



Ecological-cultural inheritance in the wetlands: the non-linear transition to plant food production in the southern Levant

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Abstract

The paper discusses a multi-proxy archaeobotanical dataset from the published macrobotanical and microbotanical research of 19 Epipalaeolithic sites over a period of 13.5 ka (ca. 25–11.5 ka cal BP) in the southern Levant. The archaeobotanical record includes over 200 phytolith samples extracted from sediments of 11 sites, macrobotanical evidence from seeds, plant tissues and wood charcoal from 11 sites and other microbotanical data from starches and starch spherulites from three sites. Phytolith assemblages show that Epipalaeolithic hunter-gatherers relied on wetland plant resources, and the macrobotanical evidence demonstrates the cultural importance of wetland resources to Late Epipalaeolithic foodways. The paper assesses the archaeobotanical data, using niche construction theory (NCT) to argue that human impacts in the wetlands over generations increased wetland productivity and created long-lasting ecological and cultural inheritances that allowed for the evolution and proliferation of a wetland-based system of wild plant food production. This paper proposes the idea that wetlands provided Epipalaeolithic people with a ‘domestication laboratory’ that allowed them to interact and modify their environment and also to experiment and gain new knowledge to build the long-lasting ecological-cultural inheritances necessary for the transition to plant food production. Importantly, the ecological-cultural inheritance of wild plant food production in the wetlands enabled the non-linear transition to cereal-based wild plant food production and domestication that took place in the southern Levant.

Keywords Multi-proxy archaeobotanical dataset · Niche construction theory · Wetlands · Macrobotanical · Microbotanical · Epipalaeolithic

Introduction

The origins of agriculture in the Levant have been explored in detail (for example, Vavilov 1926; Braidwood 1951; Childe 1952, 1956; Sauer 1952; Braidwood and Howe 1960; Bender 1975; Mellaart 1975; Cohen 1977; Rindos 1984; Hayden 1992, 1995, 2003; Cauvin 1994; Winterhalder and Kennett 2006; Gremillion and Piperno 2009), but the long-term developments of the transition to plant food production

remain unclear (Price and Bar-Yosef 2011; Asouti and Fuller 2013). The primary obstacle is the inconsistent nature of the botanical record (Asouti and Fuller 2012, 2013). Levantine Epipalaeolithic sites (ca. 25–11.5 ka cal BP) tend to have poor macrobotanical preservation of seeds, wood charcoal, fruits and nuts. Furthermore, the evidence available, for example, from the remarkable botanical assemblage at the site of Ohalo II, 23 ka BP, has centred on the remains of plant taxa that became the first domesticates, wild cereals and grasses (Kislev et al. 1992; Weiss et al. 2004a, b; Snir et al. 2015). This focus is symptomatic of a broader disciplinary preoccupation with identifying the intensification of wild cereals, a key step in the ‘broad-spectrum’ revolution outlined by Flannery (1969, 1973), and is understandable in the context of the limited macrobotanical evidence then available from the southern Levant. However, this emphasis on the pre-agricultural use of wild cereals has reinforced the notion of a linear transition (in a regular sequence of development) to plant food production and the start of agriculture.

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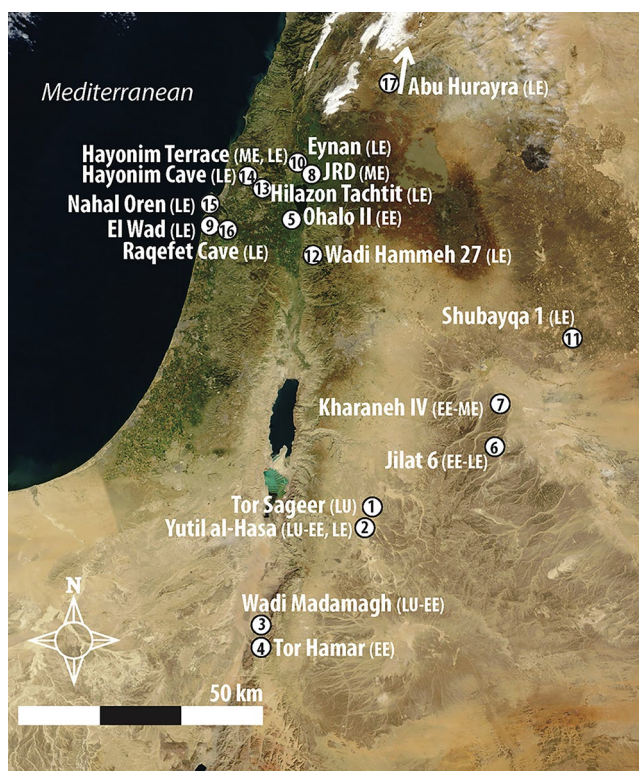


Fig. 1 Map of Southern Levant with location of sites discussed. LU, Late Upper Palaeolithic; EE, Early Epipalaeolithic; ME, Middle Epipalaeolithic; LE, Late Epipalaeolithic.

Phytoliths (microscopic silica ‘casts’ of plant cells) are now bridging the gaps in the archaeobotanical record and providing a useful long-term dataset. The phytolith evidence from Epipalaeolithic sites in the southern Levant emphasizes the importance of wetland-based plant resources (Rosen 2013; Ramsey and Rosen 2016; Ramsey et al. 2017). This paper reviews the available Epipalaeolithic phytolith research and evaluates the data against other macrobotanical and microbotanical evidence from this region (Figs. 1 and 2), within the framework of niche construction theory (NCT, see below) to argue that ecological-cultural inheritance in the wetlands facilitated a non-linear transition to plant food production (non-linear developments do not have straight or direct relationships between variables).

Epipalaeolithic hunter-gatherers relied on wetland resources and benefited from a self-reinforcing positive feedback loop whereby human use made the wetland plants such as *Cyperaceae* and *Phragmites* (reed) increasingly productive (Ramsey et al. 2015). Productive anthropogenic wetlands (under human influence) provided the resources needed to sustain generations increasingly ‘in place’, or settled. Epipalaeolithic hunter-gatherers living in wetland contexts employed a rational balance of reliable wetland resources which provided a year-round availability of edible plants such as *Cyperaceae*, *Phragmites* etc. together with

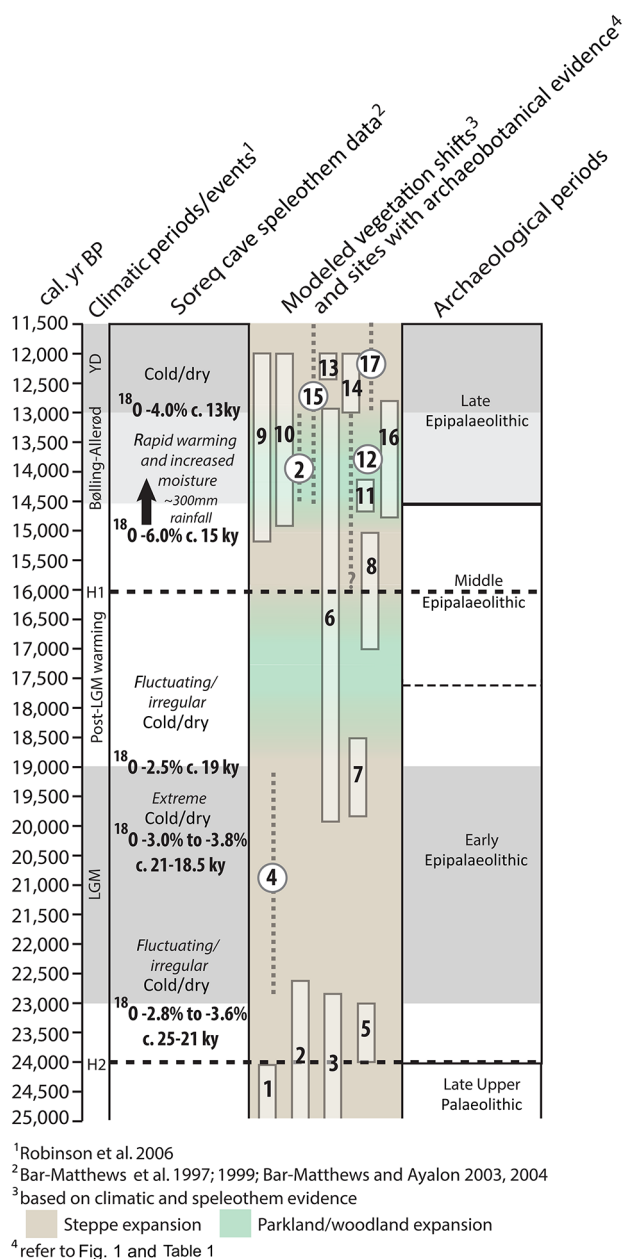


Fig. 2 Site occupation dates contextualized with climatic, vegetation and archaeological periods

animal resources and water. They also foraged strategically beyond the wetland into the surrounding steppe (xeric grass and shrub vegetation) and parkland (open vegetation with occasional trees) for highly seasonal wild cereals, grasses and other resources (Ramsey et al. 2016, p. 3). This paper hypothesizes that the wetlands provided a ‘domestication laboratory’, both in the wetlands themselves with useful *Cyperaceae* and *Phragmites* but also further afield in the steppe and parkland with wild cereals, which allowed generations of Epipalaeolithic people to interact, modify their environment, experiment and gain new knowledge to build

the long-lasting ecological and cultural inheritances necessary for plant domestication.

Unexpectedly, Epipalaeolithic peoples appear to have relied on wetland resources for their increasing use of wild grass and cereal resources. Indeed, the hypothesis put forth in this paper adds to the growing consensus that we need to rethink our view of the transition to plant food production in southwest Asia as a linear development just involving cereals. Expanding our understanding of pre-agricultural plant use by using a landscape-level approach, this paper evaluates the multi-proxy archaeobotanical evidence of foodways, material culture and palaeoenvironment over a long time period to assess other early forms of resource use and potential resource management in the wetlands. It contributes to the understanding of Neolithic plant use by exploring the origins of plant food production, assessing the evidence of wild plant use over the Epipalaeolithic period before cultivation and morphological domestication began during the Pre-Pottery Neolithic (Arranz-Otaegui et al. 2016). The Epipalaeolithic period includes the Early Epipalaeolithic (EE), Middle Epipalaeolithic (ME) and the Late Epipalaeolithic (LE) (Maher et al. 2012b; Belfer-Cohen and Goring-Morris 2014). These time periods coincide with a range of culture groups defined by tool typology (Muheisen 1988; Olszewski 2001; Nadel 2003; Kadowaki 2013), the most famous being the Natufian culture during the LE (Garrod 1957).

The Epipalaeolithic in the southern Levant, the LE in particular, is considered to be important to understanding the origins of agriculture in the region (Bar-Yosef and Belfer-Cohen 1989; Belfer-Cohen 1991; Valla 1995; Bar-Yosef 1998). Diverse wild plant resource use and broader human-environment interactions during the period produced the ecological and cultural foundations for domestication. Yet, previous macrobotanical research in the regions focused narrowly on the intensification of cereal resources (Kislev et al. 1992; Weiss et al. 2004a, b). Only recently have researchers adopted a broader perspective on wild plant use (Caracuta et al. 2016a; Arranz-Otaegui et al. 2018a, b). Moreover, most of the archaeobotanical research has employed a site level approach, producing localized models over short timescales from sites such as Ohalo II, Kharaneh IV and Shubayqa I. The transition to plant food production cannot be understood by examining any single archaeological site. As the macrobotanical syntheses of Asouti and Fuller (2012, 2013) and Arranz-Otaegui et al. (2018a, b) show, providing detailed regional archaeobotanical data is essential. Building on this, researchers have recognized the need to take a landscape level approach, which seeks to understand plant use at a broader scale, the scale of plant communities, over longer timescales (Fuller et al. 2012, 2016; Allaby et al. 2022). Archaeobotanists need to

cross the on-site and off-site boundaries, and examine the foodways, material culture and palaeoenvironmental trends, in order to build comprehensive and comparable botanical and environmental datasets. This paper will evaluate the state of the archaeobotanical record and interpret the evidence within the framework of NCT (niche construction theory) to assess the hypothesis of a non-linear shift from hunter-gatherers to wild plant food producers based on their use of wetland resources. It will conclude with some future directions for research.

Background

Changing scales and our understanding of the transition to agriculture: Niche construction theory and a landscape level approach

Humans are the ultimate niche constructing species (Smith 2007). Our ability to shape the environment precipitated the Anthropocene. Niche construction (Lewontin 1983; Odling-Smee et al. 2003) recognizes that organisms modify their ecosystems through their metabolism, activities and choices, affecting the course of their own evolutionary development (Laland et al. 2000, 2001; Odling-Smee et al. 2003). Uniquely, in shaping their environments, humans leave behind an ecological and cultural inheritance such as Jomon cultivated environments in Japan (Bleed and Matsui 2010), technological innovation (Collard et al. 2011), the development of plant food production in pre-European contact southern Ontario, Canada (Crawford 2014), the engineered landscape of Balinese rice terraces, Indonesia (Lansing and Fox 2011), prehistoric ‘conservation measures’ through the restructuring of resource communities to enhance resilience (Smith 2009), ‘wild’ plant and animal management or ecosystem engineering in small scale societies (Smith 2011a), or the evolutionary consequences of food production (Wollstonecroft 2011), that archaeology is well situated to uncover (Laland and O’Brien 2010).

Ecological inheritance, following Odling-Smee and Laland (2011), occurs when the niche constructing activities of an organism produce an ecological effect or ‘legacy effect’ (Cuddington 2011) in the environment that changes the selective pressures for subsequent generations with *evolutionarily significant consequences*. Beaver dams are an often-used example of this phenomenon in the animal world.

In the human context, the concept of ‘evolutionarily significant consequences’ is more complex, including both genetic and cultural evolution (Richerson and Boyd 2005) Mesoudi (2017) notes “[t]he emergence of this second evolutionary process [cultural evolution] saw an unprecedented

extension of genetic evolution by allowing organisms to adapt more rapidly to, and more powerfully create and shape, their environments”. Examples of evolutionarily significant cultural evolution include major phenomena such as the transition to plant food production, the start of agriculture, the rise of urban centres and the development of civilizations.

In NCT, cultural evolution is transmitted through ‘cultural inheritance’, which Odling-Smee and Laland (2011, p. 226) define as “that subset of niche construction that is the expression of culturally learned and transmitted knowledge”. This as a definition is, however, somewhat problematic from an environmental archaeology perspective. Following this definition, any interaction between humans and their environment that produces evolutionarily significant phenomena stemming from culturally learned or transmitted knowledge is considered cultural rather than ecological inheritance. In studying plant remains, for example, the archaeobotanist would be required to ascertain whether or not any interaction causing landscape modification such as landscape burning and the subsequent ecological succession, or Cyperaceae or *Phragmites* collection and the subsequent expansion of the wetland margin (phytolittoral zone), was the result of cultural learning, which would be difficult to prove. Plant domestication is a clear example of a process that required culturally transmitted learning. However, the line of knowledge transmission is less clear the further back in time we go from morphological domestication. In many contexts it is inconsequential to the broader questions whether the environmental signature is an ecological or a cultural inheritance. Moreover, Odling-Smee and Laland (2011, p. 227) view cultural inheritance as a subset of ecological inheritance, and therefore the two are closely interrelated. For these reasons, the author sees very little need to separate these two concepts in the context of understanding Epipalaeolithic plant use and the evolution of plant food production. Accordingly, in this paper, these concepts are mentioned together as ecological-cultural inheritance.

Odling-Smee and Laland (2011) recognize that the build-up of niche construction as an ecological inheritance over long time periods strongly affects the development of constructor populations, such as coral reefs or shell mounds. This time dimension to niche construction is particularly significant in human niche construction (Sterelny 2012) as ecological-cultural inheritance, and is therefore key to exploring how humans use and are affected by niche construction. This paper contends that *as successive generations build on the ecological-cultural inheritance of their ancestors, their ecological and cultural innovations become more powerful, increasing the impact of their niche construction practices and exerting evolutionarily significant phenomena*, which is cumulative cultural evolution (Mesoudi and

Thornton 2018). Therefore, the process of accumulating ecological-cultural inheritances makes NCT relevant for archaeological studies.

The application of NCT has been steadily growing over the past decade as an approach to understanding human-environment interactions and in particular plant use and domestication in archaeology (Smith 2007, 2011b; Rowley-Conwy and Layton 2011; O’Brien and Laland 2012; Crawford 2014; Florin and Carah 2018). But the number of criticisms of NCT has also grown, with some arguing that it is only useful for description and does not provide a testable explanatory mechanism (Wallach 2016; Spengler 2021, also for detailed literature review). This criticism is often levelled by optimal foraging proponents who are particularly interested in discovering the prime movers for resource selection and agricultural origins. Academic discourse has tended to pit resource depression, the prime-mover posited in optimal foraging models against resource abundance, the prime-mover that has tended to be posited by NCT models (Smith 2011b, 2015; Gremillion et al. 2014; Zeder 2015, 2018). The author does not view NCT in opposition to optimal foraging. Rather, it fits neatly as a part of human behavioural ecology which takes an evolutionary approach to human behaviour. NCT is complementary to a range of other concepts, including historical ecology (Crumley 1994; Balée and Erickson 2006) and human ecology (Butzer 1982). Findings interpreted by NCT can be usefully applied to adjust local optimal foraging models or plant food production models (Mohlenhoff et al. 2015; Mohlenhoff and Coddling 2017; Piperno et al. 2017; Florin and Carah 2018; Ready and Price 2021). This nuanced and flexible application of NCT for interpreting archaeological data has led some to suggest that it is less than straightforward or even ‘unified’ (Spengler 2021). This criticism highlights the need for a broader discussion about how NCT should be applied usefully to archaeological data. Is it, for example, simply a new term for a range of concepts we already employ such as management, cultural ecosystems and human activities? Does NCT have any explanatory mechanism or testable utility, a middle-range theory application (theories linking human behaviours and natural processes to physical remains in the archaeological record)? Or is it descriptive in use and only helpful for generating and organizing ideas like historical ecology? These are some of the questions we need to think about when using NCT for interpreting archaeological data.

This paper argues that NCT is useful in archaeology and in particular for understanding changes and transitions in plant use over long time periods. While different plant management strategies such as vegetation burning, coppicing, weeding, etc. are part of a range of human niche construction or ecosystem engineering behaviours (*synchronic*), they do not in isolation result in evolutionarily significant

phenomena, either genetically or culturally. There are two primary variables to consider when determining the utility of NCT in archaeological contexts. First, is it possible to identify and track evidence of ecological-cultural inheritance, the long-term generational impacts of niche construction (*diachronic*)? Second, can the investigation inform understanding of evolutionarily significant phenomena?

The concept of a landscape level approach is borrowed from ecology and was most clearly outlined for archaeological applications by Karl Butzer (1982). Butzer's approach emphasized a diachronic understanding of the 'landscape context' (1982, p 38). Landscapes are complex systems, they are multi-component, consisting of biotic elements such as animals and plants, and abiotic elements such as soil, water, surface gradient, etc., and these are constantly interacting, changing and affecting subsequent ecological processes (Newman et al. 2019) in the sense of niche construction and ecological inheritance. The concept of a 'landscape level' approach ('landscape framework' according to Allaby et al. 2022) has recently been applied to understanding the origins of plant domestication and human plant use with the aim of moving beyond site-level analyses (Fuller et al. 2012, 2016; Allaby et al. 2022). In the context of tracking trends of Epipalaeolithic human plant use, this paper employs a landscape level approach that shifts focus from one plant of interest such as *Schoenoplectus* (club rush), an approach typically applied in macrobotanical analysis, to viewing a range of plant taxa (plant communities) in their biotic and abiotic contexts; for wetlands, their biotic components are plants; and their abiotic components the water chemistry,

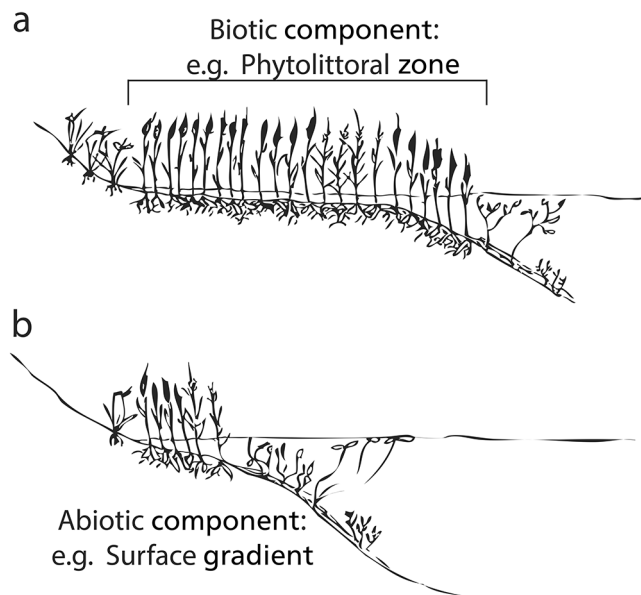


Fig. 3 Simple illustration demonstrating how biotic and abiotic components can interact to change the wetland; **a**, shallow surface gradient produces a larger phytolittoral zone; **b**, steep surface gradient produces a smaller phytolittoral zone

surface gradient, water flow, water depth, etc. (Fig. 3). A landscape level approach requires comparative diachronic archaeological datasets using appropriate scales such as landscape/population vs. taxa/individual.

This approach to NCT avoids the pitfall of being 'all-encompassing' (Spengler 2021) and favours no single assumption from first principles regarding the prime mover behind human resource selection, for instance resource depression vs. resource abundance, and emphasizes a bottom-up data-led approach. NCT requires the evaluation of the appropriateness of the datasets being used, an appraisal all researchers should make regardless of their preferred theoretical framework. In this paper, diachronic archaeobotanical evidence provides insights into Epipalaeolithic ecological-cultural inheritances and helps in understanding the development of broader cultural changes, like the transition to agriculture. It will help us refine and better apply middle-range theory, that directly links human behaviour to physical remains, such as optimal foraging theory and plant food production models.

Non-linear interactions between people and plants, and plant food production models

It is important to have a long time perspective of human plant use to be able to understand the foundations for the origins of agriculture. Ecological-cultural inheritance played a crucial part in this transition. Indeed, the accumulation of ecological-cultural inheritances and associated ecological and cultural feedbacks, which can radically alter the patterns of plant use and their changes, increases the likelihood of non-linear, or irregular, developments. Linear developments tend to be additive, *x leads to y*. Straight-line thinking is typical when modelling relationships, and simplification is necessary. Non-linear developments are not based on proportional cause and effect outcomes. Interactions between humans and their environment and with plants are co-evolutionary dynamics in which causes and their effects are not necessarily proportional. Co-evolution is one of the major mechanisms for generating non-linear interactions (Holland 2014). Indeed, as Freeman et al. (2015) point out "the feedbacks caused by niche construction... [are] known to cause non-linear trajectories of evolution". Most relationships or interactions are non-linear. In the context of long-term people-plant interactions, many of the developments are non-linear. Therefore, rather than applying a linear retrospective focused on cereal development, a data-led bottom-up approach is necessary to understand plant use during the Epipalaeolithic (Fig. 4a). The potential for non-linearity makes it important to integrate a NCT perspective in the application of plant food production models (Fig. 5; Ford 1985; Harris 1989, 1996; Smith 2001).

Fig. 4 **a** Linear and **b** non-linear models for the transition to agriculture

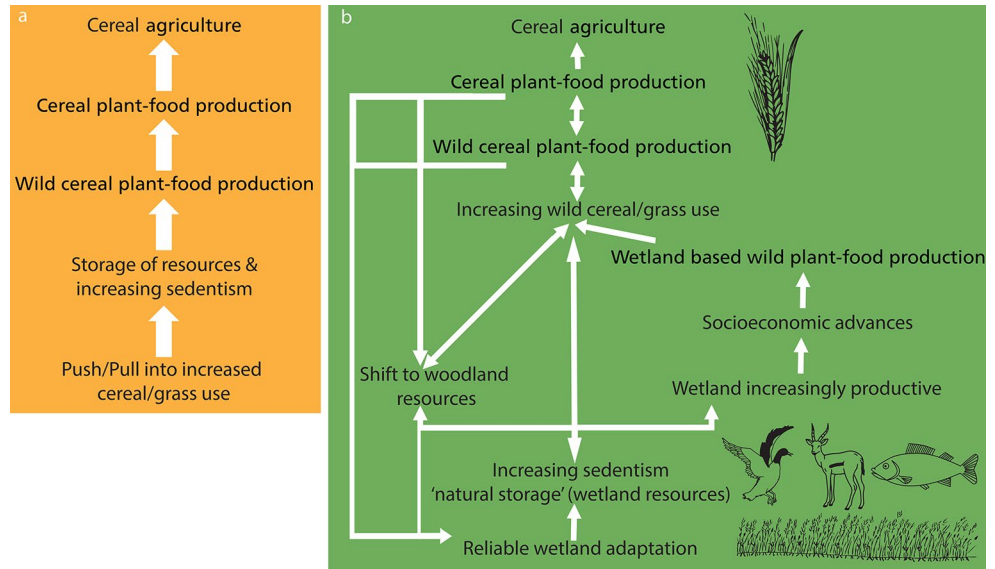


Fig. 5 Plant food production model; **a**, model based on Smith 2001; **b**, schematic model of changing plant-use proportions through time; **c**, description of hypothesized shift from wild plant-food procurement to a wetland-based wild plant-food production in the Southern Levant. Ecological-cultural inheritances outlined, with the types of archaeological samples and evidence needed to identify this transition

Food procurement		FOOD PRODUCTION	
		Low-level food production	Agriculture
Wild plant-food procurement	Hunting-gathering-fishing	Without domesticates	With domesticates
		Wild plant-food production	

decreasing dependence on wild plants for food	
wild wetland plant-use	
wild cereal and grass use	cereal and other domestic cultivar use

C Shift from wild plant-food procurement to a wetland-based wild plant-food production

*Niche constructing behaviours	Procurement	Production	Samples:	
	Burning Protective tending	Increased scale of wetland disturbance	Increased scale of wetland burning Increased growth of wetland taxa	off-site cores/sections site periphery and regional
				Evidence: micromorphology microcharcoal phytoliths pollen
More mobile settlement	Increased use of wetland taxa Increasing plant-food processing Increasing sedentism Increased social/cultural significance of wetland taxa		Samples: on-site sediments on-site food processing contexts ground stone residues Evidence: macrobotanical remains processed food remains phytoliths starches starch spherulites	

*Behaviours that may lead to an ecological-cultural inheritance

Plant food production models map the transition from hunting and gathering to agriculture. They are necessarily simplifications, but context and complexity must be added

in their application. In the ‘middle ground’ between hunting and gathering and agriculture, a range of strategies for using plants has been outlined. Ford’s (1985) model identifies cultivation as the main stage between foraging and domestication. Harris’ (1989) model is more nuanced in identifying wild plant food production and cultivation, with domestication marking agriculture. This model was revised in 1996, removing the hard boundary for domestication and focusing instead on the shift from wild plant food procurement to wild plant food production (Harris 1996). Smith’s (2001) model identifies two categories between hunting-gathering and agriculture, which are low-level food production either without domesticates or with them (Fig. 5a). These authors all mark the differences between their model categories based on the use of certain management practices and their related outcomes such as domestication. Harris’ (1989) model is particularly descriptive regarding the kinds of activities for plant use that mark each category. For example, *wild plant food procurement* includes burning vegetation and protective tending; *wild plant food production* includes transplanting, weeding, replacement planting/sowing, storage and irrigation/drainage, while *cultivation* includes land clearance and systematic soil tillage.

NCT should be applied at the macro level of analysis topically (taxa vs. landscape) and temporally (synchronic vs. diachronic). While the plant use activities listed above are examples of ecosystem engineering, they are not in isolation evidence of evolutionarily significant niche construction (Odling-Smee 2010). Rather, these activities of plant use need to accumulate through time with repeated and/or group activity, potentially over generations to exert an ecological-cultural inheritance of evolutionary significance. Accordingly, for the Epipalaeolithic in the southern Levant it is critical to take a long term diachronic view of the environmental and archaeological evidence to construct appropriate archaeological and archaeobotanical interpretations of regional transitions in plant food production.

Epipalaeolithic climate and environmental foraging opportunities

Isotope data from the Nahal Soreq cave provides a long-term palaeoclimatic record for the region. Dated by uranium/thorium and expressed as calendar years, the $\delta^{18}\text{O}$ (calibrated for rainfall) and $\delta^{13}\text{C}$ (calibrated for vegetation, C_3 vs. C_4) values are used to show changes between warm/wet and cold/dry periods in the region (Fig. 2; Bar-Matthews et al. 1997, 1999; Bar-Matthews and Ayalon 2003, 2004). The data show that during the Epipalaeolithic period there were pronounced climatic changes, with an extreme cold and dry period during the Last Glacial Maximum (LGM) followed by a less extreme period of fluctuating cold/dry

conditions before the Bølling-Allerød, which featured rapid climatic amelioration to warm and wet, before the start of the Younger Dryas, another cold/dry period (Robinson et al. 2006, for summary of climatic periods/events). These trends are now being confirmed at the local scale with studies that combine archaeobotanical remains with stable isotope analysis (Caracuta et al. 2016b; Belli et al. 2021) (El Wad and Raqefet caves, Table 1).

The climatic changes would have caused shifting environmental foraging opportunities. Warm/wet periods were characterized by the expansion of woodlands which were rich in various nuts and fruits. Cold/dry periods were characterized by the expansion of steppe and parkland which had a range of edible wild grasses and cereals growing there (Rosen and Rivera-Collazo 2012). Steppe and parkland varied greatly in primary productivity between cold/dry and warm/wet periods (Gibson 2009), with grasses and parkland resources being more productive during warm/wet periods (Ramsey et al. 2016, p. 8, Fig. 3). This variation means that the wetland environments that occurred in the region in places such as Azraq basin or Hula marsh would have been particularly important during cold/dry periods such as the LGM, when the steppe and parkland would probably have been less productive (Ramsey et al. 2016). Wetland environments provide reliable perennially available plant resources, specifically plants with edible roots like Cyperaceae, which actually increase in nutrient quality during dry periods of low growth (Wrangham et al. 2009). The phytolittoral zone, the vegetated edges typical of marshes and other shallow water environments, are identified as the most productive part of the wetlands (Ramsey and Rosen 2016; Keddy 2000). Some Cyperaceae (sedges etc.) and *Phragmites* sp. (reeds) which would have been key plant taxa of great economic and subsistence value to humans, grow in such shallow wetland environments.

Regarding subsistence, Hillman et al. (1989) outlined the processing methods and dietary uses of *Cyperus* tubers worldwide. Of the species available in the southern Levant, *C. rotundus* rhizomes are high in carbohydrates and are shown to have a calorific return of 4.435 kcal/hr gathering time, higher than most cereals (Wright 1994). Experimental work on another of the Cyperaceae available in the southern Levant, *Bolboschoenus maritimus* (sea club-rush), suggests that grinding and pulverizing of the roots would have softened the tissues and increased the bioaccessibility of nutrients through cell rupture and separation (Wollstonecroft et al. 2008) Hillman (2000) also conducted processing experiments demonstrating that *Bolboschoenus* sp. seeds can be roasted and ground into a palatable flour. Ethnobotanical studies from the Great Basin, USA, provide a useful ethnographic analog, further emphasizing the potential of wetland resources, such as those found in the southern Levant, for

Table 1 Epipalaeolithic archaeobotanical evidence in the Southern Levant, for source [] see ESM

Site (Figs. 1–2)	Dates (ka cal. BP)	Botanical remains (sample N)	Plant-use summary	Source
1 Tor Sageer	Post-dates 24.6–24.1 [1]	Phytoliths (16)	Wetland evidence (sedge cones and fan-shaped bulliforms) (wetland-type approx. 25%), but suggestive of a riparian wetland with shrubby dicots (woodland-type, see Table 1, approx. 70–75%). Grass husks also recovered	[2]
2 Yutil al-Hasa (Area C)	25.3–22.4 [1]	Phytoliths (11)	Wetland evidence (sedge cones and fan-shaped bulliforms) (wetland-type approx. 10%), but suggestive of a riparian wetland with shrubby dicots (woodland-type, see Table 1, approx. 85–90%). Grass husks also recovered	[2]
3 Wadi Madamagh	25–23 [3]	Phytoliths (11)	Wetland (sedge cones and fan-shaped bulliforms) (wetland-type approx. 25%) and woodland-type resource use (e.g. scalloped, coarse verrucate, platelets) (approx. 75%). Negligible evidence of grass husks	[2]
5 Ohalo II	24–23 [4]	Phytoliths (28), macrobotanicals, starch and starch spherulites	Phytolith evidence emphasizes wetland based (e.g., Cyperaceae and <i>Phragmites</i> sp.) (wetland-type more than 50%), but generally diverse plant use strategy that included steppe and parkland grasses and cereals (parkland-type approx. 30–40%) as well as woodland dicot resources (woodland-type, see Table 2, approx. 10%). Phytolith evidence also demonstrates that Cyperaceae and <i>Phragmites</i> sp. were used in hut construction. Macrobotanical evidence for wetland use includes <i>Phragmites</i> sp. (culm), Cyperaceae (nutlets), <i>Carex divisa</i> (nutlets), and <i>Scirpus litoralis</i> (nutlets). Steppe and parkland grasses include <i>Triticum dicoccoides</i> , <i>Hordeum spontaneum</i> , <i>Avena</i> sp., <i>Aegilops</i> sp., <i>Bromus</i> sp. and <i>Hordeum marinum/hystrix</i> . Site features evidence for cereal plant processing by-products (chaff) and twisted plant fibers. Woodland evidence includes <i>Amygdalus</i> sp., <i>Olea europaea</i> (olive), <i>Pistacia atlantica</i> (pistachio), <i>Quercus ithaburensis</i> (acorn) and a range of other shrubby and herbaceous taxa. Approx. 160,000 charred and un-charred seed and fruit remains, with over 140 identified taxa. Starch evidence on the upper face (grinding surface) of the main grindstone demonstrates that 176 of the 199 grains recovered were diagnostic of grass seed starches (AHT starch (<i>Aegilops</i> , <i>Hordeum</i> , <i>Triticum</i>) and <i>Avena</i> sp.). Starch spherulites suggest cooking of starchy plant foods	[2, 5–20]
4 Tor Hamar	Early Epipalaeolithic, Qalkhan	Phytoliths (1)	Woodland evidence (dicot), as well as grasses (although minimal husk evidence). Grasses generally C ₄ , suggests warmer drier conditions. Small component of wetland resources (<i>Cyperus</i> and <i>Juncus</i>)	[21]
6 Jilat 6	20.2–12.9 [22]	Macroremains	Chenopods, grasses and sedges. Poor macrobotanical preservation	[23–26]
7 Kharaneh IV	19.9–18.6 [22]	Phytoliths (62 EE, 13 ME), macrobotanicals (41 EE, 54 ME)	Phytolith evidence suggests wetland based (e.g. Cyperaceae and <i>Phragmites</i> sp.) (more than 50% wetland-type) with steppe grasses (parkland-type, see Table 1, approx. 30%), but transition to increased woodland use in the Middle Epi (woodland-type, see Table 1, approx. 20–25%). Response to climatic amelioration and potential woodland expansion. Phytolith evidence also demonstrates that Cyperaceae and <i>Phragmites</i> sp. were used in hut construction. Total of 95 macrobotanical samples, yielded 2,985 seeds and other plant items, including at least 16 taxa. Chenopodiaceae and <i>Atriplex</i> sp. seeds were frequent. Little evidence for tuber or legume use. Poor macrobotanical preservation	[2, 20, 27, 28]
8 Jordan River Dureijat (JRD)	17.1–15.3 [29]	Macroremains	Wetland location, with evidence of woodland plant use (fig, acorn and grape). Steppe and parkland grasses include barley (<i>Hordeum spontaneum</i>)	[29, 30]
9 el-Wad	15.2–12 [31]	Phytoliths (41 EN), macroremains	Phytolith evidence suggests wetland (Cyperaceae and <i>Phragmites</i> sp.), steppe (grass husks) and woodland (dicots) resources employed, with an emphasis on woodland resources. Wood charcoal analysis shows oak woodland predominated. Macrobotanical evidence for 261 remains from 14 taxa. Fabaceae, <i>H. spontaneum</i> , <i>Amygdalus</i> sp., <i>Craetagus</i> sp. (hawthorn) and other wild taxa. The site also features the wild progenitor of domestic <i>Vicia faba</i> . Stable isotope $\Delta^{13}\text{C}$ values from <i>Amygdalus</i> sp. suggest increased rainfall between 14.6–13.7 ka cal BP followed by a clear decrease between 13.7–12 ka cal BP	[32–36]
10 Eynan (Ain Mallaha)	ca. 15–12	Phytoliths (4 EN, 20 LN)	Shift from an emphasis on woodland (dicots) resources towards steppe and parkland grasses (monocots) during the YD. This shift also saw an increase in the use of wetland resources (e.g. Cyperaceae and <i>Phragmites</i> sp.)	[36, 37]

Table 1 (continued)

Site (Figs. 1–2)	Dates (ka cal. BP)	Botanical remains (sample N)	Plant-use summary	Source
11 Shubayqa 1	14.6–14.2 [38]	Macroremains, starch	Wetland and steppe resources employed. Earliest evidence for ‘bread’-like foodstuff, made with wild cereals and club-rush tubers. Macrobotanical analysis concentrated in two fireplaces. Total of 67,458 non-woody macroremains identified. More than 50 taxa identified, 29 taxa identified to species. High concentrations of Cyperaceae (mainly <i>Bolboschoenus</i> sp.) tubers, nutlets and seeds in fireplaces (c. 80% of plant remains in both fireplaces), followed by Brassicaceae (~ 16.7 and 18%), Poaceae and Fabaceae (< 1%) and other wild plants. Most common large seeded Poaceae was <i>Triticum</i> ssp. Wheat chaff was recovered. <i>H. spontaneum</i> and <i>Avena</i> ssp. was also recovered	[39–42]
2 Yutil al-Hasa (area D)	Late Epipalaeolithic, Early Natufian	Phytoliths (n?)	Riparian wetland, with presence of reeds (<i>Phragmites</i> sp.) and shrubby dicots. Grass husks also recovered	[43]
12 Wadi Ham-meh 27	ca. 13.9	Macroremains	Steppe and parkland grasses including wild barley (<i>H. spontaneum</i>), <i>Aegilops</i> sp., <i>Bromus</i> sp., <i>Lolium</i> sp. and <i>Stipa</i> sp. Some cereal processing by-products (chaff, three <i>H. spontaneum</i> rachis internodes). Other steppe and parkland plants include Liliaceae and Fabaceae. Woodland taxa include <i>Pistacia</i> sp. nut shells. However, low density of remains, 0.02 cm ³ per liter. Most remains 1.5 mm or less. Total of 3202 remains from 14 samples, 222 were identifiable. Poor macrobotanical preservation	[23, 44, 45]
13 Hilazon Tahtit	12.4–12 [36]	Phytoliths (4 LN)	Wetland based (Cyperaceae and <i>Phragmites</i> sp.), with heavy use of steppe and parkland grasses (grass husks)	[36]
14 Hayonim Terrace	Middle-Late Epipalaeolithic, Geometric Kebaran and Late Natufian	Phytoliths (6 LN)	Increased use of steppe and parkland grasses, wild cereals (grass husks) and importantly wetland resources (Cyperaceae and <i>Phragmites</i> sp.) in response to cooler/drier YD	[46, 47]
14 Hayonim Cave	Late Epipalaeolithic, Early Natufian	Macroremains	Steppe and parkland grasses and woodland resources were employed. However, only, four taxa identified, <i>H. spontaneum</i> (2 grains), <i>Amygdalus communis</i> (almond nutshells), <i>Lupinus pilosus</i> (lupine seeds), and possibly pea. Poor macrobotanical preservation	[48]
15 Nahal Oren	Late Epipalaeolithic, Natufian	Macroremains	Woodland resources. Taxa identified include <i>Vicia</i> sp. (vetch), <i>Olea</i> ssp. (wild olive) and <i>Vitis</i> sp. (grape)	[49]
16 Raqefet Cave	Late Epipalaeolithic, Natufian	Phytoliths (35), macroremains, plant impressions, starch and phytoliths from cup mortar residues	Phytoliths demonstrate steppe and parkland grasses (wheat, barley and small-seeded grass husks – most important), wetland (Cyperaceae and <i>Phragmites</i> sp.), and woodland resources (dicots) employed. Macrobotanicals provide evidence of <i>Amygdalus</i> sp., <i>Quercus</i> ssp., <i>Avena</i> sp., <i>H. spontaneum</i> , <i>Triticum</i> ssp., a range of Fabaceae, <i>Olea europaea</i> (olive), <i>Vitis vinifera</i> (grape) and other wild taxa. Plant impressions: <i>Salvia judacia</i> Boiss. (Judean sage), other Lamiaceae (mint family) or Scrophulariaceae (figwort family) species. Samples mainly from specialized contexts – burials and cup stone mortars. Starch residue analysis of the cup stone mortars identified a range of taxa, including wheat or barley, oats and wild grasses, <i>Cyperus</i> sp., lily bulb (1 grain) and other unidentified roots (USOs), and Fabaceae, hypothesized to have been used in the preparation of a fermented beverage. Stable isotope $\Delta^{13}\text{C}$ values from <i>Amygdalus</i> sp. suggest increased rainfall between 14–12.6 k cal BP	[51–55]
17 Abu Hureyra	Late Epipalaeolithic, Late Natufian	Macroremains	Steppe and parkland grasses include <i>Triticum</i> sp., <i>Secale</i> sp., <i>Hordeum bulbosum</i> , <i>Stipa</i> sp. and chenopods. Woodland resources include <i>Quercus</i> sp. and <i>Pistacia</i> sp. Wetland resources also feature prominently, in particular, club-rush (<i>Scirpus maritimus/tuberosus</i>). Late Natufian phases yielded approx. 31,000 remains (not including charcoal), with 95 plant taxa	[56–59]

food, providing a wealth of evidence for how wetland edge plant resources may have been employed during the Epipalaeolithic (Ramsey et al. 2017). For example, *Phragmites* sp. seeds may have been dried and ground into a flour, the young shoots and leaves boiled as pot herbs, or the stems may have been dissolved in water to make a sweet drink (Ebeling 1986). These ethnographies emphasize the use of stone tools including hand grindstones, pestles and mortars, both portable and in bedrock, for preparing wetland plant materials for food.

The climatic and environmental setting of the southern Levant during the Epipalaeolithic period made wetland resources an important part of hunting, gathering and potentially, plant food production. However, the use of wetland resources is often underestimated in the region when evidenced only from macrobotanical remains, as demonstrated by Ramsey et al. (2017) in an analysis comparing the phytolith and macrobotanical assemblages from Ohalo II. This paper emphasizes a multi-proxy archaeobotanical approach for reconstructing foodways, material culture and palaeoenvironment. These approaches are standard practice in palaeoecology, however until recently, they were less well developed in archaeobotany (García-Granero et al. 2015). In the past decade this has changed with the effective combination of macrobotanical and microbotanical studies at the site scale (Delhon et al. 2008; Dickau et al. 2012) and at the scale of individual food remains (Heiss et al. 2017; Arranz-Otaegui et al. 2018a). This paper outlines a multi-proxy approach on a regional scale.

Results

Archaeobotanical evidence: constructing a broad picture of epipalaeolithic plant use in the southern Levant

The published macrobotanical and microbotanical evidence from 19 Epipalaeolithic sites (Figs. 1 and 2; Table 1) is reviewed here to explore plant use on a regional scale in the southern Levant, mainly Israel and Jordan, although the site of Abu Hureyra, Syria, is included. Previous syntheses of plant use from the broader region and/or different time periods were based on macrobotanical remains only

Table 2 Phytolith microfossils organized according to ecozone-type

Ecozone-type	Phytolith microfossils
Wetland	Cyperaceae ‘cones’ (Ollendorf 1987, 1992), ‘fan-shaped bulliforms’ (cf. reeds), reed culm and leaf, <i>Phragmites</i> sp. culm and leaf (Ryan 2011)
Woodland	Platelets, honeycomb, coarse verrucate, polyhedron (Bozarth 1992), all irregular dicots
Steppe/parkland, grasses	Dendritic long-cells, papillae, cereal straw (Rosen 1993), all husk multi-cells (Rosen 1992)

(for example Asouti and Fuller 2012, 2013; Arranz-Otaegui et al. 2018a, b). The published microbotanical phytolith record discussed here currently includes over 200 samples extracted from the sediments of 11 sites. Macrobotanical evidence from seeds, plant tissues and wood charcoal is available from 11 sites and other lines of microbotanical evidence (starch and starch spherulites) from three sites are also included. The archaeobotanical results are provided as a qualitative summary, with references to the published data, to provide an important reference list and summary of plant use. It was not possible to compare the results between all the sites quantitatively, because the varied data sets are often either not comparably sampled and/or the raw data are not available in the publications. Moreover, using this approach to compare results quantitatively requires close control of contexts, such as that achieved at Ohalo II (Ramsey et al. 2017). However, comparing plant remains qualitatively between sites is a powerful tool for understanding trends in plant use, but issues of differential taphonomy between archaeobotanical remains and processing discrepancies must be ruled out or acknowledged as possibly contributing to the patterns in the archaeobotanical assemblages.

The results in this paper are discussed qualitatively at two scales, first in broad groupings at the landscape level, or as ecozone types (wetland, steppe and parkland, and woodland), generally shown by phytolith data following the phytolith groupings in Ramsey and Rosen (2016), Table 2; Fig. 6, and secondly in more detail at the level of taxa according to the available macrobotanical and other archaeobotanical evidence. Phytolith analysis is particularly suited to a landscape scale approach, for although phytoliths are not very taxonomically specific, they are generally more taphonomically robust than other plant remains such as seeds. This allows easier comparison between sites, and in future studies, between on-site and off-site contexts.

Wetlands

The phytolith evidence suggests that Epipalaeolithic people relied heavily on wetland resources for craft uses such as hut construction as well as for food, with plenty of evidence for Cyperaceae and *Phragmites* throughout the entire 13.5 ka period (Fig. 6, Tables 1 and 2). This interpretation is also supported by more recent archaeobotanical investigations, particularly macrobotanical evidence of Cyperaceae recovered from the hearths at Shubayqa 1, along with bread-like remains that included *Bulboschoenus* sp. tubers (probably prepared as flour), and starch evidence of *Cyperus* sp. from cupstone mortars at Raqefet cave, all of which demonstrate the use of wetland resources for food. The archaeological evidence shows the use of a grinding stone in the preparation of wetland plant resources and calls

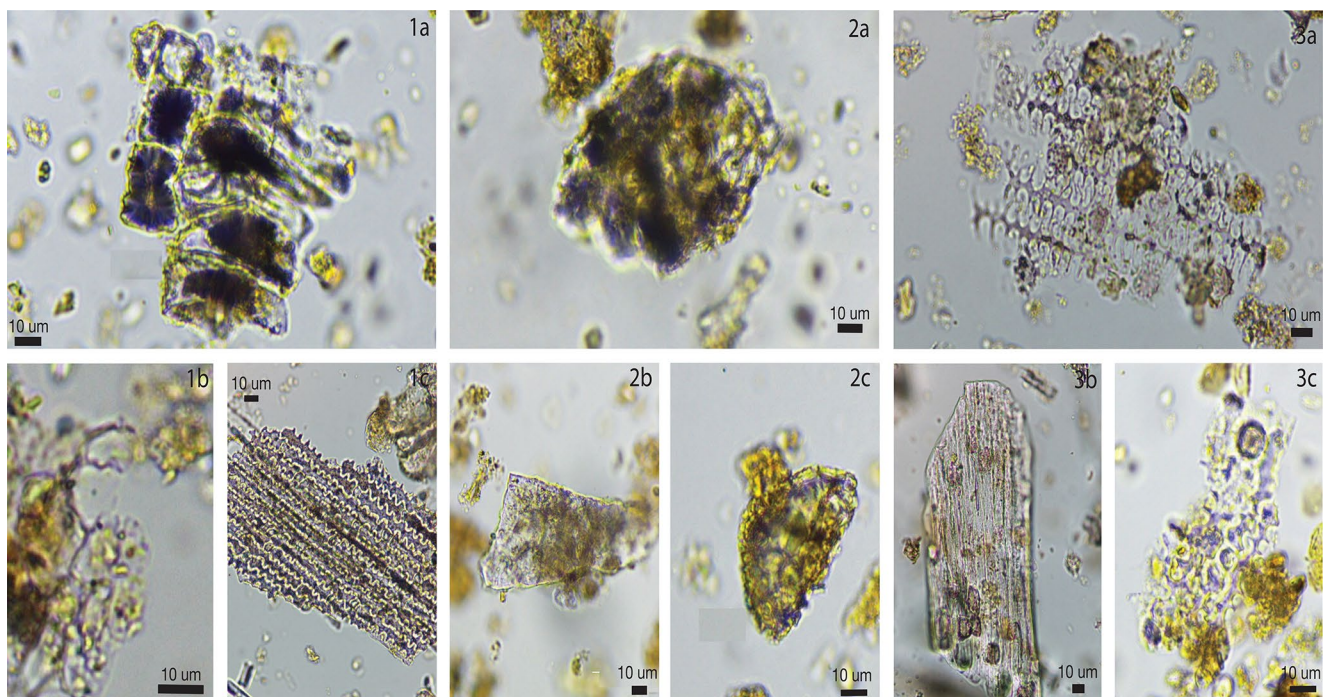


Fig. 6 Images of phytoliths recovered, organized by environment-type: **1.** wetland-type phytoliths, **1a** stacked ‘fan-shaped bulliform’ (cf. reeds) (Kharaneh IV), **1b** sedge cones cf. *Scirpus* (Ohalo II), **1c** *Phragmites* culm (Ohalo II); **2.** woodland-type phytoliths, **2a** coarse

verrucate (dicot leaf) (Kharaneh IV), **2b** platelet (dicot leaf) (Wadi Madamagh), **2c** scalloped (dicot leaf) (Kharaneh IV); **3.** parkland-type phytoliths, **3a** wild grass husk (Ohalo II), **3b** cereal straw (Ohalo II), **3c** wild grass husk (Kharaneh IV) (Ramsey and Rosen 2016)

into question previous links between increasing evidence of grinding stones (Wright 1991, 1994) and increasing cereal use (McCorriston and Hole 1991; Willcox 2005; Edwards 2007), to the exclusion of other resources in the region. It is also important to note that Cyperaceae roots and tissues are incredibly delicate, and they are almost certainly under-represented and under-identified in archaeobotanical assemblages (“missing food”, Arranz-Otaegui et al. 2018b). With many of the Epipalaeolithic sites displaying evidence for increasing sedentism (more settled life), and increasing use of grinding stones at, or close, to wetland environments, it is certainly the case that wetland plant resources formed a kind of ‘natural food storage’ (Lee and DeVore 1968), a reliable resource that enabled settlement for longer periods. Moreover, wetlands would have provided more than plants. Indeed, water itself would have been a key attraction for humans, along with a range of large animals and birds to hunt and fish to catch.

Steppe and parkland

Phytolith and macrobotanical evidence suggests that the role of pre-domestic wild cereals, wheat and barley, in Epipalaeolithic diet has been overstated. Phytolith evidence from the Early Epipalaeolithic through to and during the Natufian period suggests that small-seeded grasses (non-cereal wild

grass resources) were used, and probably played as important a role in the diet as pre-domestic wild cereals (Rosen 2010). It is clear from the macrobotanical remains that there is a range of plant taxa from steppe and parkland environments that would have been important contributors to Epipalaeolithic diets, including Chenopodiaceae and Fabaceae. This suggests that plant use through the Epipalaeolithic period was not based increasingly on cereals. Rather, a range of wild plant taxa was used according to what was available in the local environment. This is particularly evident with the changing environmental opportunities that accompanied shifts in climate through time. For example, phytolith evidence suggests that during periods of increased aridity, evidence of steppe and parkland resources, particularly wild grasses and cereals, often increases in importance along with wetland resources at sites like Ohalo II, Kharaneh IV, Eynan, Hayonim terrace and Hilazon Tahit (Fig. 2).

Woodland

Phytolith evidence suggests that woodland resources often increase in importance with climatic amelioration, such as the increased rainfall immediately after the LGM (Last Glacial Maximum) at sites like Kharaneh IV, and immediately before the Younger Dryas climatic event at sites like Eynan and Hayonim terrace (Fig. 2, Table 1). Macrobotanical

evidence of woodland use includes *Amygdalus* sp., *Pistacia*, *Quercus* (oak, acorns), *Olea* (wild olive) and *Vitis* (grape), and indicates that when these were available they were used. Poor macrobotanical preservation combined with differential phytolith records, along with the very limited number of starch residue studies, makes fully evaluating the overall importance of these resources problematic. The records are differential because dicot woodland taxa do not produce as many or as diagnostic phytoliths as monocots such as Poaceae.

Discussion

The shift from wild plant food gathering to production: ecological-cultural inheritance and the non-linearity of Epipalaeolithic plant use

Phytolittoral (water edge) resources respond positively with increased growth to disturbances such as fire, trampling or gathering (Ramsey et al. 2015). This characteristic of wetland plants produces a positive feedback loop, encouraging further human use and impact, and results in a productive self-reinforcing ecological-cultural inheritance. Therefore, the use of wetland environments and the ecological inheritance produced by human disturbance facilitated increasing sedentism (the author views sedentism as spanning a mobility spectrum from more to less sedentary) by increasing the availability of reliable perennially available wetland plant resources (Figs. 4b and 5c; Ramsey et al. 2016, 2017). This dynamic has particular significance for the sites of Ohalo II, Kharaneh IV, river Jordan Dureijat, Eynan and Shubayqa 1. These sites are all located in the direct vicinity of a marsh or lake environment with a wealth of perennially available wetland plant resources such as roots, as well as other critical animal resources. The rich animal resource availability at Ohalo II is discussed by Steiner et al. (2022), and at other sites includes, fish (Ohalo II and river Jordan Dureijat) (Zohar et al. 2018; Pedergnana et al. 2021), wetland birds (Ohalo II, Shubayqa 1) (Simmons and Nadel 1998; Yeomans and Richter 2016) and gazelle (Kharaneh IV) (Martin et al. 2010; Spyrou et al. 2019). The sites also display overwhelming archaeobotanical evidence of wetland use (Rosen 2004, 2010, 2011; Marder et al. 2015; Pedersen et al. 2016; Ramsey et al. 2016, 2017; Arranz-Otaegui et al. 2018a, b; Sharon et al. 2020). Several of these sites have strong archaeological evidence for *increasing* sedentism in the form of huts made of brushwood, then stone (Valla 1988; Nadel and Werker 1999; Maher et al. 2012a; Haklay and Gopher 2015; Richter et al. 2017; Ramsey et al. 2018) and strengthening social ties to a particular place, evidenced by on-site burial customs and a rich material assemblage that includes shell

beads, ochre and other desirable items (Muheisen 1988; Nadel 1994; Byrd and Monahan 1995; Hershkovitz et al. 1995; Simmons and Nadel 1998; Bar-Yosef Mayer 2005; Martin et al. 2010; Richter et al. 2011, 2012; Maher et al. 2012b, 2016; Pedergnana et al. 2021). The Natufian period provides the earliest published evidence for recognizably modern food innovations in the form of bread-like remains at Shubayqa 1, and potentially fermented beer-like drinks at Raqefet cave, although it must be acknowledged that there are ongoing questions about the identification of fermentation damage in archaeological starches. The processed food remains at Shubayqa 1 were made with a combination of *Bolboschoenus* tubers and wild cereals (Arranz-Otaegui et al. 2018a). The potentially fermented drinks at Raqefet cave also incorporated wetland plants and wild cereals (Liu et al. 2018). These studies demonstrate the crucial relationship between wetland plants and cereals in Epipalaeolithic diet, poetically referencing both the past and future of human cuisine. Importantly, these socio-economic advances hold the key to understanding the development of plant food production, which was a protracted non-linear process, the beginnings of which can be traced back to the Early Epipalaeolithic (~23 ka cal BP) (Asouti and Fuller 2012, 2013). Indeed, there was a period of over 15,000 years before agriculture started, when hunter-gatherers moved in and out of various types of subsistence and settlement which, when they became established later, became hallmarks of the Neolithic (Ramsey et al. 2016). The archaeobotanical evidence shows that the Epipalaeolithic hunter-gatherers were using a wide variety of types of subsistence and settlement and were not knowingly on a path towards increasing cereal use, cultivation or inevitable domestication. Accordingly, in the absence of a clear linear progression of increasing cereal use, increasing sedentism and increasing social complexity (Fig. 4a), the transition to plant food production in the southern Levant needs to be re-examined.

In this paper, it is argued that the use of wetland resources during the EE at sites like Ohalo II and Kharaneh IV laid the groundwork for a non-linear transition to plant food production (Figs. 4b and 5b -c; Ramsey et al. 2016, 2017; Ramsey and Rosen 2016). This view echoes that of Savard et al. (2006) who suggested that reliable valley bottom plant resources (such as wetland resources) were central to Epipalaeolithic diet. Indeed, the resource stability provided by the use of wetlands facilitated increasing sedentism and the development of an ecological-cultural inheritance of teaching, social learning, tools and food preparation that endured beyond site occupation. As shown at Eynan, Hilazon Tahit and Hayonim terrace, subsistence using the reliable wetland plant and animal resources was reinforced during increasingly arid and environmentally unpredictable periods such as the Younger Dryas, as originally argued by Rosen

and Rivera-Collazo (2012). The use of reliable wetland resources by Epipalaeolithic people helped make possible the socioeconomic advances usually associated with cereal cultivation before the transition to a wild plant food production based on cereals. Indeed, wetland resources arguably underpinned the increasing use of less reliable but perhaps more desirable cereal resources through the Later Epipalaeolithic (Fig. 4b).

The idea that wild cereals and grasses were a desirable resource for Epipalaeolithic people is based on several related factors. First, ethnographic studies demonstrate that taste is one of the primary factors that determine food choice by hunter-gatherers (Heim and Pyhälä 2020). While flavour is a subjective characteristic, archaeobotanical evidence strongly supports the idea that hunter-gatherers put time and effort into gathering and processing wild cereals, both in the Levant (Piperno et al. 2004; Weiss et al. 2004a; Arranz-Otaegui et al. 2018a, b) and beyond (Aranguren et al. 2007; Mariotti Lippi et al. 2015; Cristiani et al. 2021). Second, cereals and grasses can play a critical role in many processed foods (Valamoti 2011; Arranz-Otaegui et al. 2018a) and have favourable biophysical properties. For example, adding cereal flour with gluten to processed starchy foodstuffs helps create an elastic dough (Shewry 2019). Third, processed foods may have been used as luxury food items for status acquisition (Hayden 2003). For example, analysis demonstrates that the flour used to make the ‘bread-like’ remains at Shubayqa 1 was ground very finely, requiring meticulous processing, much finer than later ‘staple’ breads (Arranz-Otaegui et al. 2018a), which suggests that it may have been an early luxury food item.

Epipalaeolithic hunter-gatherers relied on wetland resources and the resulting human effects upon them caused long lasting ecological-cultural inheritances, which as the paper argues, likely led to an unexpected and non-linear shift to wild plant food production using wetland plants prior to wild grasses and cereals (Fig. 4b). The transition to a wetland based wild plant food production in the Levant can be identified by viewing resource use at a landscape level (Fig. 5c).

Hunter-gatherers often manage a range of several resources in their environments to encourage their productivity (Peacock and Turner 2000; Anderson 2005; Turner 2005). Accordingly, archaeobotanical attention needs to shift from individual taxa to a group of taxa in a landscape, with a multi-proxy archaeobotanical approach to identify when a particular environment was being used. In Harris’ (1989) model, he marks the transition to wild plant food production by naming key management activities. However, many of these are difficult to identify archaeologically and are not relevant for all plant taxa, such as transplanting, weeding, replacement planting/sowing, storage and

irrigation/drainage. This paper proposes that in the southern Levant the shift from wild plant food gathering to wild plant food production using wetlands may be detected through the introduction of new management activities, seen in the changing ratios of phytolith taxa and charcoal records in off-site cores; and the changing cultural significance of resources, detected with the introduction of new foodways, seen archaeologically via processed food remains and starch spherulites. A long-term perspective is required to build a picture of change and to detect when such a change in scale occurred, as part of the multi-proxy archaeobotanical evidence of foodways, material culture and palaeoenvironment (Fig. 5c).

The Epipalaeolithic archaeobotanical evidence from the southern Levant, strongly supports the interpretation that wetland environments were chosen for long-term occupation and the resources from them were brought back to the settlements for a range of material and food purposes. The analysis of an off-site section in the Azraq basin demonstrates that Epipalaeolithic disturbances in the wetland environments would have increased productivity of critical wetland plants (Ramsey et al. 2015). The phytolith evidence shows the scale to which wetland environments were used compared to other environments (Ramsey et al. 2016, 2017; Ramsey and Rosen 2016). The macrobotanical and microbotanical evidence is now beginning to demonstrate the range of ways in which wetland resources were incorporated into diet, including the culturally transformative introductions of ‘bread’ and potentially ‘beer’ during the Late Epipalaeolithic (Arranz-Otaegui et al. 2018a; Liu et al. 2018). This evidence, demonstrating the scale and cultural importance of wetland plant resource use, marks the first step in constructing an argument for the development of a wetland-based wild plant food production in the southern Levant during the Epipalaeolithic period (Fig. 5b, c).

A strong multi-proxy archaeobotanical dataset centred on evidence of foodways, and critically palaeoenvironment, is required to further assess this hypothesis. Building the evidence for the use of wetland resources for food is an important step and should include revisiting previous macrobotanical assemblages at sites like Ohalo II to search for unidentified plant food remains, including parenchymatous tissues and processed food remains. Identifications may be aided through the use of scanning electron microscopy (SEM) and new micro-CT (micro computed tomography) X ray imaging technologies. The capacity for studies of artefact residues and signs of use wear should also be developed in the region. Securely dated palaeoenvironmental reconstructions of the immediate areas around wetland-based sites, charting trends in microcharcoal (disturbance/management) and phytoliths (local environment), in conjunction with broader regional coring investigations including

pollen analyses should be used to track the scale and intensity of Epipalaeolithic resource management practices. To achieve regional scale palaeoenvironmental reconstructions, new machine learning algorithms are being developed to use artificial intelligence to identify phytoliths (such as Berganzo-Besga et al. 2022) and amass the large amount of archaeobotanical data needed. These lines of archaeobotanical evidence would show the impact of human management on the wetlands, and the range, scale and cultural importance of wetland plant use on-site, and when combined with archaeological evidence for increasing sedentism and cultural complexity, would demonstrate the change from wild plant food gathering to a wetland-based wild plant food production.

Conclusion

This paper provides the first multi-proxy (macrobotanical and microbotanical) synthesis of the published archaeobotanical evidence for the Epipalaeolithic period in the southern Levant. This dataset demonstrates that Epipalaeolithic hunter-gatherers relied heavily on wetland resources for materials and food. Viewed within the framework of niche construction theory (NCT), this paper argues that human impacts in the wetlands over generations increased wetland productivity, creating long-lasting ecological and cultural inheritances. This feedback is hypothesized to have promoted critical socioeconomic advances, including increasing sedentism, strengthening social ties to particular places and the rise of recognizably modern food innovations such as bread-like foodstuffs, which all contributed to changing Epipalaeolithic practices of plant use, and importantly, the evolution and proliferation of a wetland-based wild plant food production.

The wetlands provided Epipalaeolithic people with a ‘domestication laboratory’ which allowed succeeding generations to interact and modify their environments, experimenting and gaining the necessary experience to build the long-lasting ecological-cultural inheritances needed for the transition to plant food production. Importantly, the ecological-cultural inheritance of a wetland-based wild plant food production enabled the non-linear transition to cereal-based wild plant food production and their later domestication in the southern Levant. Wetland-based innovations supported increasing use and experimentation with cereal resources over the 13.5 ka Epipalaeolithic period. This hypothesis should guide future research directions.

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References

- Allaby RG, Stevens CJ, Kistler L, Fuller DQ (2022) Emerging evidence of plant domestication as a landscape-level process. *Trends Ecol Evol* 37:268–279
- Anderson MK (2005) *Tending the Wild: native american knowledge and the management of California’s Natural Resources*. University of California Press, Berkeley
- Aranguren B, Becattini R, Mariotti Lippi M, Revedin A (2007) Grinding flour in the Upper Palaeolithic Europe (25000 years BP). *Antiquity* 81:845–855
- Arranz Otaegui, A., Ibáñez, J.J., Zapata, L. (2016). Hunter-Gatherer plant use in southwest Asia: the path to agriculture. *Wild Harvest, Plants in the hominin and pre-agrarian human worlds*. K. Hardy and L. Kubiak-Martens. Oxford, Oxbow Books: 91–110.
- Arranz-Otaegui A, Carretero LG, Ramsey MN, Fuller DQ, Richter T (2018a) Archaeobotanical evidence reveals the origins of bread 14,400 years ago in northeastern Jordan. *Proc Natl Acad Sci USA* 115:7, 925–7,930

- Arranz-Otaegui A, Carretero LG, Roe J, Richter T (2018b) “Founder crops” v. wild plants: assessing the plant-based diet of the last hunter-gatherers in southwest Asia. *Quat Sci Rev* 186:263–283
- Arranz-Otaegui A, Colledge S, Zapata L, Teira-Mayolini LC, Ibáñez JJ (2016) Regional diversity on the timing for the initial appearance of cereal cultivation and domestication in southwest Asia. *Proc Natl Acad Sci USA* 113:14001–14006
- Asouti E, Fuller D (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
- Asouti E, Fuller D (2013) A Contextual Approach to the emergence of Agriculture in Southwest Asia reconstructing early neolithic plant-food production. *Curr Anthropol* 54:299–345
- Balée W, Erickson CL (2006) Time, complexity, and historical ecology. In: Balée W, Erickson CL (eds) *Time and Complexity in historical Ecology: studies in the Neotropical Lowlands*. Columbia University Press, New York, pp 1–17
- Bar-Matthews M, Ayalon A (2003) Climatic conditions in the Eastern Mediterranean during the last glacial (60 – 10 ky) and their relations to the Upper Palaeolithic in the Levant as inferred from Oxygen and Carbon Isotope Systematics of Cave deposits. In: Goring-Morris AN, Belfer-Cohen A (eds) *More than meets the Eye: studies on Upper Palaeolithic Diversity in the Near East*. Oxbow Books, Oxford, pp 13–18
- Bar-Matthews M, Ayalon A (2004) Speleothems as palaeoclimate indicators, a case study from Soreq Cave located in the Eastern Mediterranean Region, Israel. In: Battarbee RW, Gasse F, Stickley CE (eds) *Past climate variability through Europe and Africa*. Springer, Dordrecht, pp 363–391
- Bar-Matthews M, Ayalon A, Kaufman A (1997) Late quaternary paleoclimate in the Eastern Mediterranean region from stable isotope analysis of speleothems at Soreq Cave, Israel. *Quat Res* 47:155–168
- Bar-Matthews M, Ayalon A, Kaufman A, Wasserburg GJ (1999) The Eastern Mediterranean paleoclimate as a reflection of regional events: Soreq cave, Israel. *Earth Planet Sci Lett* 166:85–95
- Bar-Yosef Mayer DE (2005) The Exploitation of Shells as beads in the palaeolithic and neolithic of the Levant. *Paléorient* 31:176–185
- Bar-Yosef O (1998) The natufian culture in the Levant, threshold to the origins of agriculture. *Evol Anthropol* 6:159–177
- Bar-Yosef O, Belfer-Cohen A (1989) The origins of sedentism and farming communities in the Levant. *J World Prehist* 3:477–498
- Belfer-Cohen A (1991) The Natufian in the Levant. *Ann Rev Anthropol* 20:167–186
- Belfer-Cohen A, Goring-Morris N (2014) The Upper Palaeolithic and earlier Epi-Palaeolithic of Western Asia. In: Renfrew C, Bahn P (eds) *The Cambridge World Prehistory*. Cambridge University Press, Cambridge, 1,381-1,407
- Belli C, Caracuta V, Weinstein-Evron M et al (2021) A late pleistocene high-resolution paleoclimate reconstruction: insights from the archaeobotanical assemblage and the carbon isotope analysis of wild almond (*Amygdalus* sp.) from Raqefet Cave, Mount Carmel, Israel. *Quat Sci Rev* 268:107138
- Bender B (1975) *Farming in prehistory: from hunter-gatherer to food-producer*. St. Martin’s Press, New York
- Berganzo-Besga I, Orengo HA, Lumbreras F, Aliende P, Ramsey MN (2022) Automated detection and classification of multi-cell phytoliths using deep learning-based algorithms. *J Archaeol Sci*. <https://doi.org/10.1016/j.jas.2022.105654>
- Bleed P, Matsui A (2010) Why didn’t Agriculture develop in Japan? A consideration of Jomon Ecological Style, Niche Construction, and the Origins of Domestication. *J Archaeol Method Theory* 17:356–370
- Bozarth SR (1992) Classification of Opal Phytoliths Forms in selected Dicotyledons natives to the Great Plains. In: Rapp GJ, Mulholland SC (eds) *Phytolith Systematics: emerging issues*. Advances in Archaeological and Museum Science, vol 1. Plenum Press, New York, pp 193–214
- Braidwood RJ (1951) Discovering the world’s earliest village community. *Illustrated Lond News* Dec 15:992–995
- Braidwood RJ, Howe B (1960) Prehistoric investigations in iraqi Kurdistan. *Studies in ancient oriental civilization* 31. University of Chicago Press, Chicago
- Butzer KW (1982) *Archaeology as human ecology*. Cambridge University Press, Cambridge
- Byrd BF, Monahan CM (1995) Death, Mortuary Ritual, and Natufian Social structure. *J Anthropol Archaeol* 14:251–287
- Caracuta V, Weinstein-Evron M, Kaufmann D et al (2016a) 14,000-year-old seeds indicate the levantine origin of the lost progenitor of faba bean. *Sci Rep* 6:37399
- Caracuta V, Weinstein-Evron M, Yeshurun R et al (2016b) Charred wood remains in the natufian sequence of el-Wad terrace (Israel): new insights into the climatic, environmental and cultural changes at the end of the Pleistocene. *Quat Sci Rev* 131:20–32
- Cauvin J (1994) *Naissance des divinités, naissance de l’agriculture: la révolution des symboles au Néolithique*. CNRS Editions, Paris
- Childe VG (1952) *New light on the most ancient East*. Routledge, London
- Childe VG (1956) *Man makes himself*. Watts & Company, New York
- Cohen MN (1977) *The food crisis in prehistory: overpopulation and the origins of agriculture*. Yale University Press, New Haven
- Collard M, Buchanan B, Ruttile A, O’Brien MJ (2011) Niche Construction and the toolkits of Hunter-Gatherers and Food Producers. *Biol Theory* 6:251–259
- Crawford GW (2014) Food Production and Niche Construction in Pre-Contact Southern Ontario. *Midwest Archaeological Conference Inc. Occasional Papers* 1:135–160
- Cristiani E, Radini A, Zupancich A et al (2021) Wild cereal grain consumption among early holocene foragers of the Balkans predates the arrival of agriculture. *eLife* 10:e72976
- Crumley CL (1994) *Historical Ecology: Cultural Knowledge and changing landscapes*. School of American Research Press, Santa Fe
- Cuddington K (2011) Legacy Effects: the persistent impact of ecological interactions. *Biol Theory* 6:203–210
- Delhon C, Martin L, Argant J, Thiébault S (2008) Shepherds and plants in the Alps: multi-proxy archaeobotanical analysis of neolithic dung from “La Grande Rivoire” (Isère, France). *J Archaeol Sci* 35:2,937-2,952
- Dickau R, Bruno MC, Iriarte J et al (2012) Diversity of cultivars and other plant resources used at habitation sites in the Llanos de Mojos, Beni, Bolivia: evidence from macrobotanical remains, starch grains, and phytoliths. *J Archaeol Sci* 39:357–370
- Ebeling W (1986) *Handbook of Indian Foods and fibers of Arid America*. University of California Press, Berkeley
- Edwards PC (2007) A 14,000 year old hunter-gatherer’s toolkit. *Antiquity* 81:865–876
- Flannery KV (1969) Origins and ecological effects of early domestication in Iran and the Near East. In: Ucko PJ, Dimbleby GW (eds) *The domestication and exploitation of plants and animals*. Duckworth, London, pp 73–100
- Flannery KV (1973) The Origins of Agriculture. *Ann Rev Anthropol* 2:271–310
- Florin AS, Carah X (2018) Moving past the ‘Neolithic problem’: the development and interaction of subsistence systems across northern Sahul. *Quat Int* 489:46–62
- Ford RI (1985) The processes of Plant Food production in prehistoric North America. In: Ford RI (ed) *Prehistoric Food production in North America*. The University of Michigan, Ann Arbor, pp 1–18

- Freeman J, Peoples MA, Anderies JM (2015) Toward a theory of non-linear transitions from foraging to farming. *J Anthropol Archaeol* 40:109–122
- Fuller DQ, Asouti E, Purugganan MD (2012) Cultivation as slow evolutionary entanglement: comparative data on rate and sequence of domestication. *Veget Hist Archaeobot* 21:131–145
- Fuller DQ, Stevens C, Lucas L, Murphy C, Qin L (2016) Entanglements and entrapment on the pathway towards Domestication. In: Der L, Fernandini F (eds) *Archaeology of Entanglement*. Left Coast Press, Walnut Creek, pp 151–172
- García-Granero JJ, Lancelotti C, Madella M (2015) A tale of multiproxies: integrating macro- and microbotanical remains to understand subsistence strategies. *Veget Hist Archaeobot* 24:121–133
- Garrod DAE (1957) The natufian culture: the life and economy of a mesolithic people in the Near East. *Proc Brit Acad* 43:211–227
- Gibson DJ (2009) *Grasses and Grassland Ecology*. Oxford University Press, Oxford
- Gremillion KJ, Piperno DR (2009) Human behavioral ecology, phenotypic (developmental) plasticity, and agricultural origins: insights from the emerging evolutionary synthesis. *Curr Anthropol* 50:615–619
- Gremillion KJ, Barton L, Piperno DR (2014) Particularism and the retreat from theory in the archaeology of agricultural origins. *Proc Natl Acad Sci USA* 111:6,171–6,177
- Haklay G, Gopher A (2015) A New look at Shelter 131/51 in the Natufian Site of Eynan (Ain-Mallaha), Israel. *PLoS ONE* 10:e0130121
- Harris DR (1989) An evolutionary continuum of people-plant interactions. In: Harris DR, Hillman GC (eds) *Foraging and farming: the evolution of Plant Exploitation*. Unwin Hyman, London, pp 11–26
- Harris DR (1996) Domesticatory relations of people, plants and animals. In: Ellen RF, Fukui K (eds) *Redefining nature: Ecology, Culture, and Domestication*. Berg Publishers, Oxford, pp 437–463
- Hayden B (1992) Models of domestication. In: Gebauer AB, Price TD (eds) *Transitions to agriculture in prehistory*. Prehistory Press, Madison, pp 11–19
- Hayden B (1995) A new overview of domestication. In: Price TD, Gebauer AB (eds) *Last hunters, first farmers: new perspectives on the prehistoric transition to agriculture*. School of American Research Press, Santa Fe, pp 273–300
- Hayden B (2003) Were luxury foods the first domesticates? Ethnoarchaeological perspectives from Southeast Asia. *World Archaeol* 34:458–469
- Heim A, Pyhälä A (2020) Changing food preferences among a former hunter-gatherer group in Namibia. *Appetite* 151:104709
- Heiss AG, Antolín F, Bleicher N et al (2017) State of the (t)art. Analytical approaches in the investigation of components and production traits of archaeological bread-like objects, applied to two finds from the neolithic lakeshore settlement Parkhaus Opéra (Zürich, Switzerland). *PLoS ONE* 12:e0182401
- Hershkovitz I, Speirs MS, Frayer D et al (1995) Ohalo II H2: a 19,000 year-old skeleton from a water-logged site at the sea of Galilee, Israel. *Am J Phys Anthropol* 96:215–234
- Hillman GC (2000) Abu Hureyra I, the Epipalaeolithic. In: Moore AMT, Hillman GC, Legge AJ (eds) *Village on the Euphrates: from foraging to Farming at Abu Hureyra*. Oxford University Press, Oxford, pp 327–398
- Hillman GC, Madeyska E, Hather J (1989) Wild plant foods and diet at late palaeolithic Wadi Kubbania (Upper Egypt): evidence from charred remains. In: Wendorf F, Schild R, Close AE (eds) *The prehistory of Wadi Kubbania. Stratigraphy, subsistence and environment, vol 2*. Southern Methodist University Press, Dallas, pp 162–242
- Holland JH (2014) *Complexity A very short introduction*. Oxford University Press, Oxford
- Kadowaki S (2013) Issues of chronological and geographical distribution of Middle and Upper Palaeolithic Cultural Variability in the Levant and Implications for the Learning Behavior of Neanderthals and Homo sapiens. In: Akazawa T, Nishiaki Y, Aoki K (eds) *Dynamics of Learning in Neanderthals and Modern humans, vol 1. Cultural Perspectives*. Springer, Tokyo, pp 59–91
- Keddy PA (2000) *Wetland Ecology Principles and Conservation*. Cambridge University Press, Cambridge
- Kislev ME, Nadel D, Carmi I (1992) Epipalaeolithic (19,000 BP) cereal and fruit diet at Ohalo II, Sea of Galilee, Israel. *Rev Palaeobot Palynol* 73:161–166
- Laland KN, O'Brien MJ (2010) Niche Construction Theory and Archaeology. *J Archaeol Method Theory* 17:303–322
- Laland KN, Odling-Smee J, Feldman MW (2000) Niche construction, biological evolution, and culture change. *Behav Brain Sci* 23:131–175
- Laland KN, Odling-Smee J, Feldman MW (2001) Cultural niche construction and human evolution. *J Evol Biol* 14:22–33
- Lansing SJ, Fox KM (2011) Niche construction on Bali: the gods of the countryside. *Phil Trans R Soc B Biol Sci* 366:927–934
- Lee RB, DeVore I (eds) (1968) *Man the Hunter*. Aldine Publishing Company, Chicago
- Lewontin RC (1983) Gene, organism, and environment. In: Bendall DS (ed) *Evolution from Molecules to Men*. Cambridge University Press, Cambridge, pp 273–285
- Liu L, Wang J, Rosenberg D et al (2018) Fermented beverage and food storage in 13,000 y-old stone mortars at Raqefet Cave, Israel: investigating natufian ritual feasting. *J Archaeol Sci: Rep* 21:783–793
- Mariotti Lippi M, Foggi B, Aranguren B, Ronchitelli A, Revedin A (2015) Multistep food plant processing at Grotta Paglicci (Southern Italy) around 32,600 cal B.P. *Proc Natl Acad Sci USA* 112:12,075 – 12,080
- Maher LA, Macdonald DA, Allentuck A et al (2016) Occupying wide open spaces? Late pleistocene hunter-gatherer activities in the Eastern Levant. *Quat Int* 396:79–94
- Maher LA, Richter T, Macdonald D et al (2012a) Twenty thousand-year-old huts at a Hunter-Gatherer settlement in Eastern Jordan. *PLoS ONE* 7:e31447
- Maher LA, Richter T, Stock JT (2012b) The pre-natufian Epipalaeolithic: long-term behavioral trends in the Levant. *Evol Anthropol* 21:69–81
- Marder O, Biton R, Boaretto E et al (2015) Jordan River Dureijat - A New Epipalaeolithic Site in the Upper Jordan Valley. *J Isr Prehist Soc* 45:5–30
- Martin L, Edwards Y, Garrard A (2010) Hunting Practices at an Eastern Jordanian Epipalaeolithic Aggregation Site: the case of Kharaneh IV. *Levant* 42:107–135
- McCorriston J, Hole F (1991) The Ecology of Seasonal stress and the Origins of Agriculture in the Near East. *Am Anthropol* 93:46–69
- Mellaart J (1975) *The neolithic of the Near East*. Charles Scribner's Sons, New York
- Mesoudi A (2017) Pursuing Darwin's curious parallel: prospects for a science of cultural evolution. *Proc Natl Acad Sci USA* 114:7,853–7,860
- Mesoudi A, Thornton A (2018) What is cumulative cultural evolution? *Proc R Soc B: Biol Sci* 285:20180712
- Mohlenhoff KA, Codding BF (2017) When does it pay to invest in a patch? The evolution of intentional niche construction. *Evol Anthropol* 26:218–227
- Mohlenhoff KA, Brenner Coltrain J, Codding BF (2015) Optimal foraging theory and niche-construction theory do not stand in opposition. *Proc Natl Acad Sci USA* 112:E3093
- Muhsen M (1988) The epipalaeolithic phases of Kharaneh IV. In: Garrard AN, Gebel HG (eds) *The Prehistory of Jordan: the state*

- of Research in 1986. BAR International Series, vol S396. BAR, Oxford, pp 353–367
- Nadel D (1994) Levantine Upper Palaeolithic - Early epipalaeolithic burial customs: Ohalo II as a case study. *Paléorient* 20:113–121
- Nadel D (2003) The Ohalo II Flint assemblage and the beginning of the Epipalaeolithic in the Jordan Valley. In: Goring-Morris N, Belfer-Cohen A (eds) *More than meets the Eye: studies on Upper Palaeolithic Diversity in the Near East*. Oxbow Books, Oxford, pp 216–229
- Nadel D, Werker E (1999) The oldest ever brush hut plant remains from Ohalo II, Jordan Valley, Israel (19,000 BP). *Antiquity* 73:755–764
- Newman EA, Kennedy MC, Falk DA, McKenzie D (2019) Scaling and complexity in Landscape Ecology”. *Front Ecol Evol* 7:293
- O’Brien MJ, Laland KN (2012) Genes, Culture, and Agriculture: an example of human niche construction. *Curr Anthropol* 53:434–470
- Odling-Smee J (2010) Niche inheritance. In: Pigliucci M, Müller GB (eds) *Evolution: the extended synthesis*. MIT Press, Cambridge, pp 175–207
- Odling-Smee J, Laland KN (2011) Ecological inheritance and cultural inheritance: what are they and how do they differ? *Biol Theory* 6:220–230
- Odling-Smee FJ, Laland KN, Feldman MW (2003) *Niche Construction: the neglected process in evolution* (MPB 37). Princeton University Press, Princeton 1987
- Ollendorf AL (1992) Towards a classification Scheme of Sedge (Cyperaceae) Phytoliths. In: Rapp GJ, Mulholland SC (eds) *Phytolith Systematics: emerging issues*. Advances in Archaeological and Museum Science, vol 1. Plenum Press, New York, pp 91–112
- Ollendorf AL et al (1987) Phytoliths from some Israeli Sedges. *Isr J Bot* 68:125–132
- Olszewski DI (2001) My “backed and truncated bladelet”, your “point”: terminology and interpretation in Levantine Epipalaeolithic assemblages. In: Caneva I, Lemorini C, Zampetti D, Biagi P (eds) *Beyond Tools: Redefining the PPN Lithic Assemblages of the Levant*. (Studies in early Near Eastern production, subsistence and environment 9) *Ex oriente*, Berlin, pp 303–318
- Peacock SL, Turner NJ (2000) “Just like a Garden”: traditional plant Resource Management and Biodiversity Conservation on the British Columbia Plateau. In: Minnis P, Elisens W (eds) *Biodiversity in native America*. University of Oklahoma Press, Norman, pp 133–179
- Pedergnana A, Cristiani E, Munro N, Valletta F, Sharon G (2021) Early line and hook fishing at the epipalaeolithic site of Jordan River Dureijat (Northern Israel). *PLoS ONE* 16:e0257710
- Pedersen P, Richter T, Arranz-Otaegui A (2016) Preliminary analysis of the late natufian ground stone from Shubayqa 1, Jordan. *J Lithic Stud* 3:379–402
- Piperno DR, Ranere AJ, Dickau R, Aceituno F (2017) Niche construction and optimal foraging theory in neotropical agricultural origins: a re-evaluation in consideration of the empirical evidence. *J Archaeol Sci* 78:214–220
- Piperno DR, Weiss E, Holst I, Nadel D (2004) Processing of wild cereal grains in the Upper Palaeolithic revealed by starch grain analysis. *Nature* 430:670–673
- Price TD, Bar-Yosef O (2011) The Origins of Agriculture: New Data, New Ideas. An introduction to supplement 4. *Curr Anthropol* 52:S163–S174
- Ramsey MN, Rosen AM (2016) Wedded to wetlands: exploring late pleistocene plant-use in the Eastern Levant. *Quat Int* 396:5–19
- Ramsey MN, Jones M, Richter T, Rosen AM (2015) Modifying the marsh: evaluating early epipalaeolithic hunter-gatherer impacts in the Azraq wetland. *Holocene* 25:1:553–1:564
- Ramsey MN, Maher LA, Macdonald DA, Rosen A (2016) Risk, reliability and resilience: Phytolith evidence for Alternative ‘neolithization’ pathways at Kharaneh IV in the Azraq Basin, Jordan. *PLoS ONE* 11:e0164081
- Ramsey MN, Maher LA, Macdonald DA, Nadel D, Rosen AM (2018) Sheltered by reeds and settled on sedges: construction and use of a twenty thousand-year-old hut according to phytolith analysis from Kharaneh IV, Jordan. *J Anthropol Archaeol* 50:85–97
- Ramsey MN, Rosen AM, Nadel D (2017) Centered on the Wetland: integrating new phytolith evidence of plant-use from the 23,000-year-old site of Ohalo II, Israel. *Am Antiqu* 82:702–722
- Ready E, Price MH (2021) Human behavioral ecology and niche construction. *Evol Anthropol* 30:71–83
- Richerson PJ, Boyd R (2005) *Not by genes alone: how Culture Transformed Human evolution*. University of Chicago Press, Chicago
- Richter T, Arranz-Otaegui A, Yeomans L, Boaretto O (2017) High Resolution AMS dates from Shubayqa 1, northeast Jordan Reveal Complex Origins of Late Epipalaeolithic Natufian in the Levant. *Sci Rep* 7:17025
- Richter T, Bode L, House M et al (2012) Excavations at the late epipalaeolithic site of Shubayqa 1: preliminary Report on the first season. *Neo-Lithics* 2/12:1–14
- Richter T, Garrard AN, Allock S, Maher LA (2011) Interaction before Agriculture: exchanging material and sharing knowledge in the final Pleistocene Levant. *Camb Archaeol J* 21:95–114
- Rindos D (1984) *The Origins of Agriculture An Evolutionary Perspective*. Academic Press, Orlando
- Robinson SA, Black S, Sellwood BW, Valdes PJ (2006) A review of paleoclimates and palaeoenvironments in the Levant and Eastern Mediterranean from 25,000 to 5000 years BP: setting the environmental background for the evolution of human civilisation. *Quat Sci Rev* 25:1, 517–1, 541
- Rosen AM (1992) Preliminary identification of silica skeletons from Near Eastern archaeological sites: an anatomical approach. In: Rapp GJ, Mulholland SC (eds) *Phytolith Systematics: emerging issues*. Advances in Archaeological and Museum Science, vol 1. Plenum Press, New York, pp 129–147
- Rosen AM (1993) Phytolith evidence for early cereal exploitation in the Levant. *Current research in Phytolith Analysis: applications in Archaeology and Paleocology*. D. M. Pearsall and D. R. Piperno. University of Pennsylvania, Philadelphia, pp 160–171
- Rosen AM (2004) Phytolith evidence for plant use at Mallaha/Eynan. In: Valla FR, Khalaily H, Valladas H (eds) *Les fouilles à Mallaha en 2000 et 2001: 3ème rapport préliminaire*. (Journal of the Israel Prehistoric Society 34) Israel Prehistoric Society, Jerusalem, pp 189–201
- Rosen AM (2010) Natufian plant exploitation: managing risk and stability in an environment of change. *Eurasian Prehist* 7:113–127
- Rosen AM (2011) Change and Stability in an Uncertain Environment: foraging strategies in the Levant from the early natufian through the Beginnings of the Pre-Pottery Neolithic B. In: Miller NF, Moore KM, Ryan K (eds) *Sustainable Lifeways: Cultural Persistence in an ever-changing environment*. University of Pennsylvania Press, Philadelphia, pp 128–149
- Rosen AM (2013) Natufian Foragers and the ‘Monocot Revolution’: a Phytolith Perspective. In: Bar-Yosef O, Valla FR (eds) (the Natufian Culture in the Levant 2). University of Michigan Press, Ann Arbor, pp 638–648
- 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
- Rowley-Conwy P, Layton R (2011) Foraging and farming as niche construction: stable and unstable adaptations. *Phil Trans R Soc B Biol Sci* 366:849–862
- Ryan P (2011) Plants as material culture in the Near Eastern Neolithic: perspectives from the silica skeleton artifactual remains at Çatalhöyük. *J Anthropol Archaeol* 30(3):292–305

- Sauer CO (1952) *Agricultural Origins and Dispersals: the domestication of animals and foodstuffs*. The American Geographical Society, New York
- Savard M, Nesbitt M, Jones MK (2006) The role of wild grasses in subsistence and sedentism: new evidence from the northern Fertile Crescent. *World Archaeol* 38:179–196
- Sharon G, Grosman L, Allué E et al (2020) Jordan River Dureijat: 10,000 Years of Intermittent Epipalaeolithic Activity on the Shore of Paleolake Hula. *PaleoAnthropology* 2020:34–64
- Shewry P (2019) What is Gluten -Why is it special? *Front Nutr* 6:101
- Simmons T, Nadel D (1998) The avifauna of the early epipalaeolithic site of Ohalo II (19 400 years BP), Israel: species diversity, habitat and seasonality. *Int J Osteoarchaeol* 8:79–96
- Smith BD (2001) Low-level Food Production. *J Archaeol Res* 9:1–43
- Smith BD (2007) Niche Construction and the behavioral context of Plant and Animal Domestication. *Evol Anthropol* 16:188–199
- Smith BD (2009) Resource Resilience, Human Niche Construction, and the long-term sustainability of pre-columbian subsistence economies in the Mississippi River Valley Corridor. *J Ethnobiol* 29:167–183
- Smith BD (2011a) General patterns of niche construction and the management of ‘wild’ plant and animal resources by small-scale pre-industrial societies. *Phil Trans R Soc B Biol Sci* 366:836–848
- Smith BD (2011b) A Cultural Niche Construction Theory of initial domestication. *Biol Theory* 6:260–271
- Smith BD (2015) A comparison of Niche Construction Theory and Diet Breadth Models as explanatory frameworks for the initial domestication of plants and animals. *J Archaeol Res* 23:215–262
- Snir A, Nadel D, Groman-Yaroslavski I et al (2015) The origin of cultivation and Proto-Weeds, long before neolithic farming. *PLoS ONE* 10:e0131422
- Spengler RN III (2021) Niche Construction Theory in Archaeology: a critical review. *J Archaeol Method Theory* 28:925–955
- Spyrou A, Maher LA, Martin LA, McDonald DA, Garrard A (2019) Meat outside the freezer: drying, smoking, salting and sealing meat in fat at an epipalaeolithic megasite in eastern Jordan. *J Anthropol Archaeol* 54:84–101
- Steiner T, Biton R, Nadel D, Rivals F, Rabinovich R (2022) Abundance or stress? Faunal exploitation patterns and subsistence strategies: the case study of Brush Hut 1 at Ohalo II, a submerged 23,000-year-old camp in the sea of Galilee, Israel. *PLoS ONE* 17:e0262434
- Sterelny K (2012) *The evolved apprentice: how evolution made humans unique*. MIT Press, Cambridge
- Turner NJ (2005) *The Earth’s Blanket: traditional teachings for sustainable living*. University of Washington Press, Seattle
- Valamoti SM (2011) Ground cereal food preparations from Greece: the prehistory and modern survival of traditional Mediterranean ‘fast foods’. *Archaeol Anthropol Sci* 3:19–39
- Valla FR (1988) Aspects du sol de l’abri 131 de Mallaha (Eynan). *Paléorient* 14:283–296
- Valla FR (1995) The First settled Societies - Natufian (12,500 – 10,200 BP). In: Levy TE (ed) *The Archaeology of Society in the Holy Land*. Leicester University Press, London, pp 169–189
- Vavilov NI (1926) Studies on the origins of cultivated plants. *Bull Appl Bot Genet Plant Breed* 16:1–248
- Wallach E (2016) Niche construction theory as an explanatory framework for human phenomena. *Synthese* 193:2,595–2,618
- Weiss E, Kisley ME, Simchoni O, Nadel D (2004a) Small-grained wild grasses as a staple food at the 23 000-year-old site of Ohalo II, Israel. *Econ Bot* 58(Suppl):S125–S134
- Weiss E, Wetterstrom W, Nadel D, Bar-Yosef O (2004b) The broad spectrum revisited: evidence from plant remains. *Proc Natl Acad Sci USA* 101:9,551–9,555
- 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
- Winterhalder B, Kennett DJ (2006) Behavioral Ecology and the transition from Hunting and Gathering to Agriculture. In: Kennett DJ, Winterhalder B (eds) *Behavioral Ecology and the transition to Agriculture*. University of California Press, Berkeley, pp 1–21
- Wollstonecroft MM (2011) Investigating the role of food processing in human evolution: a niche construction approach. *Archaeol Anthropol Sci* 3:141–150
- Wollstonecroft MM, Ellis PR, Hillman GC, Fuller DQ (2008) Advances in plant food processing in the Near Eastern Epipalaeolithic and implications for improved edibility and nutrient bioaccessibility: an experimental assessment of *Bolboschoenus maritimus* (L) Palla (sea club-rush). *Veget Hist Archaeobot* 17(Suppl):S19–S27
- Wrangham R, Cheney D, Seyfarth R, Sarmiento E (2009) Shallow-water habitats as sources of fallback foods for hominins. *Am J Phys Anthropol* 140:630–642
- Wright K (1991) The origins and development of ground stone assemblages in late Pleistocene Southwest Asia. *Paléorient* 17:19–45
- Wright K (1994) Ground-Stone Tools and Hunter-Gatherer Subsistence in Southwest Asia: implications for the transition to Farming. *Am Antiqu* 59:238–263
- Yeomans L, Richter T (2016) Exploitation of a Seasonal Resource: Bird Hunting during the late Natufian at Shubayqa I. *Int J Osteoarchaeol* 28:95–108. <https://doi.org/10.1002/oa.2533>
- Zeder MA (2015) Core questions in domestication research. *Proc Natl Acad Sci USA* 112:3,191–3,198
- Zeder MA (2018) Why evolutionary biology needs anthropology: evaluating core assumptions of the extended evolutionary synthesis. *Evol Anthropol* 27:267–284
- Zohar I, Dayan T, Goren M, Nadel D, Hershkovitz I (2018) Opportunism or aquatic specialization? Evidence of freshwater fish exploitation at Ohalo II- A waterlogged Upper Paleolithic site. *PLoS ONE* 13:e0198747

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