Climate and environmental reconstruction of the Epipaleolithic Mediterranean Levant (22.0–11.9 ka cal. BP)

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ABSTRACT
This study presents, for the first time, an environmental reconstruction of a sequence spanning nearly the entire Mediterranean Epipaleolithic (~22.0–11.9 ka cal. BP). The study is based on a well-dated, high-resolution pollen record recovered from the waterlogged archaeological site Jordan River Dureijat (JRD), located on the banks of Paleolake Hula. JRD’s continuous sequence enabled us to build a pollen-based paleoclimate model providing a solid background for the dramatic cultural changes that occurred in the region during this period. Taxonomic identification of the waterlogged wood assemblage collected from JRD was used to fine-tune the paleoenvironmental reconstruction. The chronological framework is based on radiocarbon dating and the typology of archaeological findings. The LGM (~22–19 ka cal. BP) was found to be the coldest period of the sequence, marked by a distinct decrease in the reconstructed January temperatures of up to 5 °C lower than today, while mean annual precipitation was only slightly lower than the present-day average (~450 vs. 515 mm, respectively). The wettest and warmest period of the record was identified between ~14.9 and 13.0 ka cal. BP, with maximum values of 545 mm mean annual precipitation reached at ~14.5 ka cal. BP. This time interval is synchronized with the global warm and moist Bølling-Allerød interstadial as well as with the onset of the Natufian culture and the emergence of sedentism in the Levant. The Younger Dryas began around 12.9 ka cal. BP and was identified as an exceptional period by the JRD sequence with low temperatures and minimal climatic seasonality contrast: an increase in rain contribution during spring, summer, and autumn was documented concurrently with a significant decrease in winter precipitation. The detailed vegetation and climatological reconstruction presented in this study serves as backdrop to seminal events in human history: the transition from small nomadic groups of hunter-gatherers to the sedentary villages of the Natufian, eventually transitioning to the agricultural, complex communities of the Neolithic.

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1. Introduction

The period between the Last Glacial Maximum (LGM; ~23–19 ka BP) and the beginning of the Holocene interglacial (~11.7 ka BP) was an era of dramatic climatic changes in the northern hemisphere. This time interval accompanied the transition from the Last Glacial period to the Post-Glacial period, which was punctuated by short-term climatic phases (LGM, Heinrich Event 1, Bølling-Allerød, and the Younger Dryas). Yet, the actual impact of these global changes on the local Mediterranean southern Levant environment and climate (Fig. 1) is under debate. Studies of Lake Lisan, the late Pleistocene precursor to the Dead Sea, demonstrated that a high lake stand occurred during the last glacial (Bartov et al., 2002, 2003, 2006, 2007; Haase-Schramm et al., 2004; Torfstein and Enzel, 2017). It is argued that the existence of the larger Lake Lisan during the glacial period, compared to the Holocene’s smaller Dead Sea, required significantly more rainfall (Zak, 1967; Begin et al., 1974; Bartov et al., 2002, 2003, 2006, 2007; Hazan et al., 2005; Kolodny et al., 2005; Bookman et al., 2006; Enzel et al., 2008; Stein, 2014). Most speleothem records from the Mediterranean southern Levant (Soreq and Peqi’in caves) indicate contradictory, dry conditions during the last glacial period (Bar-Matthews et al., 1997, 1999, 2003, 2017, 2019).
Archaeologically, the time interval between the LGM and the Holocene is known in the Levant as the Epipaleolithic period and is characterized by significant cultural changes. It marks the shift from small nomadic groups of hunter-gatherers into larger and complex communities accompanied by reducing population mobility patterns and changing subsistence strategies, leading to the establishment of the sedentary agricultural communities of the Neolithic (Belfer-Cohen and Goring-Morris, 2013, 2014; Bar-Yosef, 2014). The interrelationship between climate and culture is a key question in Levantine Epipaleolithic research. Correlation between these two sets of evidence has proven difficult to achieve (Wright, 1993; Goring-Morris and Belfer-Cohen, 1997; Maher et al., 2011, 2012; Belfer-Cohen and Goring-Morris, 2013; Belmaker, 2017). The discussion is hampered by the scarcity of both continuous, well-dated Levantine Epipaleolithic sequences documenting cultural changes, and environmental datasets that derive directly from Epipaleolithic sites. The paucity of past environmental information is mainly due to poor preservation of organic remains and is particularly true for the Early and Middle Epipaleolithic in the Mediterranean zone of the southern Levant.

In this study, we present a high-resolution, continuous fossil pollen record that was recovered from a sediment outcrop at the Epipaleolithic site of Jordan River Dureijat (JRD). JRD is located at the southern edge of the Hula Basin, on the shore of Paleolake Hula. Its archaeological sequence is dated from ~20 to 10 ka cal. BP (Sharon et al., 2020). Previous palynological studies from Paleolake Hula were analyzed at relatively low resolution and/or suffered from chronological uncertainties (Horowitz, 1971, 1979; Tsukada, cited in Bottema and Van Zeist, 1981; Weinstein-Evron, 1983; Baruch and Bottema, 1999; Meadows, 2005; Van-Zeist et al., 2009). Palynological records from nearby archaeological sites were retrieved from much shorter time spans of the Epipaleolithic (Weinstein-Evron et al., 2015) or from different periods (Aharonovich et al., 2014). Here we provide a well-dated, high-resolution palynological record that encompasses all Levantine Epipaleolithic phases from which we have generated a quantitative reconstruction of the period’s climate changes. Additionally, we used taxonomic identification of JRD’s waterlogged wood assemblage to fine-tune our paleoclimate model. Currently, this is the only consecutive, regional wood record that covers the entire Epipaleolithic period. Previous dendroarchaeological studies from the Mediterranean southern Levant were limited to short time intervals within the Epipaleolithic. These include the wood and charcoal assemblage from the 23 ka cal. BP Ohalo II site located on the shore of the Sea of Galilee (Liphschitz and Nadel, 1997; Nadel and Werker, 1999) and the Natufian wood-charcoal remains.
recovered from the El-Wad site on Mount Carmel (Lev-Yadun and Weinstein-Evron, 1994; Caracuta et al., 2016). Because many Epipaleolithic Levantine archaeological sites are small and ephemeral, they are characterized by relatively poor preservation of botanical remains, resulting in limited and inconsistent environmental information. In contrast, JRD not only includes an assemblage of waterlogged wood, it is also endowed with a well-preserved, high-resolution fossil pollen record.

The paleoclimate reconstruction presented in this study offers a significant contribution to two primary research questions: First, what were the climate conditions in the Mediterranean Levant during the end of the last glacial period, and second, did the dramatic climate changes during the end of the Pleistocene impact the cultural shift to sedentism and agriculture? With regard to climate conditions, the climate reconstruction of seasonal changes of both precipitation and temperatures presented here contributes to unravelling the regional discrepancy between the observed lake level datasets and inferred amounts of annual precipitation derived from cave speleothem isotopes.

2. Research area

2.1. Location and geographical settings

The JRD archaeological site is situated in the Hula Valley, a northern section of the Levantine segment of the Syrian-African Rift system (also referred to as the northern Jordan Rift Valley). This narrow and elongated valley is a pull-apart basin (Schattner and Weinberger, 2008; Heimann et al., 2009). Until the mid-twentieth century, the shallow Lake Hula occupied the southern part of this small valley. The lake had a surface area of some 14 km², bordered on the north by extensive swamp area (>30 km²; Fig. 2; Dimentman et al., 1992). Large-scale drainage operations carried out during the 1950s drained most of the lake, leaving only a small nature reserve. Evidence from JRD indicates that during the end of the Pleistocene–early Holocene, Paleolake Hula extended more than 2 km south of its historically documented boundaries (Fig. 2; Sharon et al., 1999).

The Hula Valley is bordered by the Naftali carbonate mountains of the Upper Galilee (700–900 m above sea level; m asl) to the west, Mt. Hermon (up to 2814 m asl) to the northeast, and the basaltic Golan Heights (ca. 1000 m asl) to the east (Fig. 2). To the south, the basin is flanked by the Korasim basaltic block, damming the Hula Valley at its southern end. Lakes and swamps have occupied the southern half of the Hula Valley at least since the early Pleistocene, which, in combination with the continuous subsidence of the valley floor, has resulted in thick lacustrine, peat, and lignite deposits. The northern part of the valley is composed of alluvial soil deposits (Horowitz, 1979; Dimentman et al., 1992; Belitzky, 2002).

The largest stream in the area is the Jordan River. It flows south, feeding the Sea of Galilee, and continues through the Lower Jordan Valley where it finally outflows into the Dead Sea (Fig. 1). At its outflow south from the Hula Basin, the Jordan River flows at the boundary of two tectonic plates, the Sinai sub-plate (a segment of the African plate) to the west, and the Arabian plate to the east. The sediment formations exposed at the river banks range in age from the Pliocene to Holocene (Horowitz, 1973, 2001; Belitzky, 1987). The JRD site, located 60–70 m asl, was discovered during an archaeological survey preceding a massive drainage operation of the Jordan River in December 1999. The archaeological material-bearing horizons of JRD stretch over 50 m on the east bank of the artificial Jordan River trench south of the outlet of the small Dureijat Stream (Sharon et al., 1999; Marder et al., 2015).

The Hula Valley and its surroundings are characterized by a typical Mediterranean climate. Rain falls almost exclusively during winter and spring, and summers are hot and dry. Temperature and precipitation vary considerably with altitude and latitude. The mean annual rainfall is 400–520 mm in the valley and above 600 mm in the mountain ranges bordering to the west and east (Fig. 1b). Inter-annual variations in precipitation are mainly influenced by the strength of the Cyprus Low systems (Ziv et al., 2006). At Ayelet Hashahar, the nearest meteorological station west of JRD, mean temperatures in January and August are 11°C and 29°C, respectively. The mean annual temperature is 21°C and mean annual precipitation is 515 mm (Fig. 3a; Israel Meteorological Service, 2020).

From the pattern of current wind direction and intensity (Fig. 3b), it is suggested that the wind-borne pollen is embedded in the valley’s deposits by the dominant winds from the northwest, together with a degree of contribution from the east, north and south, mainly during winters. The pollen grains are then spread throughout the valley by the most common local winds, the northern and southern winds, which change direction during the day (Weinstein-Evron, 1983; Israel Meteorological Service, 2020). Pollen grains that are deposited by fluvial transportation originate primarily from the north, transported by the Jordan River and its
north of the now drained Hula Lake is dominated by Cyperus papyrus — Polygonum acuminatum (Persicaria acuminata) association accompanied by various other marsh plants such as Thelypteris palustris (Dryopteris thelypteris), Rorippa amphibia (great yellow-cress), Galium elongatum (marsh bedstraw), and Lycopus europaeus (bugleweed) (Zohary, 1973; Dimentman et al., 1992). Before the draining, a few other marsh-plant associations formed the outer belt of the swamp (Zohary, 1973, 1982). On the east and west, the lake was fringed by a marsh-vegetation belt consisting of riparian plants such as: Phragmites australis (common reed), Typha latifolia (bulrush), Scirpus lacustris (common club-rush), Sparganium erectum (simplestem bur-reed), Lythrum salicaria (purple loosestrife), Mentha longifolia (horse mint), and Cyperus longus (galingale). Water plants include a few Potamogeton (pondweed) species, Myriophyllum spicatum (spiked water-milfoil), Nuphar lutea (yellow water-lily), Nymphaea alba (white water rose), Ceratophyllum demersum (hornwort) and Ranunculus peltatus (= aquatilis, pond water-crowfoot; Van-Zeist et al., 2009). Currently, the natural landscape of the Hula Valley is heavily damaged due to millennia of overgrazing, tree clearance and agricultural activities (Palmisano et al., 2019, Fig. 8). The natural vegetation is restricted to protected areas and to less accessible deep canyons and steep mountain slopes.

2.3. The archaeological site of Jordan river Dureijat (JRD)

For over 10,000 years, during the Epipaleolithic period, people repeatedly returned to the site of JRD on the shore of Paleolake Hula to fish, hunt, and exploit other aquatic resources (Sharon et al., 2020). The excavation exposed a thick sequence of sediments that accumulated within the fluctuating water levels of Paleolake Hula. The archaeological horizons were deposited within near-shore layers that were embedded during low water stands. These layers are separated by archaeologically sterile, fine silt layers, deposited tributaries. Some contribution is observed, however, from smaller streams, originating from the Golan Heights in the east and the Naftali Ridge in the west (Weinstein-Evron, 1983; Aharonovich et al., 2014).

2.2. Vegetation

The region supports typical Mediterranean vegetation. Beyond the lake and marshland, the natural vegetation of the Hula Valley and the nearby lower slopes is the Quercus ithaburensis — Pistacia atlantica (Mount Tabor oak — Atlantic terebinth) woodland or park-forest (Zohary, 1973, 1982). The open terrain between the widely spaced trees is covered by herbaceous vegetation, while various shrubs such as Styrax officinalis (storax), Ziziphus lotus (wild jujube) and Ziziphus spin-

Fig. 3. a) Ayelet Hashahar weather station data (under 5 km from JRD). Average monthly temperature and precipitation for the period of 2010–2020. Red bars represent seasonal average. Data downloaded from Israel Meteorological Service (2020); b) Normalized wind roses (m/s) for Jan 2015–Dec 2016, and seasonal for Dec–Feb (2014–2017, DJF) and Jun–Aug (2015–2016; JJA) (taken from Besc, 2018: Fig. 2.5) (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
during higher water stands of the lake. The stratigraphic sequence and chronology were established in Area B, the primary site excavation area. The chronology was based on numerous radiocarbon dates obtained on wood-charcoal remains (Sharon et al., 2020). The lowest excavated layer (Layer 5) dates to ~20 ka cal. BP and is characterized by an Early Epipaleolithic lithic tradition. The lithics from Layer 4 ascribed to the Middle Epipaleolithic, i.e., the Geometric Kebaran tradition and date to 17.46–15.75 ka cal. BP. The three upper layers, 3c, 3b and 3a, belong to the Late Epipaleolithic Natufian culture (15–11.5 ka cal. BP) based on radiocarbon dates and on the presence of typical flint artifacts such as microlithic lunates (Grosman, 2018; Sharon et al., 2020).

The unique waterlogged conditions at the site captured an unusually well-preserved record of perishable plant remains attesting to both human activities and to the local environmental conditions along much of the Epipaleolithic (Sharon et al., 2020). The primary activity documented at the JRD archaeological horizons was fishing (Fig. 4; Pedergnana et al., 2021) and utilization of additional aquatic resources such as mollusks, crabs, amphibians, turtles and, equally significant, aquatic and near-shore plants (Sharon et al., 2020). The importance of fishing is evident by the presence throughout the sequence of limestone cobbles that served as net sinkers, forming the largest collection of such tools in the Levant (Sharon et al., 2020). Fishbones are also abounded in all archaeological layers. In the Natufian layers, as many as 19 bone fishhooks were found, accompanied by small grooved pebbles used as line weights (Sharon et al., 2020; Pedergnana et al., 2021). The presence of shell horizons (Sharon et al., 2020), the wealth of mollusk shells and of non-marine ostracod taxa (Björgvinsson, 2017), and the high number of valves (Valdimarsson, 2017), also point to the existence and exploitation of a shallow freshwater lake environment at JRD.

![Fig. 4. 1. JRD bone fish hooks; 2. JRD small grooved pebbles (line weights); 3. JRD stone tools by layers and cultural affinity: a. Early Neolithic; b. Natufian; c. Geometric Kebaran; d. Early Epipaleolithic.](image-url)
3. Materials and methods

3.1. Archaeological context and chronology

The eastern border of Area B (the primary archaeological excavation area; 33°19′N/35°37′E) is the type locality for the site’s full stratigraphic sequence. This outcrop forms the longest exposure of the site’s sedimentology and yielded both palynological and 14C radiocarbon samples (Sharon et al., 2020). Several lines of evidence indicate that the sedimentation environment of the JRD archaeological horizons is a nearshore water stand (shallow lake environment). Hence, the horizons document fishing and aquatic resources utilization during short-term visits rather than a long-term permanent occupation. This reconstruction explains, for example, the absence of identified hearths at the site, coupled by a widespread distribution of charcoal remains throughout the layers. This is probably due to the flooding of small fire-places by rising lake water levels and spreading of charcoals on the surface. This reconstruction of wet depositional environment also explains the excellent preservation of pollen and wood remains, as well as other botanical remains (charcoal, seeds, fruits) in the site’s waterlogged layers.

Even if the context of the archaeological remains is not that of a settlement (Fig. 4), the stratigraphy and archaeological context of the finds are secure, due to the separation of the archaeological horizons by sterile layers of fine silt formed during high water lake stands. Hence, each assemblage has good chronological control. Furthermore, there is a clear chrono-cultural affinity between the various flint tools and the specific layers from which they originated (Sharon et al., 2020). This solid stratigraphy of cultural sequences enables correlation of specific pollen zones to specific cultural units and discussion of their interrelations (Fig. 5).

The eight 14C radiocarbon samples used for the chronological age-depth model in the current study (Table 1) were selected from the available JRD dates (Sharon et al., 2020: Table 1). These samples were chosen due to their location in the eastern sediment outcrop (where the pollen samples were collected), as well as for their reliability (dubious samples due to size or state of preservation were excluded). The aim was to achieve good chronological control and the highest possible accuracy. All the wood and charcoal remains submitted for 14C radiocarbon dating were identified as terrestrial plants to avoid bias from the reservoir effect of the water body. When possible, young branches rather than old or unknown wood trunk sections were preferred for radiocarbon dating.

The 14C samples were analyzed at the Poznań Radiocarbon Laboratory and at the Beta Analytic Laboratory. 14C ages were calibrated using the default calibration data set IntCal13 northern Hemisphere radiocarbon (Table 1). The age-depth model presented in Fig. 6 was processed using the Bayesian Bacon 2.3.6 software package (Blaauw and Christen, 2011).

Fig. 5. Archaeological layers, cultural affiliation, radiocarbon chronology (with calibrated dates) and pollen zones of the Jordan River Dureijat (JRD) sequence (after Sharon et al., 2020: Fig. 4a).
Table 1

<table>
<thead>
<tr>
<th>Lab. Number</th>
<th>Depth, above sea level (m)</th>
<th>Archaeological layer</th>
<th>$^{14}$C Age (cal. yrs BP)</th>
<th>Calibrated age range, 1σ (cal. yrs BP)</th>
<th>Calibrated age range, 2σ (cal. yrs BP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Poz-94159</td>
<td>57.73</td>
<td>3–0</td>
<td>10,010 ± 60</td>
<td>11,391–11,620</td>
<td>11,269–11,744</td>
</tr>
<tr>
<td>Beta-457488</td>
<td>57.15</td>
<td>3b</td>
<td>11,490 ± 40</td>
<td>13,316–13,411</td>
<td>13,298–13,462</td>
</tr>
<tr>
<td>Poz-94158</td>
<td>57.03</td>
<td>3c</td>
<td>12,350 ± 60</td>
<td>14,181–14,475</td>
<td>14,102–14,617</td>
</tr>
<tr>
<td>Beta-457489</td>
<td>56.73</td>
<td>3c</td>
<td>13,320 ± 40</td>
<td>15,933–16,105</td>
<td>15,841–16,182</td>
</tr>
<tr>
<td>Poz-94160</td>
<td>56.58</td>
<td>4b</td>
<td>13,960 ± 80</td>
<td>16,839–17,081</td>
<td>16,657–17,142</td>
</tr>
<tr>
<td>Poz-100258</td>
<td>56.49</td>
<td>4c</td>
<td>14,433 ± 40</td>
<td>17,456–17,627</td>
<td>17,397–17,823</td>
</tr>
<tr>
<td>Poz-100321</td>
<td>55.98</td>
<td>5</td>
<td>16,612 ± 72</td>
<td>19,950–20,179</td>
<td>19,874–20,293</td>
</tr>
<tr>
<td>Poz-100295</td>
<td>55.40</td>
<td>6</td>
<td>16,867 ± 71</td>
<td>20,312–20,480</td>
<td>20,200–20,542</td>
</tr>
</tbody>
</table>

Fig. 6. Age-depth model for the Jordan River Dureijat (JRD) sedimentological outcrop using the Bayesian Bacon software from the R package rbacon v2.3.9.1 (Blaauw and Christen, 2011).
3.2. Palynology

Fifty-four sediment samples were collected for palynological investigation from the JRD eastern sediment outcrop during the 2016 and 2017 excavation seasons (Fig. 5). Samples of 1-cm thickness were taken at 5-cm intervals along the 2.70-m long sequence from 55.33 to 58.03 m asl. In addition, a recent Jordan River mud surface sample was collected ca. 20 m east of the sediment outcrop to examine the relationship between the fossil pollen results and the modern pollen rain in the region.

Pollen extraction procedure followed a physical-chemical treatment successfully employed in other Dead Sea Rift Valley lacustrine sediments (Langgut et al., 2014a). Samples were immersed in HCl to remove the calcium carbonates. In order to float the organic material, a density separation was carried out using a ZnBr₂ solution (with a specific gravity of 1.95), together with 5 min of sonication. After sieving (150 μm mesh screen), the unstained residues were homogenized and mounted onto microscope slides using glycerin. Acetylation was not carried out in order to enable the identification of any non-pollen palynomorph (NPP) such as algae (e.g., Langgut, 2018). Pollen grains were identified under a light microscope at magnifications of 200 ×, 400 × and 1000 × (oil immersion), to the most detailed possible systematic taxonomic level.

For pollen identification, a comparative reference collection of the Israeli pollen flora of Tel Aviv University (The Steinhardt Museum of Natural History) was used, in addition to pollen atlases (Horowitz and Baum, 1967; Reille, 1995, 1998, 1999; Beug, 2004). At least 500 pollen grains were counted from each sample.

For the preparation of the palynological diagram (Fig. 7), PolPal software was used (Walansus and Nalepka, 1999). The total sum of the palynological diagram is composed of Arboreal Pollen (AP), trees and large shrubs) and Non-Arboreal Pollen (NAP). The latter includes herbaceous plants and dwarf shrubs of the upland vegetation. The proportions of all pollen taxa are expressed as percentages of this total pollen sum. Pollen taxa counted in less than five samples were not included in the pollen diagram (for a detailed palynological diagram that presents all identified taxa, see Figure A1). Cyperaceae, Sparganium, Typha, Phragmites type and various trees and shrubs that inhabit banks of permanent and intermittent streams such as Salix, Tamarix and Vitis were grouped together. This group was excluded from the basic sum (AP + NAP) but was calculated as ratios of the total sum. Aquatic plants and spores were not included in the total sum and are presented in the last section of the pollen diagram. This category also includes the green algae Pediasstrum (P. simplex type and P. boryanum type). The zonation of the pollen record is based primarily on changes in AP/NAP ratios, together with principal component analysis (PCA) and cluster analysis.

3.3. Waterlogged wood

The waterlogged, un-burned wood fragments exposed during the JRD excavation were recorded on-site using a Leica Total Station to indicate their exact location. All excavated sediments were collected from sub-squares, wet sieved in the Jordan River and sorted for wood remains. The remains were stored in plastic bags, covered with water and transferred to the Laboratory of Archaeobotany and Ancient Environments, Tel Aviv University, for identification, analysis and conservation.

Wood remains were identified to the lowest possible taxonomic level. Each wood sample was cut and examined along three observational axes (transverse, radial longitudinal and tangent longitudinal) using a stereoscopic Carl Zeiss SteREO Discovery.V20 microscope with magnifications of up to 360 × under oblique-angled top-lighting. A Scanning Electron Microscope (SEM: Tescan VEGA 3) was used when higher magnifications were needed. The abundance, arrangement and size of the wood’s anatomical structures (e.g., vessels, rays, fibers, annual growth rings), along with several other diagnostic characteristics of the eastern Mediterranean arboreal flora, were noted. Observations were compared with the modern reference collection of tissue structure of the southern Levant flora (The Steinhardt Museum of Natural History) and with literature on plant anatomy (Fahn et al., 1986; Wheeler et al., 1989; Schweingruber, 1990; Richter et al., 2004; Akkemike and Yaman, 2012; Crivellaro and Schweingruber, 2013).

3.4. Paleoclimate reconstruction

The pollen-based climate reconstruction enabled us to quantify monthly precipitation and temperature for the time span encompassed by the JRD fossil pollen record (Fig. 8). The statistical approach used to infer the climate variables from pollen samples was designed to minimize two major, known palynological difficulties: (1) the potential lack of analogy between the fossil pollen assemblages and the modern ecosystems; and/or (2) the potential adaptation of species to different climatic ranges over time which may lead to a misuse of the modern climate to infer past climate variables (Cheddadi et al., 2016, 2017). The model applied in the current study hypothesizes that plant species may co-occur only if their climatic ranges intersect.

The first step of the climate reconstruction was the assignment of the fossil pollen taxa to their most probable corresponding present-day plant species. In the second step, we computed the weighted median of the present-day climatic range of each assigned species (Figure A2). The reconstructed temperature and precipitation values correspond to the weighted median value of the climatic ranges of the plant species that correspond to pollen taxa identified in a fossil sample. Pollen taxa abundances (percentages) within each fossil sample are used as normalized (between 0 and 1) weight for computing the weighted median climatic values.

The standard deviations were computed using a leave-one-out approach: For each fossil pollen sample, one taxon was removed and a median climatic value for the remaining taxa was computed. This computation was performed as many times as the number of taxa used in the climate reconstruction model. The standard deviation of each reconstructed climatic value corresponds to the median value of all leave-one-out iterations.

The pollen-based climate reconstruction required modern plant species geographic distribution data as well as the dataset of their corresponding climatic ranges. The modern plant species distributions were georeferenced from the Atlas Florae Europaeae (Jalas and Suominen, 1973, 1979, 1980) and downloaded from the Global Biodiversity Information Facility (https://www.gbif.org). The modern climate dataset was obtained from the WORLDCLIM database (Hijmans et al., 2005). The temperature and precipitation range of each plant species was obtained by interpolating the present-day climate values onto the geographical species occurrences. The statistical approach code was written with R software (R Core Team, 2020) using the following packages: RMySQL (Ooms et al., 2019),...
Fig. 7. Simplified pollen diagram of the Jordan River Dureijat (JRD) sequence. A 10-fold exaggeration is used to show changes in low taxa percentages. Chronology is based on the age-depth model established in this study. *At zone 6, pollen was not preserved.
Fig. 8. Jordan River Dureijat (JRD) paleoclimate model. a). average temperature (°C): mean January (Tjan), mean annual (Tann) and mean August (Taug); b). δ18O of Soreq Cave; c). Annual precipitation (mm); d). Winter precipitation (December–February); e). Spring precipitation (March–May); f). Summer precipitation (June–August); g). Autumn precipitation (September–November); Red bars represent recent geographical settings. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
4. Results

4.1. The palynological record

Pollen was preserved in most sections of the JRD sediment outcrop. The section of 55.33–57.73 m asl provided 45 fertile pollen samples, whereas the nine samples from the upper 70 cm of the sequence (57.33–58.03 m asl) were pollen barren. In all fertile samples, a large variety of well preserved pollen types was identified. The full fossil pollen results are presented in Figure A1.

The chronological framework of the JRD pollen diagram is based on the age-depth model presented in Fig. 6. It covers the time interval between ~22 and 12 ka cal. BP. The diagram was divided into six pollen zones based on changes in the AP/NAP ratios together with the cluster analysis and the PCA analysis results. The uppermost part of the JRD section, where pollen was not preserved, was marked as pollen zone 6 (Figs. 5 and 7). The following description of the diagram presents the observed pollen zones from bottom to top.

Pollen Zone 1 (55.40–56.58 m asl; ~21.6–17.3 ka cal. BP).

The lower part of the JRD sequence, corresponding to the later stages of the Last Glacial period and to the Early Epipaleolithic, is characterized by relatively low percentages of Mediterranean arboreal pollen (0–18.1%) and relatively high frequencies of Artemisia and Chenopodiaceae (up to 21.4% and 28.6%, respectively). At ~20.9 ka cal. BP, no arboreal pollen was documented. High values of riparian taxa were observed between ~19.5–20.5 ka cal. BP (the highest being 10.3%). Zone 1 was subdivided into two subzones, Zone 1a (~21.6–18.5 ka cal. BP) and Zone 1b (~18.5–17.3 ka cal. BP). Subzone 1b is distinguished from subzone 1a by a decline in Poaceae and an increase in Chenopodiaceae and Apiaceae, together with a slight decrease in the ratios of Quercus ithaburensis type and a total disappearance of Cedrus libani.

Pollen Zone 2 (56.58–56.85 m asl; ~17.3–15.6 ka cal. BP).

This zone, archaeologically corresponding to the Middle Epipaleolithic Geometric Kebaran lithic assemblage, is marked by a rise in the ratios of the tree taxa, with a peak of 29.4% at ~15.9 ka cal. BP. Another significant feature is the regular appearance of Quercus calliprinos and Pisatucia sp. during this time interval. Artemisia, Poaceae, Chenopodiaceae and Apiaceae are present but in medium ratios. At the upper part of this zone, a slight drop in the ratios of the stream/marsh-bank vegetation was documented (0.3–3.1%).

Pollen Zone 3 (56.85–56.96 m asl; ~15.6–15.0 ka cal. BP).

This short time interval, preceding the appearance of the Natufian culture at JRD, is characterized by a sharp decline of AP ratios (5.7–8.5%). While both oak types (Q. ithaburensis and Q. calliprinos) and Pinus are present in lower frequencies, the total disappearance of other tree taxa was documented. This zone also exhibits a profound increase in Artemisia values (15.4–20.3%) and the first appearance of the alga Pediastrum. The stream/marsh-bank vegetation was again characterized by relatively low values (3.0–4.3%).

Pollen Zone 4 (56.96–57.30 m asl; ~14.9–13.0 ka cal. BP).

This zone is equivalent to the early stages of the Natufian culture at JRD. The most striking feature of zone 4 is the strong increase in the total tree pollen values, with maximum ratios documented at ~14.2–13.2 ka cal. BP (reaching up to 53.1%). This increase is almost entirely due to Quercus ithaburensis type with a maximum at 13.4 ka cal. BP of 32.1%. Almost at the same time, at ~14.2–13.1 ka cal. BP, Olea pollen shows a relatively high and constant presence (0.3–1.5%). The significant rise in the tree percentages is accompanied by a profound decline in the ratios of both Artemisia and Chenopodiaceae (0.7–8.1% and 7.7–13.1%, respectively). Poaceae and Apiaceae are present in medium ratios.

Pollen Zone 5 (57.30–57.55 m asl; ~13.0–12.0 ka cal. BP).

In this pollen zone, archaeologically documenting the Late Natufian at JRD, a drop in AP ratios was registered (9.3–28.2%). Both oak curves, evergreen and deciduous, declined, as well as the Pistacia and Olea curves. Asteraceae Asteroideae and Asteraceae Cichorioideae as well as Apiaceae values are relatively high. Artemisia and Chenopodiaceae are present in relatively low frequencies (not exceeding 2.6% and 16.2%, respectively). Asphodelus pollen is characterized by a constant appearance and relatively high percentages. Zone 5’s palynological assemblages are also typified by high ratios of the alga Pediastrum and relatively low percentages of aquatic plants. A slight increase in the group of riparian taxa was also observed (up to 5.8%).

Pollen Zone 6 (57.55–58.03 m asl; ~11.9–11.0 ka cal. BP).

This is equivalent to the uppermost archaeological layer at JRD, Layer 3–0 (archaeologically, it seems that this layer was modified by later inhabitants, possibly of the Early Neolithic, as evident by the El-Khiam arrowheads and limestone axes; Sharon et al., 2020). Pollen was not preserved in this uppermost section (Fig. 5), most probably due to oxidation when lake levels decreased, causing loss of the waterlogged conditions.

Recent sample.

The recent river mud surface sample collected as a comparative control sample demonstrates that the arboreal pollen spectrum is dominated by the following taxa: Olea, Pinus, Cupressus type, and neophytic trees such as Eucalyptus spp. (Table A1). The presence of these tree taxa is most likely due to modern afforestation rather than representing the natural flora. The Hula Valley environment has been subject to thousands of years of human disturbances. Similar to other southern Levantine areas, the intensity of human interference increased dramatically in the last 100 years due to modern agriculture, forestry and development. Human interference completely transformed the vegetation of the Hula Basin into an artificial environment. Hence, the contribution of the recent pollen sample to the interpretation of the fossil pollen data is limited.

4.2. Waterlogged wood assemblage

The waterlogged wood assemblage analyzed in the current study is composed of 227 fragments from all layers tested. Twenty-five different taxa were identified (Table 2 and Fig. 9). The assemblage can be subdivided into two groups: Trees and shrubs typical of the Mediterranean forest/maquis comprise 37.3% of the assemblage, while riparian trees and shrubs form the majority, comprising 59.6% of the samples. Undetectable taxa include only 3.1% of the assemblage. The first group is dominated by the two deciduous oaks species, Quercus boissieri and Q. ithaburensis. In the second group, the identified samples belong to various trees and shrubs common today on banks of permanent and intermittent water bodies and streams in the Hula Valley. The most abundant taxa among this group are Fraxinus syriaca, Salix/Populus and monocots (mainly reeds).

The potential of this wood assemblage to provide a robust ecological picture documenting changes in the Mediterranean woodland on a time trajectory is limited. This is due to the relatively small size of the assemblage (when subdivided according to stratigraphic location) and its high ratios of riparian taxa, as water bank vegetation is less sensitive to climatic changes in the region (Melamed et al., 2011). However, the JRD wood assemblage was instrumental in refining the pollen results when wood identification was possible to a lower systematic level than the identification achieved by the pollen, as in the cases of Pistacia and the deciduous oak pollen type. Three Pistacia species are native to the southern...
Levant: *P. palaestina*, *P. lentiscus* and *P. atlantica*. Whereas *Pistacia* pollen cannot be distinguished from one another, the species can be easily identified based on the anatomical structure of the wood (Grundwag and Werker, 1976). Among the deciduous oak pollen type, the most abundant species in the studied area today are *Q. ithaburensis*, a thermophilic deciduous tree typical of low elevations and *Q. boissieri*, a deciduous oak species of the upper mountain zones of the Galilee, Golan Heights and Mount Hermon (Zohary, 1973). However, as in the case of *Pistacia* species, the two deciduous oak species are palynologically indistinguishable. The results of the JRD wood assemblage presented in Table 2 indicate that *P. atlantica* grew at the vicinity of JRD and that *Q. boissieri* was more prevalent in the study region than *Q. ithaburensis*.

### 5. Discussion

#### 5.1. Vegetation reconstruction at the Hula Basin

The most dominant component of the arboreal pollen vegetation in and around the Hula Valley was the deciduous *Quercus ithaburensis* (Mount Tabor oak) pollen type (Fig. 7). Some pollen grains of this type may have been of *Q. boissieri* (Aleppo oak), which is a deciduous oak species of the surrounding higher mountain zones, and some may have derived from the thermophilic deciduous *Q. ithaburensis*, typical of lower elevations. Palynologically, these two deciduous oaks are indistinguishable and therefore appear in the pollen diagram as *Q. ithaburensis* pollen type. In the JRD wood assemblage, *Q. boissieri* was slightly more common than *Q. ithaburensis* (Table 2). In contrast to the pollen record, human agency was most likely involved in the accumulation of the archaeological wood assemblage — people collected wood as raw material for construction, firewood, and for preparing various wooden tools. Based on the assumption that the timber for everyday use was usually collected in the site vicinity (Deckers et al., 2007; Lev-Yadun, 2007), it can be argued that both deciduous oak species were growing around JRD. Hence, both contributed to the pollen rain over Paleolake Hula. The other two dominant taxa in the palynological record are the evergreen oak (*Q. calliprinos*) and *Pistacia*. Their occurrence with nearly identical trends throughout the pollen record reflects the expansion and reduction of the Mediterranean woodland/maquis. For example, the increasing values of their curves together with the rising values of *Quercus ithaburensis* pollen type at the beginning of pollen zone 2 (~17 ka cal. BP), point to a gradual expansion of the Mediterranean woodland/maquis in the environs of the Hula Valley. The presence of sclerophyllous trees such as evergreen oak and *Pistacia*, though in very low frequencies and inconsistent appearance during the LGM, suggests that the mountains near JRD (Upper Galilee; Figs. 1 and 2) may have served as glacial plant refugia. The same phenomenon was observed in other Mediterranean pollen studies (Tzedakis et al., 2002; Carrion et al., 2013; Cheddadi and Khater, 2016).

The pollen values of *Pinus* are relatively low throughout the JRD sequence, but its occurrence is almost constant except during two short phases: at ~21 ka cal. BP, and around ~13 ka cal. BP. These episodes may be related to the LGM and Younger Dryas cold climates. *Pinus halepensis* (Aleppo pine) is the only pine species native to Israel and it is sensitive to frost (Pardos et al., 2003). Typically, it is a minor arboreal component of the Mediterranean maquis/forest (Zohary, 1973; Weinstein-Evron and Lev-Yadun, 2000), though some *Pinus* pollen grains may have originated from Lebanon where at present *P. brutia* (Turkish pine) is the predominant pine (Zohary, 1973; Van Zeist and Bottema, 2009). *Pinus* pollen is usually overrepresented in palynological assemblages, owing to its high production, efficient long-distance transport ability, and high resistance to degradation (Cheddadi and Rossignol-Strick, 1995; Van Zeist et al., 2009). The total lack of waterlogged pine wood remains at JRD (Table 2) supports the hypothesis of long-distance transportation of *Pinus* pollen and/or its presence as a very minor component in the Mediterranean woodland/maquis in the area around the Hula Valley.

*Olive* (*Olea europaea*) was always a minor component of the

### Table 2
Identified waterlogged wood remains recovered from the JRD archaeological site in absolute numbers and percentages.

<table>
<thead>
<tr>
<th>Category</th>
<th>Taxon</th>
<th>Absolute number</th>
<th>Percentages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mediterranean woodland/maquis</td>
<td><em>Quercus calliprinos</em> (Kermes oak)</td>
<td>2</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td><em>Quercus ithaburensis</em> (Mount Tabor oak)</td>
<td>13</td>
<td>5.7</td>
</tr>
<tr>
<td></td>
<td><em>Quercus boissieri</em> (Aleppo oak)</td>
<td>20</td>
<td>8.8</td>
</tr>
<tr>
<td></td>
<td><em>Quercus deciduous (unidentifiable deciduous oak)</em></td>
<td>20</td>
<td>8.8</td>
</tr>
<tr>
<td></td>
<td><em>Quercus sp. (unidentifiable oak)</em></td>
<td>8</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td><em>Laurus nobilis</em> (laural)</td>
<td>2</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td><em>Platanus orientalis</em> (oriental plane)</td>
<td>3</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td><em>Pistacia sp. (terebinth)</em></td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td><em>Pistacia atlantica</em> (Atlantic turpentine)</td>
<td>2</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td><em>Ziziphus spinosa</em> (jujube)</td>
<td>2</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td><em>Paliurus spinosa</em> (Jerusalem thorn)</td>
<td>2</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td><em>Cercis silicquastrum</em> (Judas tree)</td>
<td>2</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td><em>Rhus coriaria</em> (elm-leaved sumac)</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td><em>Ononis natrix</em> (yellow restharrow)</td>
<td>3</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td><em>Viburnum tinus</em> (lauretine)</td>
<td>2</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td><em>Myrtus communis</em> (true myrtle)</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td><em>Rosa sp.</em> (rosa)</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Riparian trees</td>
<td><em>Fraxinus syriaca</em> (ash)</td>
<td>30</td>
<td>13.2</td>
</tr>
<tr>
<td></td>
<td><em>Salix/Populus</em> (willow/poplar)</td>
<td>27</td>
<td>11.9</td>
</tr>
<tr>
<td></td>
<td><em>Tamarix parviflora</em> (smallflower tamarisk)</td>
<td>7</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td><em>Tamarix sp.</em> (tamarisk unidentifiable)</td>
<td>14</td>
<td>6.2</td>
</tr>
<tr>
<td></td>
<td><em>Vitis vinifera</em> (grapevine)</td>
<td>2</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td><em>Arundo donax</em> (giant reed)</td>
<td>7</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td><em>Phragmites australis</em> (common reed)</td>
<td>7</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td><em>Monocots</em></td>
<td>41</td>
<td>18.1</td>
</tr>
<tr>
<td></td>
<td><em>Undetectable</em></td>
<td>7</td>
<td>3.1</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>227</td>
<td>100.0</td>
</tr>
</tbody>
</table>
Levantine native Mediterranean maquis/forest (Langgut et al., 2019, and references therein). This observation is supported by the total absence of *Olea* remains in the JRD wood assemblage (Table 2). After its domestication during the early Chalcolithic (ca. 7,000 years BP), olive became the most dominant tree in wood-charcoal assemblages of the Mediterranean southern Levant Bronze and Iron Ages sites (e.g., Benazaqen et al., 2019). *Olea* is a predominantly wind-pollinated species that releases large amounts of pollen into the atmosphere and is usually well-represented in palynological spectra (Bottema and Sarpaki, 2003; Mercuri et al., 2013; Langgut et al., 2014b). *Olea* pollen appears in the JRD pollen sequence mainly at the time interval of 14.2−13.1 ka cal. BP. Olive does not grow in areas where winter temperatures fall below 3°C (Zohary, 1973); therefore, increasing *Olea* pollen levels signal warmer climate conditions in the region (Cheddadi and Rossignol-Strick, 1995; Aharonovich et al., 2014; Langgut et al., 2011, 2018). In contrast, *Cedrus libani*, only sporadically occurring in the JRD pollen record, is usually an indicator of colder climate conditions, since it is restricted to cold and sunny high elevation slopes in the region (Weinstein-Evron, 1983; Cheddadi et al., 1991). Scattered cedar populations are still found today in the mountains of Lebanon, in the mountain ranges of southern Turkey and in northwestern Syria (Seals, 1965; Hajar et al., 2010), probably relics of a formerly extensive distribution. Indeed, no cedar wood remains were found at JRD nor at other Pleistocene sites in Israel. Beginning in the Middle-Holocene, the cedar of Lebanon was imported to ancient Israel as a prestigious tree (Lev-Yadun, 1992; Langgut and Gleason, 2020; Langgut et al., 2021).

The arboreal pollen and wood results demonstrate that the Mediterranean maquis/forest was always present in the region during the end of the Pleistocene, and was composed of the same components. Changes were, however, observed in taxa proportions in the different periods investigated, resembling shrinkage and expansion of the maquis/forest.

5.1.2. Open fields vegetation

The lower part of the JRD sequence (pollen zones 1−3) is characterized by high ratios of *Artemisia* and Chenopodiaceae pollen. In the southern Levant, *Artemisia* (in non-hot-desert conditions) is considered the best palynological marker for dryer and colder climate conditions (Cheddadi and Rossignol-Strick, 1995; Langgut et al., 2011). Similarly, members of Chenopodiaceae family are found in the same environmental conditions since they are common constituents of *Artemisia* dwarf-shrub steppe. However, they can also thrive in saline habitats (Van-Weziet et al., 2009).

Pollen zone 4 (−14.9−13.0 ka cal. BP) is marked by a decrease in *Artemisia* and Chenopodiaceae values. This decline represents a profound shift in the vegetation cover of the Hula Basin, from extensive dwarf-shrub steppe (at pollen zones 1−3) to an open steppe cover and widening of the Mediterranean woodland/maquis. Pollen zone 5, which begins at −13 ka cal. BP, corresponds to the Younger Dryas event (Andres et al., 2003). This zone is typified by an exceptional non-arboreal palynological spectrum. *Artemisia* frequencies show their lowest values anywhere along the sequence. Yet, unlike previous pollen zones, the *Artemisia* low percentages were accompanied by a significant rise of the following taxa: *Asphodelus*, Asteraceae Asteroideae type (aster-like), Asteraceae Cichorioideae type (dandelion-like) and Apiceae. These ecosystem changes indicate a significant shift in the regional vegetation cover in the JRD area during the Younger Dryas. Assemblages of pollen zone 5 indicate a decline in Mediterranean arboreal pollen and an increase in the abundance of Mediterranean open field small shrubs and herb components. In contrast, in previous JRD pollen zones, a decrease in Mediterranean trees was accompanied by a rise in open field steppe environment components such as *Artemisia* and Chenopodiaceae.

The occurrence of Cerealia pollen type is scattered throughout the JRD pollen record without a specific trend that can be attributed to environmental change and/or human interference.

5.1.3. Marsh-bank vegetation and aquatic plants

Slightly higher pollen percentages of the marsh-bank vegetation group were documented for the lower part of the palynological diagram (−22.0−16.5 ka cal. BP), covering pollen zone 1 and the lower section of zone 2. This may indicate that the edge of the lake was closer to the studied site. It is therefore suggested that slightly lower lake levels characterized Paleolake Hula from −22.6−16.5 ka cal. BP. After −16.5 ka cal. BP, during the accumulation of the upper part of zone 2 and until the end of the diagram, a minor decrease in the percentages of the riparian plants was recorded, probably representing an increase in the lake level stands.

The pollen and the waterlogged wood assemblages from JRD enable characterization of the Paleolake Hula bank vegetation during site occupation. They provide direct evidence for the aquatic vegetation resources that were available to the Epipaleolithic fishers and gatherers. The marsh-bank palynological spectra include pollen of *Plagmites* type (reed), *Cyperaceae*, *Typha* (cattail), and *Salix* (willow), all ethnographically and experimentally known to be used in basketry and rope interweaving (Kristal, 2019). Water plants are highly reproductive and abundant and they are known to be used in the production of various fishing gear, including fishline, nets and traps (Salls, 1989; Nadel et al., 1994; Dounias et al., 2016). Other components of this group, such as *Vitis* (grape), have been used as food, while woody taxa such as *Tamarix* (tamarisk) may have been used as raw material for the preparation of wooden objects (Nadel and Werker, 1999; Nadel et al., 2006; Langgut et al., 2016). Various Poaceae plants (grasses) could have been used for bedding (Nadel et al., 2004). The JRD wood assemblage confirms the high riparian taxa diversity that was available to the site’s inhabitants, including ash, tamarisk, poplar/willow and grapevine, as well as monocots such as giant reed (Table 2 and Fig. 9).

A significant observation emerging from the study of JRD palynomorphs is the first appearance of two types of freshwater alga, *Pediastrum simplex* type and *P. boryanum* type. This alga appears at the upper segment of the JRD section, after −15.5 ka cal. BP. Typically, increasing percentages of these two algae taxa are indicative of warmer climate conditions and a nutrient-rich environment (Jankovská and Komárek, 2000, and references therein). The appearance of *Pediastrum* is almost parallel to the marked rise in Mediterranean arboreal pollen and a decrease in pollen of aquatic plants. Van Zeist et al. (2009), who identified the same phenomenon in a previous Paleolake Hula pollen investigation, suggested that the growth of *Pediastrum* was encouraged by a rise in the influx of organic material into the lake. It was proposed that increased density of upland vegetation cover resulted in more organic debris being washed into the lake, enriching the organic nutrients available in the water. The decline in aquatic pollen percentages is probably a result of the rise in lake levels. The lake became (locally) too deep for water plants to take root in the lake bottom (Van Zeist et al., 2009). The observation regarding the increase in lake levels since −16.5 ka cal. BP based on the increase in pollen of riparian taxa is, therefore, corroborated by the declining pollen values of the aquatic taxa.

5.2. Climate reconstruction of the Mediterranean southern levant:

−22.0−11.9 ka cal. BP

5.2.1. Last Glacial Maximum (LGM): −22−19 ka cal. BP

Our paleoclimate model indicates that the reconstructed annual precipitation exhibits no dramatic changes throughout the later
**Fig. 9.** SEM Images of wood sections of taxa identified at Jordan River Dureijat (JRD). a: *Quercus ithaburensis*, transverse section, 50x, scale 300 μm; b: *Quercus* sp. (calliprinos?), transverse, 30x, scale 500 μm; c: monocot (*Arundo donax*?), transverse, 137x, scale 300 μm; d: monocot (*Phragmites australis*?), transverse, 246x, scale 100 μm; e: *Tamarix* sp., transverse, 40x, scale 500 μm; f: *Fraxinus syriaca*, transverse, 181x, scale 100 μm; g: *Cercis siliquastrum*, transverse, 40x, scale 400 μm; h: *Salix/Populus*, transverse, 50x, scale 400 μm; i: *Pistacia atlantica*, transverse, 110x, scale 200 μm; j: *Vitis vinifera*, transverse, 105x, scale 400 μm; k: *Ziziphus spina-christi*, transverse, 137x, scale 300 μm; l: *Rhus coriaria*, transverse, 173x, scale 200 μm; m: *Laurus nobilis*, transverse, 60x, scale 200 μm. Note that due to preservation conditions, not all identified taxa were able to be imaged satisfactorily. In other cases, only certain parts of the examined samples were able to be photographed. Images a, b, c, g, h, i, and m were taken using a stereoscopic Carl Zeiss SteREO Discovery.V20 microscope. Images c, d, f, j, k, and l were taken using a Tescan VEGA3 LMH scanning electron microscope.
part of the LGM represented in this study (~22–19 ka cal. BP) with an average of 450 mm (Fig. 8c). However, mean January (Tjan), August (Taug) and annual (Tann) temperatures fluctuated greatly during this time interval (Fig. 8a). Tjan ranged between 5.5°C and 10°C (present-day value is 11°C). Both the Taug and the overall mean annual temperature were ca. 4°C lower than today, which had a positive effect on the precipitation/evaporation ratio of the region. Previous regional studies confirm that during the LGM, temperatures in the Levant were cooler than at present; fluid inclusion δD from Soreq Cave speleothems yielded calculated annual average temperatures of ~5–7°C at the cave during the height of the LGM, 9–11°C cooler than today (McGarry et al., 2004). Annual average temperatures on the Mitzpe Shelagim summit of Mount Hermon (2224 m asl) were below 0°C (Ayalon et al., 2013). Dryer and cooler conditions during the LGM are also evidenced by erosion in the Negev Desert (Goodfriend, 1987; Goodfriend and Magaritz, 1988). However, speleothem deposition at the northern Negev Desert at ~23–13 ka signifies that the climate was not extremely arid; moisture was available from a Mediterranean source for the formation of these cave deposits (Vaks et al., 2006).

Slightly before the beginning of the JRD sequence, at ~27–23 ka BP, the reconstructed Lake Lisan reached its highest levels (Bartov et al., 2002, 2003, 2006, 2007; Hazan et al., 2005; Torfstein and Enzel, 2017). Our palaeoclimate model (Fig. 8) suggests that temperature was the critical climate variable influencing the lake level changes of the Jordan Rift Valley. While the reconstructed annual precipitation was only slightly below that of today (~450 mm vs. 515 mm, respectively), annual mean temperatures were much lower during the end of the last glacial period. These low temperatures most probably reduced evaporation, resulting in high lake levels. This scenario is in line with south Levantine speleothems studies (Ayalon et al., 2013; Bar-Matthews et al., 2019 for a recent review) and climate model simulations (Stockhecke et al., 2016), but contradicts claims explaining high lake levels by an extensive increase in precipitation (Bartov et al., 2003; Enzel et al., 2008; Stein, 2014; Torfstein and Enzel, 2017). The vegetation patterns that emerged from this study for the LGM indicate a reduction of the Mediterranean woodland/maquis and the prevalence of steppe vegetation, which translates into a reduction in the overall amounts of annual precipitation. The decrease in the total woodland density resulted in a reduction in the overall amounts of annual precipitation (Chen and Litt, 2018; Miebach et al., 2017). A palynological and environmental study of a northern Levantine core from Lake Yammouneh in Lebanon also indicates that the LGM was one of the coldest periods during the last 250 ka BP (Develle et al., 2011). Eastern Mediterranean marine pollen records are also characterized by low values of Mediterranean arboreal pollen during the LGM, with almost no occurrence of frost-sensitive and summer-drought-adapted trees such as Olea and Pistacia, indicating cooler climate conditions (Cheddadi and Rossignol-Strick, 1995; Langgut et al., 2011). The total lack of speleothems growth at Mizpe Shelagim Cave during Marine Isotope 2 suggests permafrost conditions along the higher elevations of Mount Hermon (Ayalon et al., 2013). The vegetation cover could have been shaped by effective moisture in the habitats, while additional precipitation was stored as snow in high mountains (Haase-Schirrmann et al., 2008). Rapid snowmelt in spring would have fed the Jordan Rift lakes but would have hardly affected the vegetation cover (Miebach et al., 2017). A palynological study from the Dead Sea reveals an expansion of the Artemisia steppe from 60 to 20 ka BP under a drier and cooler climate with an average of 3°C lower during MIS 3 than today (Miebach et al., 2019; Richter et al., 2020). According to recent Dead Sea pollen studies (Chen and Litt, 2018; Miebach et al., 2019; Richter et al., 2020), the decline in temperatures during glacial periods reduced evaporation, yet sufficient moisture was available in the Dead Sea region to support steppe vegetation. Thus, the Lisan Lake level rose without a corresponding increase in the annual amount of precipitation (Chen and Litt, 2018; Miebach et al., 2019; Richter et al., 2020).

5.3. 2: The post-glacial time interval: ~18.7–11.9 ka cal. BP

This time span began with a marked rise in temperatures (mean annual, winter and summer) of between 3 and 5°C from ~19 to ~17 ka cal. BP (Fig. 8a). A similar pattern emerged from the reconstruction of average annual temperatures for Soreq Cave, based on speleothem fluid inclusion δD, with 7–9°C at ~19.2–18.9 ka increasing to 9–12°C at ~18.9–18.6 ka (McGarry et al., 2004). The JRD palaeoclimate model also indicates a slight increase in winter precipitation (Fig. 8d) accompanied by a slight decrease for the three other seasons, indicating a rise in seasonality contrast (Fig. 8e–g). At ~16–15 ka cal. BP the model points to a decline in temperatures as well as a decrease in winter and spring precipitation (Fig. 8d and e). This climatic shift to cooler and drier climate conditions is most probably related to Heinrich Event 1. This short-duration cooler and dryer episode was also identified in other southern Levantine palaeoclimate records: 16.5 ka at Soreq Cave (Bar-Matthews et al., 1999) and 16 ± 1 ka at Lake Lisan (Bartov et al., 2003).

The wettest and warmest time interval throughout the JRD sequence was identified between ~14.9 and 13.0 ka cal. BP. This period coincides with the global warm and moist Belling-Allerød interstadial (=Greenland Interstadial 1, Lowe et al., 2008) (Fig. 8a and d). This warm trend reached its maximum at ~14 ka cal. BP, with reconstructed January temperatures similar to today’s average (~11°C; Fig. 8a). The mean annual temperature values during the warm Belling-Allerød interstadial remained ca. 2°C lower than today, which is consistent with the global temperature ice record (GRIP Members, 1993), the Mediterranean Sea surface temperature (Cacho et al., 1999) and regional climate records (Cheddadi and Khatner, 2016).

Speleothem formation at Mizpe Shelagim beginning at ~15 ka (after a total lack of growth during the time interval of ~34–15 ka) was due to the melting of permafrost at the higher elevations of Mount Hermon, indicating the onset of a warm phase in the Levant (Ayalon et al., 2013). Based on the reconstructed seasonal precipitation from the JRD model, not only did winter precipitation increase, but also spring and autumn precipitation (Fig. 8e–g). This multi-seasonal increase in precipitation likely resulted from multiple contributors, with autumn and winter moisture originating from the Mediterranean (Cyprus Low) and spring moisture from a southern source (Red Sea Low).

Lake Lisan levels during the Belling-Allerød were relatively high, suggesting an increase in precipitation to evaporation ratio in comparison to conditions during Heinrich Event 1 (Bartov et al., 2002). The Soreq Cave speleothem stable isotope data are also suggestive of an increase in temperatures and precipitation during this time interval (Bar-Matthews et al., 1997, 1999). The Belling-Allerød period was also identified in the eastern Mediterranean marine pollen record based on a marked rise in Mediterranean arboreal pollen values (Langgut et al., 2011).

The onset of the Younger Dyas event is dated in the JRD sequence to ~12.9 ka cal. BP. At the uppermost part of the JRD record, pollen grains were not preserved (Pollen zone 6); hence, the end of the Younger Dyas is missing. The reconstructed palaeoclimate conditions for this time interval are exceptional, as for the
first time in the JRD record, temperature and precipitation show opposite trends: While temperatures decreased, annual precipitation slightly increased (Fig. 8a and c). A higher contribution of moisture derived from spring, summer and autumn rains, while winter precipitation decreased in comparison to the previous periods (Fig. 8d–g). This reconstruction points to a reduced seasonal contrast during the Younger Dryas. Identical observations emerged from the study of fluorescent banding patterns of Soreq Cave speleothems, revealing that during Heinrich Event 1 and the Younger Dryas, the supply of drip water to Soreq Cave was more consistent year-round (Orland et al., 2012). Thus, a reduced gradient of seasonal precipitation, occasional snowfall, and vegetation cover differences may have all contributed to the isotope and fluorescent banding patterns observed for these two exceptionally short time intervals that led to less distinct wet and dry seasons (Orland et al., 2012). The decrease in the magnitude of difference in δ18O values between the wet and dry seasons in the Mediterranean Levant during the Younger Dryas is supported by an isotopic study of hunted gazelles (Hartman et al., 2016). Similar seasonality trends were also observed during the same time period from palynological records of the northern Levant (Cheddadi and Khater, 2016). These records show a lowering of winter precipitation over Lebanon during the Younger Dryas and a slight increase of summer precipitation, resulting in a more balanced contribution of moisture from the southwest and northwest Mediterranean basin during summer and winter (Cheddadi and Khater, 2016; Figs. 1 and 5). Today, the Mediterranean climate is characterized by a highly marked amplitude of precipitation between summer and winter, related to the dominant northwest storm tracks during winter. The cooler temperatures during the Younger Dryas reconstructed for the JRD record are corroborated by other isotope studies available from the Mediterranean Levant (Orland et al., 2012; Hartman et al., 2016).

The JRD reconstructed precipitation during the Younger Dryas is also intensively fluctuating, potentially pointing to climate instability (Fig. 8c–f). Based on multiple Levantine paleoclimate datasets, Robinson et al. (2006) proposed that the Younger Dryas was colder in comparison to the Bølling-Allerød and the Holocene (Robinson et al., 2006; Fig. 15C). The Younger Dryas was also depicted in other Levantine terrestrial and marine palynological records, based on the identification of steppe dominating plant taxa, primarily Artemisia and Chenopodiaceae (Kadosh et al., 2004; Langgut et al., 2011; Cheddadi and Khater, 2016). Unfortunately, the beginning of the Holocene is not recorded in the JRD pollen sequence. Other palynological records in the vicinity of JRD reveal increasing percentages of arboreal pollen accompanied by an abundance of frost-sensitive and summer-drought-adapted taxa such as Olea, Pistacia, and evergreen oaks during the early Holocene (Lake Hula: Van-Zeist et al., 2009, based on their revised chronology; Sea of Galilee: Schiebel and Litt, 2018). Similar vegetation and environmental patterns were observed in the northern Levant during the Early Holocene (Develle et al., 2011; Gasse et al., 2015; Cheddadi and Khater, 2016).

5.4. Environmental preconditions to sedentism and the onset of agriculture

The transition from small nomadic groups of hunter-gatherers, to the sedentary villages of the Natufian, followed by the agricultural communities of the Neolithic period, is a seminal process in human history. This transition involved not only a shift to food production-based subsistence strategies, but also the creation of the complex societies of early civilizations. Yet, the exact location, reasons, and processes that led to this dramatic cultural change remain in dispute (e.g., Lev-Yadun et al., 2000; Fuller et al., 2011). The current study does not aim to resolve this debate; however, the long and well-dated stratigraphic sequence of JRD yielded a continuous, site-based palynological record covering the great majority of the Levantine Epipaleolithic. Our record is especially important due to the correlation achieved between the palynological and the paleoclimatic reconstruction with the cultural changes evident at JRD, based on well-defined archaeological horizons. This correlation enables identifying several unique environmental circumstances which characterized the Mediterranean southern Levant, forming the background for the dramatic shift toward sedentism and Neolithization (Table 3).

The paleoclimate reconstruction generated from the Epipaleolithic JRD sequence demonstrates that a significant climate shift to warmest and wettest conditions occurred during the time interval of −14.9–13.0 ka cal. BP (Fig. 8). This warm and humid interval was accompanied by a high seasonal contrast of precipitation. Significantly, the beginning of this phase is synchronous with the onset of the Natufian culture, characterized by reduced population mobility and sedentism in the Hula Valley and the entire southern Levant (Bar-Yosef and Belfer-Cohen, 1989, 1992; Kaufman, 1992; Moore and Hillman, 1992; Grosman, 2003, 2018; Byrd, 2005; Maher et al., 2011; Bar-Yosef and Valla, 2013; Yeshurun et al., 2014). The data indicate that the Early Natufian documented by archaeological finds from the Hula Valley, characterized by suitable climatic conditions and abundant resource availability. Such conditions may have augmented the capability of the first sedentary communities to face the environmental and subsistence challenges that surely accompanied early sedentism and population increase (Belfer-Cohen and Bar-Yosef, 2000; Boyd, 2006).

The JRD Younger Dryas pollen assemblages differ from all other pollen spectra observed during the glacial/interglacial time intervals (Fig. 7; Table 3). They are characterized by high frequencies of Mediterranean open-forest taxa. The pollen assemblages of the Late Natufian (~12.9–11.6 cal. BP) populations, reveals that the Younger Dryas event (Fig. 8). The pollen record shows an increase in annual plants. This may have enriched the plant-gathering opportunities of the inhabitants of the Mediterranean Levant. The proliferation of herbs, and specifically of annuals, may have paved the way to the emergence of agriculture in the Near East, since all seven Neolithic founder crops are annuals. Munro (2003), based on the archaeozoological record of the southern Levant, also sees the Younger Dryas as forcing Late Natufian (~12.9–11.6 cal. BP) populations to cope with the changing climate and environment by shifting to a wide spectrum diet. In parallel, Belfer-Cohen and Bar-Yosef (2000) noted that the Late Natufian hunter-gather communities are characterized by increasing population mobility patterns.

The exceptional climatic and environmental conditions during the Younger Dryas event are evidenced by its vegetation change and the lowest climatic seasonal contrast reconstructed for the JRD sequence. The primary expression of this observation is an increase in rains during spring, summer and autumn, together with a significant reduction in winter precipitation (Fig. 8c–f). In contrast, at the beginning of the Holocene, the regional climate was typical Mediterranean, of stronger seasonality than today, with mild winters and hyper-arid summers (Orland et al., 2012; Cheddadi and Khater, 2016). The early Holocene seasonal stress of long, hot dry summers probably increased the need for food storage by sedentary communities. We suggest that the significant vegetation and climate changes at the late Pleistocene-Holocene boundary contributed to the development of agriculture-based subsistence
Admittedly, similar environmental changes also occurred during earlier phases of the Pleistocene. Yet, the climate changes that occurred during the Pleistocene-Holocene boundary were, for the first time, accompanied by sedentism, complex social organization, food storage and curating technologies for harvesting and processing of wild plants. Sickles (Groman-Yaroslavski et al., 2016; Maeda et al., 2016), grinding stones (Weiss et al., 2008; Marder et al., 2013; Rosenberg and Nadel, 2010; Marder et al., 2013; Rosenberg and Nadel, 2014), as well as storage facilities (Liu et al., 2018), are all well documented in the Levantine Epipaleolithic.

This study suggests that the confluence of separate natural events and cultural developments promoted the emergence of agriculture in the Mediterranean Levant. The sudden, exceptional Younger Dryas climate induced a major vegetation change, which was followed by a severe seasonality during the Early Holocene and related changes in vegetation cover. Together with the shrinking of the Jordan Valley lakes, these conditions presented new subsistence challenges to the sedentary communities of the Mediterranean Levant. A similar synergic scenario was suggested three decades ago by McCorriston and Hole (1991). Yet, their proposal lacks a solid paleo-vegetation dataset and detailed paleoclimate model as presented in this study. McCorriston and Hole (1991) claimed that the convergence of several cultural and environmental factors, each forming a piece of the puzzle, generated the Neolithization process. They list a series of social, ideological, cultural, technological, climatological and environmental preconditions that must have existed before Natufian groups could cross the threshold to agriculture-based subsistence. Hence, agricultural economy developed because the right people were in the right place, at the right time, with the right decisions.
demonstrates that during this time interval, the mean annual temperature was lower than today (in the range of 14.5–19°C vs. 21°C on average today). During most of the period, the mean annual precipitation was slightly lower than today (average 450 mm vs. 515 mm today). However, from ~15 ka cal. BP, mean annual precipitation increased (reaching maximum values of 545 mm at 14.5 ka cal. BP). Our climate model of seasonal changes for both temperatures and precipitation enabled us to reconstruct in detail the climatic conditions of the region, providing the environmental background for the dramatic socio-cultural human shifts that occurred at this time interval.

1. During the Early Epipaleolithic period, corresponding to the LGM, a limited Mediterranean woodland/maquis with a lush dwarf shrub steppe vegetation covered the area around Paleolake Hula. Our paleoclimate model points to low temperatures, reaching the lowest values of the sequence at 20.5 and 19.5 ka cal. BP, with reconstructed January temperatures 5°C lower than today. Average annual precipitation was only slightly lower than today, with some summer precipitation.

2. After the LGM, at ~19–17.5 ka cal. BP, dwarf shrub-steppe vegetation continued to dominate the region. The mean annual temperature remained relatively low and a slight increase in precipitation associated with an additional contribution of summer rainfall was inferred. By ~17.5 ka cal. BP, a well-developed Mediterranean woodland probably already existed in the area. The reconstructed climate points to a significant increase in temperature and winter precipitation with increased seasonality.

3. The greatest cover of the Mediterranean woodland/maquis was identified at the beginning of the Late Epipaleolithic period. The paleoclimate reconstruction of the time interval ~14.9 to 12.9 ka cal. BP demonstrates a striking climatic shift to the warmest and wettest conditions in the Epipaleolithic JRD sequence. These are likely correlated with the warm and humid Belling-Allerød interstadial as well as with the onset and duration of the Natufian culture in the Levant. The humid and warm climate certainly helped the early settlers overcome the many challenges of sedentism. The palynological evidence also points to an increase in Paleolake Hula levels.

4. Two cold, short-term climate events were identified. The first is dated to ~16–15 ka cal. BP and may be related to the cold and dry Heinrich Event 1. The second episode began at ~12.9 ka cal. BP and corresponds to the Younger Dryas. The JRD sequence ends at ~11.9 ka cal. BP and probably lacks the last phase of the Younger Dryas (~11.9–11.7 ka cal. BP). Our paleoclimate model indicates that this period was characterized by unique climatic conditions, with the least contrast of climatic seasonality. There was an increase in precipitation contribution during spring, summer and fall, along with a significant decrease in winter precipitation. The reconstructed vegetation suggests the presence of Mediterranean open field vegetation, probably rich with annuals. We therefore suggest that the extensive herbaceous landscape probably increased the opportunities for plant gathering, specifically of annuals, paving the way towards agriculture. In the following period, the early Holocene, as well as at present, the region is characterized by seasonal stress, with long, hot dry summers.

5. We propose that the significant vegetation and climate changes at the late Pleistocene-Holocene boundary contributed to the development of agriculturally-based subsistence communities in the Mediterranean Levant. Undoubtedly, environmental changes similar to those of the Younger Dryas/Early Holocene transition occurred previously during earlier phases of the Pleistocene. But, for the first time, these climatic changes were accompanied by sedentism, more complex social organization, and technologies for harvesting and for food storage.

Declaration of competing interest

The authors declare that they have no known competing financial interests.

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Author statement

All the authors materially participated in the research and article preparation.

Appendix A. Supplementary data

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