while the associations of small-mammals come from the entire archaeological level, which in MIR4 encompasses a minimum range of 140 years (between 3530 and 3390 cal BP) and a maximum of 660 years (between 3730 and 3070 cal BP), according to calibrated radiocarbon data (Vergès et al., 2016), thus exceeds the temporal limit for the effect of time averaging on relative abundances of the different species to be significant (Terry, 2008). A second difference is that the comparison of associations made up exclusively of small-mammals with grouped taphocenoses of mostly herpetofauna (78.98% in MIR4 and 92.22% in MIR5) may affect interpretation due to the physiological and ethological differences and ecological requirements between the two samples, mainly endothermy versus ectothermy. A third point is the possible contribution to the small-vertebrate record from other sources, as referred to above, although last taphonomic studies point to the action of the eagle owl *B. bubo* as the agent of coprocoenotic accumulation for the small-mammals in MIR4 and MIR5 levels (García-Morato et al., 2023), the same predator previously identified for the pellets (Bisbal-Chinesta et al., 2020).

Despite the differences between these two records, both the small-mammals from the disaggregated sediment and the pellets indicate the existence of a climate similar to the present one, except for the higher rainfall. The differences in temperatures are within the standard deviation and are therefore not significant. However, the divergences between the data provided by the two small-vertebrate samples are pronounced in the palaeoenvironmental records. Among the small-mammals, representatives of shrub and forest environments predominate, whereas rocky and periaquatic environments are absent. In MIR5, evidence of wet meadow environments doubles in percentage compared to that of dry open areas, but in MIR4 the percentages of both habitats are equal. On the other hand, the content of the pellets testifies to a mostly open and humid landscape, with abundant water points, wooded areas and, to a much lesser extent, rocky areas (Table 7).

The comparison between the small-mammal and the pellet assemblages is much more complicated, as pellets have a much more pronounced bias because they are directly associated with the selection of the predator, while the associations of small-mammals could be contributed to the sedimentary record of the cave by a variety of sources, from different predators to in situ natural mortality. Taphonomic marks within the small-mammal associations from of the whole El Mirador sequence, except MIR4 and MIR5 levels, indicate that their remains were contributed by a category 1 predator (Bañuls-Cardona et al., 2017a), such as *Asio otus* (long-eared owl) or *T. alba*, opportunistic predators that prefer semi-forested and open areas (Bañuls-Cardona et al., 2017b). Meanwhile, taphonomic analyses link the pellets (Bisbal-Chinesta et al., 2020) and the small-mammals from MIR4 and MIR5 levels (García-Morato et al., 2023) to the eagle owl *B. bubo*, more eclectic in its environmental preferences as a generalist predator (Hagen, 1950; Hiraldo et al., 1975; Pérez-Mellado, 1978; Vericad et al., 1976; Frey and Walter, 1986; Serrano, 1998; Penteriani and Delgado, 2016).

The location of El Mirador cave in the Atapuerca Mountains, on the biogeographical border between the Mediterranean and Eurosiberian regions of influence, makes it a place of special interest to monitor the changes associated with the 4.2 ka BP Bond event. The archaeobotanical data coincide with the scenario proposed for the southern regions, with a marked increase in aridity (Allué and Euba, 2008; Rodríguez et al.,

Table 7
Comparative between habitat and climatic data from small-vertebrate records (small-mammals according Bañuls-Cardona et al., 2017a).

Habitats	MIR4				MIR5		
	Small-Mammals	Pellets	Pellets MIR4.A	Pellets MIR4.B	Small-Mammals	Pellets	Pellets (without *Hyla*)
Open Dry (%)	20.80	5.32	2.13	9.00	14.60	3.11	11.41
Open Humid (%)	19.80	31.71	31.87	32.08	30.90	44.62	30.22
Woodland (%)	59.40	26.29	23.47	29.00	54.50	23.79	33.91
Rocky (%)	0	10.82	2.00	21.00	0	2.46	9.02
Water Edge (%)	0	25.86	40,53	8.92	0	26.04	15.43

Climate	Current	MIR4				MIR5	
	Ibeas de Juarros	Small-Mammals	Pellets	Pellets MIR4.A	Pellets MIR4.B	Small-Mammals	Pellets
MAT (in °C)	10.1	9.94	9.8	10.5	11.1	10.03	9.8
SD		1.5	-	1.1	1.8	1.6	-
MTC (in °C)	2.6	2.54	2.3	3.8	3.9	2.65	2.3
SD		1.2	-	1.6	2.3	1.2	-
MTW (in °C)	18.7	18.53	17.9	17.9	18.9	18.60	17.9
SD		1.4	-	0.7	1.4	1.4	-
MAP (in mm)	594	794	721	826	806	846	721
SD		221	-	84.2	17.7	284	-

2016; Expósito et al., 2017, 2022), as well as the low incidence of manganese coatings and carbonate crusts deposits in bone remains from MIR5 (García-Morato et al., 2023). On the other hand, the record of the small-vertebrates suggests a typical scenario of the northern regions, with a continuance of the humid conditions in the environment. In the small-mammal sample, MIR5 is the sequence level with the highest percentage of species with Eurosiberian requirements (64%) (Bañuls-Cardona et al., 2017b), while in MIR4 they represent the second highest group in the association (36.5%).

Among the herpetofauna, the presence of the common brown frog *R. temporaria* in the pellets of MIR4 and MIR5 is diagnostic of wet Eurosiberian climatic and environmental conditions. This frog is highly conditioned by temperature, environmental humidity and rainfall (Álvarez, 2014), so it is highly susceptible to be negatively affected by aridity events. This species is currently absent from the Sierra de Atapuerca and its closest populations are located 60 km to the north and northeast, already within the Eurosiberian bio-region (Diego-Rasilla and Ortiz-Santaliestra, 2009; AHE, 2025; own data). The distribution retraction of *S. araneus*, another typically Eurosiberian species present in MIR4, is even more extreme, as nowadays its Iberian populations are limited to the eastern Pyrenees (López-Fuster, 2007a, 2007b). The presence of both species between 4530 cal BP to 3530 cal BP means that environmental humidity was high during the 4.2 ka BP Bond event and that locally there was no significant increment in aridity, in contrast what is described based on the archaeobotanical data from El Mirador and many other palynological sequences from the Iberian Peninsula (Jalut et al., 2000; Gil-García et al., 2002; Carrión et al., 2010). This data also adds to the already compelling arguments for human impact as the primary factor in the degradation of the vegetation communities observed from archaeobotany in the latest sequence of El Mirador cave.

6. Conclusions

The comparative study of the accumulations of MIR4 and MIR5, interpreted as pellets, suggests the existence of seasonal variations in the dietary composition of the accumulating agent. Through the ethology, phenology, annual activity and reproductive cycles of the documented preys, the existence of a determining seasonal factor is postulated. The MIR4 pellets point to a double seasonality, represented by the two groups separated by correspondence analyses. The MIR4.A group is mainly composed of amphibians with a reproductive cycle and increased activity after hibernation and during the first weeks of spring. The second group, MIR4.B, is made up mainly of reptiles and species of more Mediterranean influence compared to the other group. For this reason, MIR4.B is situated in a period between mid-spring and summer, when reptiles reproduce and when the most thermophilic species begin their annual activity. In contrast, MIR5 is monopolised by *Hyla* gr. *H. arborea*, which reproduces massively in large agglomerations during the mid-spring wet phase.

The taxonomic composition and number of preys in the pellets from MIR4 and MIR5 are very unusual and have no parallel in contemporary literature. Modern data also suggest that human impact may cause changes in the diets of nocturnal raptors, as an adaptation to pressure from anthropogenic changes. Archaeobotanical data and the small-mammal record support the hypothesis of human impact as a conditioning factor for the predator in the Sierra de Atapuerca environment. Possibly in the absence or scarcity of more optimal preys, the predator opted for other less optimal but more abundant prey available in the surroundings, especially during their reproductive phases in accordance with seasonal cycles. The palaeoenvironmental reconstruction through the different seasonal associations suggests changes in the distribution of the main habitats, with increased wet areas between late winter and mid-spring, and increased dryness between mid-spring and summer. The palaeoclimatic reconstruction points to a climate remarkably similar to today's, albeit slightly wetter.

The separated calculations according to seasonal criteria did not show significant differences in annual or monthly temperatures, although there were increases in precipitation from the associations assigned to winter through mid-spring. Though the record of pellets from El Mirador is exceptional in comparison with the usual scenario in karst sites, the new data provided in this research suggest the combined use of small-vertebrate associations and archaeobotanical sequences for a higher degree of confidence in our reconstructions and interpretations of the past.

CRediT authorship contribution statement

Josep Francesc Bisbal-Chinesta: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Hugues-Alexandre Blain:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition. **Sandra Bañuls-Cardona:** Writing – review & editing. **Iván Rey-Rodríguez:** Writing – review & editing, Methodology. **Carmen Núñez Lahuerta:** Writing – review & editing. **Ethel Allué:** Writing – review & editing. **Isabel Expósito:** Writing – review & editing. **Gloria Cuenca-Bescós:** Writing – review & editing. **Josep Maria Vergès:** Writing – review & editing.

Declaration of competing interest

We, Josep Francesc Bisbal-Chinesta, Hugues-Alexandre Blain, Sandra Bañuls-Cardona, Iván Rey-Rodríguez, Carmen Núñez Lahuerta, Ethel Allué, Isabel Expósito, Gloria Cuenca-Bescós and, Josep Maria Vergès, the authors of the manuscript "*Influences of seasonal prey availability and anthropogenic landscape on small-vertebrate based palaeoecological reconstructions: a case study from the mid-late Holocene transition at El Mirador cave (Sierra de Atapuerca, Spain)*", declare that we have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

J.F.B.C. thanks the Dr. Marta Calvo for the access to the reference collections of the Museo Nacional de Ciencias Naturales-CSIC de Madrid, and Dr. Salvador Bailon and Dr. Emmanuelle Stoetzel for the access to the pellet collections of the Musée de l'Homme and Muséum National d'Histoire Naturelle of Paris. The authors are grateful to editor Marian Berihuete Azorín and reviewer Elisa Luzi for their comments on improving the original manuscript. This publication is part of the R&D&I project PID2021-122533NB- I00 "Using climate envelope models to predict spatial and temporal distribution patterns of climate-related Quaternary extinctions", funded by MCIN/AEI/10.13039/501100011033/and by ERDF, EU. J.F.B.C. was supported by FI Predoctoral Fellowship 2016FI_B00286 with the financial sponsorship of the Agència de Gestió d'Ajuts Universitaris i de Recerca of the Generalitat de Catalunya. I.R.R. is supported by the Axudas de apoio á etapa de formación posdoutoral grant (ED481B-2023-040), from the Consellería de Cultura, Educación, Formación Profesional e Universidades, Xunta de Galicia. J.F.B.C., H.-A.B. and I.R.R. belongs to the Consolidated Research Group "Paleoecology of Pliocene and Pleistocene and Human Dispersals (PalHum)", funded by AGAUR-Generalitat de Catalunya, 2021SGR-1238 and URV 2023PFR- URV-01238.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2026.110186.

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