



Agropastoral practices and woodland management shaped the Irano-Turanian steppe-forest vegetation during the Transitional PPNA/B–Early PPNB (8895–8210 cal BCE) at Kharaysin, Jordan

Andoni Mateos-Cabero¹ · Josu Aranbarri¹ · Eneko Iriarte² · Marta Portillo³ · Amaia Arranz-Otaegui^{1,4} · Aroa García-Suárez⁵ · Luis C. Teira⁶ · Juan R. Muñoz⁷ · Juan J. Ibáñez³

Received: 5 December 2025 / Accepted: 16 March 2026
© The Author(s) 2026

Abstract

The present study reconstructs vegetation change and human–environment interactions from the Transitional Pre-Pottery Neolithic A/B (8895–8415 cal BCE) to the Early Pre-Pottery Neolithic B (8465–8210 cal BCE) at the Kharaysin archaeological site (Zarqa, Jordan). For the first time at this site, integrated pollen, wood charcoal and phytolith analyses have been carried out in combination with a detailed archaeostratigraphic and Bayesian-modelled chronological framework. The results obtained suggest the presence of open steppe–forest communities dominated by *Quercus ithaburensis*-type–*Pistacia* near the archaeological site, as well as riparian woodlands used for structural purposes and for firewood. Furthermore, herbaceous communities have been identified, which include grazing-resistant and nitrophilous taxa, as well as steppe herb elements, suggesting likely agropastoral impacts. Conversely, the low but continuous presence of Fabaceae and Cerealia-type pollen, as evidenced by phytolith data, could indicate their small-scale local exploitation and processing but also their role as part of the herbaceous component of an increasingly open landscape. These findings imply that sedentary societies brought about a moderate yet sustained long-term transformation of the plant landscape, favoured by a regionally stable climate background.

Keywords Irano-Turanian steppe-forest · Archaeobotany · Grazing · Pre-Pottery Neolithic · Southern Levant

Introduction

The Southern Levant is particularly vulnerable to desertification and land degradation (Khresat et al. 1998). In this region, deforestation and extensive grazing, exacerbated

by millennial-scale climatic fluctuations, has significantly altered both historical and contemporary patterns of tree distribution (Henry et al. 2017; Deckers et al. 2025). Today, only a few remnants stand, or isolated trees persist, primarily

Communicated by A. Weide.

✉ Andoni Mateos-Cabero
andoni.mateos@ehu.eus

¹ Department of Geography, Prehistory and Archaeology, University of the Basque Country, Francisco Tomás y Valiente, s/n, 01006 Vitoria-Gasteiz, Spain

² IsoTOPIK Lab, Department of History, Geography and Communication, University of Burgos, Misael Bañuelos Square s/n, 09001 Burgos, Spain

³ Milà i Fontanals Institute for Humanities Research, Spanish National Research Council, Egipcíacues 15, 08001 Barcelona, Spain

⁴ Ikerbasque - Basque Foundation for Science, 48011 Bilbao, Spain

⁵ Department of Prehistory and Archaeology, University of Granada, Campus Universitario de Cartuja s/n, 18071 Granada, Spain

⁶ Instituto Internacional de Investigaciones Prehistóricas de Cantabria (Universidad de Cantabria/Gobierno de Cantabria/Santander), Av. de Los Castros, 52, 39005 Santander, Spain

⁷ Department, Saint Esteban Pontifical Faculty of Theology, Concilio de Trento Square, 37001 Salamanca, Spain

in remote mountainous areas or in locations with topographic conditions that limit human access and land-use.

Recent research has identified the rise in temperature and humidity during the Early Holocene (Bar-Matthews et al. 2019; Stein et al. 2025) as key drivers in the formation of new ecological conditions that may have facilitated the emergence of agropastoral societies in the Levant (Borrell et al. 2015; Roberts et al. 2018). These environmental shifts likely supported the adoption of agriculture and a growing reliance on livestock (Ibáñez et al. 2018) and subsequent demographic expansion (Palmisano et al. 2019). Nevertheless, the extent to which early Neolithic communities actively modified their landscapes remains a subject of debate. Practices such as fire management, selective timber harvesting, deforestation, and early farming practices have been proposed as potential agents of anthropogenic environmental change (Roberts 2002; Willcox et al. 2009; Fuller and Lucas 2025). Some scholars (e.g. Rollefson and Köhler-Rollefson 1992; Yasuda et al. 2000; Migowski et al. 2006) argue that this period marked the onset of long-term ecological transformations, leading to significant shifts in biodiversity.

Despite the central role of palynology in reconstructing the interactions between Neolithic societies and the surrounding vegetation across the Mediterranean realm (e.g. Aranbarri et al. 2015; Revelles et al. 2015), case studies in the Levant, particularly in the Jordanian Plateau, remain scarce. As a result, the composition and spatial distribution of vegetation communities, as well as the environmental impact and land-use strategies of early societies, are still not fully understood. This gap in palaeobiogeographical knowledge is largely attributable to the scarcity of continuous sedimentary records and persistent taphonomic biases that hinder accurate pollen identification (Rambeau 2010; Cordova et al. 2026). In contrast, wood charcoal assemblages have provided a foundational understanding of regional vegetation dynamics, including evidence for the expansion of deciduous oak communities at the onset of the Holocene (Asouti and Kabukcu 2014). Notably, a clear north–south and west–east gradient in vegetation trajectories has been identified (Asouti 2025). Wood charcoal data from sites such as Tell Qarassa North (Arranz-Otaegui et al. 2017) and ‘Ain Ghazal (Neef 2004a) document the spread of *Quercus* sp. deciduous, *Pistacia* sp., and *Amygdalus* sp. open parkland between 8750–7950 and 7200–6500 cal BCE, respectively. In contrast, eastern and southern regions influenced by drier climatic conditions show local assemblages dominated by *Juniperus* sp., *Pistacia* sp., *Tamarix* sp., and/or Amaranthaceae (e.g. El-Hemmeh, Asouti et al. 2015; Basta, Neef 2004b; WF16, Austin 2007; Mithen et al. 2007; Asifir, Crassard et al. 2025). Overall, the available data suggest a gradual transition in tree resource exploitation, from

opportunistic woodland harvesting to more selective, and in some cases intensive, timber procurement, driven by an increased anthropogenic pressure (Willcox 1999; Asouti and Austin 2005; Willcox et al. 2009). This shift may explain the long-term persistence of anthropogenically managed tree resources, including elements of the Irano-Turanian steppe-forest (Asouti and Kabukcu 2014).

In this context, the archaeological site of Kharaysin (Zarqa, Jordan) offers valuable insights into the architectural evolution associated with the transition from hunter-gatherer lifestyles to planned, sustainable housing. These developments reflect increasing social complexity and local adaptation to regional environmental conditions (Ibáñez et al. 2025a). Beyond architecture, Kharaysin has proven to be a key site for exploring burial practices and the manipulation of human remains (Iriarte et al. 2020; Santana et al. 2020, 2022), lithic technology (Borrell et al. 2019; Ibáñez et al. 2020; Milić et al. 2025), further providing early evidence of crop cultivation and processing (Douché et al. 2025; Ibáñez et al. 2025b). Despite these advances, the palaeoenvironmental framework of the site remains largely unexplored, which offers a unique opportunity to reconstruct the vegetation landscape through detailed palynological and anthracological analyses. The current research focuses on examining human–vegetation interactions during the Transitional Pre-Pottery Neolithic A/B (Trans. PPNA/B) (8895–8415 cal BCE) and the Early Pre-Pottery Neolithic B (Early PPNB) (8465–8210 cal BCE) periods using an integrated archaeobotanical approach. This study aims to clarify the environmental drivers that shaped vegetation history in the Southern Levant during the emergence of agricultural societies, to identify potential woodland management strategies employed by Neolithic communities, and to explore the spatial variability of vegetation communities in relation to settlement dynamics and resource exploitation. Through this integrated perspective, this research seeks to deepen our understanding of both regional and local vegetation patterns, as well as of the ways in which early Neolithic populations interacted with and transformed their surrounding landscapes.

Geographical framework

The archaeological site of Kharaysin is in Northern Jordan, within the municipality of Quneya, Zarqa Governorate, at the confluence of the Zarqa River and Wadi Kharaysin (Ibáñez et al. 2016) (Fig. 1). The regional geology is dominated by Mesozoic sedimentary formations, along with Upper Cretaceous and Lower Tertiary sequences composed primarily of limestones, marls, dolomites, and sandstones (Bender 1975). This geological diversity has shaped heterogeneous

Fig. 1 Location of the Kharaysin archaeological site in the context of the Levant



landscape, where active erosion processes have contributed to the formation of fertile alluvial soils and river terraces, offering favourable conditions for early human settlement and land use.

The Zarqa River Basin is characterised by a Mediterranean climate, marked by hot, dry summers and mild, rainy winters. Precipitation exhibits strong inter- and intra-annual variability, with an average annual rainfall of approximately 195 mm, most of which occurs between October and April. Mean winter temperatures range between 12 and 14 °C, whereas summer temperatures average between 24 and 26 °C (Freiwan and Kadioğlu 2008).

From a biogeographical perspective, the site of Kharaysin is situated within a transitional zone between the Mediterranean and Irano-Turanian regions. The Mediterranean biogeographic region supports a mosaic of ecotones, including forest, maquis, garrigue, and batha, that intersect across the landscape, reflecting varying degrees of woodland degradation and landscape openness. Forest communities in nearby mountainous areas, such as the Ajloun and Dibein Forest

Reserves, are dominated by *Quercus ithaburensis* and *Pinus halepensis*, forming relatively dense stands on rendzina soils (Al-Eisawi 1996). These are accompanied by sclerophyllous thermo-Mediterranean tree species including *Quercus calliprinos*, *Pistacia palaestina*, *P. lentiscus*, *Arbutus andrachne*, and *Pyrus syriaca*, along with a dense shrub layer composed of *Calycotome villosa*, *Cistus creticus*, *C. salvifolius*, and *Phlomis kurdica*. On limestone substrates, open woodlands of *Q. ithaburensis* are found alongside *Ceratonia siliqua* and *Styrax officinalis*. The understory is diverse, featuring species such as *Crataegus azarolus* and *Amygdalus communis*, with open shrublands of *Rhamnus lycioides*, *Retama raetam*, and *Sarcopoterium spinosum* occupying areas with shallow soils or those affected by anthropogenic degradation. In contrast, the Irano-Turanian region is characterised by dwarf shrubs, grasses, and geophytes thriving on poorly developed calcareous soils and rocky outcrops (Al-Eisawi 1996; Djamali et al. 2012; Manafzadeh et al. 2017). Vegetation here includes sparse woody species such as *Pistacia atlantica*, *Amygdalus korschinskii*, *Retama*

raetam, and *Ziziphus lotus*, along with xerophytic taxa like *Artemisia herba-alba*, *Anabasis syriaca*, *Caroxylon vermiculatum*, *Noaea mucronata*, and *Suaeda vermiculata*. Geophytes such as *Asphodelus ramosus*, *Drimia aphylla*, *Crocus moabiticus*, *Colchicum* spp., and *Tulipa* spp. are also prominent. Local vegetation communities have been significantly altered by irrigated agriculture and the widespread cultivation of olive groves, which have reshaped the natural landscape.

Archaeological context

Kharaysin (444 m a.s.l., 32° 12' 23.7" N, 35° 59' 47.7" E) is recognised as a 'mega-site' due to its extensive size and archaeological significance (Ibáñez et al. 2025a). It stands as a key settlement for understanding early cultural

transformations during the transition from the PPNA to the PPNB in the Southern Levant (Milić et al. 2025). The site is located on the southern slope of a naturally formed terrace system along the Zarqa River, where successive occupation layers have been identified across six excavation zones (A to F). The stratigraphy reveals a complex occupation sequence, with some architectural structures having collapsed or been truncated by different phases, compounded by natural erosion processes affecting the slope (Monik et al. 2018; Ibáñez et al. 2025a) (Fig. 2). The occupation sequence comprises a Late PPNA phase, dated to the end of the 10th millennium BCE (Zones A and B), a Trans. PPNA/B phase dated to the first half of the 9th millennium BCE (Zones A and B), overlain by an Early PPNB phase in the second half of the 9th millennium BCE (Zone B). This is succeeded by a Middle PPNB phase at the end of the 9th and the beginning of the 8th millennium BCE (Zones A, B and C), a Late PPNB phase

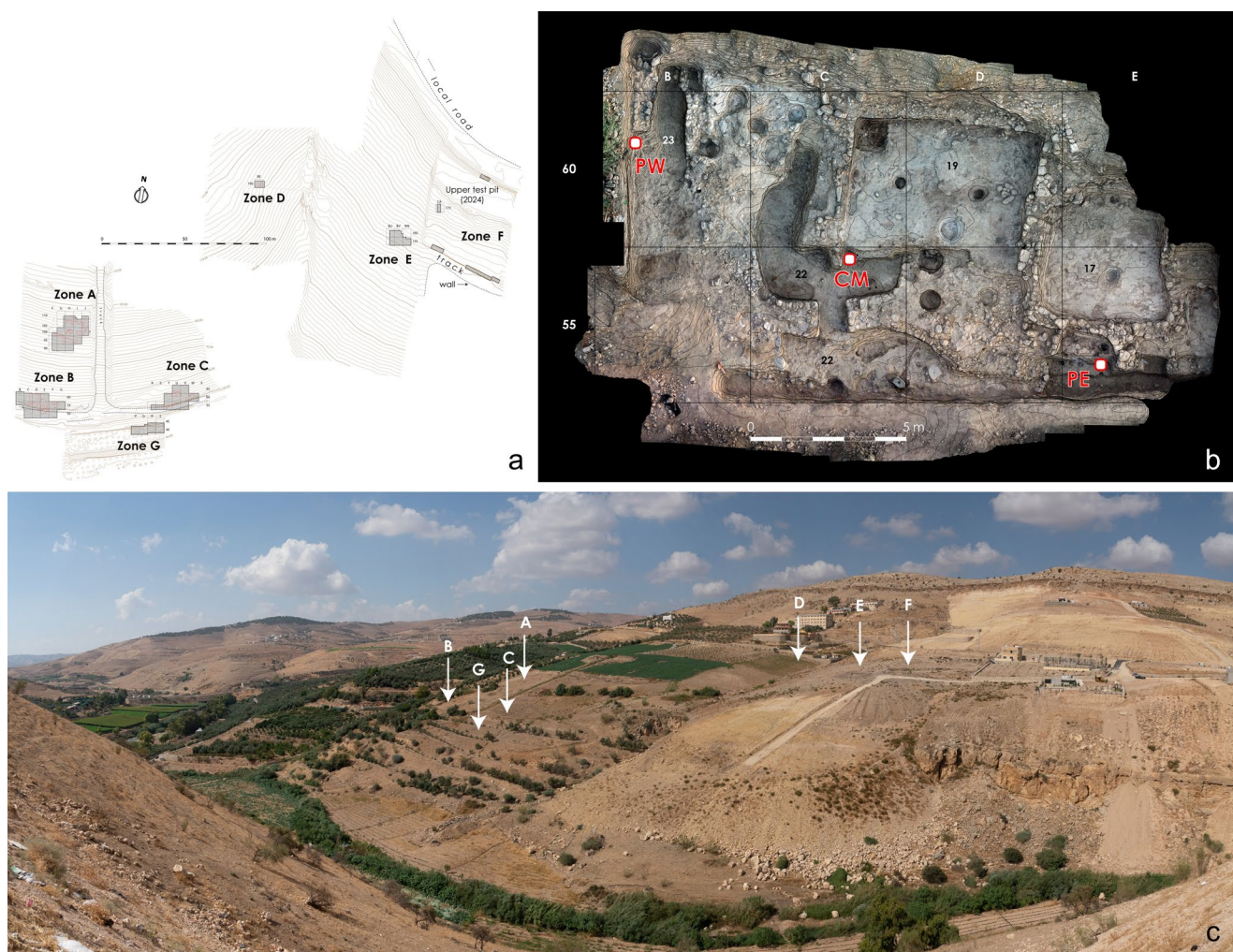


Fig. 2 **a** Map of the Kharaysin archaeological complex with its different excavation zones (from A to F; G=2025's last field season). **b** Aerial orthophoto of Zone B. The locations of the studied PE, CM, and PW profiles are indicated. The wood charcoal was taken from SU 1047

and SU 1041 (C-55: House 22), SU 905 (D-60: House 19), SU 781 (E-55: House 17) and SU 607 (D-55: House 21). The latter is not visible in the image, as it lies above the current level. **c** Panoramic image of the Wadi Kharaysin and the sites of the different excavation zones

dated to the second half of the 8th millennium (Zones E and F) and a Late PPNB/PPNC phase dated to the beginning of the 7th millennium BCE (Zone D). More recent excavations have also revealed Pottery Neolithic (PN) layers, primarily concentrated in a newly investigated area (Zone F), that expands the site's chronological and cultural framework.

Material and methods

Stratigraphy

The sampled profiles derive from excavation Zone B of Kharaysin (Fig. 2). Three profiles were selected from the eastern (PE) and western (PW) margins and from the central sector of the excavation zone (CM). The archaeostratigraphic sequence excavated in Zone B comprises up to four superimposed construction phases, ranging from the Late PPNA to the Middle PPNB (Ibáñez et al. 2025a). Each phase exhibits the lateral and vertical alternation of distinct stratigraphic units associated with architectural features (lime floors, rubble-built walls, and/or adobe walls) and open-air contexts (unbuilt spaces or the remains of collapsed dwellings) (Figs. 2, 3).

Site chronology

The chronology of the different stratigraphic units and construction phases identified in the area under study has been obtained through systematic chronostratigraphic work carried out over multiple excavation seasons (ESM Table S1). This effort has produced stratigraphically continuous radiocarbon determinations that provide an excellent dating framework for the different construction phases (Ibáñez et al. 2025a). 35 radiocarbon dates were processed using a Bayesian statistical framework implemented in Oxcal v4.4 (Bronk Ramsey 2009). The primary objective was to refine the chronological sequence of the archaeological stratigraphy by integrating the radiocarbon measurements with the relative order of the stratigraphic units and construction phases. Prior to modelling, all radiocarbon ages were calibrated using the IntCal20 calibration curve (Reimer et al. 2020).

The stratigraphic information was translated into a hierarchical Bayesian model composed of a series of phases, each corresponding to a discrete stratigraphic unit or group of units sharing the same architectural phase. Within each phase, individual radiocarbon dates were treated as unordered, while the phases themselves were constrained according to the stratigraphic superposition observed during excavation. This approach allowed the model to estimate not only posterior probability distributions for each

individual sample but also the start and end boundaries of each phase.

Outlier analysis was conducted using the General Outlier Model with a prior probability of 5%. Posterior outlier probabilities were inspected to assess the consistency of dates with their stratigraphic assignments. All modelled age estimates are reported at the 95.4% Highest Posterior Density (HPD) intervals.

This Bayesian approach allowed us to incorporate archaeological context directly into the chronological model, resulting in more precise and stratigraphically coherent age estimates for the formation and occupation events of the settlement, and the pollen, phytolith and wood charcoal assemblages of the site.

Pollen analysis

Three sediment profiles (PE, CM, and PW) (Fig. 3) were sampled from Zone B, encompassing the Trans. PPNA/B through to the Early PPNB. A total of 25 sediment samples were collected (PE=11; CM=11; PW=3), systematically labelled and documented using photographs and schematic diagrams in accordance with established archaeopalynological protocols (Dimbleby 1985; Moore et al. 1991). Sample preparation was conducted at the Pyrenean Ecology Institute (IPE-CSIC), employing standard chemical processing procedures, including the use of a Thoutlet-solution. Residues were mounted in glycerol and analysed at the Lydia Zapata Palaeobotany Laboratory (University of the Basque Country) using a Nikon Eclipse 50i light microscope. A minimum of 300 palynomorphs per sample was counted. Monospecific pollen clumps were also recorded. Palynomorph identification was performed using modern reference collections, supplemented by key atlases (Reille 1999) and specialised literature on pollen–vegetation relationships in arid environments (El-Moslimany 1990). Pollen data was expressed as relative percentages, with indeterminate grains and Cichorioideae excluded from the terrestrial pollen sum. Taxa with low representativeness not shown in the diagrams are listed in ESM Table S2. Pollen diagrams were generated using Psimpoll 4.27 and ecological groupings were assigned based on contemporary vegetation studies (Davies and Fall 2001). Zonation into stratigraphic thresholds was guided by results from CONISS cluster analysis; however, dendrograms were not included in the diagrams.

Wood charcoal analysis

The wood charcoal remains analysed in this study were collected from 40 sediment samples processed with machine-assisted flotation. From these, 19 samples were taken from two stratigraphic units (SU 1047 and SU 1041)

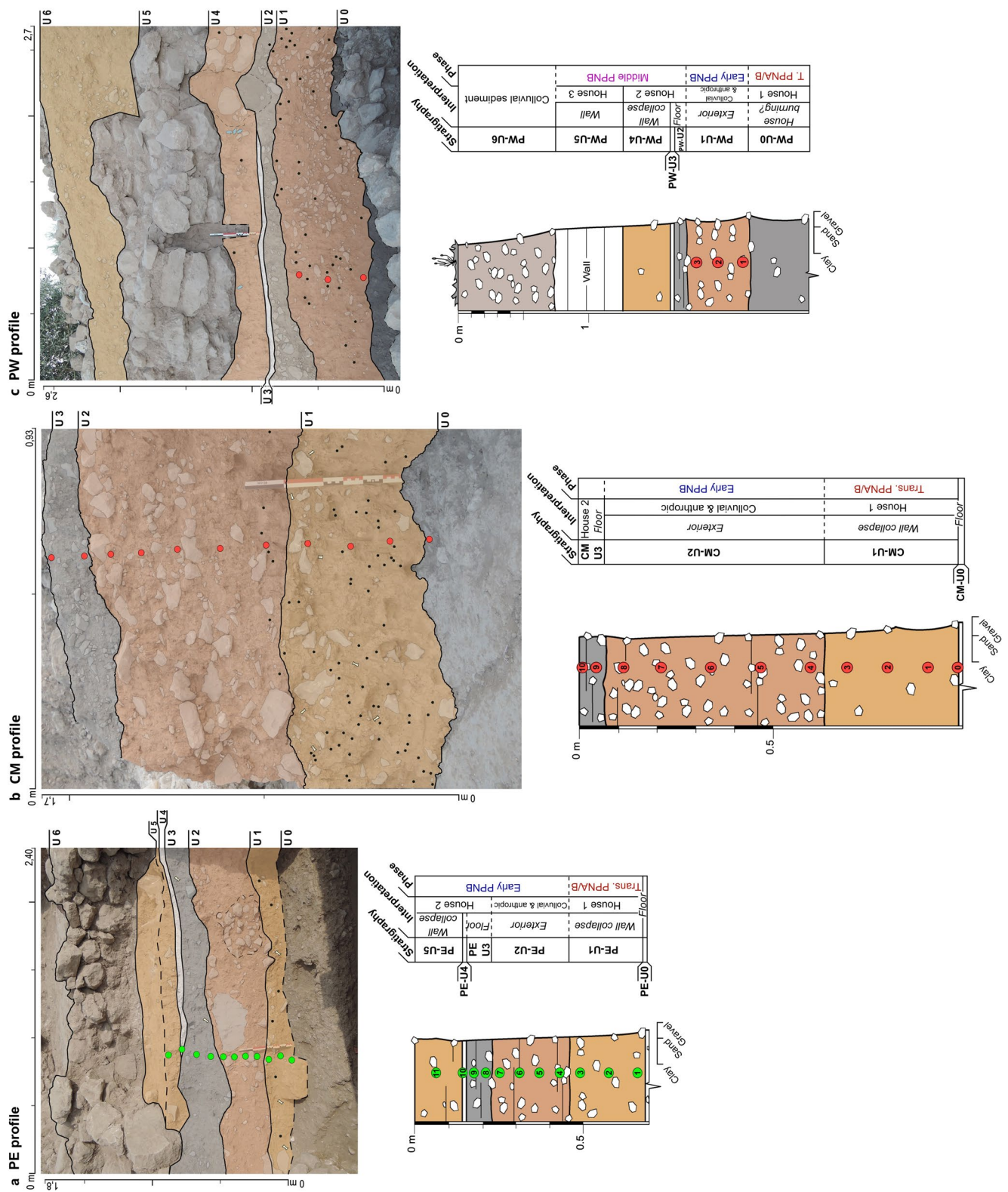


Fig. 3 PE, CM, and PW stratigraphy profiles of Kharaysin showing site architectural phases and chronology. The sampling points for both pollen and phytoliths are indicated by red dots, whereas the green dots represent samples collected exclusively for pollen analysis

corresponding to a destruction/abandonment fill of House 22 and dated in the Trans. PPNA/B phase. 21 samples were taken from three stratigraphic units (SU 905, SU 781, and SU 607), which correspond to the destruction/abandonment levels of Houses 19, 17 and 21 respectively. These samples are dated to the Early PPNB phase (Fig. 2). However, 8 of the 40 samples analysed were found to be sterile and have been removed from the results section.

All the studied samples come from flotation samples and correspond to wood charcoal fragments found in contexts such as infill of structures, open areas, and plant processing areas. However, two samples, one hand-picked and one from a flotation sample, represent wood charcoal concentrations identified during excavation and probably representing structural remains (i.e. primary deposit). These were quantified separately from the secondary/contextual assemblages.

The wood charcoal remains were identified using modern reference collections (Fahn et al. 1986; Schweingruber 1990) and atlases housed at the Lydia Zapata Palaeobotany Laboratory, University of the Basque Country. The analyses were carried out with the aid of an incident light microscope (Olympus BX50) with different magnifications (10× to 50×). Saturation curves were initially used to establish the minimum number of charcoal fragments to be analysed, but in most cases the entire charcoal assemblage was analysed due to the low number of available remains. Prior to quantification, indeterminate wood, non-wood tissues, and not positively identified taxa were separated from the taxon sum. Percentages were calculated exclusively on positively identified wood charcoal fragments, while indeterminate and non-wood categories are reported separately.

Taphonomic analyses included the evaluation of the presence of vitrification, radial cracks, fungal hyphae, boreholes and deformed or wavy patterns, as conducted in contemporary sites (Arranz-Otaegui 2017). These results are available in ESM Table S3. Taphonomic features were quantified as percentages to evaluate their relative frequency by taxon and across the assemblage, allowing comparison between taxa and samples with different fragment counts (e.g. Arranz-Otaegui 2017; Arranz-Otaegui et al. 2017). Percentages were calculated based on identified fragments per taxon; cf. specimens were included for consistency with the taxonomic dataset and transparency. As these are often more affected by anatomical alteration and therefore less securely identified, they should be interpreted cautiously in taxon-specific assessments.

Phytolith analysis

Fourteen sediment samples were selected from profiles CM and PW for phytolith analyses (CM=11; PW=3, Fig. 4). These analyses were conducted at the Institució Milà i

Fontanals (IMF-CSIC) in Barcelona. Phytolith extraction and quantitative methods followed Katz et al. (2010). Weighed aliquots of ca. 40 mg of dried sediment were treated with 50 µl of a volume solution of 6N HCl and 450 µl 2.4 g/ml of sodium polytungstate [$\text{Na}_6(\text{H}_2\text{W}_{12}\text{O}_{40})$]. Microscope slides were mounted with aliquots of 50 µl of sample. A minimum of 200 phytoliths with consistent morphologies were counted at 200× and 400× magnifications using a Zeiss Axioscope 5 optical microscope. The estimated phytolith numbers per gram of sediment are related to the initial sample weight and allow quantitative comparisons between the samples and the sediment profiles. Percentages of multicellular phytoliths (multi-celled or in anatomical connection) in addition to percentages of weathered morphotypes (phytoliths showing pitted surfaces because of weathering and alteration by dissolution, which can no longer be assigned to specific morphotypes) were also recorded (Portillo et al. 2021). Morphological identification was based on specialised literature and modern plant reference collections (Piperno 2006; Albert et al. 2008, 2016; Portillo et al. 2014). The terms used to describe phytolith morphologies followed the standards of the International Code for Phytolith Nomenclature, ICPN v. 2.0 (ICPT et al. 2019).

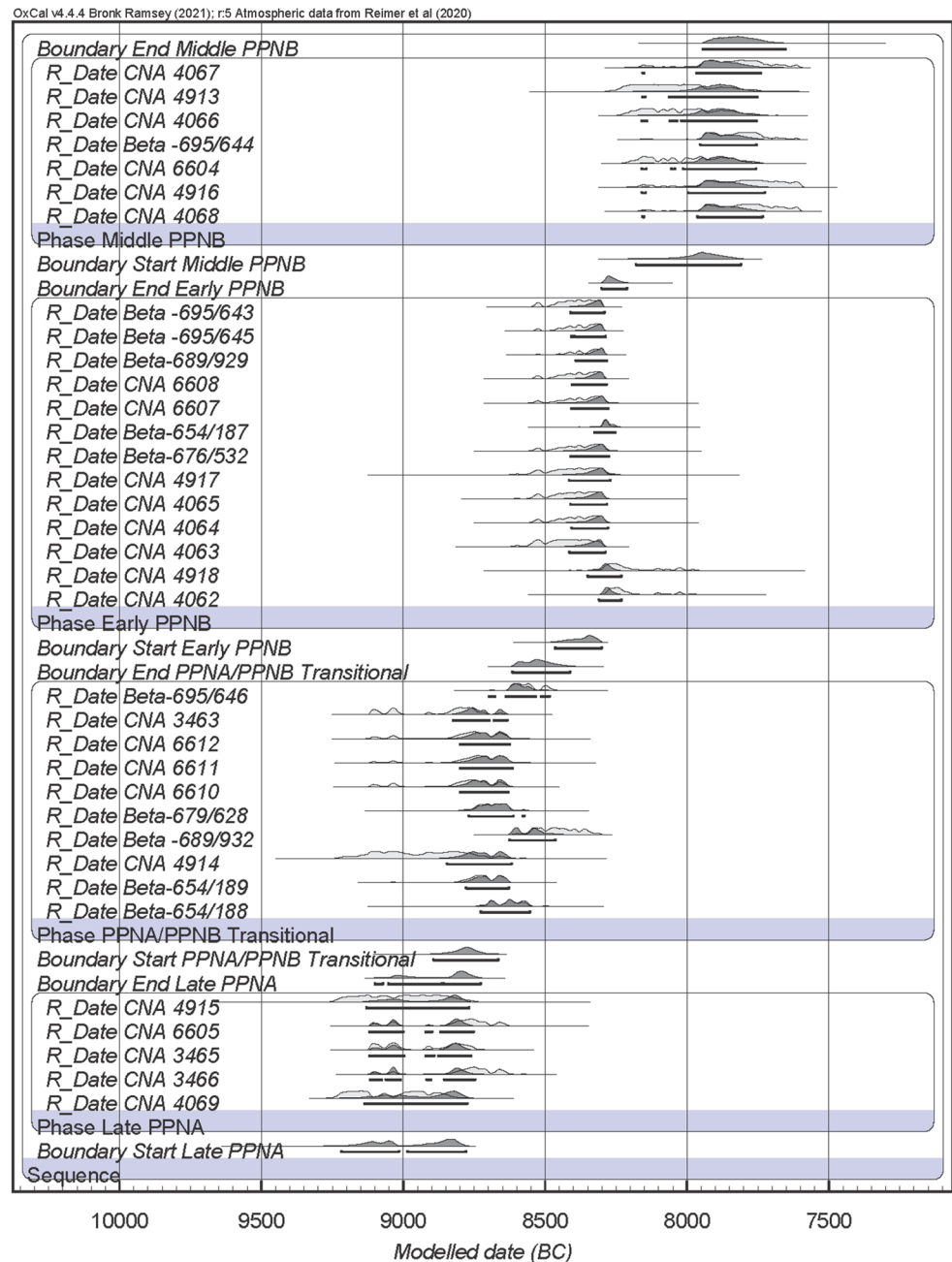
Results

Stratigraphy

In the PW profile (Fig. 3), the sequence contains a beaten-earth floor at the bottom (PW-U0) belonging to Structure 23 (Ibáñez et al. 2025a) and dated to the Trans. PPNA/B phase. This floor is overlain by a massive silty-sand deposit (PW-U1) containing abundant limestone and basalt lithoclasts and numerous charcoal fragments and anthropogenic materials. This unit represents the accumulation and reworking of possibly burned adobe wall material accumulated after the building abandonment and collapse, followed by its transformation into an exterior activity area. During the Early PPNB, this exterior space was intentionally levelled with an archaeologically rich fill to provide a stable foundation for the construction of a new building with an interior lime floor (units PW-U2 and PW-U3, respectively) during the Middle PPNB phase.

In the CM profile (Fig. 3), the basal sampled unit (CM-U1) consists of a massive orange silty-sand sediment rich in charcoal fragments and containing few lithoclasts, along with scattered bone and flint remains. This deposit overlies a beaten-earth floor (CM-U0) belonging to a dwelling adjacent to the structure recorded at the base of the PE profile; both attributed to the same Trans. PPNA/B architectural phase (Figs. 2, 3). CM-U1 has been interpreted in the field as

Fig. 4 Modelled dates of Khayrains using four-phase Bayesian analysis



(possibly burnt) adobe debris resulting from the collapse of this dwelling. Above it lies a thick unit (CM-U2) composed of ashy silty clay sediments with abundant lithoclasts and artefacts and including thin, discontinuous layers of finer sediment, likely of colluvial origin. This sampled sequence represents an open-air accumulation zone that received substantial inputs of sediment derived from the erosion, redistribution, and reworking of nearby anthropogenic deposits throughout the Early PPNB. The sequence is capped by a lithoclast-rich levelling unit (CM-U3) that prepared the area for the construction of a subsequent building (Structure 19; Ibáñez et al. 2025a) with a lime floor.

Finally, in the PE profile (Fig. 3), the basal unit PE-U1 consists of massive orange to reddish silty-sand sediments with abundant embedded charcoal, corresponding to the burnt and collapsed adobe of a Trans. PPNA/B structure (Structure 25) deposited above a beaten-earth floor (PE-U0). Overlying this unit lies PE-U2, a deposit like CM-U2, an open-area accumulation of reworked anthropogenic sediments, characterized by a greater proportion of heterometric limestone clasts and a fine, ashy sediment rich in archaeological artefacts, defining one or more episodic activity surfaces within an outdoor context. PE-U2 unit includes a small carbonate-lithoclast-filled pit and an ash-filled hearth,

reflecting discrete activity episodes nearby to Early PPNB structures. As in the other profiles, this is overlain by a levelling layer (PE-U3) that supported the construction of a Middle PPNB building with a lime floor (PE-U4) (Structure 18 in Ibáñez et al. 2025a). Finally, a deposit (PE-U5) analogous in character to PE-U1 accumulated above the lime floor, representing the collapse and abandonment of the second adobe-built structure.

Site chronology

The Bayesian model constructed in OxCal using a phases structure provides a refined and internally consistent chronological framework for the Late PPNA, Trans. PPNA/B, Early PPNB and Middle PPNB occupations at Kharaysin. All radiocarbon dates demonstrated excellent agreement indices (Amodel and Aoverall consistently above 95%), indicating strong statistical coherence between the radiocarbon measurements and the stratigraphic priors (Fig. 4; ESM Table S4).

The Late PPNA phase is tightly constrained by the modelled boundaries. The start of the phase is estimated at approximately 9220 cal BCE, while the end boundary is placed around 9100 cal BCE, indicating a relatively short and well-defined occupational span. Individual dates within this phase cluster predominantly between ca. 9240 and 8715 cal BCE, showing high internal consistency and supporting the integrity of the architectural and depositional sequence corresponding to the Late PPNA levels.

The Trans. PPNA/B phase represents a distinct occupational horizon at the site, separating the Late PPNA structures from the earliest PPNB construction episodes. The modelled start boundary is estimated at 8895 cal BCE, and the end boundary is projected around 8615 cal BCE. The radiocarbon determinations from this phase span between ca. 9200 and 8640 cal BCE, with the modelled posterior distributions showing a marked contraction relative to the unmodelled ranges. This tightening reflects the chronological coherence of the deposits and supports the interpretation of this horizon as a discrete and relatively short-lived transitional interval.

The Early PPNB phase shows a modelled start boundary around 8465 cal BCE, with posterior later density estimates for individual samples clustering between ca. 8550 and 7960 cal BCE. These results suggest the onset of a more substantial architectural reorganization at Kharaysin sometime in the mid-9th millennium BCE, consistent with broader regional patterns of Early PPNB development.

Finally, the modelled end boundary of the Middle PPNB falls between 7945 and 7655 cal BCE, marking the latest well-dated constructional activity preserved in the sampled stratigraphic units. Radiocarbon determinations assigned to this

phase show posterior modelled ranges generally between ca. 8220 and 7600 cal BCE, exhibiting narrow highest-posterior-density intervals and strong statistical agreement.

Overall, the Bayesian model significantly improves chronological resolution across the site's major constructional phases. The resulting sequence documents a continuous and structured occupation spanning more than a millennium, from the late 10th to the mid-8th millennium BCE and clearly differentiates the architectural and cultural transitions between the Late PPNA, the Trans. PPNA/B interface, and the successive stages of PPNB development at Kharaysin.

Pollen results

PE profile

The first analysed profile encompasses the Trans. PPNA/B and Early PPNB phases. Overall, pollen preservation is relatively good, with indeterminate percentages remaining below 20%. Nonetheless, several samples exhibit signs of thermal alteration and mechanical degradation of pollen grains. Pollen concentration is notably high, ranging from 1,858 to 360,921 grains/g, and a total of 84 distinct taxa have been identified. Arboreal pollen is well represented during the Trans. PPNA/B, with an average of 38.5% but declines markedly in the Early PPNB to 29.2%. Based on CONISS clustering, two principal pollen assemblage zones have been distinguished (Fig. 5).

UNIT-1 (samples PE-1 to PE-7): This unit is characterised by the highest frequencies of arboreal pollen (ca. 33.75%), predominantly represented by the *Q. ithaburensis*-type, followed by *Pistacia*, *Q. calliprinos*, and *Prunus*-type. *Pinus halepensis*, Cupressaceae, and other Mediterranean trees and shrubs occur sporadically. Riparian taxa such as *Salix* and *Tamarix* are also present. Shrub pollen frequencies remain below 4.5%, with *Rosa*- and *Ephedra fragilis*-type being the most frequently recorded. Among herbaceous taxa, Cichorioideae increases at the end of the unit, accompanied by thistles (*Carthamus*-, *Carduus*- and *Centaurea nigra*-type), *Suaeda*-type, and Poaceae (<35 µm). Cerealia-type pollen is consistently present, as is Fabaceae. Notably, taxa associated with ruderal and synanthropic vegetation, including *Heliotropium*, *Papaver*-type and *Rumex*, contribute significantly to the assemblage. *Typha/Sparganium* is also represented.

UNIT-2 (samples PE-8 to PE-11): This unit is defined by a minor decline in arboreal pollen frequencies, which decrease to ca. 28.2%. The most affected taxa include *Q. ithaburensis*-type and *Pistacia*, along with *Q. calliprinos* and *Tamarix*. *Prunus*-type and *Salix* appear sporadically throughout the unit. Shrub taxa such as *Rosa*- and *Ephedra*

fragilis-type are consistently recorded. Poaceae (<35 µm) and thistles (mainly *Carthamus*- and *Carduus*-type) show reduced representation. Conversely, Cichorioideae representation remains significant but decreases slightly. *Suaeda*-type also rises moderately. Ruderal taxa remain consistently present. Notably, Cerealina-type maintains stable values, while Fabaceae exhibits a substantial increase, reaching nearly to 13.5%.

CM profile

A total of 11 samples were analysed from the CM profile, spanning the Trans. PPNA/B and Early PPNB phases. Pollen preservation is considered adequate, with indeterminates comprising less than 15.7%. Pollen concentrations range from 4,915 to 324,010 grains/gr, and 81 distinct taxa have been identified. Compared to the PE profile, the CM samples exhibit greater homogeneity in tree pollen frequencies, but in slightly lower quantities in both cultural phases. CONISS cluster analysis defines two pollen assemblage zones (Fig. 6):

UNIT-1 (samples CM-0 to CM-7): Within the arboreal component, *Q. ithaburensis*-type is the most dominant taxon, with frequencies increasing from 10.9 to 15.5%. This is followed by *Pistacia* (4.4–12%), *Q. calliprinos* (0.8–14.6%) and Cupressaceae (<2%). *Tamarix* is constantly represented, and to a lesser extent *Salix* concentrating its values in the first samples of Trans. PPNA/B. Among shrub taxa, *Rosa*-type is recorded (0.7–1.9%), along with *Ephedra fragilis*-type. Cichorioideae is overrepresented, particularly in samples associated with the Early PPNB. A similar trend is observed for Poaceae (<35 µm), *Carduus*- and *Carthamus*-type, with the latter peaking in selected samples. Although present in low frequencies, *Mentha*-type and ruderal taxa such as *Heliotropium* are noteworthy. Cerealina-type pollen remains below 5.1%, while Fabaceae is prominently represented in the upper samples of the Trans. PPNA/B, with values ranging from 10 to 27%.

UNIT-2 (samples CM-8 to CM-10): This unit exhibits a slight decline in arboreal pollen representation, although it shows a modest recovery compared to the previous samples. For example, the frequencies of *Q. ithaburensis*-type decrease slightly (13–11.6%). Cupressaceae is nearly absent (<0.9%), and *Pistacia* is recorded in low quantities (4–5.6%). No significant changes are observed among shrub taxa, with *Rosa*- and *Ephedra fragilis*-type consistently present throughout the unit. Herbaceous taxa show marked shifts, with Cichorioideae reaching values above 54%, accompanied by a rise in *Suaeda*-type (<21.5%). Poaceae (<35 µm) and thistles (e.g. *Carduus*- and *Carthamus*-type) exhibit a declining trend but remain consistently represented at moderate levels (<4.2 and <11.6%, respectively). Other

herbaceous taxa, including *Heliotropium*, *Mentha*-type, Apiaceae, and Asparagaceae, maintain low yet stable frequencies. Cerealina-type is still present but with a downward trend (<1%), while Fabaceae remain present, oscillating between 14 and 21.5%, slightly lower than in the preceding unit.

PW profile

Three samples were analysed from contexts associated with the Early PPNB phase. Pollen preservation is generally good, with indeterminate grain percentages ranging from 16.1 and 19.8%. A total of 62 taxa were identified. Pollen concentrations vary between 6,261 and 41,293 grains/gr in stratigraphic units linked to exterior contexts. Arboreal pollen frequencies are comparable to those observed in the Early PPNB levels of the PE and CM profiles, varying between 23.4 and 29.9% (Fig. 7).

For this third and last profile, only one unit has been defined, UNIT-1 (samples PE-1 to PE-3). *Quercus ithaburensis*-type is the dominant arboreal taxon, reaching its highest frequency at the upper sample of the Early PPNB phase (>14%). It is followed by *Pistacia*, which remains constant around 4%. *Tamarix* also peaks within this unit. As observed in other profiles, *Q. calliprinos*, *Prunus*- and *Rosa*-type are consistently present, albeit at low frequencies (<3.5%). Among herbaceous taxa, Cichorioideae and *Suaeda*-type are notably abundant, attaining approximately 48.9 and 22.2%, respectively. Poaceae (<35 µm) shows a slight decline, ranging from 6.1 to 3.2%. Other herb taxa including *Bellis*-, *Carduus*-, *Carthamus*-type, *Heliotropium*, *Mentha*-, *Papaver*-type, and *Rumex* remain low but consistently represented. Geophytes such as Asparagaceae are also recorded. Cerealina-type pollen is present in all samples (<1.3%), while Fabaceae increases significantly to reach 18.9%. Instead, Apiaceae displays a pronounced peak in the lowermost sample, with values up to 27.3%.

Wood charcoal results

A total of 599 wood charcoal remains were analysed at Khayrayin, representing a minimum of 10 taxa, identified both in the concentrated and dispersed wood charcoal assemblages.

The two wood charcoal concentrations (primary deposits) dated to the Early PPNB were monospecific (see ESM Table S5 for the results by sample). In sample number 38,255 (SU 781), 40 Salicaceae wood charcoal remains were identified, whereas in sample number 219 (SU 905) 40 *Fraxinus* sp. remains were registered. In terms of taphonomy, the Salicaceae remains were all in optimal condition, showing no alterations. However, in the case of *Fraxinus* sp., 10% of the wood charcoal fragments showed tyloses, and 17.5% of

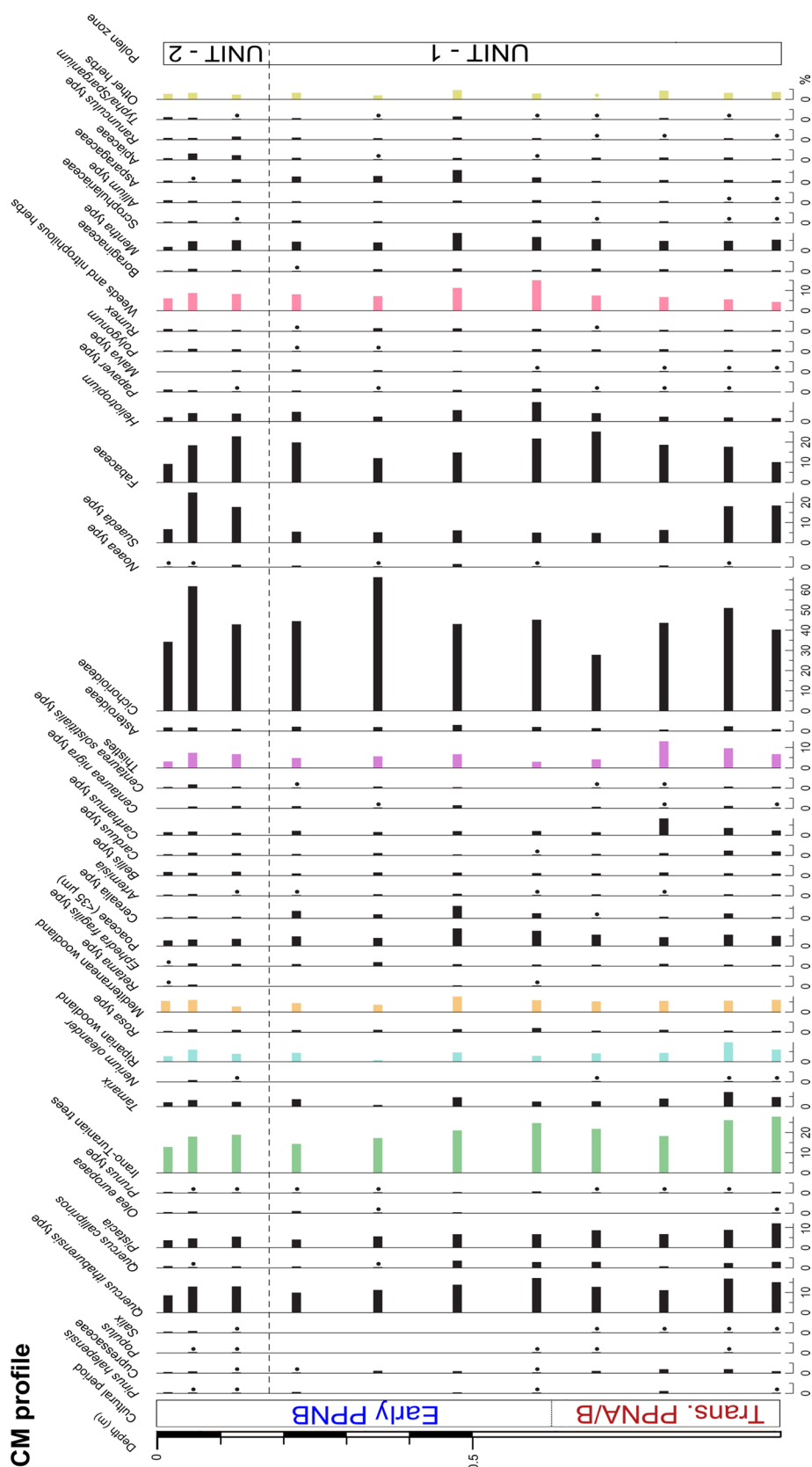


Table 1 Results of the dispersed wood charcoal analysis from Khaysin

these, *Pistacia* sp. predominated both in frequency counts and ubiquity values (57.9% counts and present in all the samples), followed by *Quercus* sp. (ca. 35% counts and present in >50% of the samples). *Quercus* sp. deciduous (7.7% counts and present in 25% of the samples) was more common than *Quercus* sp. evergreen (2.2% counts and present in 6.3% of the samples). *Amygdalus* sp. was present in ca. 30% of the samples, but it showed low frequency (3.3% counts). The remaining taxa accounted for less than 5% of the assemblage.

Early PPNB (SU 905, 781 and 607): A total of 283 wood charcoal remains were analysed, which represented at least 8 different taxa. The assemblage includes the same taxa identified in the transitional phase along with *Amaranthaceae* and cf. *Olea europaea*. In this case, *Quercus* sp. dominated the assemblage (37.8% counts, and present in >70% of the samples), followed by *Fraxinus* sp. (34.8% counts and present in 68.8% of the samples) and *Salicaceae* (11.6% counts and 56.3% of the samples). *Pistacia* sp. was also present, but it was less abundant (10.3% counts and present in 62.5% of the samples), showing a marked decrease compared to earlier phases, with values like those reported for *Salicaceae*. The rest of the taxa were rare (frequency counts <5% and present in less than 20% of the samples).

CM profile

The rest of the charcoal samples, 519 remains, represented dispersed wood charcoal fragments (Table 1; see ESM Tables S6, S7 for the results per sample, and ESM Table S3 for the results of the taphonomic analyses of the dispersed wood charcoal remains). In terms of size, 87.4% of the total charcoals analysed at the site were of 2–4 mm and 12.5% of the remains fell within the >4 mm fraction, limiting the comparison of the results by size range. The detailed results by phase are described below.

Trans. PPNA/B (SU 1047 and 1041): A total of 236 remains were analysed to characterise this phase, representing a minimum of 8 taxa: *Amygdalus* sp., Euphorbiaceae-type, Fabaceae, *Fraxinus* sp., *Pistacia* sp., *Quercus* sp. deciduous, *Quercus* sp. evergreen, and Salicaceae. From

A total number of 11 phytolith samples were analyzed from the CM profile, comprising the Trans. PPNA/B and Early PPNB phases (Table 2, Fig. 8a, b). Phytoliths were abundant in most of the samples throughout the Trans. PPNA/B depositional sequence (ranging from ca. 670,000 to 1.1 million phytoliths per gram of sediment, stratigraphic unit 1, Table 2). The presence of multicellular phytoliths (multi-celled or in anatomical connection, Fig. 8a) in these latter samples (between 1.4 and 3.6%), in addition to the relatively low proportion of weathered morphotypes (below 3%, Fig. 8a), were indicative of the general good state of

preservation of the phytolith assemblages. In contrast, the Early PPNB samples displayed relatively lower phytolith concentrations (ca. 32,000–92,000 phytoliths/g in stratigraphic unit 2; 28,000–41,000 phytoliths/g in stratigraphic unit 3, Table 2). The relatively low proportions of phytoliths in both stratigraphic units, together with the almost complete absence of multi-celled phytoliths (only 0.2%, samples CM-7 and CM-8 in unit 2; whereas up to 2.5% sample CM-9, unit 3) and higher percentages of weathering (up to 25%, sample CM-9, Table 2), appears to be indicative of the state of preservation of the assemblages and type of contextual deposit (interior floors and wall collapse vs. exterior-colluvial and anthropic levels more exposed to external agents).

The phytolith morphological results point towards a general similarity between all samples, with dominance of monocotyledonous phytoliths, particularly of grasses from the Pooideae subfamily according to the short cell morphologies, mainly composed of RONDELS, CRENATES and TRAPEZOIDS (average ca. 85% of all the counted morphotypes, Fig. 8a, b). In addition to Pooideae grass phytoliths, diagnostic hat-shaped morphotypes from the Cyperaceae family (sedges), which are also common in wet environments, occur only in Trans. PPNA/B assemblages, whereas they are completely absent in Early PPNB samples (Fig. 8a). Similarly, diagnostic phytoliths from the Chloridoideae subfamily (SADDLES) were only common in Trans. PPNA/B samples although into a lesser extent (up to 1.4%, sample PW-2), whereas these were almost completely absent from Early PPNB assemblages, with the only exception of sample CM-8 (ca. 4.3%, Fig. 8a). Phytoliths from the leaves and culms of grasses, including, ACUTE BULBOSUS (trichomes), BULLIFORM FLABELLATE and ELONGATE ENTIRE phytoliths, were common in most of the samples (Fig. 8a). Interestingly, certain diagnostic morphotypes, such as DENDRITIC and DENTATE ELONGATES, in addition to epidermal cells such

as papillate from the floral parts of grasses, occur in greater proportions in Trans. PPNA/B assemblages (Fig. 8b). Of note is the dominance of phytoliths from the inflorescences of grasses in Trans. PPNA/B assemblages (ca. between 40 and 48%, sample CM-0, unit 1, Fig. 8a, b). Furthermore, multi-celled phytoliths from the husks and culms of Pooideae grasses, including *Triticum* sp. and *Hordeum* sp. were also noted in these latter samples.

PW profile

Three samples were analysed from contexts belonging to the Early PPNB phase defined as exterior contexts (Fig. 8c, d). Like the exterior Early PPNB samples from the CM profile, the samples from the PW profile yielded relatively lower phytolith concentrations in comparison to indoor Trans. PPNA/B samples from the CM profile (ranging from ca. 110,000 to 330,000 phytoliths per g of sediment, Stratigraphic Unit 1, Table 3). Multi-celled phytoliths were also recorded in PW profile samples (up to 4.4%, sample PW-1), with the only exception of sample PW-2 where multi-celled morphologies were completely absent (Table 2).

Coeval to CM profile samples, monocotyledonous plants and particularly grasses from the Pooideae subfamily dominated the phytolith record (average ca. 76% of all the counted morphotypes, Fig. 8c). Multi-celled dendritic phytoliths from the husks and culms of *Triticum* sp. and *Hordeum* sp. were also recorded. Contrary to CM profile samples, diagnostic chloridoid grass morphotypes (SADDLES) were completely absent (Fig. 8d). Interestingly, characteristic hat-shaped morphologies from the Cyperaceae family (sedges), were only noted in the lowermost sample from the Early PPNB depositional sequence, although into lesser amounts (ca. 5.5%, sample PW1, Fig. 8c). Also of significance is the increased proportions of dicotyledonous morphotypes observed in the uppermost sample of the Early

Table 2 Description of samples and main phytolith quantitative results from CM and PW profiles

Sample number	Strati. Unit	Cultural period (phase)	Phytoliths 1 g of sediment	Weathered phytoliths (%)	Multi-celled phytoliths (%)	Context
CM-10	3	Early PPNB	41,000	8.3	2.5	House 2, floor
CM-9	3		28,000	25	1.3	House 2, floor
CM-8	2		83,000	8.7	0.2	Exterior, colluvial and anthropic
CM-7	2		32,000	11	0.2	Exterior, colluvial and anthropic
CM-6	2		92,000	4.2		Exterior, colluvial and anthropic
CM-5	2		57,000	6.7		Exterior, colluvial and anthropic
CM-4	2		46,000	15		Exterior, colluvial and anthropic
CM-3	1	Trans. PPNA/B	670,000	2.9	2.4	House 1, wall collapse
CM-2	1		1,100,000	1.8	3.6	House 1, wall collapse
CM-1	1		670,000	1.9	2.8	House 1, wall collapse
CM-0	0		850,000	2.3	1.4	House 1, floor
PW-3	1	Early PPNB	110,000	6.5	3.2	Exterior, colluvial and anthropic
PW-2	1		130,000	5.1		Exterior, colluvial and anthropic
PW-1	1		330,000	9.9	4.4	Exterior, colluvial and anthropic

PPNB sequence, including SPHEROIDS and tracheary phytoliths (ca. 26.5%, sample PW3, Fig. 8c).

Discussion

Early Holocene (8895–8210 cal BCE) vegetation communities in the Jordanian Plateau

The Southern Levant underwent pronounced climatic adjustments from the Late Pleistocene into the Early Holocene (Robinson et al. 2006; Enzel et al. 2008; Blockley and Pinhasi 2011), eventually stabilising at around 7000 cal BCE (Stein et al. 2025). Most palaeoclimatic records concur that both precipitation regimes and, notably, summer temperatures recovered rapidly following the regionally arid and less seasonal conditions of the Younger Dryas (Migowski et al. 2006), resulting in complex palaeohydrological responses. Sedimentary evidence from the Dead Sea basin indicates a marked reduction in lake size during the transition from the Late Glacial to the Holocene (Müller et al. 2022), with low water levels persisting throughout much of the Holocene (Stein et al. 2010; Lev et al. 2019). Simultaneously, high-resolution speleothem records from Soreq (Bar-Matthews et al. 2019) and Jeita caves (Verheyden et al. 2008; Cheng et al. 2015) suggest relatively stable precipitation patterns, while summer insolation and evaporation rates gradually declined toward the Middle Holocene (Cheng et al. 2015). Several studies (e.g. Almogi-Labin et al. 2009) propose that increased humidity originated from the Mediterranean, associated with the northward shift of the Azores High and the winter rain belt, underscoring the significant influence of Mediterranean climatic dynamics on the Levant during the Early Holocene (Arz et al. 2003; Burstyn et al. 2019). Within this climatic framework, both PPNA and PPNB periods emerged during a phase of renewed environmental stability, which facilitated the development of communities capable of managing their immediate landscapes for agricultural and woodland management (Robinson et al. 2006; Turner et al. 2010; Rosen and Rivera-Collazo 2012).

The pollen profiles obtained from Kharaysin indicate that the Irano-Turanian steppe-forest, characterised by the *Q. ithaburensis*-type–*Pistacia*–*Prunus*-type association, was widespread across the Jordanian Plateau between 8895 and 8210 cal BCE. This vegetation assemblage is typical of the modern Mediterranean–Irano-Turanian transition zone (Al-Eisawi 1996), although it may have represented a denser arboreal cover than observed in the present-day landscape. Notably, arboreal pollen reached significant proportions during the Trans. PPNA/B phase (8895–8415 cal BCE) and slightly declined during the Early PPNB (8465–8210 cal BCE) (Figs. 5, 6). This is particularly evident in the case

of *Pistacia*, a taxon known for its low pollen productivity (Cordova 2010) and frequent underrepresentation in palynological records (Davies and Fall 2001). Nevertheless, its presence with frequencies up to 13% in Kharaysin indicates that *Pistacia* was not represented by scattered individuals but rather formed significant stands near the settlement. Similarly, *Q. ithaburensis*-type pollen scores oscillated between 5 and 15% across the three profiles, implying a substantial contribution to the local woodland structure, consistent with modern pollen–vegetation relationship (Davies and Fall 2001), which adapts to more continental and harsh environments. Wood charcoal assemblages further support the preferential use of *Pistacia* sp., *Quercus* sp. deciduous, and *Amygdalus* sp. as primary fuelwood taxa (Table 2), suggesting that these species were likely sourced from nearby stands. Additionally, Mediterranean taxa such as *Q. calliprinos*, Cupressaceae, *Pinus halepensis* and *Rosa*-type reached their highest pollen frequencies during the Trans. PPNA/B phase (Figs. 5, 6), potentially reflecting a broader distribution of thermophilous elements into more continental zones under milder and moister climatic conditions. However, the practically absence of warm-adapted taxa in both the wood charcoal assemblages (Table 1) and in the carpological spectra (Douché et al. 2025) suggests that continental climatic influences continued to shape Early Holocene plant distributions in the region.

At a regional scale, the obtained pollen profiles, and charcoal assemblages at Kharaysin correlate with the available regional data and support a contemporary spread of both Mediterranean woodland and Irano-Turanian steppe-forest across the Southern Levant, reaching areas under modern steppe and desert communities (Asouti et al. 2015). For example, the pollen profiles of Aammiq and Chamsine/Anjar wetlands, both placed in the Bekka Valley, as well as the Al-Jourd marsh, located in Northern Lebanon, reveal a rapid shift from a dense Amaranthaceae–Cichorioideae herbaceous steppe towards an open woodland with deciduous and evergreen oak forests as the main taxon towards the Early Holocene (Hajar et al. 2008, 2010; Cheddadi and Khater 2016). At Lake Hula, the pollen section points to a predominantly steppe-like character of the vegetation with scattered *Q. ithaburensis*-type, and to a lesser extent, *Q. calliprinos* trees in the valleys (van Zeist et al. 2009), which points to continental climate with reduced amount of rainfall. Even so, the uppermost section of the Yammoûneh record evidence an exponential rise in arboreal pollen during the Holocene onset, primarily derived from deciduous oak communities (Gasse et al. 2011). In Tell Qarassa, open oak-woodland steppe (*Q. ithaburensis*-type, *Q. calliprinos*, *Pistacia*, and *Prunus*-type) coexisted with local hygrophilous communities and with a high-mountain mixed coniferous forest (*Betula*, *Cedrus*, and *Pinus nigra*-type), indicating a

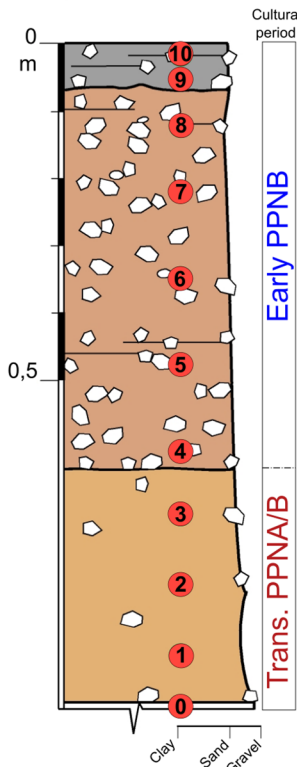
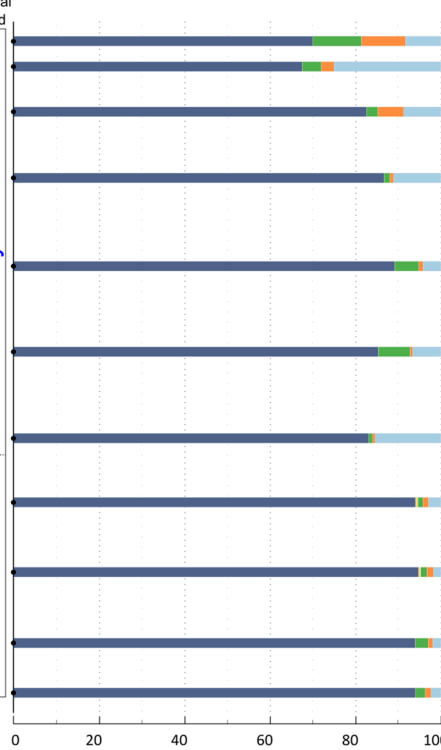
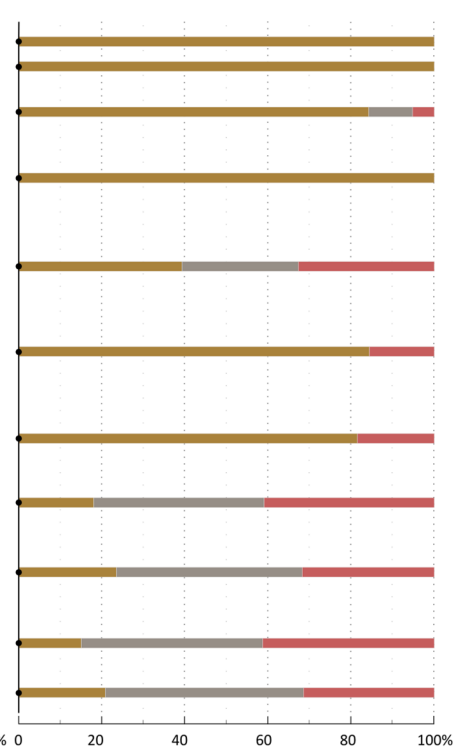
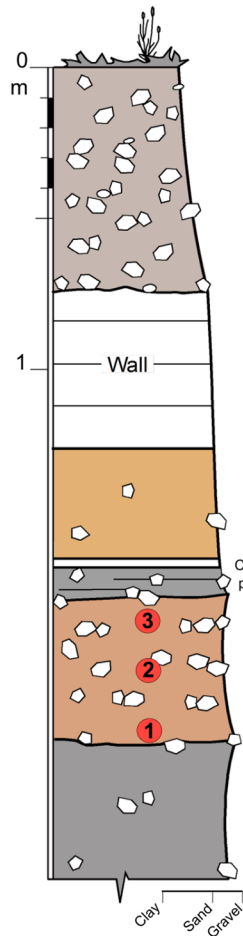
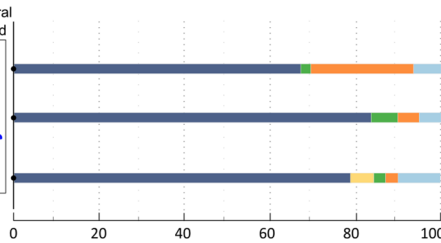
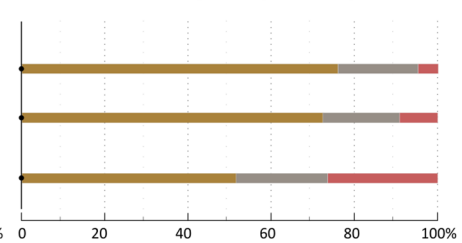
CM profile**a relative abundances of phytoliths****b anatomical origin of grass phytoliths****PW profile****c relative abundances of phytoliths****d anatomical origin of grass phytoliths**

Fig. 8 **a** Relative abundance of phytoliths from grasses, dicotyledonous leaves, dicotyledonous wood/bark, sedges and weathered morphotypes from CM profile samples. **b** Anatomical origin of grass phytoliths from CM profile samples. **c** Relative abundance of phytoliths from PW profile samples. **d** Anatomical origin of grass phytoliths from PW profile samples. Photomicrographs of identified phytoliths are visible in ESM Fig. S1

climate shift towards humid conditions between ca. 8675 and 7875 cal BCE (Arranz-Otaegui et al. 2017). Moreover, the pollen profile from Lake Birkat-Ram in the Golan Heights evidences a dry climate at the beginning of the Holocene with reduced trees but with a noticeable representation of Irano-Turanian and batha communities (e.g. *Quercus* spp., Rosaceae) (Weinstein-Evron 1976). The charcoal results coming from the nearby 'Ain Ghazal demonstrate that the *Quercus* sp. deciduous–*Pistacia* sp.–*Crataegus* sp./*Pyrus* sp. steppe-forest widespread in the Jordanian Plateau during and Early PPNB periods (Neef 2004a).

The diversity and sustained presence of riparian woodland in the pollen assemblages, represented primarily by *Tamarix* and *Salix* but also by *Populus*, *Fraxinus angustifolia*-type and *Nerium oleander*, alongside hygrophilous herbaceous species such as *Typha/Sparganium* as well as Cyperaceae phytoliths, indicate that fluvial ecosystem remained active during this period. In addition, the recovery of Salicaceae, *Fraxinus* sp., and to a lesser extent Salicaceae *Populus*-type and *Quercus* sp./*Tamarix* sp. wood charcoal from primary deposits provides direct evidence that Early PPNB communities at Kharaysin systematically exploited riparian forests for firewood and/or construction purposes. In addition, carpological data highlights the exploitation of riparian plant resources, including fruits like *Ficus carica*, *Vitis vinifera*, and *Sambucus* sp., along with sedges such as *Carex* sp., during the Trans. PPNA/B and Early PPNB phases (Douché et al. 2025).

However, the most conspicuous feature of the palynological profiles is the high representation of herbaceous taxa, particularly during the Early PPNB phase (Figs. 4, 5, 6). Cichorioideae and, overall, diverse members of Asteraceae are prominently represented in the pollen profiles from Kharaysin. Their presence in archaeological contexts from arid regions has been extensively debated and has been often attributed to local taphonomic processes. Cichorioideae pollen exhibits greater resistance to degradation compared to other types and is frequently considered an over-represented component in archaeological pollen spectra. Moreover, Cichorioideae pollen has been observed to enter the sedimentary records due to recurrent burrowing insect activity (Bottema 1975). Therefore, this can be considered a case of partial bioturbation, and even disturbances caused by trampling, grazing or ruderal growth within or in the vicinity of the site, whereby certain amounts of Cichorioideae pollen could have been displaced vertically downwards in the

sampled profiles, contributing to its increased abundance in the sections. For this reason, this taxon has been excluded from the pollen sum to avoid possible taphonomic biases. Nevertheless, it is worth noting that the high abundance of Cichorioideae in profiles coincides with elevated pollen concentration samples, high palynological diversity, and low proportions of indeterminate pollen, suggesting that taphonomic distortion alone is insufficient to account for its prevalence. Indeed, the possibility that Cichorioideae was a genuine component of open land steppe vegetation, should not be ruled out. This interpretation is supported by modern pollen rain studies (Davies and Fall 2001; Hajar et al. 2008) and is consistently reflected in Holocene pollen records from the Southern Levant (e.g. van Zeist et al. 2009; Hajar et al. 2010; Litt et al. 2012).

In a similar way, the high abundance of species included within the pollen taxa like Poaceae (<35 µm), *Suaeda*-type, as well as the various representatives of Boraginaceae, *Mentha*-type, or Scrophulariaceae, complicates the inference of ecological signals, particularly when these taxa encompass elements with a broad distribution range within the Irano-Turanian phytogeographic region (Djamali et al. 2012). The phytolith assemblage from Kharaysin shows a clear predominance of Poaceae, particularly Pooideae, during the Trans. PPNA/B, indicating an open, grass-dominated landscape (Fig. 8). This interpretation is consistent with the site carpological record related to wild taxa (Douché et al. 2025). In the Early PPNB, the morphological diversity is lower and there is an absence of elements linked to humid habitats (e.g. Cyperaceae) pointing to drier environment (Fig. 8). In addition, the increase of Amaranthaceae in the pollen profiles has been commonly interpreted as an indicator of disturbed environments linked to long-term human activities (e.g. Baruch and Bottema 1991; Hajar et al. 2008, 2010). Despite, *Suaeda*-type is continuously present in high frequencies in the three pollen profiles (Figs. 5, 6, 7), whereas wood charcoal analysis report scattered Amaranthaceae wood fragments in the Early PPNB phase of Kharaysin (Table 1). Therefore, this taxon could also have been part of the shrub component, associated with both wet and saline areas and in arid or semi-arid environments, accompanied by other xerophytic shrubs/herbs, specifically of the *Retama*-type, *Artemisia*, and/or *Ephedra fragilis*-type. In a similar way, the presence of geophytes (e.g. *Allium*-type, Asparagaceae, or *Ranunculus*-type, see the complete list in the ESM Table S2), potential edible species, in pollen during the Trans. PPNA/B and Early PPNB, more abundant at the beginning of the latter, suggests the recolonization of open areas. However, it is possible that some recorded frequencies are directly associated with ruderal plant species, as will be discussed in the following section.

Table 3 Synthetic archaeobotanical summary of the vegetation landscape and human–environment interactions at Kharaysin during the Trans. PPNA/B–Early PPNB

Pollen analysis	Phytolith analysis	Wood charcoal analysis	Carpological analysis (Douché et al. 2025)
Early PPNB (8465–8210 cal BCE)			
Open landscape with a slight decline in arboreal taxa (mainly <i>Quercus ithaburensis</i> -type and <i>Pistacia</i>) along a progressive increase in herbaceous and nitrophilous taxa dominated by Cichorioideae and Asteraceae (<i>Bellis</i> -, <i>Carthamus</i> -, <i>Centaurea</i> - and <i>Carduus</i> -type). The presence of Cerealia-type and expansion of Fabaceae and ruderal elements indicate intensified agropastoral pressure on vegetation cover	A scarcity of multicellular cereal remains (<i>Triticum</i> sp. and <i>Hordeum</i> sp.) and the near disappearance of the Cyperaceae and Chloridoideae. The increase in dicotyledonous morphotypes could indicate a possible disturbance of the vegetation, a gradual opening of the landscape, and comparatively drier conditions	Dominance of <i>Quercus</i> sp., with high representation of <i>Fraxinus</i> sp. and Salicaceae, indicating continued reliance on riparian and nearby woody resources. The decline of <i>Pistacia</i> sp. and the low presence of other taxa suggest reduced availability (limited wood charcoal assemblage)	High representation of legumes, mainly <i>Vicia narbonensis</i> , <i>V. faba</i> , and <i>Lens</i> spp., indicating possible plant management practices. Secondary role of cereals as indicated by Cerealia spp., <i>Triticum monococcum</i> ssp. <i>boeoticum/monococcum</i> and <i>Hordeum vulgare</i> ssp. <i>spon-taneum/vulgare</i> presences
Trans. PPNA/B (8895–8415 cal BCE)			
Predominantly open woodland–grassland mosaic dominated by <i>Q. ithaburensis</i> -type and <i>Pistacia</i> , accompanied by herbaceous communities rich in Cichorioideae and Asteraceae (<i>Carthamus</i> -, <i>Carduus</i> - and <i>Centaurea nigra</i> -type), also <i>Suaeda</i> -type and Poaceae (<35 µm). The continuous presence of Fabaceae, Cerealia-type and ruderal taxa indicates sustained local agropastoral activity	The dominance of C ₃ grasses (Pooideae), with abundant inflorescence morphotypes and multicellular remains of <i>Triticum</i> sp. and <i>Hordeum</i> sp., points to the existence of local cereal processing activities. The presence of Cyperaceae and Chloridoideae suggests the existence of humid microenvironments within an open landscape dominated by herbaceous vegetation	Exploitation of local open woody communities dominated by <i>Pistacia</i> sp. and <i>Quercus</i> sp., both deciduous and evergreen, with minor contribution of <i>Amygdalus</i> sp., <i>Fraxinus</i> sp. and Salicaceae, reflecting the use of local woodland and scrub resources as fuel and/or building material (limited wood charcoal assemblage)	Assemblage dominated by herbaceous wild/weed taxa (e.g. <i>Buglossoides tenuiflora</i> and <i>Chenopodium</i> sp.) and the exploitation of fruit resources (<i>Ficus carica</i> , <i>Vitis vinifera</i> , <i>Sambucus</i> sp.). Minor contribution of cereals (<i>H. vulgare</i> , <i>T. monococcum/dicoccum</i>) and legumes (<i>Lens culinaris</i> , <i>V. narbonensis</i> -type) (limited carpological assemblage)

The absence of abrupt shifts in the pollen spectra obtained in Kharaysin implies that anthropogenic pressure was moderate and did not result in large-scale woodland clearance. Instead, the vegetation landscape appears to have undergone a slow and continuous modification, likely reflecting incremental changes in land-use practices rather than disruptive ecological interventions. The continued presence of Irano-Turanian elements in both pollen and wood charcoal assemblages highlights the resilience of steppe-adapted taxa throughout the Trans. PPNA/B (8895–8415 cal BCE) and Early PPNB (8465–8210 cal BCE) phases. This long-term persistence cannot be fully explained by climatic factors alone and instead suggests a form of human-mediated landscape management that allowed these steppe elements to maintain their ecological niche despite increasing anthropogenic intervention.

It is important to note that pollen data from the archaeological contexts at Kharaysin mainly reflect local vegetation change and anthropogenic processes occurring within and around the site. Taxa associated with disturbance, ruderal species, low pollen producers, and/or entomophilous taxa (e.g. *Pistacia*, *Prunus*-type, or Fabaceae) likely represent a predominantly local signal. In contrast, highly productive anemophilous taxa, such as *Q. ithaburensis*-type, *Pinus halepensis* and/or Poaceae, may incorporate a broader extra-local component. Consequently, although comparisons with

regional palaeoecological records allow us to situate Kharaysin within broader Early Holocene vegetation trends, local anthropogenic processes modulated the vegetation at the site scale. This distinction clarifies the separation between ecological dynamics operating at the settlement level and the wider climatic and phytogeographic patterns.

Agropastoral and woodland management activities as drivers of local vegetation change

During the Trans. PPNA/B and Early PPNB periods, agropastoral activities became widespread in the Southern Levant (Colledge et al. 2004). Although the first evidence of cereal domestication, possibly opportunistically (Asouti and Fuller 2012), began to appear during these periods, the exploitation of the so-called “founder crops” (Weiss and Zohary 2011; Arranz-Otaegui and Roe 2023) and wild cereals was carried out in earlier periods, such as the Middle (Lev et al. 2005) and Upper (Kabukcu et al. 2023) Palaeolithic. Wetter climatic conditions, particularly at the onset of the Holocene, presumably favoured this expansion (Weninger et al. 2009). Despite this asynchronous and regionally variable change, small-scale cultivation of cereals, legumes, and fruit trees expanded in diverse ways (Fuller and Lucas 2025) favoured by climatic and cultural drivers. These factors had a gradual impact on the natural vegetation cover,

which may have resulted in localised landscape degradation (Henry et al. 2017). In this context, hunting (Sapir-Hen et al. 2009) and gathering (Asouti and Fuller 2012) remained common during the transition to the Early PPN societies in the Mediterranean Levant, while plant resource management, woodland management, and animal domestication gradually became widespread in certain regions (Palmisano et al. 2019). In the period leading up to the Early PPNB, plant management practices, such as sowing, underwent a multifaceted expansion (Willcox 2005; Fuller et al. 2011; Ibáñez et al. 2025b). Simultaneously, there was an increase in goat breeding (Zeder and Hesse 2000). Otherwise, vegetation clearance and the use of fire on a small-scale were driven by the need for land suitable for agriculture and livestock grazing (Asouti 2025). In fact, it is conceivable that human intervention contributed to the controlled expansion of heliophilous forests and scrublands, as well as the maintenance of grasslands, thus shaping a more anthropogenic landscape around the site. All these practices could have been linked to the progressive population growth in Mediterranean regions and to changes in land use, although this relationship would vary geographically and would not be due to a simple cause-and-effect dynamic (Palmisano et al. 2019; Roberts et al. 2019). Nevertheless, in the case of Kharaysin, pollen, charcoal, and phytolith analyses demonstrate a slight and progressive transformation in the structure of the local vegetation, attributable to both climatic stability and the intensification of human practices, particularly grazing, firewood collection, and plant exploitation.

One of the most compelling indicators of agropastoral activity is the presence of thistles identified within the pollen records. These communities, belonging mainly to the Asteraceae family, have a complex relationship with long-term grazing practices in the Levant and other Mediterranean rangelands (Sternberg et al. 2000; Ronel and Lev-Yadun 2009). Because of their spiny leaves and stems, most thistle species are unpalatable to livestock, especially cattle and sheep, which tend to avoid them (Deckers et al. 2025). Under conditions of heavy or continuous grazing, more palatable grasses are selectively consumed (Lu 1988), leaving bare patches of soil that thistles readily colonize (Segev et al. 2022). As a result, thistles often increase in abundance and can become dominant indicators of overgrazed or degraded rangelands. In this frame, the reduced values of grasses (Poaceae < 35 µm) alongside the marked increase of the thistle group (*Carduus*-, *Carthamus*-, *Centaurea nigra*- and *C. solstitialis*-type, see the complete list in the ESM Table S2) supports the hypothesis of local overgrazing around Kharaysin. This interpretation is consistent with archaeozoological data from the site, which shows an increasing specialization in goat exploitation and human-controlled feeding practices towards the Early and

Middle PPNB (Jiménez-Manchón et al. 2023; Ibáñez et al. 2025c). The phytolith results point to a gradual transition from dense grasslands, which were influenced by a more humid climate during the Trans. PPNA/B period, to more open habitats. This is also supported by reduced grass inflorescence morphotypes and relatively low phytolith concentrations, including multicellular forms of *Triticum* sp. and *Hordeum* sp. These microfossil records further suggest grazing dynamics and the early exploitation of cereals near the settlement. Increased relative abundances of dicotyledonous, which are minor phytolith producers, are noted in the upper levels of the Early PPNB, alongside the predominance of Pooideae. This may suggest increasing vegetation disturbance and the expansion of shrubs or woody taxa, which are linked to the anthropogenic landscape.

Besides, the high and constant presence of Fabaceae in the pollen profiles of Kharaysin (Figs. 5, 6, 7) could potentially be indicative of local legume cultivation (Douché et al. 2025). Although unfortunately the preservation of pollen does not allow for a detailed taxonomic ascription, the dominance of *Vicia narbonensis*, *V. faba*, and *Lens* spp., and the sporadic appearance of *Lathyrus sativus* and *Vicia ervilia* in the Early PPNB carpological record suggests plant management practices, probably linked to the combination of mixed subsistence including both cultivation and wild plant gathering (Douché et al. 2025). In addition, the continuous presence of Fabaceae pollen clumps, in some samples forming aggregates of up to ten pollen grains, could be evidencing systematic plant collection and processing activities, since pollen grain clumps are typically associated with pollen-rich anthers and deliberate handling of floral material (Eastwood et al. 2018; Miras et al. 2018). In fact, some species within Fabaceae have enclosed anthers and, due to its poor dispersal capacity, are rarely found in high frequencies in fossil pollen assemblages (Davies and Fall 2001), so, scores up to 27% as seen in Kharaysin (Figs. 6, 7), should be linked to cultivated fodder grown around the archaeological site. However, they could also indicate an abundance of small-seeded legumes, both cultivated and wild, in the vicinity of the site, indicating increasing grazing pressure on grasslands (Asouti et al. 2015). High-resolution surface textural analysis and plant micro residues recovered from grinding stone tools in domestic contexts at Kharaysin provide a detailed perspective on legume exploitation strategies and offer new insights into plant transformation and food preparation practices among the earliest Neolithic farmers. The archaeobotanical significance of legumes during the PPNB phases is not particular to Kharaysin, as it has been demonstrated by their recurrent presence across numerous archaeological sites in the Southern Levant (Arranz-Otaegui et al. 2016; Caracuta et al. 2017; Douché and Willcox 2018, among others).

Conversely, Cereal-type pollen counts are notably lower, with sporadic appearances of pollen aggregates. In addition, no significant differences in pollen frequencies have been identified between the Trans. PPNA/B and Early PPNB phases (Figs. 5, 6). Due to its specific characteristics, namely low pollen productivity, and relatively large grain size ($>40\text{ }\mu\text{m}$), Cereal-type pollen exhibits limited potential for long-distance dispersal. Consequently, its presence in the pollen record is generally interpreted as evidence of cereal exploitation near the settlement (Fyfe 2006). Nonetheless, contributions from natural Cereal-type communities cannot be entirely excluded, as wild grass taxa with morphologies resembling domesticated cereals may also produce similar pollen types (Bottema 1992), complicating the interpretation of early agricultural signals (Schiebel and Litt 2018). In any case, the recurrent presence of Cereal-type pollen, in association to *Triticum* sp. and *Hordeum* sp. multi-cellular or anatomically connected phytoliths in both phases correlates with the carpological spectra with Cereal spp., *Triticum monococcum* ssp. *boeoticum/monococcum* and *Hordeum vulgare* ssp. *spontaneum/vulgare* as main contributors. Overall, cereals constitute a minor component of the carpological assemblage, always below 15%, regardless of the occupational phase (Douché et al. 2025) and, while the analysis of ground stone tools clearly indicates cereal processing by grinding, these products do not appear to have been the primary or preferred plant foods.

Conclusions

The integration of pollen, wood charcoal and phytolith analyses has provided new data on Neolithic landscape transformation and management activities at Kharaysin, complementing previous work in the Southern Levant. The findings of this study are of significant value to elucidate the Trans. PPNA/B (8895–8415 cal BCE) and Early PPNB (8465–8210 cal BCE) vegetation history and the landscape dynamics in the Jordanian Plateau, as well as the role of early agricultural societies in transforming the environment (Table 3).

Overall, the data from this study indicate that the vegetation around the Kharaysin archaeological site was dominated by Irano-Turanian steppe-forest together with a riparian woodland, which constituted the primary sources of fuel and construction materials. The strong representation of steppe herb taxa further suggests that open environments coexisted with arboreal taxa such as *Pistacia* and *Q. ithaburensis*-type, indicating that these woodland patches were locally abundant and significant within the settlement. Grazing pressure, inferred by the abundant presence of thistles, weeds and ruderal species, together with early legume and

cereal exploitation, indicates significant human impact and disturbance in the area immediately surrounding the site, which helped in the contribution of the progressive opening of the landscape.

This work indicates that all these transformations of the vegetation landscape were gradual and cumulative rather than abrupt, reflecting moderate but persistent management strategies under generally temperate climatic conditions. Local pollen assemblages capture site-specific ecological and anthropogenic signals, while their correlation with regional datasets places Kharaysin within the trend of Early Holocene vegetation in the Southern Levant.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00334-026-01100-y>.

Acknowledgements Andoni Mateos-Cabero acknowledges the predoctoral funding received from the Basque Country Government (ref. PRE_2025_2_0151). Elena Royo and Inés de la Parra are also thanked for their help with pollen extractions.

Author contributions Conceptualisation: A. Mateos-Cabero, J. Aranbarri. Data curation: A. Mateos-Cabero. Methodology: A. Mateos-Cabero, J. Aranbarri, E. Iriarte, M. Portillo, A. Arranz-Otaegui, JJ. Ibáñez. Formal analysis and research: A. Mateos-Cabero, J. Aranbarri, E. Iriarte, M. Portillo, A. Arranz-Otaegui, JJ. Ibáñez. Writing—original draft preparation: A. Mateos-Cabero. Writing—review and editing: A. Mateos-Cabero, J. Aranbarri, E. Iriarte, M. Portillo, A. Arranz-Otaegui, JJ. Ibáñez, A. García-Suárez. Resources: LC. Teira (cartography and orthophotos), A. Mateos-Cabero, E. Iriarte, M. Portillo, A. Arranz-Otaegui (figures and tables). Funding acquisition: JJ. Ibáñez. Supervision: J. Aranbarri. Validation: A. Mateos-Cabero, J. Aranbarri, E. Iriarte, M. Portillo, A. Arranz-Otaegui, A. García-Suárez, LC. Teira, J. Muñiz, JJ. Ibáñez.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This research was funded by the Spanish Ministry of Science and Innovation through the research Project NEONET (PID2022-142075NB-I00), as well as by the GIZAPRE Research Team supported by the Basque Government (IT-1852-26) and the Fundación Palarq. Wood charcoal analysis was supported by the ERC Starting Grant PalaeOrigins (ERC-2021-STG Project 101039060).

Data availability The datasets produced during this study are available from the corresponding author (A. Mateos-Cabero, andoni.mateos@ehu.eus) upon reasonable request.

Declarations

Competing interests The authors declare that they have no competing interests.

Ethical approval This study did not include human participants, clinical samples, or experiments on live animals. Analysis of the archaeological materials recovered from the Kharaysin site was conducted with authorisation from the Jordanian Department of Antiquities.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Albert RM, Shahack-Gross R, Cabanes D et al (2008) Phytolith-rich layers from the late Bronze and Iron Ages at Tel Dor (Israel): mode of formation and archaeological significance. *J Archaeol Sci* 35:57–75. <https://doi.org/10.1016/j.jas.2007.02.015>
- Albert RM, Ruiz JA, Sans A (2016) PhytCore ODB: a new tool to improve efficiency in the management and exchange of information on phytoliths. *J Archaeol Sci* 68:98–105. <https://doi.org/10.1016/j.jas.2015.10.014>
- Al-Eisawi D (1996) Vegetation of Jordan. Regional Office for Science and Technology for the Arab States, UNESCO, Cairo
- Almogi-Labin A, Bar-Matthews M, Shriki D et al (2009) Climatic variability during the last ~90 ka of the southern and northern Levantine Basin as evident from marine records and speleothems. *Quat Sci Rev* 28:2882–2896. <https://doi.org/10.1016/j.quascirev.2009.07.017>
- Aranbarri J, González-Sampériz P, Iriarte E et al (2015) Human–landscape interactions in the Conquezueta-Ambrona Valley (Soria, continental Iberia): from the early Neolithic land use to the origin of the current oak woodland. *Palaeogeogr Palaeoclimatol Palaeoecol* 436:41–57. <https://doi.org/10.1016/j.palaeo.2015.06.030>
- Arranz-Otaegui A (2017) Evaluating the impact of water flotation and the state of the wood in archaeological wood charcoal remains: implications for the reconstruction of past vegetation and identification of firewood gathering strategies at Tell Qarassa North (South Syria). *Quat Int* 457:60–73. <https://doi.org/10.1016/j.quaint.2016.06.030>
- Arranz-Otaegui A, Roe J (2023) Revisiting the concept of the ‘Neolithic Founder Crops’ in Southwest Asia. *Veget Hist Archaeobot* 32:475–499. <https://doi.org/10.1007/s00334-023-00917-1>
- Arranz-Otaegui A, Colledge S, Ibáñez JJ, Zapata L (2016) Crop husbandry activities and wild plant gathering, use and consumption at the EPPNB Tell Qarassa North (South Syria). *Veget Hist Archaeobot* 25:629–645. <https://doi.org/10.1007/s00334-016-0564-0>
- Arranz-Otaegui A, López-Sáez JA, Araus JL et al (2017) Landscape transformations at the dawn of agriculture in southern Syria (10.7–9.9 ka cal. BP): plant-specific responses to the impact of human activities and climate change. *Quat Sci Rev* 158:145–163. <https://doi.org/10.1016/j.quascirev.2017.01.001>
- Arz HW, Lamy F, Pätzold J, Müller PJ, Prins M (2003) Mediterranean moisture source for an early-Holocene humid period in the northern Red Sea. *Science* 300:118–121. <https://doi.org/10.1126/science.1080325>
- Asouti E (2025) Beyond the ‘Principle of Least Effort’—culture and the natural environment in the interpretation of archaeological data. *Environ Archaeol*. <https://doi.org/10.1080/14614103.2025.2498286>
- Asouti E, Austin P (2005) Reconstructing woodland vegetation and its exploitation by past societies, based on the analysis and interpretation of archaeological wood charcoal macro-remains. *Environ Archaeol* 10:1–18. <https://doi.org/10.1179/env.2005.10.1.1>
- Asouti E, Fuller DQ (2012) From foraging to farming in the southern Levant: the development of Epipalaeolithic and Pre-pottery Neolithic plant management strategies. *Veget Hist Archaeobot* 21:149–162. <https://doi.org/10.1007/s00334-011-0332-0>
- Asouti E, Kabukcu C (2014) Holocene semi-arid oak woodlands in the Irano-Anatolian region of Southwest Asia: Natural or anthropogenic? *Quat Sci Rev* 90:158–182. <https://doi.org/10.1016/j.quascirev.2014.03.001>
- Asouti E, Kabukcu C, White CE et al (2015) Early Holocene woodland vegetation and human impacts in the arid zone of the southern Levant. *Holocene* 25:1,565–1,580. <https://doi.org/10.1177/0959683615580199>
- Austin P (2007) The wood charcoal macroremains. In: Finlayson B, Mithen S (eds) *The early prehistory of Wadi Faynan, Southern Jordan: archaeological survey of Wadis Faynan, Ghuwayr and Al Bustan and evaluation of the Pre-Pottery Neolithic A site of WF16*. Oxbow Books, Oxford, pp 408–419
- Bar-Matthews M, Keinan J, Ayalon A (2019) Hydro-climate research of the late Quaternary of the Eastern Mediterranean-Levant region based on speleothems research—a review. *Quat Sci Rev* 221:105872. <https://doi.org/10.1016/j.quascirev.2019.105872>
- Baruch U, Bottema S (1991) Palynological evidence for climatic changes in the Levant ca. 17000–9000 B.P. In: Bar-Yosef O, Valla FR (eds) *The Natufian Culture in the Levant*. International Monographs in Prehistory, Ann Arbor, pp 11–20
- Bender F (1975) *Geology of the Arabian Peninsula*. Jordan. United States Geological Survey, Washington
- Blockley SPE, Pinhasi R (2011) A revised chronology for the adoption of agriculture in the Southern Levant and the role of Lateglacial climatic change. *Quat Sci Rev* 30:98–108. <https://doi.org/10.1016/j.quascirev.2010.09.021>
- Borrell F, Junno A, Barceló JA (2015) Synchronous environmental and cultural change in the emergence of agricultural economies 10,000 years ago in the Levant. *PLoS ONE* 10:e0134810. <https://doi.org/10.1371/journal.pone.0134810>
- Borrell F, Ibáñez JJ, Muñiz J, Teira L (2019) The PPNB chipped stone industries from Kharaysin (Zarqa Valley, Jordan): preliminary Insights. In: Astruc L, McCartney C, Briois F, Kassianidou V (eds) *Near Eastern lithic technologies on the move. Interactions and contexts in Neolithic traditions*. Studies in Mediterranean Archaeology 150. Astrom Editions, Uppsala, pp 257–266
- Bottema S (1975) The interpretation of pollen spectra from prehistoric settlements (with special attention to Liguliflorae). *Palaeohistoria* 17:17–35
- Bottema S (1992) Prehistoric cereal gathering and farming in the Near East: the pollen evidence. *Rev Palaeobot Palynol* 73:21–33. [https://doi.org/10.1016/0034-6667\(92\)90042-F](https://doi.org/10.1016/0034-6667(92)90042-F)
- Bronk Ramsey C (2009) Bayesian analysis of radiocarbon dates. *Radiocarbon* 51:337–360. <https://doi.org/10.1017/S0033822200033865>
- Burstyn Y, Martrat B, Lopez JF et al (2019) Speleothems from the Middle East: an example of water limited environments in the SISAL database. *Quaternary* 2:16. <https://doi.org/10.3390/quat2020016>
- Caracuta V, Vardi J, Paz Y, Boaretto E (2017) Farming legumes in the pre-pottery Neolithic: new discoveries from the site of Ahihud (Israel). *PLoS ONE* 12:e0177859. <https://doi.org/10.1371/journal.pone.0177859>
- Cheddadi R, Khater C (2016) Climate change since the last glacial period in Lebanon and the persistence of Mediterranean species. *Quat Sci Rev* 150:146–157. <https://doi.org/10.1016/j.quascirev.2016.08.010>

- Cheng H, Sinha A, Verheyden S et al (2015) The climate variability in northern Levant over the past 20,000 years. *Geophys Res Lett* 42:8,641–8,650. <https://doi.org/10.1002/2015GL065397>
- Colledge S, Conolly J, Shennan S (2004) Archaeobotanical evidence for the spread of farming in the eastern Mediterranean. *Curr Anthropol* 45(Suppl 4):S35–S58. <https://doi.org/10.1086/422086>
- Cordova CE (2010) Palynology of anthropicized landscapes in Jordan: A survey of modern and fossil records of *Quercus*, *Pistacia* and *Olea* pollen. In: Dean RM (ed) *The archaeology of anthropogenic environments*. Southern Illinois University Press, Carbondale, pp 95–121
- Cordova CE, Ames CJH, Boyd KC et al (2026) Phytoliths and pollen from a desert wetland through the Last Glacial–Interglacial cycle in Azraq, Jordan. *Quaternary* 9:18. <https://doi.org/10.3390/quat9010018>
- Crassard R, Hilbert YH, Dinies M et al (2025) Early Arabian Neolithic agropastoral communities from Asifir, Northwestern Saudi Arabia. *Archaeol Anthropol Sci* 17:130. <https://doi.org/10.1007/s12520-025-02234-2>
- Davies CP, Fall PL (2001) Modern pollen precipitation from an elevational transect in central Jordan and its relationship to vegetation. *J Biogeogr* 28:1,195–1,210. <https://doi.org/10.1046/j.1365-2699.2001.00630.x>
- Deckers K, Riehl S, Karakaya D et al (2025) Fuel use in ancient Southwest Asia based on wood charcoal and seed data from fire installations. *J Archaeol Sci Rep* 62:104999. <https://doi.org/10.1016/j.jasrep.2025.104999>
- Dimbleby GW (1985) *The palynology of archaeological sites*. Academic Press, London
- Djamali M, Brewer S, Breckle SW, Jackson ST (2012) Climatic determinism in phytogeographic regionalization: a test from the Irano-Turanian region, SW and Central Asia. *Flora Morphol Distrib Funct Ecol Plants* 207:237–249. <https://doi.org/10.1016/j.flora.2012.01.009>
- Douché C, Willcox G (2018) New archaeobotanical data from the Early Neolithic sites of Dja'de el-Mughara and Tell Aswad (Syria) a comparison between the Northern and the Southern Levant. *Paléorient* 44:45–58
- Douché C, Arranz-Otaegui A, Zupancich A et al (2025) Exploitation and consumption of legumes during the Early Neolithic at Kharaysin, Jordan. *Veget Hist Archaeobot*. <https://doi.org/10.1007/s00334-025-01074-3>
- Eastwood WJ, Fairbairn A, Stroud E et al (2018) Comparing pollen and archaeobotanical data for Chalcolithic cereal agriculture at Çatalhöyük, Turkey. *Quat Sci Rev* 202:4–18. <https://doi.org/10.1016/j.quascirev.2018.11.012>
- El-Moslimany AP (1990) Ecological significance of common nonarborescent pollen: examples from drylands of the Middle East. *Rev Palaeobot Palynol* 64:343–350. [https://doi.org/10.1016/0034-6667\(90\)90150-H](https://doi.org/10.1016/0034-6667(90)90150-H)
- Enzel Y, Amit R, Dayan U et al (2008) The climatic and physiographic controls of the eastern Mediterranean over the late Pleistocene climates in the southern Levant and its neighbouring deserts. *Glob Planet Change* 60:165–192. <https://doi.org/10.1016/j.gloplacha.2007.02.003>
- Fahn A, Werker E, Baas P (1986) *Wood anatomy and identification of trees and shrubs from Israel and adjacent regions*. The Israel Academy of Sciences and Humanities, Jerusalem
- Freiwan M, Kadioğlu M (2008) Spatial and temporal analysis of climatological data in Jordan. *Int J Climatol* 28:521–535. <https://doi.org/10.1002/joc.1562>
- Fuller DQ, Lucas L (2025) Contrasting pathways to domestication and agriculture around Southwest Asia. *Archaeol Anthropol Sci* 17:74. <https://doi.org/10.1007/s12520-025-02190-x>
- Fuller DQ, Willcox G, Allaby RG (2011) Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East. *World Archaeol* 43:628–652. <https://doi.org/10.1080/00438243.2011.624747>
- Fyfe R (2006) GIS and the application of a model of pollen deposition and dispersal: a new approach to testing landscape hypotheses using the POLLANDCAL models. *J Archaeol Sci* 33:483–493. <https://doi.org/10.1016/j.jas.2005.09.005>
- Gasse F, Vidal L, Develle A-L, Van Campo E (2011) Hydrological variability in the Northern Levant: a 250 ka multiproxy record from the Yammouneh (Lebanon) sedimentary sequence. *Clim Past* 7:1,261–1,284. <https://doi.org/10.5194/cp-7-1261-2011>
- Hajar L, Khater C, Cheddadi R (2008) Vegetation changes during the late Pleistocene and Holocene in Lebanon: a pollen record from the Bekaa Valley. *Holocene* 18:1,089–1,099. <https://doi.org/10.1177/0959683608095580>
- Hajar L, Haïdar-Boustani M, Khater C, Cheddadi R (2010) Environmental changes in Lebanon during the Holocene: Man vs. climate impacts. *J Arid Environ* 74:746–755. <https://doi.org/10.1016/j.jaridenv.2008.11.002>
- Henry DO, Cordova CE, Portillo M et al (2017) Blame it on the goats? Desertification in the Near East during the Holocene. *Holocene* 27:625–637. <https://doi.org/10.1177/0959683616670470>
- Ibáñez JJ, Muñoz J, Iriarte E et al (2016) Kharaysin: a PPNA and PPNB site by the Zarqa River 2014 and 2015 field seasons. *Neo-Lithics* 2(15):11–19
- Ibáñez JJ, González-Urquijo J, Teira-Mayolini LC, Lazuén T (2018) The emergence of the Neolithic in the Near East: a protracted and multi-regional model. *Quatern Int* 470:226–252. <https://doi.org/10.1016/j.quaint.2017.09.040>
- Ibáñez JJ, Muñoz JR, Huet T et al (2020) Flint ‘figurines’ from the Early Neolithic site of Kharaysin, Jordan. *Antiquity* 94:880–899. <https://doi.org/10.15184/aqy.2020.78>
- Ibáñez JJ, Muñoz J, Teira L et al (2025a) Architecture in Kharaysin from the late PPNA to the middle PPNB. *Archaeol Res Asia* 41:100584. <https://doi.org/10.1016/j.ara.2024.100584>
- Ibáñez JJ, Pichon F, Mazzucco N, Anderson P (2025b) Leaning on to rise up: from high to low cutting at the origins of cereal agriculture in the Near East. *J Archaeol Sci Rep* 61:104962. <https://doi.org/10.1016/j.jasrep.2024.104962>
- Ibáñez JJ, Abdo K, Arranz-Otaegui A et al (2025c) The Early Pre-Pottery Neolithic B in the Southern Levant. contributions from Tell Qarassa North (Sweida, Syria) and Kharaysin (Zarqa, Jordan). *Paléorient* 50:49–82. <https://doi.org/10.4000/145z7>
- International Committee for Phytolith Taxonomy (ICPT) (2019) International code for phytolith nomenclature (ICPN) 2.0. *Ann Bot* 124:189–199. <https://doi.org/10.1093/aob/mcz064>
- Iriarte E, García-Tojal J, Santana J et al (2020) Geochemical and spectroscopic approach to the characterization of earliest cremated human bones from the Levant (PPNB of Kharaysin, Jordan). *J Archaeol Sci Rep* 30:102211. <https://doi.org/10.1016/j.jasrep.2020.102211>
- Jiménez-Manchón S, Gourichon L, Muñoz J, Ibáñez JJ (2023) Discriminating dietary behaviour between wild and domestic goats using dental microwear texture: first results from a modern reference set and early Neolithic goat exploitation in the southern Levant. *J Archaeol Sci* 155:105779. <https://doi.org/10.1016/j.jas.2023.105779>
- Kabukcu C, Hunt C, Hill E et al (2023) Cooking in caves: palaeolithic carbonised plant food remains from Franchthi and Shanidar. *Antiquity* 97:12–28. <https://doi.org/10.15184/aqy.2022.143>
- Katz O, Cabanes D, Weiner S et al (2010) Rapid phytolith extraction for analysis of phytolith concentrations and assemblages during an excavation: an application at Tell es-Safi/Gath, Israel. *J Archaeol Sci* 37:1,557–1,563. <https://doi.org/10.1016/j.jas.2010.01.016>

- Khresat SA, Rawajfih Z, Mohammad M (1998) Land degradation in north-western Jordan: causes and processes. *J Arid Environ* 39:623–629. <https://doi.org/10.1006/jare.1998.0385>
- Lev E, Kislev ME, Bar-Yosef O (2005) Mousterian vegetal food in Kebara Cave, Mt. Carmel. *J Archaeol Sci* 32:475–484. <https://doi.org/10.1016/j.jas.2004.11.006>
- Lev L, Stein M, Ito E et al (2019) Sedimentary, geochemical and hydrological history of Lake Kinneret during the past 28,000 years. *Quat Sci Rev* 209:114–128. <https://doi.org/10.1016/j.quascirev.2019.02.015>
- Litt T, Ohlwein C, Neumann FH, Hense A, Stein M (2012) Holocene climate variability in the Levant from the Dead Sea pollen record. *Quat Sci Rev* 49:95–105. <https://doi.org/10.1016/j.quascirev.2012.06.012>
- Lu CD (1988) Grazing behavior and diet selection of goats. *Small Rumin Res* 1:205–216. [https://doi.org/10.1016/0921-4488\(88\)90049-1](https://doi.org/10.1016/0921-4488(88)90049-1)
- Manafzadeh S, Staedler YM, Conti E (2017) Visions of the past and dreams of the future in the Orient: the Irano-Turanian region from classical botany to evolutionary studies. *Bio Rev* 92:1,365–1,388. <https://doi.org/10.1111/brv.12287>
- Migowski C, Stein M, Prasad S, Negendank JFW, Agnon A (2006) Holocene climate variability and cultural evolution in the Near East from the Dead Sea sedimentary record. *Quat Res* 66:421–431. <https://doi.org/10.1016/j.yqres.2006.06.010>
- Milić B, Pichon F, Ibáñez JJ, Gourichon L (2025) Assessing socio-economic changes between the Northern and Southern Levant through the function of projectile points from the Pre-Pottery Neolithic Kharaysin (Jordan) and Dja'de (Syria). *J Archaeol Sci Rep* 66:105280. <https://doi.org/10.1016/j.jasrep.2025.105280>
- Miras Y, Ejarque A, Barbier-Pain D et al (2018) Advancing the analysis of past human/plant relationships: methodological improvements of artifact pollen washes. *Archaeometry* 60:1,106–1,121. <https://doi.org/10.1111/arc.12375>
- Mithen S, Austen P, Kennedy A et al (2007) Early Neolithic woodland composition and exploitation in the southern Levant: a comparison between archaeobotanical remains from WF16 and present-day woodland at Hammam Adethni. *Environ Archaeol* 12:49–70. <https://doi.org/10.1179/174963107x172741>
- Moník M, Lendáková Z, Ibáñez JJ et al (2018) Revealing early villages: pseudo-3D ERT geophysical survey at the pre-pottery Neolithic site of Kharaysin, Jordan. *Archaeol Prospect* 25:339–346. <https://doi.org/10.1002/arp.1713>
- Moore PD, Webb JA, Collinson ME (1991) Pollen analysis, 2nd edn. Blackwell Scientific Publications, Oxford
- Müller D, Neugebauer I, Ben Dor Y et al (2022) Phases of stability during major hydroclimate change ending the Last Glacial in the Levant. *Sci Rep* 12:6052. <https://doi.org/10.1038/s41598-022-10217-9>
- Neef R (2004a) Vegetation and climate. A comparison between PPNB 'Ain Ghazal and Basta. In: Bienert H-D, Gebel HGK, Neef R (eds) Central settlements in Neolithic Jordan. Studies in Early Near Eastern Production, Subsistence, and Environment (SENEPSE) 5. Ex Oriente, Berlin, pp 289–299
- Neef R (2004b) Vegetation and plant husbandry. In: Nissen HJ, Muheisen M, Gebel HGK (eds) Basta I: the human ecology. Ex Oriente, Berlin, pp 187–218
- Palmisano A, Woodbridge J, Roberts CN et al (2019) Holocene landscape dynamics and long-term population trends in the Levant. *Holocene* 29:708–727. <https://doi.org/10.1177/0959683619826642>
- Piperno DR (2006) Phytoliths: a comprehensive guide for archaeologists and paleoecologists. AltaMira Press, Lanham
- Portillo M, Kadowaki S, Nishiaki Y, Albert RM (2014) Early Neolithic household behavior at Tell Seker al-Aheimar (Upper Khabur, Syria): a comparison to ethnoarchaeological study of phytoliths and dung spherulites. *J Archaeol Sci* 42:107–118. <https://doi.org/10.1016/j.jas.2013.10.038>
- Portillo M, Dudgeon K, Allistone G, Raeuf Aziz K, Matthews W (2021) The taphonomy of plant and livestock dung microfossils: an ethnoarchaeological and experimental approach. *Environ Archaeol* 26:439–454. <https://doi.org/10.1080/14614103.2020.1800344>
- Rambeau CMC (2010) Paleoenvironmental reconstruction in the Southern Levant: synthesis, challenges, recent developments and perspectives. *Philos Trans R Soc Math Phys Eng Sci* 368:5225–5248. <https://doi.org/10.1098/rsta.2010.0190>
- Reille M (1999) Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, Marseille
- Reimer PJ, Austin WEN, Bard E et al (2020) The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* 62:725–757. <https://doi.org/10.1017/RDC.2020.41>
- Revelles J, Cho S, Iriarte E et al (2015) Mid-Holocene vegetation history and Neolithic land-use in the Lake Banyoles area (Girona, Spain). *Palaeogeogr Palaeoclimatol Palaeoecol* 435:70–85. <https://doi.org/10.1016/j.palaeo.2015.06.002>
- Roberts N (2002) Did prehistoric landscape management retard the post-glacial spread of woodland in Southwest Asia? *Antiquity* 76:1,002–1,010. <https://doi.org/10.1017/S0003598X0009181X>
- Roberts N, Woodbridge J, Bevan A et al (2018) Human responses and non-responses to climatic variations during the last Glacial-Interglacial transition in the eastern Mediterranean. *Quat Sci Rev* 184:47–67. <https://doi.org/10.1016/j.quascirev.2017.09.011>
- Roberts N, Woodbridge J, Palmisano A et al (2019) Mediterranean landscape change during the Holocene: synthesis, comparison and regional trends in population, land cover and climate. *Holocene* 29:923–937. <https://doi.org/10.1177/0959683619826697>
- Robinson SA, Black S, Sellwood BW, Valdes PJ (2006) A review of palaeoclimates and palaeoenvironments in the Levant and Eastern Mediterranean from 25,000 to 5000 years BP: setting the environmental background for the human civilisation. *Quat Sci Rev* 25:1,517–1,541. <https://doi.org/10.1016/j.quascirev.2006.02.006>
- Rollefson GO, Köhler-Rollefson I (1992) Early Neolithic exploitation patterns in the Levant: cultural impact on the environment. *Popul Environ* 13:243–254. <https://doi.org/10.1007/BF01271025>
- Ronel M, Lev-Yadun S (2009) Spiny plants in the archaeological record of Israel. *J Arid Environ* 73:754–761. <https://doi.org/10.1016/j.jaridenv.2009.02.009>
- Rosen AM, Rivera-Collazo I (2012) Climate change, adaptive cycles, and the persistence of foraging economies during the late Pleistocene/Holocene transition in the Levant. *Proc Natl Acad Sci USA* 109:3,640–3,645. <https://doi.org/10.1073/pnas.1113931109>
- Santana J, Iriarte E, Teira LC et al (2020) Transforming the ancestors: early evidence of fire-induced manipulation on human bones in the Near East from the Pre-Pottery Neolithic B of Kharaysin (Jordan). *Archaeo Anthropol Sci* 12:112. <https://doi.org/10.1007/s12520-020-01065-7>
- Santana J, Muñiz J, Iriarte E, Teira LC, Ibáñez JJ (2022) Grasping ritual activities in the Pre-Pottery Neolithic B funerary spaces based on evidence from Tell Qarassa North and Kharaysin (Southern Levant). In: Ackerfeld D, Gopher A (eds) Dealing with the dead. Studies in early Near Eastern production, subsistence, and environment (SENEPSE) 23. Ex Oriente, Berlin, pp 109–134
- Sapir-Hen L, Bar-Oz G, Khalaily H, Dayan T (2009) Gazelle exploitation in the early Neolithic site of Motza, Israel: the last of the gazelle hunters in the southern Levant. *J Archaeol Sci* 36:1,538–1,546. <https://doi.org/10.1016/j.jas.2009.03.015>
- Schiebel V, Litt T (2018) Holocene vegetation history of the southern Levant based on a pollen record from Lake Kinneret (Sea of Galilee), Israel. *Veget Hist Archaeobot* 27:577–590. <https://doi.org/10.1007/s00334-017-0658-3>

- Schweingruber FH (1990) Anatomy of European woods. An atlas for the identification of European trees, shrubs and dwarf shrubs. Paul Haupt, Bern
- Segev O, Golodets C, Henkin Z, Gorelik H, Dovrat G (2022) Long-term proliferation of large annual thistles in dry Mediterranean rangelands. *Ecosphere* 13:e4340. <https://doi.org/10.1002/ecs2.4340>
- Stein M, Torfstein A, Gavrieli I, Yechieli Y (2010) Abrupt aridities and salt deposition in the post-glacial Dead Sea and their North Atlantic connection. *Quat Sci Rev* 29:567–575. <https://doi.org/10.1016/j.quascirev.2009.10.015>
- Stein M, Goring-Morris N, Ben Dor Y, Erel Y (2025) Environmental setting of the Neolithic Agricultural Revolution across the Fertile Crescent. *Quat Sci Rev* 355:109265. <https://doi.org/10.1016/j.quascirev.2025.109265>
- Sternberg M, Gutman M, Perevolotsky A, Ungar ED, Kigel J (2000) Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. *J Appl Ecol* 37:224–237. <https://doi.org/10.1046/j.1365-2664.2000.00491.x>
- Turner R, Roberts N, Eastwood WJ, Jenkins E, Rosen A (2010) Fire, climate and the origins of agriculture: micro-charcoal records of biomass burning during the last glacial-interglacial transition in Southwest Asia. *J Quat Sci* 25:371–386. <https://doi.org/10.1002/jqs.1332>
- Van Zeist W, Baruch U, Bottema S (2009) Holocene palaeoecology of the Hula Area, Northeastern Israel. In: Kaptijn E, Petit LP (eds) *A Timeless Vale*. Leiden University Press, Leiden, Archaeological and related essays on the Jordan Valley in honour of Gerrit van der Kooij on the occasion of this sixty-fifth birthday, pp 29–64
- Verheyden S, Nader FH, Cheng HJ, Edwards LR, Swennen R (2008) Paleoclimate reconstruction in the Levant region from the geochemistry of a Holocene stalagmite from the Jeita cave, Lebanon. *Quat Res* 70:368–381. <https://doi.org/10.1016/j.yqres.2008.05.004>
- Weinstein-Evron M (1976) The late Quaternary vegetation of the northern Golan. *Pollen Spores* 18:553–562
- Weiss E, Zohary D (2011) The Neolithic Southwest Asian founder crops: their biology and archaeobotany. *Curr Anthropol* 52(Suppl 4):S237–S254. <https://doi.org/10.1086/658367>
- Weninger B, Clare L, Rohling E et al (2009) The impact of rapid climate change on prehistoric societies during the Holocene in the Eastern Mediterranean. *Doc Praehist* 36:7–59. <https://doi.org/10.4312/dp.36.2>
- Willcox G (1999) Charcoal analysis and Holocene vegetation history in southern Syria. *Quat Sci Rev* 18:711–716. [https://doi.org/10.1016/S0277-3791\(98\)00106-1](https://doi.org/10.1016/S0277-3791(98)00106-1)
- Willcox G (2005) The distribution, natural habitats and availability of wild cereals in relation to their domestication in the Near East: multiple events, multiple centres. *Veget Hist Archaeobot* 14:534–541. <https://doi.org/10.1007/s00334-005-0075-x>
- Willcox G, Buxo R, Herveux L (2009) Late Pleistocene and early Holocene climate and the beginnings of cultivation in northern Syria. *Holocene* 19:151–158. <https://doi.org/10.1177/0959683608098961>
- Yasuda Y, Kitagawa H, Nakagawa T (2000) The earliest record of major anthropogenic deforestation in the Ghab Valley, northwest Syria: a palynological study. *Quat Int* 73–74:127–136. [https://doi.org/10.1016/S1040-6182\(00\)00069-0](https://doi.org/10.1016/S1040-6182(00)00069-0)
- Zeder MA, Hesse B (2000) The Initial Domestication of Goats (*Capra hircus*) in the Zagros Mountains 10,000 Years Ago. *Science* 287:2,254–2,257. <https://doi.org/10.1126/science.287.5461.2254>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.