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REVIEW

Orphan crops of archaeology-based crop history research

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Societal Impact Statement

Agrobiodiversity is central to sustainable farming worldwide. Cultivation, conservation and reintroduction of diverse plant species, including 'forgotten' and 'underutilized' crops, contribute to global agrobiodiversity, living ecosystems and sustainable food production. Such efforts benefit from traditional and historical knowledge of crop plants' evolutionary and cultural trajectories. This review is a first attempt at systematically gauging species representativeness in studies of archaeological plant remains. Results indicate that, in addition to discipline-specific methodological sources of bias, modern agricultural biases may replicate themselves in crop history research and influence understandings of 'forgotten crops'. Recognizing these biases is an initial stride towards rectifying them and promoting agrobiodiversity in both research and practical applications.

Summary

So-called 'forgotten' or 'orphan' crops are an important component of strategies aimed at preserving and promoting biodiversity. Knowledge of historical cultivation, usage, and geographic and evolutionary trajectories of plants, that is, crop history research, is important for the long-term success of such efforts. However, research biases in the crops chosen for study may present hurdles. This review attempts to systematically identify patterns in crop species representativeness within archaeology-based crop history research. A meta-analysis and synthesis of archaeological evidence (and lack thereof) is presented for 268 species known to have been cultivated for food prior to 1492 CE from the Mediterranean region to South Asia. We identified 39 genera with known crop plants in this geographical and historical context that are currently absent from its archaeobotanical record, constituting

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‘orphan’ crops of archaeobotany. In addition, a worldwide synthesis of crop species studied using geometric morphometric, archaeogenetic and stable isotope analyses of archaeological plant remains is presented, and biases in the species represented in these disciplines are discussed. Both disciplinary methodological biases and economic agenda-based biases affecting species representativeness in crop history research are apparent. This study also highlights the limited geographic diffusion of most crops and the potential for deeper historical perspectives on how crops become marginalized and ‘forgotten’.

KEYWORDS

agrobiodiversity, archaeobotany, archaeogenetics, archaeology, food crop, geometric morphometrics, stable isotope analysis, underutilized crops

1 | INTRODUCTION

Agrobiodiversity is widely recognized as key to sustainable farming systems worldwide, especially in the face of steadily declining global crop diversity (FAO, 2019; Khoury et al., 2014). At least 7000 species are used for human food; yet, only three cereals (wheat, maize and rice) are thought to comprise nearly half of human caloric intake globally (Ulian et al., 2020). Efforts to research, improve and cultivate ‘forgotten’, ‘underutilized’, ‘neglected’ or ‘orphaned’ crops form a key component of strategies for promoting agrobiodiversity and

agricultural sustainability. Research on crops used in the ancient and historical past provides essential background to understanding, conserving and reintroducing ‘forgotten’ crops.

By delving into the history of agricultural plants, researchers have gained valuable insights into the diversity of evolutionary paths taken by cultivated plants. Some crops, such as bread wheat (*Triticum aestivum*) and sugar cane (*Saccharum officinarum*) overcame the restricted natural distributions of their wild progenitors to become among the most widely grown plants on the planet (FAO, 2020). Others, such as hulled wheat, several minor millets and pili nut

(*Canarium ovatum*) exist only in small pockets marked by rare micro-environments and cultural contexts, whereas still others, like domesticated erect knotweed (*Polygonum erectum* subsp. *watsoniae*), may have become extinct entirely (Hammer & Khoshbakht, 2005; Mueller, 2017). Yet another category subject to dwindling knowledge and availability are the so-called ‘famine food’ plants, traditionally used for coping with starvation during extreme weather conditions, political conflict and so forth. For instance, the seminal works of Maurizio (1932, 1939) on European plant use preserve a largely forgotten relic of knowledge regarding edible plants, including the documented utilization of some 90 wild plant taxa by soldiers in captivity. Such traditional and indigenous knowledge is rapidly disappearing due to urbanization, migration, industrialized food systems and socio-cultural changes affecting people's preferences. Considering agricultural crop diversity, the expansion and contraction of crop species distributions encompass a complex set of processes that involve the evolution of numerous agricultural varieties, ecotypes and landraces. Developed and nurtured by farmers over thousands of years, these taxa tend to be specifically adapted to diverse environmental and cultural conditions. On a recent timescale, various drivers, including the adoption of high-yielding crop varieties, market changes and climate change, have effected changes in crop diversity, leading in particular to genetic erosion and spatial homogeneity of cultivated plants (Khoury et al., 2021).

Crop history research has long been recognized as key to modern crop improvement and agricultural progress (de Candolle, 1885; Vavilov, 2009).¹ Yet, this motivation may affect choices about which species to study, potentially introducing substantial and persistent biases favoring staple and commodity foods of current and perceived future global markets. To take a specific example, horse gram (*Macrotyloma uniflorum*) is the fifth most widely planted grain legume (pulse) in India, and the fourth most often encountered archaeologically in South Asia. Yet, horse gram is much less researched and covered in agricultural textbooks published in India than less widely planted pulses with higher economic value in Europe, such as lentil (*Vicia lens* syn. *Lens culinaris*) and pea (*Lathyrus oleraceus* syn. *Pisum sativum*) (Fuller & Murphy, 2018). Moreover, it has been suggested that a bias towards the ‘eight Neolithic founder crops’ (sensu Zohary & Hopf, 1988), likely resulting from modern industrialized perceptions of agriculture, has blinded researchers to other food plants in Southwest Asian archaeobotany (Arranz-Otaegui, 2021; Arranz-Otaegui & Roe, 2023). Such research biases might impede the preservation and promotion of underrepresented crops. These biases need to be identified and addressed if we want to ensure the conservation of all crops, promote diversity and

achieve sustainable agricultural practices. Our objective in this paper is to comprehensively evaluate biases in crop species representativeness within archaeology-based crop history research, as a crucial initial step toward rectifying them and promoting a more inclusive, unbiased approach to studying and conserving crop diversity.

2 | BACKGROUND: CROP HISTORY RESEARCH

In its broadest sense, crop history research includes any research into the cultivation, utilization, geography, ecology and evolution of domesticated plants, their wild progenitors and associated plant species over time. Crop history differs from agricultural history in that the former focuses on the crops themselves whereas the latter may also include other aspects of agricultural systems, such as technology, infrastructure and institutional frameworks. Crop history research includes, among other topics, ethnobotanical studies of cultivation, utilization and ecology in traditional contexts; linguistic and philological studies of plant references in spoken and written language; archaeobotanical studies of ancient plant remains; and genetic studies of modern, historical and archaeological specimens. Genetic studies of archaeological plant remains are one example of further analyses of archaeobotanical remains, along with geometric morphometrics (GMM) and stable isotope analysis (SIA), which are increasingly producing new information on ancient cultivation conditions and intra-species diversity.

Long before these more recent analytical techniques were developed, the interdisciplinary approach to crop history research was mastered by Alphonse de Candolle in *Origine des plantes cultivées*, originally published in 1882. This work set a standard by which all available sources of evidence were used to reconstruct crop histories—which for de Candolle included those deriving from phyto-geography, archaeological and palaeontological evidence (including archaeobotany and palaeobotany), historical records and philology. De Candolle's work strongly influenced Nikolai I. Vavilov, who devoted his life to uncovering genetic, evolutionary and geographic trajectories of plants with the aim of eliminating famine (Zakharov, 2005) and was one of the first scientists to discuss declining cultivar diversity due to agricultural modernization (Nabhan, 2009). Vavilov identified centers of diversity as probable domestication centers, but his wider goal was to focus research and conservation efforts on those regions most likely to host useful genetic variation for breeding and food security (Vavilov, 2009). Although this work has since been updated, Vavilov's approach to crop diffusion is still highly influential (e.g., Liu, Chen, et al., 2019; Maxted & Vincent, 2021). Vavilov's ideas concerning centers of diversity were refined and revised by Jack Harlan (1971)—yet another agronomist and botanist who personified interdisciplinary crop history research through his involvement in archaeology, ethnobotany, weed ecology, crop genetics and evolution (Hymowitz, 2003).

While botanists and agronomists of the late-19th and 20th centuries mustered historical and archaeological knowledge in constructing crop histories, historians and linguists continued to be an important

¹De Candolle lists agriculturalists first among groups interested in crop history research: ‘The knowledge of the origin of cultivated plants is interesting to agriculturists, to botanists, and even to historians and philosophers concerned with the dawnings of civilization’ (de Candolle, 1885: v). Writing half a century later, Vavilov is more explicit: ‘The questions concerning the origin of a given plant—how it became cultivated, where its original native land was, where the sources of the development of varieties were found, and where the clues to the wealth of forms could be discovered—are not only of general importance for explaining the historical destiny of peoples but also of actual and practical importance for the present agronomical work toward the exploration of varieties for plant breeding’ (Vavilov, 2009: 1).

source of knowledge about crop histories (e.g., Laufer, 1919) and archaeologists became increasingly interested in botanical and agronomic knowledge for constructing human history. The idea that the Neolithic invention of agriculture was a precursor to urbanism and ‘civilization’ increasingly gained currency in archaeology, particularly thanks to popularization by V. Gordon Childe (1936, 1954). This led to research aimed at empirically identifying the transition from foraging to farming, such as the influential excavations by Robert Braidwood on the ‘hilly flanks’ of the Zagros Mountains in the 1950s and 1960s (e.g., Braidwood, 1958, 1972). These involved collaborations with several pioneering archaeobotanists, most prominently Hans Helbæk and Willem van Zeist. They generated archaeobotany-based crop histories and reconstructions of agricultural origins (Helbæk, 1959, 1966).² By this time, archaeobotany was over a century old, but it was this period that saw the development of larger scale systematic sampling methods and flotation (Fuller, 2008; Miksicsek, 1987; Watson, 1997). In the ensuing period, specialist archaeobotany labs were established at multiple institutions and archaeobotany developed as one of the main disciplines producing new empirical data on crop histories (for historical overviews of archaeobotany, see Warnock, 1998; Pearsall, 2015: 28–31; Marston et al., 2014, and references; see also Background S1).

Archaeobotany developed into multiple subdisciplines, each focusing on different plant organs, including carpological remains (seeds and fruits), pollen, charcoal and wood, parenchyma, starch granules and phytoliths (Lancelotti & Madella, 2023). These subdisciplines all employ morphological and/or anatomical identification of plant remains using modern reference material, which often involves diagnostic measurements or morphometry. Geometric morphometrics (GMM) applied to archaeobotanical remains developed in the early 2000s (Evin et al., 2022). This innovative approach introduced a quantification of shape, enabling more precise and refined morphometric analyses than had been standard using traditional measurements in archaeobotany (see Method S1). It has contributed to enhancing the accuracy and reliability of taxonomic identification for some types of archaeobotanical specimens. Another significant advance in the study of crop histories came with the emergence of archaeogenetics, which began in the 1990s, experienced notable progress in the 2000s and continues to develop today (Kistler et al., 2020). Archaeogenetics (based on sequencing ancient DNA or aDNA) provides a fascinating window into the past, allowing researchers to investigate the genetic diversity of ancient crops. After a pioneering study in the 1980s (DeNiro & Hastorf, 1985), stable isotope analysis (SIA) became an additional part of the archaeobotanical toolkit, with methodological, experimental and archaeological applications growing in number from the 1990s. SIA can reveal direct information about plant growth conditions which can be used to infer past environment and agrarian practices, including water status, irrigation, manuring and seasonal variability. Typically, carbon and nitrogen isotopes are analyzed to explore these factors, however, other isotopes such as oxygen, sulphur and strontium have been applied to investigate growing

conditions including potential water sources, landscape zone and non-local cultivation, respectively (Fiorentino et al., 2015; see Background S1, for brief overviews of archaeobotany and GMM, aDNA and SIA applied to archaeological plant remains).

The above historiographic survey highlights the interdisciplinary nature of crop history research from the beginning and the development of archaeology-based crop history research. A strong interest in agricultural origins and initial domestication is still a prominent feature of this field. Two common primary starting points for such inquiries are botanical/agronomic and archaeological, stemming from underlying assumptions that documenting domestication is key to (1) future advances in modern crop improvement and (2) illuminating the essential trajectories of human history (Childe, 1954; Vavilov, 2009). These two assumptions no doubt have a common source, namely the belief that the course of post-Neolithic history has been/will be determined by a select group of domesticates (e.g., Diamond, 2002; Scott, 2017). Indeed, the caloric and economic significance of grain crops, particularly in modern high-income economies, may make it difficult to imagine alternatives moving forward, despite the fact that several tuber crops are more productive per unit of land than cereals (Denham et al., 2020). Although both archaeobotanical and genetics-based crop history research have developed well beyond the focus on origins and grain crops, these are still inherent biases with a long historiography. Meanwhile, taphonomy, or factors affecting preservation, retrieval and identification, is the primary default source of bias affecting species representativeness in archaeobotany and associated research. However, other factors, such as cultural perceptions and economic priorities, could conceivably also be at play. Our research question is, what patterns are evident in the set of species represented in, as well as those absent from, archaeology-based crop history research, and what sources of research bias do they point to? While attempting to systematically analyze species representativeness in archaeology-based crop history research, the data we collected also indicated interesting patterns concerning the natural distributions of crop plants in the study region and global diffusion. Presented and discussed below, these patterns demonstrate how archaeology-based crop history synthesis work can offer a deeper time perspective on the phenomenon of ‘forgotten crops’.

3 | METHODS

3.1 | Disciplines

This study is based on a meta-analysis of crop species figuring in archaeobotany and in studies applying GMM, aDNA and SIA to archaeobotanical materials. It attempts to systematically determine which crop species have been subject to such studies, which have not and why. We distinguish between archaeobotany on one hand and on the other, GMM, aDNA and SIA applied to archaeobotanical specimens. Application of these latter disciplines to ancient plant material is derivative of archaeobotanical research, still in its early stages and the corpus of such studies is relatively small. Therefore, we did not

²Incidentally, Jack Harlan was also on the team for his expertise in agronomy and genetics.

limit our synthesis of GMM, aDNA and SIA studies by species or region (Method S1). By contrast, archaeobotanical studies are extremely numerous, and it was necessary to limit the number of crop plants considered in the meta-analysis, before determining which have and which have not figured in archaeobotanical studies.

3.2 | Data collection

In order to systematically identify crop species representativeness in archaeobotany, we began by constructing as comprehensive a list as possible of food crops in our study regions and recording presence/absence in the archaeobotanical record of these regions, for each species. Food crops and regional boundaries were delineated as follows:

1. Food crop species: We limited the archaeobotanical analysis exclusively to crops cultivated for human food. Following Meyer et al. (2012), we adopt a broad understanding of ‘food’: ‘... a plant species must have been used at some time as a food, spice, edible oil, beverage, or fasting aid with nutritional value (e.g., khat)’. This includes crops for which food usage is secondary, for example, cotton, flax and hemp. Food crops of today were included even if their status as such in the past is uncertain. Analysis was generally conducted at the species level, even if domestication status is determined by subspecies or varietal classification. In very few cases, species from the same genus were combined if they are not usually distinguished as archaeobotanical specimens (*Musa acuminata/balbisiana* × *paradisiaca*, *Lathyrus cicera/sativus*, *Ziziphus jujuba/mauritanica*), have too much taxonomic overlap to justify separation (*Rheum australe/emodi/webbianum*) or represent a domesticate and its wild progenitor (*Camelina microcarpa/sativa*). Wheat species taxonomy followed the genomic approach. A single

functional category was assigned to each species from cereal/pseudocereal, pulse, tree fruit/nut, vegetable and condiment. Where species cover multiple functional categories, the primary one was chosen. Edible tubers were included in the vegetable category (see Method S1 for extended methodology).

2. Geographical scope: For the archaeobotanical meta-analysis, we limited the study scope to the following regions: Southwest Asia, Southern Europe, the Caucasus, South Asia, North Africa and Central Asia (Figure 1; see Method S1 for country lists). For lack of a better term, we loosely describe this region as the ‘Mediterranean and Middle East interaction sphere’, abbreviated MME+.

We constructed a list of food crop species native to these regions or introduced prior to 1492 CE and the Columbian exchange (Crosby, 1972), to the best of our knowledge (see Method S1 for full details). Introductions from the Americas were excluded from the analysis. To construct this ‘MME+ food crop list’, crop species were collected from several published lists and studies (Meyer et al., 2012; FAO, 2017; Muthukumar, 2023; Farooq and Siddique [eds], 2023; Malik et al., 2021; Valamoti et al., 2022; Valamoti, 2023). Additional species were added from archaeobotanical databases and papers consulted during the searches. *Plants for a Future* (PFAF, 2023) and *Useful Tropical Plants* (Fern, 2014) online databases were the main sources used to determine food usage and cultivation status (see Method S1 for additional sources).

Each species on the MME+ food crop list was subject to searches in academic search engines, conducted separately for each discipline. Archaeobotany was subject to Google Scholar and Web of Science database searches, complemented by further searches of databases compiled by archaeobotanists working in each of the study regions. Online databases that were used include the Botanical Records of Archaeobotany Italian Network for Italian archaeobotany (Mariotti

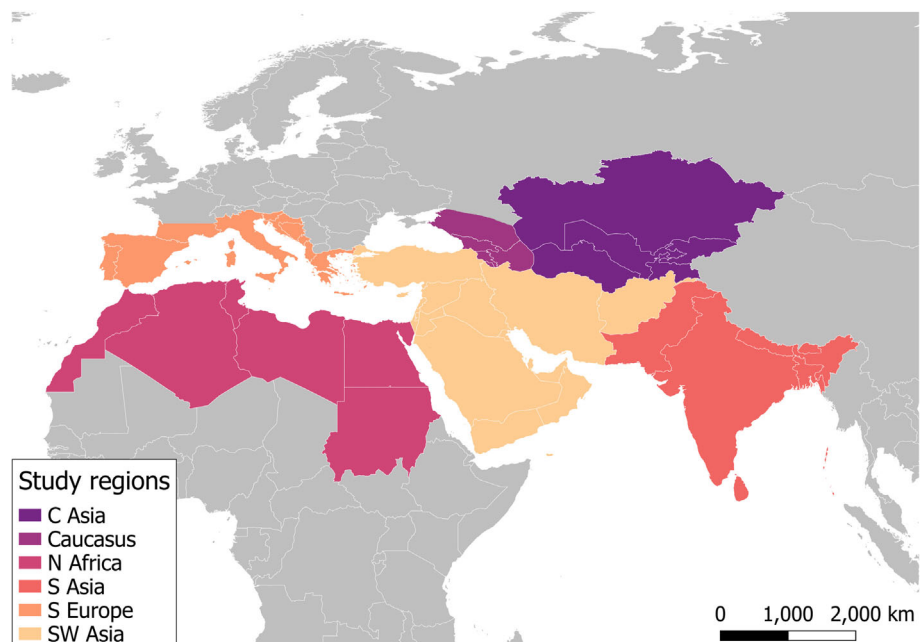


FIGURE 1 Study regions of the archaeobotany meta-analysis. Archaeobotanical presence/absence data for color-coded regions appear in Dataset S1. For country lists see Method S1. Note that GMM, aDNA and SIA meta-analyses were not limited geographically.

TABLE 1 Food crop species absent from archaeobotanical records of the Middle East, Mediterranean, Caucasus, Central Asia and South Asia.

Functional category	Common name	Species	Family	Simplified natural range
Vegetable	Okra	<i>Abelmoschus esculentus</i> (L.) Moench	Malvaceae	S Asia; SE Asia
Tree fruit/nut	Baobab	<i>Adansonia digitata</i> L.	Malvaceae	SW Asia; sub-Saharan Africa
Condiment	Grains of paradise	<i>Aframomum melegueta</i> K.Schum.	Zingiberaceae	Sub-Saharan Africa
Vegetable	Sissoo spinach; Periquito sessil	<i>Alternanthera sessilis</i> (L.) DC.	Amaranthaceae	SW Asia, Caucasus, S Asia, SE Asia, Oceania, Americas
Vegetable	Callaloo/Chinese spinach	<i>Amaranthus tricolor</i> L.	Amaranthaceae	S Asia; SE Asia
Vegetable	Elephant (foot) yam	<i>Amorphophallus paeoniifolius</i> (Dennst.) Nicolson	Araceae	S Asia, SE Asia, E Asia, Oceania
Condiment	Angelica	<i>Angelica archangelica</i> L.	Apiaceae	Caucasus, W Europe, N Europe, E Europe, N Asia
Vegetable	Ceylon/Indian/vine spinach	<i>Basella alba</i> L.	Basellaceae	S Asia; SE Asia; Oceania
Vegetable	Tinda/wax gourd	<i>Benincasa fistulosa/hispida</i>	Cucurbitaceae	S Asia, SE Asia, Oceania
Vegetable	Star gooseberry	<i>Breynia androgyna</i> (L.) Chakrab. & N.P.Balacr.	Phyllanthaceae	S Asia, SE Asia
Condiment	Tea	<i>Camellia sinensis</i> (L.) Kuntze	Theaceae	SE Asia; E Asia
Tree fruit/nut	Bengal currant and Num-num	<i>Carissa carandas/spinarum</i> L.	Apocynaceae	SW Asia, S Asia, Africa, SE Asia, E Asia, Oceania
Condiment	Khat	<i>Catha edulis</i> (Vahl) Forssk. ex Endl.	Celastraceae	Sub-Saharan Africa
Vegetable	Gotu kola/Asian pennywort	<i>Centella asiatica</i> (L.) Urb.	Apiaceae	SW Asia, Caucasus, S Asia, SE Asia, sub-Saharan Africa, E Asia, Oceania
Condiment	Saffron	<i>Crocus sativus</i> L.	Iridaceae	S Europe
Pulse	Guar/cluster bean	<i>Cyamopsis tetragonoloba</i> (L.) Taub.	Fabaceae	S Asia
Vegetable	Lemon grass	<i>Cymbopogon citratus</i> (DC.) Stapf	Poaceae	S Asia
Vegetable	Ube, water/mountain yam (Japanese)	<i>Dioscorea alata/opposita</i>	Dioscoreaceae	S Asia, SE Asia
Vegetable	Vegetable fern	<i>Diplazium esculentum</i> (Retz.) Sw.	Aspleniaceae	S Asia, SE Asia, E Asia
Tree fruit/nut	Governor's/Indian coffee plum	<i>Flacourtia indica/jangomas</i>	Salicaceae	S Asia, SE Asia, E Asia, sub-Saharan Africa
Condiment	Noog, Niger seed	<i>Guizotia abyssinica</i> (L.f.) Cass.	Asteraceae	Sub-Saharan Africa
Condiment	Kenaf and Roselle	<i>Hibiscus cannabinus/sabdariffa</i> L.	Malvaceae	SW Asia, N Africa, sub-Saharan Africa
Vegetable	Kangkong, water spinach	<i>Ipomoea aquatica</i> Forssk.	Convolvulaceae	SW Asia; S Asia; sub-Saharan Africa; Oceania
Condiment	Lavender	<i>Lavandula angustifolia</i> Mill.	Lamiaceae	S Europe
Condiment	Lovage	<i>Levisticum officinale</i> W.D.J.Koch.	Apiaceae	SW Asia
Vegetable	Bitter melon/spine gourd	<i>Momordica charantia/dioica</i>	Cucurbitaceae	S Asia, sub-Saharan Africa, Oceania, SE Asia
Tree fruit/nut	Noni	<i>Morinda citrifolia</i> L.	Rubiaceae	S Asia, SE Asia, Oceania
Vegetable	Horseradish tree	<i>Moringa oleifera</i> Lam.	Moringaceae	S Asia
Vegetable	Water mimosa	<i>Neptunia oleracea</i> Lour.	Fabaceae	S Asia, SE Asia, sub-Saharan Africa, America
Pulse	Tree bean	<i>Parkia biglobosa</i> Benth.	Fabaceae	S Asia, SE Asia, Oceania
Pulse	Winged bean	<i>Psophocarpus tetragonolobus</i> (L.) DC.	Fabaceae	Sub-Saharan Africa
Vegetable	Himalayan/Indian rhubarb	<i>Rheum australe/emodi/webbianum</i>	Polygonaceae	S Asia
Vegetable	Common golden thistle	<i>Scolymus hispanicus</i> L.	Asteraceae	SW Asia, Caucasus, S Europe, E Europe, W Europe
Vegetable	Scorzonera	<i>Scorzonera hispanica</i> L.	Asteraceae	N Africa, Europe
Vegetable	Climbing wattle	<i>Senegalia pennata</i> (L.) Maslin	Fabaceae	S Asia, SE Asia, E Asia

TABLE 1 (Continued)

Functional category	Common name	Species	Family	Simplified natural range
Vegetable	Siamese cassia	<i>Senna siamea</i> (Lam.) H.S.Irwin & Barneby	Fabaceae	S Asia; SE Asia
Vegetable	West Indian pea	<i>Sesbania grandiflora</i> (L.) Poir.	Fabaceae	SE Asia, Oceania
Tree fruit/nut	Hog plum	<i>Spondias pinnata</i> (L.f.) Kurz	Anacardiaceae	S Asia, SE Asia, E Asia
Vegetable	Snake- and pointed gourd	<i>Trichosanthes cucumerina/dioica</i>	Cucurbitaceae	S Asia, SE Asia, E Asia, Oceania

TABLE 2 Unrepresented crops in the archaeobotany of the study region by functional category.

Functional category	Species in group	Not in MME+ archaeobotany	% absent per group
Cereal/pseudocereal	30	1	3.3
Pulse	24	3	12.5
Tree fruit/nut	73	9	12.3
Condiment	51	12	23.5
Vegetable	90	28	31.1

Lippi et al., 2018; Mercuri et al., 2015) and the Archaeobotanical Database of Eastern Mediterranean and Near Eastern Sites for Southwest Asia (Riehl, 2015). Anthologies such as that by Núñez et al. (2011) were also consulted. Citing literature and additional sources were further scanned for relevant crop species. For practical reasons, only presence/absence data was collected for archaeobotany. Presence was recorded even where the specimens present are unlikely to represent cultivation or consumption within the context in which they were found.

For GMM, aDNA and SIA, an attempt was made to quantify the number of studies conducted per species, without geographical or thematic limitations (including non-food crops, unlike the archaeobotany search). Search retrieval focused on analyses of archaeobotanical remains only, removing those based on samples dating post-1492 CE (as for the archaeobotany search), and thereby excluding historical herbarium studies and methodological papers. For each crop, we obtained its natural range from *Plants of the World Online* (POWO, 2023). Additionally, we utilized the FAO-STAT (2021) database to examine patterns associated with global production by species. Our query focused on data from the region 'World (total)' and specifically targeted the element of 'Production quantity' for the item 'Crops, primary' (see Method S1 for full details).

4 | RESULTS

4.1 | Archaeobotany

Our 'MME+ food crop list' is a working list of food crop species used in the pre-1492 Mediterranean and Middle East interaction sphere (S Europe, N Africa, SW Asia, Caucasus, C Asia and S Asia), numbering 268 species or species groups across 196 genera and 66 families

(Dataset S1; Table S1). Among these, at least 199 species have been identified in the archaeobotany of these regions, mostly as seeds and fruits. For 53 species, we found no evidence in archaeobotanical literature (Table 1; Table 2; Dataset S1), whereas the remaining species represent questionable, unpublished and genus-level-only identifications. The 53 absent crop species come from 45 genera; however, some of them have present co-genera: monkey jackfruit (*Artocarpus lacucha*), East Indian arrowroot (*Curcuma angustifolia*), Indian almond (*Terminalia catappa*), betel and long pepper (*Piper betle*; *P. longum*), pepperweed (*Lepidium latifolium*) and Zhukovsky's wheat (*Triticum zhukovskiy*). Although these species are absent from the archaeobotanical record of the study region, other food crop species from the same genus are present: jackfruit (*Artocarpus heterophyllus*), turmeric (*Curcuma longa*), belleric myrobalan (*Terminalia bellirica*), black pepper (*Piper nigrum*), cress (*Lepidium sativum*) and Timopheev's wheat (*Triticum timopheevii*), respectively. We excluded all of these species from Table 1 to avoid any possibility of over-counting archaeobotany's 'orphan crops'. In the same vein, Table 1 combines species from genera that were absent from the archaeobotanical record: snake- and pointed gourd (*Trichosanthes cucumerina/dioica*), kenaf and roselle (*Hibiscus cannabinus/sabdariffa*), governor's and Indian coffee plum (*Flacourtia indica/jangomas*), tinda and wax gourd (*Benincasa fistulosa/hispida*), ube or water yam and mountain yam (*Dioscorea alata/opposita*), bitter melon and spine gourd (*Momordica charantia/dioica*) and Bengal currant and num-num (*Carissa carandas/spinarum*). Thus, the 39 entries in Table 1 represent a conservative, genus-level summary of archaeobotany's 'orphan' crops in the study region. Over two-thirds of these are native to tropical Asia. The full dataset informs on species representativeness in archaeobotany in other ways, such as indicating patterns of crop introduction into this wide region. We present these results in more detail below, addressing the representativeness of archaeobotanical subdisciplines, plant families, functional categories and natural distributions.

4.1.1 | Subdisciplines

Thanks to its greater taxonomic power and to the fact that it is one of the most established archaeobotanical sub-disciplines, carpological (seed/fruit) identifications account for the overwhelming majority of species in our archaeobotanical dataset. By contrast, parenchyma, starch granule, phytolith and food remain analyses have contributed little to archaeobotanical crop species diversity in our dataset; their contribution to crop history research in the MME+ region tends toward more localized aspects of plant economy and ecology.³ Wood and pollen can sometimes provide evidence for local cultivation (as opposed to import) of a crop plant, but most food crop plant species in the records of the MME+ region identified by these techniques have also been identified as carpological remains, at least on the multi-regional scale. A very small number of species are represented exclusively by wood/charcoal identifications, including wood apple (*Limonia acidissima*) and bael (*Aegle marmelos*). In a few cases, wood identifications provide the main evidence for early cultivation, such as finds of jackfruit (*Artocarpus heterophyllus*) and mango (*Mangifera indica*) wood on sites in India well outside their natural distribution, implying local cultivation (Kingwell-Banham & Fuller, 2012).

4.1.2 | Crop species per family and functional category

Sixty-six families are represented in our MME+ food crop list (Dataset S1). Over half of them include only one species, whereas seven families contain over 10 species each (Fabaceae, Poaceae, Rosaceae, Brassicaceae, Apiaceae, Cucurbitaceae and Lamiaceae). The families with the greatest number of food crop species are legumes (Fabaceae) with 31 species and grasses (Poaceae) with 30. Within these families, the proportion of species present in the archaeobotanical record also varies. All Rosaceae and most Brassicaceae, Lamiaceae, Poaceae, Fabaceae and Apiaceae species on our list were found in archaeobotany. Within the gourd family (Cucurbitaceae), 7/13 food crop species on the list have apparently not yet been identified in archaeobotanical research; once combined by genus, the number absent becomes 4/7.⁴ The food crop genera absent from the MME+ archaeobotanical record accounted for here (Table 1) come from 25 different families.

The functional category with the greatest number of species or species groups on the MME+ food crop list was vegetable (90), followed by tree fruit/nut (73), condiment (51), cereal/pseudocereal (30) and pulse (24). However, the cereal/pseudocereal group covers only two families (mostly Poaceae, plus Polygonaceae in the case of two buckwheat pseudocereal species), and pulses cover a single family

(Fabaceae).⁵ By contrast, the vegetable and tree fruit/nut categories each contain 31 and 29 families in the database, respectively; condiments cover 26 (Dataset S1).

Species representativeness in archaeobotany diverges according to functional category. Note that Table 1 presents genera absent from the MME+ archaeobotanical record, whereas Table 2 summarizes species-level representativeness, based on Dataset S1. In cases where a species remains unidentified but there exist genus-only identifications, we did not count the species in question as absent (marked as 'genus' in Dataset S1). This includes taxa for which only genus-level identification exists: asparagus (*Asparagus*), mint (*Mentha*) and salsify (*Tragopogon*), as well as species for which other co-generic species have been identified, but genus-only identifications also exist: persimmon (*Diospyros kaki*), red oat (*Avena byzantina*), angled loofah (*Luffa acutangula*) and sweet orange (*Citrus sinensis*). Similarly, non-definitive identifications (marked as "cf." in Dataset S1) were also not counted among the absent crops. This left 53 species absent from the MME+ archaeobotanical record from among 268 taxa on our MME+ food crop list. Of these 53 'orphan' crop species of the MME+ archaeobotanical record, 28 are vegetable crops, 12 are condiments, nine are tree fruits/nuts, three are pulses and only one is a cereal. However, these differences need to be adjusted for the representativeness of each category in the full list. When expressed as a percentage of crop species absent per group, the contrast between cereals and vegetables is still apparent, with 28/90 (31.1%) absent among the vegetables compared with 1/30 (3.3%) among the cereal/pseudocereal group (Table 2). The tree fruit/nuts and pulses display relatively low levels of absence from the archaeobotanical record of the study region (9/73 or 12.3% and 3/24 or 12.5%, respectively).

4.1.3 | Crop species by natural distribution

The natural range of over 85% of the species in our database, or that of their wild progenitors, falls within the MME+ region; only 35 out of 268 may be classified as introductions from other regions (Table 3). The introduced species mostly originate in East and Southeast Asia and Sub-Saharan Africa; only three were originally endemic to Oceania: coconut (*Cocos nucifera*), sugar cane (*Saccharum officinarum*) and clove (*Syzygium aromaticum*); only two come from non-Mediterranean Europe: horseradish (*Armoracia rusticana*) and cabbage and derivatives (*Brassica oleracea*). When East and Southeast Asia are combined, they account for the greatest number of introductions ($n = 17$); when separated, introductions from Sub-Saharan Africa are the most abundant ($n = 13$). Only Sub-Saharan Africa has produced introductions for all functional categories (when 'pseudocereal' is combined with 'cereal'),

³In other world regions, particularly the tropical Americas and Oceania, much foundational archaeobotanical research has been built on non-carpological techniques (e.g., Piperno, 1985; Hather, 1994 [ed]; Piperno et al., 2000; Lentfer, 2009; Denham et al. [eds], 2007).

⁴*Luffa acutangula* is marked 'cf./genus' rather than 'n' in Dataset S1. We consider it absent from the set of reliable gourd species identifications but do not count it among the total 53 absent crop species from MME+ archaeobotany.

⁵While the 'pulse' functional category includes only members of the legume family (Fabaceae), there are several Fabaceae in other functional categories, namely the tree fruits, carob (*Ceratonia siliqua*) and tamarind (*Tamarindus indica*), the vegetables, water mimosa (*Neptunia oleracea*), climbing wattle (*Senegalia pennata*), Siamese cassia (*Senna siamea*) and West Indian pea (*Sesbania grandiflora*), and the condiment, liquorice (*Glycyrrhiza glabra*). Similarly, one grass (Poaceae) species is considered a condiment (sugarcane, *Saccharum officinarum*) and one a vegetable (lemongrass, *Cymbopogon citratus*).

TABLE 3 Introduced food crop species to the study region.

Simplified nat range	Functional category	Species	Family	Common name
Europe - C	Vegetable	<i>Armoracia rusticana</i> G. Gaertn., B.Mey. & Scherb.	Brassicaceae	Horseradish
Europe - N/W	Vegetable	<i>Brassica oleracea</i> L.	Brassicaceae	Cabbage & derivatives
E Asia	Cereal	<i>Setaria italica</i> (L.) P.Beauv.	Poaceae	Foxtail millet
E Asia	Cereal	<i>Oryza sativa</i> L.	Poaceae	Rice (Asian)
E Asia	Cereal	<i>Echinochloa esculenta</i> (A.Braun) H.Scholz	Poaceae	Barnyard millet
E Asia	Pseudocereal	<i>Fagopyrum esculentum</i> Moench	Polygonaceae	Buckwheat
E Asia	Pseudocereal	<i>Fagopyrum tataricum</i> (L.) Gaertn.	Polygonaceae	Tartarian buckwheat
E Asia	Tree fruit/nut	<i>Morus alba</i> L.	Moraceae	White mulberry
E Asia	Tree fruit/nut	<i>Citrus sinensis</i> (L.) Osbeck	Rutaceae	Sweet orange
E Asia; SE Asia	Condiment	<i>Camellia sinensis</i> (L.) Kuntze	Theaceae	Tea
SE Asia	Condiment	<i>Piper longum</i> L.	Piperaceae	Long pepper
SE Asia	Condiment	<i>Piper betle</i> L.	Piperaceae	Betel
SE Asia	Tree fruit/nut	<i>Mangifera indica</i> L.	Anacardiaceae	Mango
SE Asia	Tree fruit/nut	<i>Areca catechu</i> L.	Arecaceae	Areca nut
SE Asia	Tree fruit/nut	<i>Citrus × aurantium</i> L.	Rutaceae	Bitter orange
SE Asia	Tree fruit/nut	<i>Citrus × limon</i> (L.) Osbeck	Rutaceae	Lemon
SE Asia	Tree fruit/nut	<i>Citrus maxima</i> (Burm.) Merr.	Rutaceae	Pomelo
SE Asia, Oceania	Vegetable	<i>Sesbania grandiflora</i> (L.) Poir.	Fabaceae	West Indian pea
SE Asia, Oceania	Vegetable	<i>Benincasa hispida</i> (Thunb.) Cogn.	Cucurbitaceae	Wax gourd
Oceania	Condiment	<i>Syzygium aromaticum</i> (L.) Merr. & L.M.Perry	Myrtaceae	Clove
Oceania	Condiment	<i>Saccharum officinarum</i> L.	Poaceae	Sugar cane
Oceania	Tree fruit/nut	<i>Cocos nucifera</i> L.	Arecaceae	Coconut
Sub-saharan Africa	Cereal	<i>Pennisetum glaucum</i> (L.) R.Br.	Poaceae	Pearl millet
Sub-Saharan Africa	Cereal	<i>Eleusine coracana</i> (L.) Gaertn.	Poaceae	Finger millet
Sub-Saharan Africa	Condiment	<i>Guizotia abyssinica</i> (L.f.) Cass.	Asteraceae	Noog, Niger seed
Sub-Saharan Africa	Condiment	<i>Catha edulis</i> (Vahl) Forssk. ex Endl.	Celastraceae	Khat
Sub-Saharan Africa	Condiment	<i>Coffea arabica</i> L.	Rubiaceae	Coffee
Sub-Saharan Africa	Condiment	<i>Aframomum melegueta</i> K.Schum.	Zingiberaceae	Grains of paradise
Sub-Saharan Africa	Pulse	<i>Vigna unguiculata</i> (L.) Walp.	Fabaceae	Cowpea
Sub-Saharan Africa	Pulse	<i>Psophocarpus tetragonolobus</i> (L.) DC.	Fabaceae	Winged bean
Sub-Saharan Africa	Tree fruit/nut	<i>Tamarindus indica</i> L.	Fabaceae	Tamarind
Sub-Saharan Africa	Tree fruit/nut	<i>Vitellaria paradoxa</i> C.F.Gaertn.	Sapotaceae	Shea
Sub-Saharan Africa	Vegetable	<i>Celosia argentea</i> L.	Amaranthaceae	Plumed cockscomb
Sub-Saharan Africa	Vegetable	<i>Lagenaria siceraria</i> (Molina) Standl.	Cucurbitaceae	Bottle gourd
Sub-Saharan Africa	Vegetable	<i>Hibiscus sabdariffa</i> L.	Malvaceae	Roselle

thanks to the introduction of pulses only from this region. Twenty-two of the 35 introductions have been securely identified in the archaeobotanical record. In terms of the regional origin of species more poorly reflected in the archaeobotanical record, the gourd family (*Cucurbitaceae*) appears to reflect the wider pattern. All seven food crop species of this family not found in archaeobotany originate in South/East Asia and Oceania, whereas the six that were found in archaeobotany have more westerly natural distributions (Table 4).

4.2 | Geometric morphometrics

Our literature review of crop history research applying geometric morphometrics to archaeobotanical remains built upon the work of Evin et al. (2022) and identified a total of 40 studies in 15 taxa (genus or species) (Table 5; Table S2; Figure 2). The first application of GMM to crop history research dates back to 2004, with a study of olive (*Olea europaea*) endocarps (Terral et al., 2004) (Figure 2a). Most taxa are represented by three

TABLE 4 Gourd species by presence in archaeobotany and simplified natural range.

Species	Common name	Simplified natural range	Present in MME+ archaeobotany
<i>Benincasa fistulosa</i>	Tinda	S Asia	n
<i>Luffa acutangula</i>	Loofah	S Asia	n
<i>Momordica dioica</i>	Spine gourd	S Asia, SE Asia	n
<i>Trichosanthes dioica</i>	Pointed gourd	S Asia, SE Asia	n
<i>Trichosanthes cucumerina</i>	Snake gourd	S Asia, SE Asia, E Asia, Oceania	n
<i>Momordica charantia</i>	Bitter melon	S Asia, sub-Saharan Africa, Oceania, SE Asia	n
<i>Benincasa hispida</i>	Wax gourd	SE Asia, Oceania	n
<i>Luffa aegyptiaca</i>	Loofah	S Asia	y
<i>Cucumis sativus</i>	Cucumber	S Asia, SE Asia	y
<i>Coccinia grandis</i>	Ivy gourd	SW Asia, S Asia, SE Asia, E Asia, sub-Saharan Africa	y
<i>Cucumis melo</i>	Melon	SW Asia; S Asia, Oceania, sub-Saharan Africa	y
<i>Citrullus lanatus</i>	Watermelon	N Africa, sub-Saharan Africa	y
<i>Lagenaria siceraria</i>	Bottle gourd	Sub-Saharan Africa	y

Note: Presence/absence data refer to the entire region in Figure 1.

TABLE 5 Summary of geometric morphometrics (GMM) studies per crop taxon.

Functional category	Common name	Species	Family	Natural distribution	GMM studies
Tree fruit/nut	Grape	<i>Vitis vinifera</i> L.	Vitaceae	SW Asia; C Asia	18
Tree fruit/nut	Olive	<i>Olea europaea</i> L.	Oleaceae	SW Asia; N Africa; S Europe; SE Asia; sub-Saharan Africa	6
Cereal	Barley	<i>Hordeum vulgare</i> L.	Poaceae	SW Asia, N Africa; C Asia; E Asia	4
Cereal	Wheat	<i>Triticum</i> spp.	Poaceae	SW Asia; C Asia; Europe	3
Tree fruit/nut	Date palm	<i>Phoenix dactylifera</i> L.	Arecaceae	SW Asia; S Asia	3
Condiment	Opium poppy	<i>Papaver somniferum</i> L.	Papaveraceae	N Africa, S Europe	2
Pulse	Broad bean	<i>Vicia faba</i> L.	Fabaceae	SW Asia; S Asia	2
Cereal	Browntop millet	<i>Urochloa ramosa</i> (L.) T.Q. Nguyen	Poaceae	SW Asia, N Africa, sub-Saharan Africa, S Asia, SE Asia; Oceania	1
Cereal	Foxtail millet	<i>Setaria italica</i> (L.) P.Beauv.	Poaceae	E Asia	1
Pulse	Grass pea	<i>Lathyrus sativus</i> L.	Fabaceae	S Europe	1
Pulse	Lentil	<i>Lens culinaris</i> Medik.	Fabaceae	SW Asia; S Europe; N Africa	1
Tree fruit/nut	Cherry	<i>Prunus avium</i> L.; <i>P. cerasus</i> L.	Rosaceae	SW Asia; Europe; N Africa	1
Tree fruit/nut	Citrus	<i>Citrus</i> spp.	Rutaceae	E Asia	1
Vegetable	Melon	<i>Cucumis melo</i> L.	Cucurbitaceae	SW Asia; S Asia; sub-Saharan Africa; Oceania	1
Vegetable	Watermelon	<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai	Cucurbitaceae	N Africa; sub-Saharan Africa	1

Note: Article citations for each taxon appear in Table S2, with references in Reference S2.

studies or less, except grape (*Vitis vinifera*; $n = 18$), olive ($n = 6$) and barley (*Hordeum vulgare*; $n = 4$) (Figure 2b). Below, we provide a detailed analysis of the results, focusing on the representation of plant families, functional categories and natural distributions. In specific instances, the count of mentions for larger groups may not align with the total mentions for their individual components because some publications include data pertaining to multiple taxa within each group, for example, barley and wheat.

4.2.1 | Crop species per family and functional category

Nine families are represented in GMM studies applied to archaeobotanical remains (Figure 2c). The Vitaceae family stands out with the highest number of studies (18), all focused on grapevine (*Vitis vinifera*). The Poaceae family follows with six GMM studies, primarily focusing

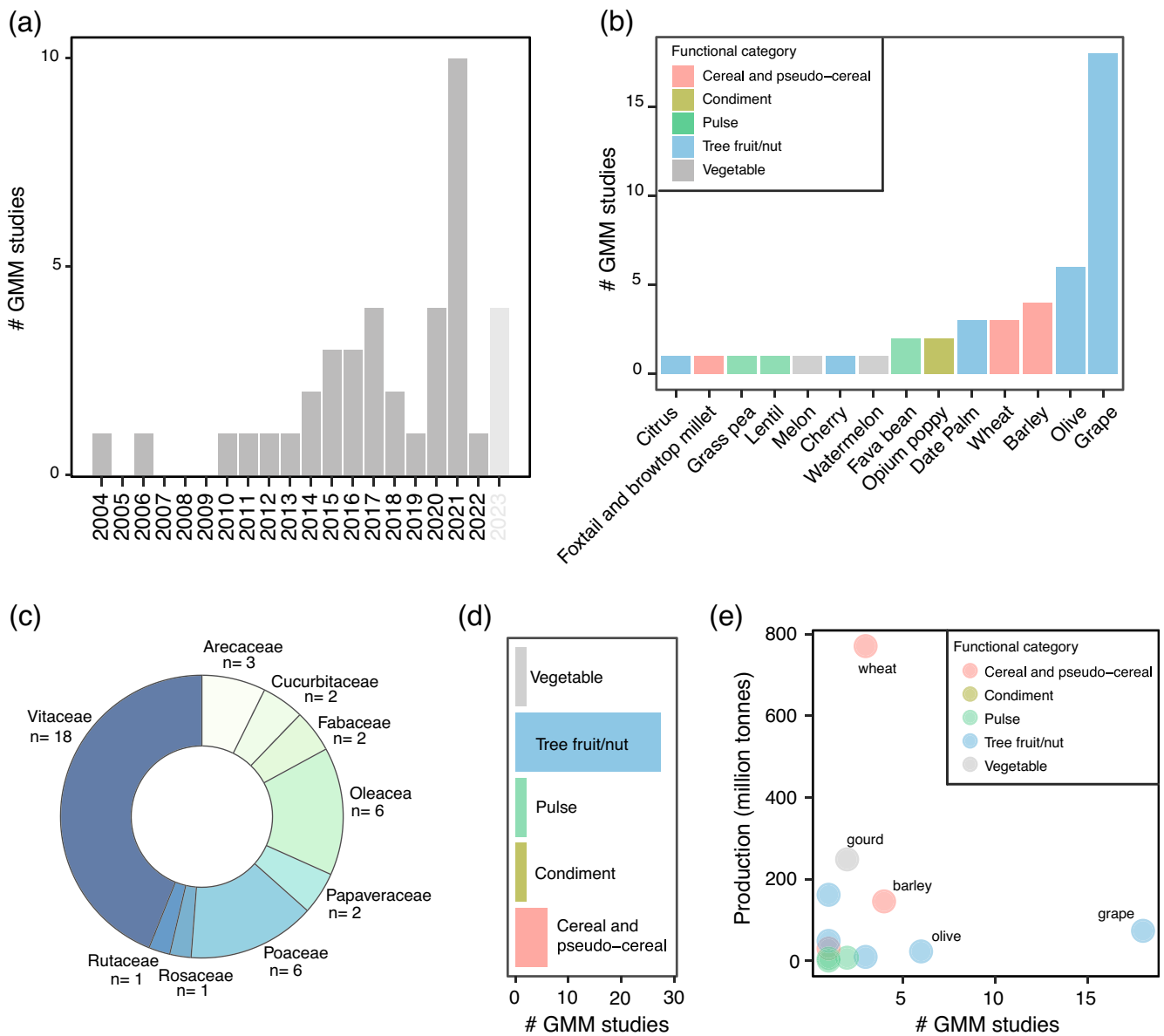


FIGURE 2 Exploration of geometric morphometric studies of archaeobotanical specimens. (a) Number of studies per year. The value for 2023 is in light grey given that the review stops at studies published by May 2023. (b) number of studies per crop, (c) number of studies per family, (d) number of studies per functional category and (e) relationship between the number of geometric morphometric studies and crop production quantity (FAOSTAT, 2021).

on wheat and barley, and Oleaceae with six studies on olive. Other families are represented by four (Fabaceae: grass pea, *Lathyrus sativus*; lentil, *Vicia lens* syn. *lens culinaris*; and two for fava/broad bean, *Vicia fava*), three (Arecaceae: date palm, *Phoenix dactylifera*) or two (Papaveraceae: opium poppy, *Papaver somniferum*; Cucurbitaceae: melon, *Cucumis melo*, and watermelon, *Citrullus lanatus*). Families with only one study include Rutaceae (citrus, *Citrus* spp.) and Rosaceae (cherry, *Prunus avium*, *P. cerasus*). Three quarters of the studies focus on fruit crops ($n = 28$), whereas cereals and pulses are represented in six and two studies, respectively (Figure 2d). Despite the prevalence of GMM studies in fruit crops, there remains a noticeable gap in the application of GMM to many iconic fruit crop species.

4.2.2 | Crop species by natural distribution

Taxa with natural distributions in Southwest Asia or Central Asia are well-represented, accounting for 36 studies out of 40 (88%), in part due to the abundance of studies focusing on grape ($n = 18$). Sub-Saharan Africa ($n = 1$) and South Asia ($n = 7$) have a relatively lower number of GMM studies compared to their high crop diversity and natural distribution. A single crop (grass pea) whose natural range is restricted to Europe (specifically, the Balkan Peninsula) forms the focus of one GMM study. Species native to the Americas were not found to have been the focus of GMM studies of archaeobotanical specimens based on our literature search.

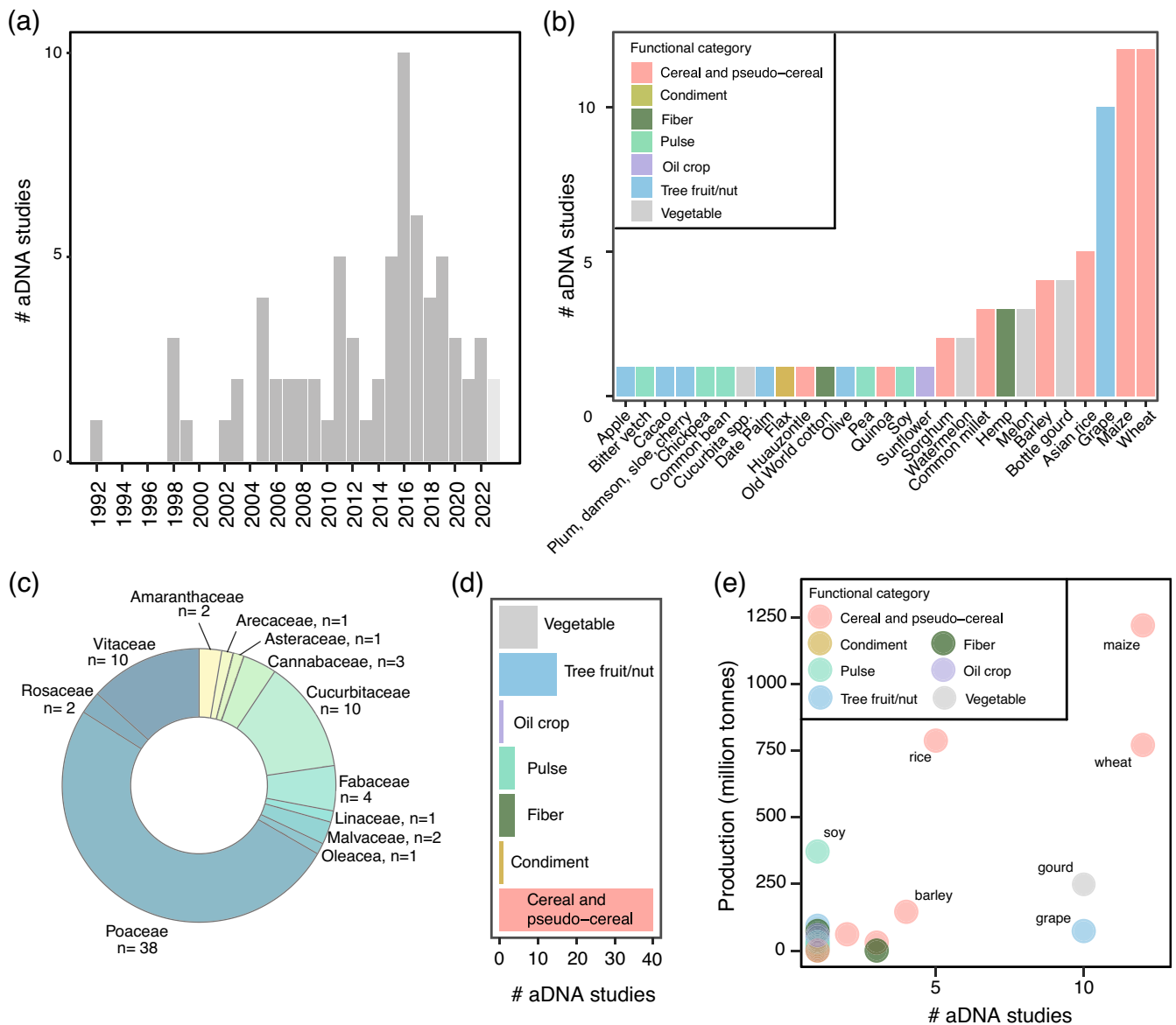


FIGURE 3 Exploration of archaeogenetic studies of archaeobotanical specimens. (a) Number of studies per year. The value for 2023 is in light grey given that the review stops at studies published by May 2023, (b) number of studies per crop, (c) number of studies per family, (d) number of studies per functional category and (e) relationship between the number of archaeogenetic studies and crop production quantity (FAOSTAT, 2021).

4.2.3 | Crop species by annual production quantity

The relationship between the number of GMM studies and global crop production, as reported by FAOSTAT (2021), does not show a significant association (linear model, $p = 0.93$, adjusted $R^2 = -0.10$) but reveals interesting patterns (Figure 2e; Table S3). First, it is worth noting that grapes exhibit a high number of GMM studies despite their relatively low global production. Meanwhile, among the top three cereals in terms of production (wheat, maize and rice), wheat is the only taxon that has been studied by GMM, and despite the prime importance of this crop, only three studies have been published as of May 2023. Of the 14 crops present in the FAOSTAT database having a production >100 million tonnes a year, only three have been studied

by GMM (wheat, barley and watermelon), whereas some iconic species like tomato, potato or soy are absent.⁶

4.3 | Archaeogenetics

Our review of archaeogenetic research focusing on crop histories identified a total of 72 plant archaeogenetics studies on 27 taxa (genus/species) (Figure 3; Table S4). Before 2000, ancient DNA

⁶Among the 14 top-producing crops (FAOSTAT, 2021), 10 were not the focus of any geometric morphometric (GMM) study: sugar cane, maize, rice, oil palm, potato, soy, cassava, sugar beet and tomato, listed in descending order of production quantity by weight.

TABLE 6 Summary of archaeogenetic studies per crop taxon.

Functional category	Common name	Species	Family	Natural distribution	aDNA studies
Cereal/pseudo-cereal	Maize	<i>Zea mays</i> L.	Poaceae	C America; N America	12
Cereal/pseudo-cereal	Wheat	<i>Triticum</i> spp.	Poaceae	SW Asia; C Asia; Europe	12
Tree fruit/nut	Grape	<i>Vitis vinifera</i> L.	Vitaceae	SW Asia; C Asia	10
Cereal/pseudo-cereal	Asian rice	<i>Oryza sativa</i> L.	Poaceae	E Asia	5
Cereal/pseudo-cereal	Barley	<i>Hordeum vulgare</i> L. subsp. <i>vulgare</i>	Poaceae	SW Asia; N Africa; C Asia; E Asia	4
Vegetable	Bottle gourd	<i>Lagenaria siceraria</i> (Molina) Standl.	Cucurbitaceae	Sub-Saharan Africa	4
Cereal/pseudo-cereal	Common millet	<i>Panicum miliaceum</i> L.	Poaceae	S Asia	3
Fiber	Hemp	<i>Cannabis sativa</i> L.	Cannabaceae	C Asia; S Asia	3
Vegetable	Melon	<i>Cucumis melo</i> L.	Cucurbitaceae	SW Asia; S Asia; sub-Saharan Africa; Oceania	3
Cereal/pseudo-cereal	Sorghum	<i>Sorghum bicolor</i> (L.) Moench	Poaceae	Sub-Saharan Africa; S Asia	2
Vegetable	Watermelon	<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai	Cucurbitaceae	N Africa; sub-Saharan Africa	2
Cereal/pseudo-cereal	Huauzontle	<i>Chenopodium berlandieri</i> Moq.	Amaranthaceae	N America; C America	1
Cereal/pseudo-cereal	Quinoa	<i>Chenopodium quinoa</i> Willd.	Amaranthaceae	S America	1
Condiment	Flax	<i>Linum usitatissimum</i> L.	Linaceae	SW Asia; C Asia	1
Fiber	Old World cotton	<i>Gossypium herbaceum</i> L.	Malvaceae	Sub-Saharan Africa, SW Asia, C Asia	1
Pulse	Bitter vetch	<i>Vicia ervilia</i> (L.) Willd.	Fabaceae	SW Asia; C Asia; S Europe; N Africa	1
Pulse	Chickpea	<i>Cicer arietinum</i> L.	Fabaceae	SW Asia	1
Pulse	Common bean	<i>Phaseolus vulgaris</i> L.	Fabaceae	C America; N America	1
Pulse	Pea	<i>Pisum sativum</i> L.	Fabaceae	N Africa; S Europe; SW Asia	1
Pulse	Soy	<i>Glycine max</i> (L.) Merr.	Fabaceae	E Asia	1
Oil crop	Sunflower	<i>Helianthus annuus</i> L.	Asteraceae	C America; N America	1
Tree fruit/nut	Apple	<i>Malus domestica</i> (Suckow) Borkh.	Rosaceae	C Asia	1
Tree fruit/nut	Cacao	<i>Theobroma cacao</i> L.	Malvaceae	C America; S America	1
Tree fruit/nut	Date palm	<i>Phoenix dactylifera</i> L.	Arecaceae	SW Asia; S Asia	1
Tree fruit/nut	Olive	<i>Olea europaea</i> L.	Oleaceae	SW Asia; N Africa; S Europe; SE Asia; sub-Saharan Africa	1
Tree fruit/nut	Plum, damson, sloe, cherry	<i>Prunus</i> spp. ^a	Rosaceae	Europe, N Africa, SW Asia, Caucasus, C Asia	1
Vegetable	Gourd and squash	<i>Cucurbita</i> spp.	Cucurbitaceae	Americas	1

Note: Citations and references for each taxon appear in Table S4 and Reference S3, respectively.

^aFruit stones of the groups *P. insititia/spinosa* and *P. avium/cerasus*.

studies of crops were scarce (Figure 3a) and focused on the development of suitable extraction methods; they are thus mostly not counted in the analysis that follows. Only a few articles from this period interpreted the DNA sequences recovered from an evolutionary viewpoint and are reported here. From the late 2000s onwards, the number of studies per year increased, as well as the number of taxa studied. Most studies focus on a single taxon (Table 6; Figure 3). There is a large variance in the number of studies per taxon (on average: 2.8): more than half of the taxa ($n = 16$) are represented by a single study, whereas three taxa form the focus of 10 studies or more (maize: $n = 12$, wheat: $n = 12$ and grape: $n = 10$). In certain situations, the tally of references to broader categories may not correspond to the cumulative mentions of their smaller constituents since some publications encompass data pertaining to multiple taxa within each category, for example, flax and hemp.

4.3.1 | Crop species per family and functional category

Twelve families are represented in archaeogenetic studies devoted to archaeology-based crop history (Figure 3c). Among them, Poaceae is by far the most extensively studied, with a total of 38 aDNA studies on six different taxa. Vitaceae (grape only) and Cucurbitaceae (with four taxa represented) are represented by 10 studies each. Fabaceae follows with four studies on five different species. Other families, such as Cannabaceae ($n = 3$), Rosaceae ($n = 2$), Malvaceae ($n = 2$) and Amaranthaceae ($n = 2$), exhibit a lower number of studies.

Considering functional categories (Figure 3d), cereals/pseudo-cereals overwhelmingly dominate the research landscape ($n = 40$). They account for the largest share of studies by a significant margin, representing 56% of the total number of studies. This notable predominance can primarily be attributed to the substantial number of studies conducted on wheat ($n = 12$) and maize ($n = 12$). Studies of cereals/pseudo-cereals are followed by studies of tree fruit ($n = 15$), vegetables and pulses ($n = 10$ and $n = 4$, respectively) and finally fiber crops, oil crops and condiments ($n = 4$, $n = 1$ and $n = 1$, respectively).

4.3.2 | Crop species by natural distribution

Overall, varying levels of aDNA research activity are evident across crop species' regions of natural distribution. Numerous studies have been conducted on crops originating from Southwest Asia ($n = 34$). Central America also garners attention ($n = 17$), primarily driven by the 12 studies of maize. Crop species originating in other regions, including North America, South America, South Asia, East Asia and Europe are represented by fewer studies. Natural distributions of Cucurbitaceae (bottle gourd, melon and watermelon), sorghum, olive and old-world cotton include Sub-Saharan Africa (according to POWO, 2023), but none of the aDNA studies were conducted on

specimens excavated in Sub-Saharan Africa. In fact, all the apparent natural distribution regional foci come down to a few key crops that have successfully globalized.

4.3.3 | Crop species by annual production quantity

For the represented taxa, crop production volumes correlate significantly with the extent of archaeogenetic research focused on specific crops (linear model, $p = 1.06 \times 10^{-4}$, adjusted $R^2 = 0.50$) (Figure 3e; Table S5). In line with this, the top three globally cultivated cereals (each with annual production above 500 million tonnes) have some of the highest numbers of studies, with 12 studies on wheat and 12 on maize. Although rice is less represented with five studies, it is still one of the most archaeogenetically studied crops. Meanwhile, despite being under the 250 M tonne production threshold, grape and the gourd family stand out with 10 studies each.

Only a few 'minor' crops (based on FAOSTAT production data) have been subjected to archaeogenetic studies, such as broomcorn millet (*Panicum miliaceum*, $n = 3$), which is a cereal, and hemp (*Cannabis sativa*, $n = 3$) with even less attention paid to vegetable or tree crops. Bottle gourd (*Lagenaria siceraria*), with four aDNA studies, is not a global market crop but is and was an important food and container crop across a wide portion of the globe. Interestingly, *Chenopodium berlandieri*, which is absent from FAOSTAT because it is a lost crop of ancient North America (Gremillion, 2014), was the subject of a dedicated aDNA study (Kistler & Shapiro, 2011). Although there is a tendency for the most archaeogenetically studied species to be high-production crops globally, the reverse is not necessarily the case: sugar cane, tomatoes (*Solanum lycopersicum*) and potatoes (*Solanum tuberosum*) are among the highest yielding crops globally but at the time of writing lack archaeogenetic studies.

4.4 | Stable isotope analysis

We identified a total of 135 publications involving SIA of archaeological seeds, grains and fruits (See Dataset S2 for full breakdown). The vast majority of these publications analyze carbon and nitrogen isotopes, with strontium ($n = 4$), sulphur ($n = 1$) and oxygen ($n = 1$) less represented. This reflects that carbon and nitrogen analysis of charred grain is relatively straightforward when compared to other isotopes which come with additional preservation, contamination and analytical difficulties that are only starting to be addressed (Bogaard et al., 2014; Larsson et al., 2020; Nitsch et al., 2019; Ryan et al., 2021; Williams et al., 2005). Most publications analyze more than one plant species. Our literature survey indicates that studies of SIA held fast with around 10 studies per decade through the 1990s and 2000s until around 2010, when the field exploded, exceeding 15 per year during 2020–2022 (Figure 4a). The number of papers published since the first major review of SIA applied to archaeobotanical research by Fiorentino et al. in 2015 has doubled, with the total number of published studies involving SIA of archaeobotanical remains rising from 43 to 92 between

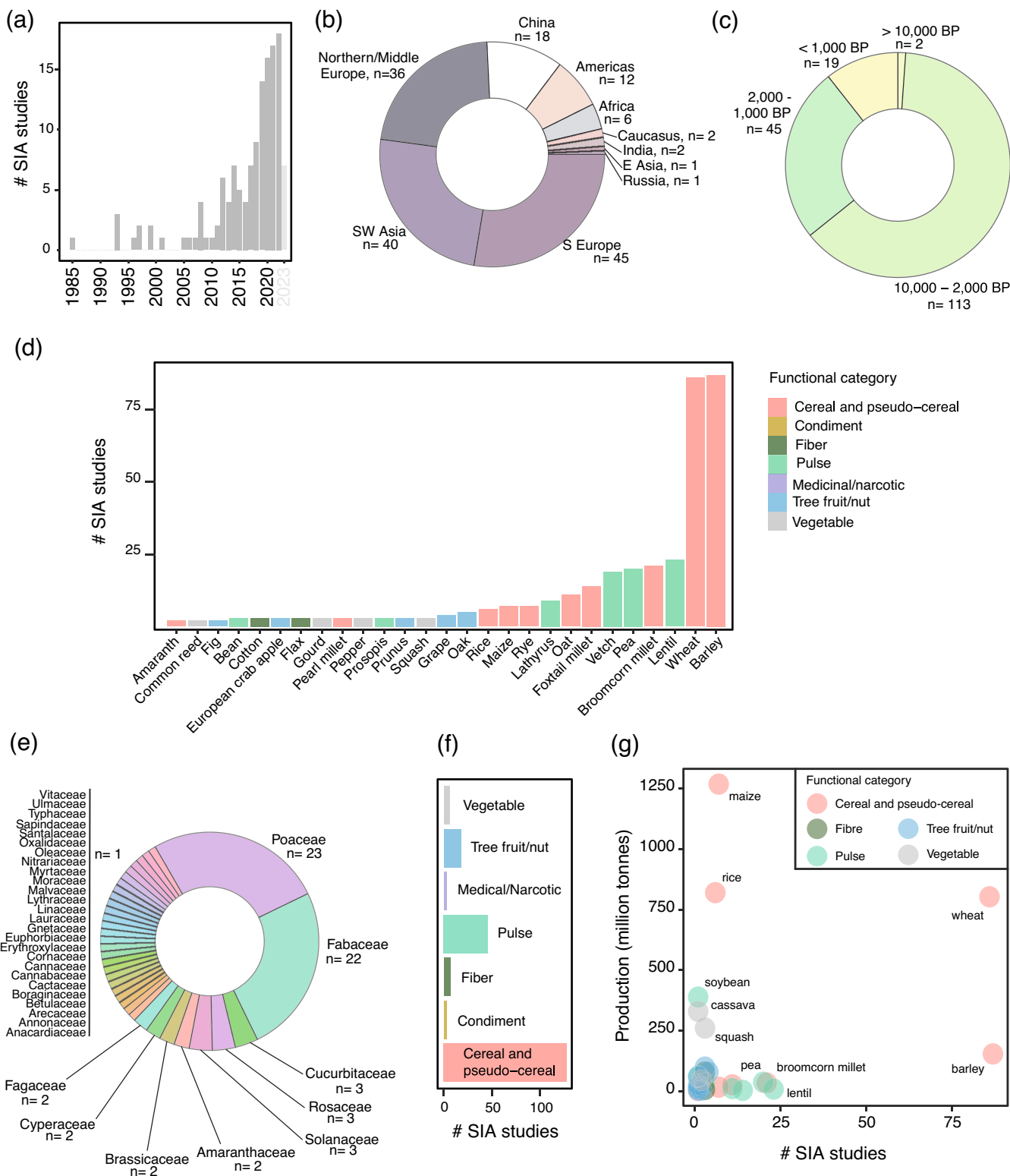


FIGURE 4 Exploration of stable isotope analysis studies of archaeobotanical specimens. (a) Number of studies per year. The value for 2023 is in light grey given that the review stops at studies published by May 2023, (b) geographic distribution of publications on SIA of archaeological plant remains, (c) chronological distribution of publications on SIA of archaeological plant remains, (d) number of studies per crop (only crops present in more than one study are represented), (e) number of studies per family, (f) number of studies for each category, (g) relationship between the number of stable isotope analysis studies and crop production quantity (FAOSTAT, 2021; note that the data point representing squash includes all the studies for the Cucurbitaceae family [*Cucurbita* spp., *C. moschata*, *Lagenaria* spp. and *L. siceraria*], the data point representing broad beans [*Vicia faba*] combines the data for the entries green and dry broad beans and horse bean from FAOSTAT, and the entry vetches from FAOSTAT includes the studies for *Vicia* spp., *V. ervilia*, *V. sativa*, *L. clymenum*, *L. ochrus* and *L. sativus*). For data, see Table S6.

TABLE 7 Plant taxa analyzed using stable isotope analysis applied to archaeobotanical remains and quantification of the publications mentioning them.

Functional category	Common name	Genus	Family	Count	Main species included
Cereal	Barley	Hordeum	Poaceae	87	<i>H. vulgare</i> (64), <i>H. v. var. nudum</i> (13), <i>H. v. ssp. vulgare</i> (9)
Cereal	Wheat	Triticum	Poaceae	86	<i>T. dicoccon</i> (48), <i>T. aestivum/durum</i> (35), <i>T. monococcum</i> (26)
Pulse	Lentil	Lens	Fabaceae	23	<i>L. culinaris/orientalis</i> (23)
Cereal	Broomcorn millet	Panicum	Poaceae	21	<i>P. miliaceum</i> (21)
Pulse	Pea	Pisum	Fabaceae	20	<i>P. sativum</i> (20)
Pulse	Vetch	Vicia	Fabaceae	19	<i>V. faba</i> (11), <i>V. ervilia</i> (7), <i>V. sativa</i> (1)
Cereal	Foxtail millet	Setaria	Poaceae	14	<i>S. italica</i> (14)
Cereal	Oat	Avena	Poaceae	11	<i>A. sativa</i> (11)
Pulse	Lathyrus	Lathyrus	Fabaceae	9	<i>L. clymenum</i> (1), <i>L. ochrus</i> (1), <i>L. sativus</i> (1)
Cereal	Rye	Secale	Poaceae	7	<i>S. cereale</i> (7)
Cereal	Maize	Zea	Poaceae	7	<i>Z. mays</i> (7)
Cereal	Rice	Oryza	Poaceae	6	<i>O. sativa</i> (6)
Tree fruit/nut	Oak	Quercus	Fagaceae	5	<i>Q. pubescens/virgiliana</i> (4), <i>Q. gambelii</i> (1)
Tree fruit/nut	Grape	Vitis	Vitaceae	4	<i>V. vinifera</i> (4)
Cereal	Pearl millet	Pennisetum	Poaceae	3	<i>P. glaucum</i> (3)
Fiber	Flax	Linum	Linaceae	3	<i>L. usitatissimum</i> (3)
Fiber	Cotton	Gossypium	Malvaceae	3	-
Pulse	Bean	Phaseolus	Fabaceae	3	<i>P. vulgaris</i> (3), <i>P. lunatus</i> (2)
Pulse	Various	Prosopis	Fabaceae	3	<i>P. farcta</i> (1), <i>P. pallida</i> (1)
Tree fruit/nut	European crab apple	Malus	Rosaceae	3	<i>M. sylvestris</i> (3)
Tree fruit/nut	Various	Prunus	Rosaceae	3	<i>P. amygdalus</i> (2)
Vegetable	Squash	Cucurbita	Cucurbitaceae	3	<i>C. moschata</i> (2)
Vegetable	Gourd	Lagenaria	Cucurbitaceae	3	<i>L. siceraria</i> (2)
Vegetable	Pepper	Capsicum	Solanaceae	3	<i>C. baccatum</i> (1)
Cereal	Amaranth	Amaranthus	Amaranthaceae	2	-
Vegetable	Common reed	Phragmites	Poaceae	2	<i>P. communis</i> (2)
Tree fruit/nut	Fig	Ficus	Moraceae	2	<i>F. carica</i> (2)
Cereal	Goatgrass	Aegilops	Poaceae	1	-
Cereal	Blue wild rye	Leymus	Poaceae	1	<i>L. secalinus</i> (1)
Condiment	Gold of pleasure	Camelina	Brassicaceae	1	<i>C. sativa</i> (1)
Condiment	Wood club-rush	Scirpus	Cyperaceae	1	-
Condiment	Bastard toadflax	Comandra	Santalaceae	1	<i>C. pallida</i> (1)
Condiment	Maple	Acer	Sapindaceae	1	<i>A. grandidentatum/negundo</i> (1)
Medicinal/narcotic	Cocaine	Erythroxylum	Erythroxylaceae	1	-
Pulse	Peanut	Arachis	Fabaceae	1	<i>A. hypogaea</i> (1)
Pulse	Jack-bean	Canavalia	Fabaceae	1	-
Pulse	Chickpea	Cicer	Fabaceae	1	<i>C. arietinum</i> (1)
Pulse	Coral tree	Erythrina	Fabaceae	1	-
Pulse	Chañar	Geoffroea	Fabaceae	1	<i>G. decorticans</i> (1)
Pulse	Soybean	Glycine	Fabaceae	1	<i>G. max</i> (1)
Pulse	Ice-cream bean/ Pacay	Inga	Fabaceae	1	<i>I. edulis/feuillei</i> (1)
Pulse	Horsegram	Macrotyloma	Fabaceae	1	<i>M. uniflorum</i> (1)
Pulse	Adzuki bean	Vigna	Fabaceae	1	<i>V. angularis</i> (1)

TABLE 7 (Continued)

Functional category	Common name	Genus	Family	Count	Main species included
Cereal	Quinoa	Chenopodium	Amaranthaceae	1	<i>C. quinoa</i> (1)
Medicinal/narcotic	Kudouzi	Sophora	Fabaceae	1	<i>S. alopecuroides</i> (1)
Tree fruit/nut	Unknown	Nitraria	Nitrariaceae	1	<i>N. pamirica</i> (1)
Fiber	Cana-do-rio	Gynerium	Poaceae	1	<i>G. sagittatum</i> (1)
Tree fruit/nut	Terebinth	Pistacia	Anacardiaceae	1	<i>P. terebinthus</i> (1)
Tree fruit/nut	Soursop	Annona	Annonaceae	1	<i>A. muricata</i> (1)
Tree fruit/nut	Date palm	Phoenix	Arecaceae	1	<i>P. dactylifera</i> (1)
Tree fruit/nut	Hazelnut	Corylus	Betulaceae	1	<i>C. avellana</i> (1)
Medicinal/narcotic	Common gromwell	Lithospermum	Boraginaceae	1	<i>L. officinale</i> (1)
Tree fruit/nut	Prickly pear	Opuntia	Cactaceae	1	-
Tree fruit/nut	Cornelian cherry	Cornus	Cornaceae	1	<i>C. mas</i> (1)
Tree fruit/nut	Avocado	Persea	Lauraceae	1	<i>P. americana</i> (1)
Tree fruit/nut	Pomegranate	Punica	Lythraceae	1	<i>P. granatum</i> (1)
Tree fruit/nut	Guava	Psidium	Myrtaceae	1	<i>P. guajava</i> (1)
Tree fruit/nut	Olive	Olea	Oleaceae	1	<i>O. europaea</i> (1)
Tree fruit/nut	Whitebeam/Service tree	Sorbus	Rosaceae	1	<i>S. aria/domestica</i> (1)
Tree fruit/nut	Elm	Ulmus	Ulmaceae	1	-
Vegetable	Club-rush	Schoenoplectus	Cyperaceae	1	-
Vegetable	Winter cress	Barbarea	Brassicaceae	1	-
Vegetable	Caucasian hackberry	Celtis	Cannabaceae	1	<i>C. caucasica</i> (1)
Vegetable	Canna lily	Canna	Cannaceae	1	-
Vegetable	Cassava	Manihot	Euphorbiaceae	1	<i>M. esculenta</i> (1)
Vegetable	Eru	Gnetum	Gnetaceae	1	<i>G. africanum</i> (1)
Vegetable	Yams	Oxalis	Oxalidaceae	1	<i>O. tuberosa</i> (1)
Vegetable	Various	Solanum	Solanaceae	1	-
Vegetable	Lesser bulrush	Typha	Typhaceae	1	<i>T. angustifolia</i> (1)

Note: Only the three most frequent species in SIA literature are listed under 'main species included'. A comprehensive list of species and references, as well as natural distributions, can be found in Dataset S2.

2016 and mid-2023.⁷ In the following sections, we quantify the taxa, geographic areas and chronologies analyzed, providing in brackets the number of publications presenting new data about each of these categories. In certain cases, the number of mentions to broad groups may not match the sum of the mentions to its smaller components because many publications report data about more than one taxon in each group, for example, wheat and barley discussed below (Table 7).

Geographically (Figure 4b), most studies have been carried out on plant remains excavated from Southern Europe ($n = 45$), SW Asia ($n = 40$) and northern/middle Europe ($n = 36$), followed by China ($n = 18$) and the Americas ($n = 12$). Within Europe, the main focus has been Spain ($n = 16$), where the use of carbon stable isotopes to explore water status ($\Delta^{13}\text{C}$) was pioneered in the 1990s. Plant

remains from Greece represent the second greatest number of studies in Europe ($n = 13$), followed by the United Kingdom ($n = 10$), Germany ($n = 9$) and Italy ($n = 7$). Africa ($n = 6$), the Caucasus ($n = 2$), India ($n = 2$), East Asia ($n = 1$) and Russia ($n = 1$) have seen the fewest number of publications so far. There are also regions of the world where SIA has yet to be applied to archaeobotanical specimens, for example, Oceania and the majority of the Americas.

Chronologically (Figure 4c), the majority of studies concentrate on 10,000–2000 BP ($n = 113$), a broad time period that witnessed the development of agriculture in many parts of the globe. The geographical focus on SW Asia and to some extent Southern Europe (Greece and Spain) reflects research oriented towards crop management and environmental status during the early dynamics of agriculture in these regions, more specifically during the Neolithic and Bronze Age. Another period that has received considerable interest, especially in recent years, is the Middle Ages in Western and Central Europe (1500–500 BP, $n = 23$). In contrast, the smaller

⁷Fiorentino et al. (2015) counted all papers involving SIA in archaeobotanical research, including methodological papers measuring modern material. Hence, they counted around 70 papers, while we have only considered those that directly analyzed archaeological plant remains.

number of studies focused on the Classical period (2500–1500 BP, $n = 19$) is surprising, considering the abundance of sites dating to this period in Europe, SW Asia and North Africa. Studies on contexts older than 10,000 BP are rare ($n = 2$), probably due to a smaller number of sites and well-preserved assemblages, in addition to greater interest in questions related to agricultural management within SIA.

4.4.1 | Crop species per family and functional category

Published papers on SIA of archaeobotanical remains include data on 35 plant families (Table 7, Figure 4e), but the number of species represented from each family is unevenly distributed. The families most frequently represented are Poaceae and Fabaceae, with 25 and 24 species, respectively. A small number of families have two or three species analyzed for stable isotopes. These are Cucurbitaceae, Rosaceae, Amaranthaceae, Brassicaceae, Cyperaceae, Fagaceae and Solanaceae. The other 26 plant families are represented by one species and in most instances only appear in a single publication. These numbers agree with the trends observed in archaeobotany and archaeogenetics studies, where Poaceae and Fabaceae are also the predominant families. In contrast, Vitaceae, the most frequent family targeted in GMM publications, is only represented in SIA by just four ($n = 4$) papers on grape pips.

The application of SIA to ancient plant remains is dominated by cereals ($n = 128$; Figure 4d,f). The two most prevalent are wheat (*Triticum* spp., $n = 87$) and barley (*Hordeum vulgare*, $n = 86$), and it is frequent to find both in the same study. These cereals are today some of the most globally significant crops in terms of area cultivated and production (FAOSTAT, 2021). Among those publications that specified taxonomic groups within wheat, naked wheat (55 total publications; *Triticum aestivum*, $n = 17$; *T. durum*, $n = 6$; *T. aestivum/durum*, $n = 35$) are about equally researched as hulled wheat (53 total publications; *T. dicoccon*, $n = 48$; *T. monococcum*, $n = 26$; *T. spelta*, $n = 14$). Among barley, 13 of 86 were specified as naked (*Hordeum vulgare* var. *nudum*), and those specified as six-row barley (*H. vulgare* subsp. *hexastichum*, $n = 6$) are more common than those specified as two-row barley (*H. vulgare* subsp. *distichon*, $n = 1$). A wild specimen of both wheat (*Triticum boeoticum*, $n = 1$) and barley (*Hordeum spontaneum*, $n = 1$) have also been analyzed, just once in each case. Millets have received much attention too, both broomcorn millet (*Panicum miliaceum*, $n = 21$) and foxtail millet (*Setaria italica*, $n = 14$), and more rarely pearl millet (*Pennisetum glaucum*, $n = 3$). Other cereals are less frequent, including oat (*Avena sativa*, $n = 11$), rye (*Secale cereale*, $n = 7$), maize (*Zea mays*, $n = 7$) and rice (*Oryza sativa*, $n = 6$).

Beyond the major cereals, pulses ($n = 46$) are the second largest group of crops analyzed, including lentils (*Lens culinaris/orientalis*, $n = 23$), peas (*Pisum sativum*, $n = 20$), vetches (*Vicia* spp., $n = 19$) and lathyrus (*Lathyrus* spp., $n = 9$). Tree fruits and nuts ($n = 18$) have also been subjected to SIA occasionally. Acorn/oak (*Quercus* spp., $n = 5$), a plant resource that has long been exploited and

managed by humans, stands out in this group, followed by grapes (*Vitis vinifera*, $n = 4$). Other fruits and nuts only have a few or single examples of SIA studies such as apple (*Malus sylvestris*, $n = 3$), fig (*Ficus carica*, $n = 2$), almond (*Prunus amygdalus*, $n = 2$), olive (*Olea europaea*, $n = 1$), Cornelian cherry (*Cornus mas*, $n = 1$), hazelnut (*Corylus avellana*, $n = 1$), avocado (*Persea americana*, $n = 1$), date palm (*Phoenix dactylifera*, $n = 1$), guava (*Psidium guajava*, $n = 1$) and pomegranate (*Punica granatum*, $n = 1$). Vegetables ($n = 6$) are infrequent, with only pepper (*Capsicum* spp., $n = 3$) and squash/gourd (*Cucurbita* spp., $n = 3$; *Lagenaria* spp., $n = 3$) analyzed in more than one publication. Finally, we also found a few examples of SIA on condiments (*Acer grandidentatum/negundo*, $n = 1$) and fibres (*Gossypium* spp., $n = 3$; *Linum usitatissimum*, $n = 3$), as well as medicinal/narcotic plants (*Erythroxylum* spp., $n = 1$), although they are always incidental.

4.4.2 | Crop species by natural distribution

Wild distributions of species subjected to SIA are loosely related to the geographic origin of the archaeological plant remains analyzed (Dataset S2). More than half of the plant species with published stable isotope data originate from SW Asia ($n = 54$) and approximately a third of them from Southern Europe ($n = 35$), the two regions with the greatest volume of published isotopic data. This is followed by studies of plants native to the Americas (North America, $n = 27$; Central America, $n = 23$; South America, $n = 28$), Africa (North Africa, $n = 27$; Central Africa, $n = 18$; South Africa, $n = 16$) and Oceania ($n = 11$). Most of the plants studied by SIA recorded as native to these latter regions have very broad natural distributions and the samples actually analyzed derive from excavations in different regions (e.g., *Amaranthus* sp., *Solanum* sp., *Prunus* sp.). Plants exclusively native to the Americas (e.g., *Chenopodium quinoa*, *Cucurbita moschata* and *Zea mays*) and Africa (e.g., *Lagenaria siceraria*, *Gnetum africanum* and *Pennisetum glaucum*) have significantly smaller numbers of SIA studies. So far, no plants originally endemic to Oceania have been analyzed for stable isotopes according to our literature survey.

4.4.3 | Crop species by annual production quantity

FAOSTAT data exist for 28 species analyzed for stable isotopes, with no significant relation between modern annual production and the representation of crops in the SIA literature (linear model, $p = 0.17$, adjusted $R^2 = 0.03$) (Figure 4g; Dataset S2; Table S6). Of the most significant modern species with over 750 M tonnes, maize (*Zea mays*) and rice (*Oryza sativa*) have featured in less than 10 archaeological SIA studies each, although wheat (*Triticum* spp.) has high figures in both variables. Barley (*Hordeum* spp.) stands out as the species with the greatest number of SIA studies but with moderate modern production, under 250 M production tonnes. Several other cereals (broomcorn millet and oats) and pulses (lentil,

pea and fava bean) with lower global production levels have been featured in over 10 SIA publications. In contrast, two crops with higher production (over 250 M tonnes)—soybean (*Glycine max*) and cassava (*Manihot esculenta*)—have only been analyzed in one publication each. The majority of plant species analyzed in archaeological SIA studies do not appear in the FAO database. This may be because they are wild resources (e.g., blue wild rye [*Leymus secalinus*], oaks [*Quercus* spp.]), because they are no longer commonly cultivated (e.g., gold of pleasure [*Camelina sativa*]) or because they are not globally significant enough to be included (e.g., foxtail and pearl millets).

5 | DISCUSSION

The aim of this study was to identify ‘invisible’ or ‘orphan’ crops within archaeology-based crop history research and the factors contributing to their absence. More specifically, we sought to systematically assess the representativeness of food crop species in archaeobotanical research, as well as geometric morphometric (GMM), ancient DNA (aDNA) and stable isotope analyses (SIA) applied to archaeobotanical plant remains. For archaeobotany, the attempt began with compiling a list of food crops from the Middle East, Mediterranean, Caucasus, Central Asia and South Asia. The resultant ‘MME+ food crop list’ of 268 species and species groups, as well as the tally of 53 species across 45 genera absent from the archaeobotanical record of this region, both yielded several interesting patterns. As might be expected, families and functional categories were unevenly represented in the MME+ food crop list, with just eight families (out of 66) accounting for over half of its 268 species. Similarly, roughly 60% of these are vegetable and tree fruit/nut crops, whereas pulses and cereals combined account for 20%. Taking this into account, a higher proportion of vegetables is absent from the archaeobotanical record than that of cereals, pulses and tree fruit/nuts. The families with more species on the total list also tended to have relatively few ‘orphan’ crops. Perhaps related to this, the ‘orphan’ crops are, without exception, minor crops. Natural distributions of the crop species—‘orphan’ crops included—span the Old World and many are cosmopolitan, with natural ranges cutting across much of the study region. At the same time, a disproportionate number of species on both the MME+ food crop list and the ‘orphan’ crops of MME+ archaeobotany seem to originate in South/East Asia. Such patterns trickle down to GMM, aDNA and SIA analyses applied to archaeobotanical remains; South/East Asian crops and those of the southern hemisphere in general are far less likely to be subject to these analyses. However, it is important to note that each discipline also exhibits its own unique set of biases. A study of species representativeness in archaeology-based crop history research has never been attempted on such a wide geographic and multidisciplinary scale, and the effort is confounded by numerous methodological hurdles. Therefore, the meta-analysis and synthesis presented here should be understood as a first attempt, which will be improved upon and expanded in the future. At the same time, several illuminating patterns emerge

from this study, which may be relevant to a deeper understanding of ‘forgotten’ crops and agendas for promoting sustainable agriculture. The causes of the observed patterns and their implications are the focus of the following discussion. Overall, the patterns can be explained by site formation process and taphonomy, research agendas and wider patterns in plant species diversity.

5.1 | Limitations and methodological challenges

The primary limitations of this study of species representativeness in crop history research concern the choice of disciplines and the choices involved in producing the MME+ food crop reference list of pre-Columbian crops in the region. The choice of disciplines follows archaeology-based crop history research, but it must be acknowledged that some of archaeobotany’s ‘orphan’ crops presented above are attested to in historical sources. Within the context of the current study, the presence in historical sources of some of archaeobotany’s ‘orphan’ crops (Table 1) is an apparent reflection of taphonomic bias in archaeobotany. Among these crops is saffron (*Crocus sativus*), which is identified as a useful plant in several ancient written sources from the Mediterranean to South Asia (Cardone et al., 2020) and numerous Minoan iconographic depictions (Dewan, 2015). Kenaf (*Hibiscus cannabinus*) and okra (*Abelmoschus esculentus*) are both mentioned in Sanskrit texts, supporting their presence in historical India and hinting at an African/South Arabian crop introduction in the case of kenaf (Singh & Nigam, 2017). The absence of okra in MME+ archaeobotany could be explained by the fact that okra seeds are consumed together with the unripe fruit, leaving little chance for deposition and preservation of mature seeds. Saffron is propagated vegetatively, and its stigmas are harvested for spice; hence, there would be no opportunity for seeds to be deposited archaeologically; its bulbs are unlikely to be identified to species. Meanwhile, the practical choice to limit the archaeobotanical meta-analysis to food crops from the Mediterranean to South Asia presents both a limitation of this study and potentially ambiguous boundaries (see Method S1). We would also like to stress that the archaeobotanical database and meta-analysis presented here are no substitute for regional databases and studies, where sample-level data (including different studies, sites, microregions, periods, quantities etc.) are recorded and analyzed.

5.2 | Factors affecting crop species representativeness

5.2.1 | Site formation processes and taphonomy

Site formation processes and taphonomy include factors affecting deposition, preservation, retrieval and identification. These play a key role in the representativeness of archaeobotanical assemblages and go a long way in explaining the results of this study. As regards the representativeness of functional categories and families in archaeobotany, higher seed density is more conducive to preservation by

charring, the main pathway to archaeobotanical visibility. This could explain the excellent representation in the archaeobotanical record of the Rosaceae family and other tree fruits with hard endocarps. Preservation by charring also favors legume and grass grains over vegetables, especially since vegetables are often exploited for leafy, fleshy or other low-density organs and are notoriously underrepresented in archaeobotany (e.g., Harris, 2012; Hather, 1994; Zohary et al., 2012). Another taphonomic advantage for cereals and pulses over vegetables is that crops requiring multi-stage processing conducted on-site are more likely to be deposited in archaeological contexts (Fuller et al., 2014). For certain fruit endocarps and nuts, archaeological preservation is likely to be highly fragmented, making identification reliant on background studies of reference materials or methods such as SEM investigation of tissue patterns (e.g., Fairbairn & Florin, 2022). The observed bias against species from tropical regions in MME+ archaeobotany might be related to the greater importance of microscopic identification techniques in tropical archaeobotany compared with MME+ archaeobotany. More taxonomic reference work on phytoliths, starch granules and parenchyma has been conducted in tropical regions outside the MME+, particularly Central and South America and Oceania (e.g., Cassino et al., 2021; Denham et al., 2003; Denham et al., 2007; Florin, 2022; Hather, 1994; Lentfer, 2009; Piperno, 1985; Piperno et al., 2000; Scheel-Ybert & Boyadjian, 2020) and relatively little work of this kind has been conducted in the MME+ (Ahituv & Henry, 2022; Arranz-Otaegui & Roe, 2023).

Crop species representation in GMM, aDNA and SIA studies of archaeobotanical remains may reflect taphonomic biases in archaeobotany more strongly or in ways not apparent from archaeobotanical presence/absence data. These analyses often require large numbers of specimens (esp. GMM and SIA) or well-preserved material (esp. aDNA), meaning that species which are rare in archaeobotany are likely to be absent from these analyses. The chronological and geographic biases observed for SIA—favoring Neolithic–Bronze Age SW Asia and Europe—are a direct reflection of greater archaeobotanical focus on these contexts. Ancient DNA tends to preserve best under desiccated conditions, which could explain the relative paucity of aDNA studies of rice ($n = 5$) compared to the other two major global grains, wheat ($n = 12$) and maize ($n = 12$). Historically, rice was rarely grown or consumed in arid environments, which provide the best recovery potential for aDNA (Kistler et al., 2020; Spengler et al., 2021). The near absence of desiccated plant remains of crops such as potatoes, citrus, sugar cane or bananas probably explains the lack of archaeogenetic studies of these global commodities. Scarcity in the archaeobotanical record may also explain the relative paucity of GMM studies of citrus ($n = 1$) and apple (*Malus domestica*, $n = 0$), whereas the wealth of grape GMM studies ($n = 18$) may be the product of abundant grape pips in archaeobotanical assemblages of the Mediterranean region. Archaeobotanical scarcity explains somewhat, but not fully, the absence of archaeological GMM studies on crops whose hard endocarps/seeds are otherwise conducive to intact preservation, for example, peach (*Prunus persica*), plum (*Prunus domestica*), jujube (*Ziziphus* spp.) or pine nuts (*Pinus pinea*).

5.2.2 | Biodiversity

Overall species diversity within plant families, functional categories and geographic regions comprises another key factor affecting the observed patterns in species representativeness within archaeobotany. This provides another possible explanation for the higher representation of legumes (Fabaceae) and grasses (Poaceae) in our MME+ food crop list, followed by the rose family (Rosaceae), since these three families contain the highest numbers of edible species and crop wild relatives worldwide (Vincent et al., 2013; Willis, 2017). Perhaps the larger families are also better studied and better represented in archaeobotanical reference collections. One reason that South/East Asia is the source of a greater number of food crops absent from the archaeobotanical record may have to do with greater overall biodiversity in the tropics, including more edible plant species. In other words, greater crop diversity could mean that there are more species to miss. Perhaps a historically slower pace of industrialization in the ‘Global South’ has also contributed to the greater survival of agricultural species diversity there.

5.2.3 | Agricultural research agendas

Crop history research agendas do appear to affect the observed patterns by influencing aspects of taphonomic bias related to retrieval and identification, among other possible routes. A general grain bias may be a carryover from the grain bias in SW Asian archaeobotany, where cereals and pulses are among the best-represented families in prehistoric archaeobotany (Arranz-Otaegui & Roe, 2023) and almost exclusively comprise the so-called Neolithic founder crops (Zohary et al., 2012). The interest in these crops associated with agricultural origins may contribute in part to a self-fulfilling prophecy in the archaeobotanical literature (Arranz-Otaegui & Roe, 2023), since archaeobotanists are often better skilled at identifying cereals and pulses, due to their common over-representation in reference collections and identification manuals. Even in South Asia, where potential crop species diversity is greater, more studies have apparently been conducted on rice than any other crop.

In addition to the grain bias, a focus on grapes in plant GMM and aDNA research likely derives, at least in part, from economic and cultural priorities in modern, as well as ancient, agriculture. Grapes have been the focus of 18 archaeobotanical GMM studies—by far the highest for any taxon—not including studies on modern specimens ultimately aimed at applications to archaeobotanical materials (e.g., Karasik et al., 2018; Landa et al., 2021). Grapes have also been subject to 10 archaeogenetic studies and even more genomic marker mapping. Despite not being a staple crop, wine is a globally traded commodity driven by its cultural significance in many high-income countries. In many ancient contexts, wine was also culturally significant, and grapes are often the most abundant non-grain species in archaeobotanical assemblages. Thus, both ancient and modern cultural factors may be at play.

Another way in which archaeobotanical, geometric morphometric, archaeogenetic and stable isotope studies of crop plants depend on wider agricultural research agendas concerns the availability of modern reference material. For instance, existing modern data (e.g., short reads and genome assembly) can significantly influence the feasibility and depth of genetic investigations in the context of ancient DNA research.

5.2.4 | Additional factors

Additional biases specific to each discipline or crop type may also explain some of the patterns presented in our analyses. For example, SIA of plant remains often aims to understand crop management and/or provide baseline data for human and animal diets, which will necessarily focus on the prominent plants in agriculture and diet. Moreover, SIA studies of crop management are best suited to annual plants, which would explain why olive is only represented once in SIA of ancient plant remains, despite its longstanding importance in many societies in Southern Europe and SW Asia and its high ubiquity in archaeobotanical assemblages. Another case in point is the greater focus on tree fruit seeds than on cereal grains in GMM, despite (or perhaps because of) frequent use of traditional morphometric approaches in archaeobotanical reports of cereal grains. Perhaps GMM is perceived as having relatively less added value over linear morphometrics in the case of grains, where changes in a single dimension (cereal grain breadth; legume grain length) are correlated with domestication (e.g., Fuller et al., 2019). Detecting meaningful patterns through GMM might be more likely to succeed with perennial clones, that is, fruit/nut trees, than annual crops, which could perhaps partly explain the observed focus on grapes and olives. However, since our own literature review for this paper was completed (May 2023), new publications demonstrate the potential of GMM for identifying wheat species and subspecies (Roushannafas et al., 2023; Roushannafas & McKerracher, 2023), perhaps foreshadowing more GMM applications to ancient grains in the future. Meanwhile, GMM applications to archaeobotany are still in early stages, and with future experience and breakthroughs, including machine-learning and 3D capture, it is likely that GMM will be applied to a greater variety of crops and research questions (Bonhomme et al., 2023; Evin et al., 2022).

Yet another source of bias is cultural, discussed briefly above in the context of wine. Cannabis appears to be under-reported in FAO-STAT data, which lacks production data specifically for 'true hemp' and only provides information on 'hempseed'. Furthermore, even if such data were available, it is likely that cannabis production would be underreported due to significant parts of its cultivation occurring in hidden economies. Nevertheless, the decision of researchers to sequence ancient cannabis (Mukherjee et al., 2008; Murphy et al., 2011; Russo et al., 2008) may be influenced by its cultural significance in many high-income countries today.

5.3 | Implications for crop diffusion

The results of this study also have implications for understanding crop diffusion. It has long been thought that the later first millennium CE, the Early Islamic period, was a critical moment for the diffusion of crop plants originally from tropical Asia into the Middle East and Mediterranean. Watson (1974, 2008 [1983]) discussed some 18 crop species (including a few African crops) claimed to be part of this phenomenon. Whereas Zohary (1998) wondered why it took so long for tropical Asian domesticates to travel further west, Muthukumarana's (2023) study of textual and linguistic materials demonstrated much earlier introductions of several tropical Asian crops into the Middle East and Mediterranean. Meanwhile, a growing body of archaeobotanical research has emphasized Roman-period crop introductions into the Mediterranean region (Bosi et al., 2020; Fuks et al., 2023; Langgut, 2022; Peña-Chocarro et al., 2019; Van der Veen et al., 2018; Van der Veen & Morales, 2017) and beyond (Livarda, 2011; Van der Veen et al., 2008). Prehistoric crop diffusion across Eurasia has been widely discussed and investigated (Boivin et al., 2012; Jones et al., 2011; Liu, Jones, et al., 2019; Sherratt, 2006; Stevens et al., 2016; Zhou et al., 2020), not least as a supposed driver of enduring patterns of global hegemony (Diamond, 1997). Others have charted crop diffusion in the Indian Ocean world (e.g., Rangan et al., 2012; Crowther et al., 2016; cf. Grimaldi et al., 2022) or as a global phenomenon (e.g., Boivin et al., 2016). Despite this wealth of research on Old World crop diffusion, our meta-analysis suggests that all known examples of pre-1492 intercontinental introductions are few and far between.

The fact that relatively few of the food crops in the pre-Columbian Mediterranean, Middle East, Central Asia and South Asia were introduced from outside this albeit very broad region seems to indicate a degree of conservatism when it comes to crop migrations. Even within this region, the impact of crop migrations was uneven, resulting in a 'unified ecological contact zone' of overlapping but not uniform sets of cultivars (Mikhail, 2011). The spatial extent of crop migrations was determined, above all, by ecological and cultural constraints. Ecological barriers could partially explain the sparseness of introductions from northern Europe to Southern Europe (alongside a relatively small number of food crops originally endemic to northern Europe). Evidence suggests that in ancient times crop diffusion was often a slow process (Stevens et al., 2016).

Among the species introduced to the study region, only a handful have become major economic food and beverage crops globally, including orange, lemon, buckwheat, rice, foxtail millet, coconut, sugar cane, mango, tea and coffee. These species' global economic significance today might be more a product of post-Columbian imperial and colonial ventures than ancient diffusion, although these, in turn, were often influenced by more ancient trajectories of crop expansion. Interestingly, only one of them—coffee—originates in Sub-Saharan Africa. Notwithstanding, other African crops have diffused widely and/or become important food crops outside their wild range, such as sorghum, pearl millet, finger millet (*Eleusine coracana*), cowpea (*Vigna*

unguiculata), shea (*Vitellaria paradoxa*) and bottle gourd (*Lagenaria siceraria*). Relative to their numbers on our MME+ food crop list, vegetable crops appear to be the least likely to diffuse widely, followed by pulses. This suggests that broadly speaking, vegetable and pulse species consumed in traditional societies might be more reflective of long-standing local traditions than other food crop types.

Archaeobotany, increasingly augmented by GMM and aDNA, is uniquely poised to examine the chronological depth of local agricultural traditions, past distributions of crops and genetic/phenotypic diversity of crops in ancient times (Fuller et al., 2023). Whether because of, or in spite of, the grain bias in crop history research, studies of wheat demonstrate the potential of these disciplines to reconstruct patterns of past agrobiodiversity, with direct implications for understanding 'lost' and 'forgotten' crops in the usual sense. For instance, recent aDNA analysis (Czajkowska et al., 2020), further supported by GMM (Roushannafas et al., 2022), has confirmed previous identification of the so-called 'New Glume Wheat'—originally discovered in the archaeobotanical record of northern Greece (Jones et al., 2000) and subsequently recognized in a number of sites in Europe and Western Asia (e.g., Filipović et al., 2023; Kohler-Schneider, 2003; Toulemonde et al., 2015; Ulaş & Fiorentino, 2021)—as Timopheev's wheat. Today, Timopheev's wheat survives only in the Caucasus. Surely, its vastly wider distribution in the past was associated with wider genotypic and phenotypic diversity than observable today, the extent of which might be clarified by future archaeobotanical, GMM and aDNA analyses. Timopheev's wheat is just one example of a wheat type whose cultivation has diminished significantly or entirely since ancient times, alongside the modern globalization of bread wheat (*T. aestivum*) (Fuks & Marom, 2021; Mosulishvili et al., 2017; Nesbitt & Samuel, 1996). A similar scenario probably impacted Old World cotton (*Gossypium arboreum/herbaceum*) following the introduction of New World cotton (*Gossypium hirsutum/barbadense*), which now dominates global cotton production (Bouchaud et al., 2019; Brite & Marston, 2013). Indeed, the process by which certain crop species diffuse widely and cause other crop species to recede must have played out many times in history for a number of crops. In other words, the phenomenon of 'lost' and 'forgotten' crops has a much deeper history than is usually considered.

5.4 | For future research

Following from the above insights on crop diffusion, one question for future research might be what are the qualities that help transform a plant species into a global food crop? In a counterfactual world, bitter melon (*Momordica charantia*), mountain yam (*Dioscorea opposita*) and Ceylon spinach (*Basella alba*) might have had the success that banana (*Musa × paradisiaca*), orange (*Citrus × aurantium*) and cucumber (*Cucumis sativus*) enjoy today. Why did some crop species travel far and even become nativized while others did not? Is it possible to disentangle nutritional, cultural, logistical, agronomic and geopolitical factors? One long-term research objective might be to map the long-term geographic trajectories of a wide range of food crops—both the

cosmopolitan ones and the more provincial ones. In so doing, emphasis should be placed on crops whose geographic range has receded, in addition to those that have expanded. This will generate a much deeper chronological understanding of the 'forgotten' crops phenomenon. Where applicable, aDNA and GMM studies may immensely enhance understanding of changing infraspecies diversity that accompanies crop diffusion and recession.

A related goal could be to actively seek archaeobotany's underrepresented crop species, with improved methods of excavation, retrieval and identification. Wider application of archaeobotanical research, especially in the tropics, including more flotation at archaeological sites and better reference collections for identification, could significantly improve crop history research towards refined understandings of crop diffusion and evolution. Considering the bias toward carpological remains in archaeobotany of the MME+, one advantage of phytolith, starch granule and parenchyma analyses is their potential to identify remains of leafy or starchy plant parts (e.g., García-Granero et al., 2015, and references; Florin et al., 2020; Ahituv & Henry, 2022). Development and wider application of more precise taxonomic identification keys for these techniques may hold potential for expanding species representation in archaeobotany. Perhaps sedimentary DNA analyses applied to archaeology could offer an even broader range of identifiable taxa. SIA analyses may expand knowledge of past cultivation conditions, complementing GMM and aDNA research on ancient crop diversity and evolution. However, simply targeting underrepresented crops will not necessarily lead to better crop history research. Methods need to be appropriate to the research questions, and in many cases, the methods require further development before they can be applied more widely.

Controlled growing experiments in the field and laboratory continue to provide essential reference data for inferring past agronomic practices, the limitations of comparing modern with ancient notwithstanding (Ferrio et al., 2020). This enables the interpretation of stable isotope results in the context of a range of potential environments and agrarian regimes, specific to C₃ and C₄ plants (e.g., Araus et al., 1997; Flohr et al., 2011; Fraser et al., 2011; Lightfoot et al., 2020; Sanborn et al., 2021; Styring et al., 2016). These experiments help us to unlock information on the variation and trajectory in crop management through time. Controlled studies, however, need to be expanded to other species beyond cereals and pulses, including traditional cultivars from more diverse geographic regions. They also need to capture multi-seasonal data to better understand the variability of local environmental and climatic conditions and the effect they have on inter-species variability in isotopic values. A small number of studies have moved beyond $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to explore the potential for analyzing strontium ($^{87}\text{Sr}/^{86}\text{Sr}$; Bogaard et al., 2014; Larsson et al., 2020; Ryan et al., 2021), sulfur ($\delta^{34}\text{S}$; Nitsch et al., 2019; Wozniak & Belka, 2022) and oxygen ($\delta^{18}\text{O}$; Williams et al., 2005) isotopes in archaeological plants to better characterize the isotopic baselines of local ecosystems and provenancing, which may have an impact on our understanding of crop diffusion.

Finally, much valuable synthesis work can be attained by expanding and improving upon this study of crop species representativeness, including broadening the geographic, disciplinary and crop type

boundaries. Integrating philological and linguistic studies in the analysis of crop species representativeness will surely improve the picture presented here. Indeed, some ‘orphan’ crops of archaeobotany, including saffron, kenaf and okra noted above, are known from ancient textual evidence. Integration of historical studies with archaeobotany is a long-standing and valuable approach (e.g., Amichay et al., 2019; de Candolle, 1885; Heiss et al., 2012; Muthukumar, 2023), and its application to multi-regional synthesis studies will present an even clearer and more nuanced picture of the ‘orphan’ crops of crop history research. Inclusion of herbarium studies in the synthesis of plant archaeogenetics will be another worthwhile avenue for expanding this study. It would also be rewarding to take a quantitative approach to species representativeness in archaeobotany, which was beyond the scope of the present study. To do so for some regions will prove very challenging, and it must be stressed that the present meta-synthesis and analysis is no replacement for regional databases and syntheses. At the multi-regional, interdisciplinary level, the Crop History Consortium, of which this paper is a first output, aims toward improved synthesis research of this type.

6 | CONCLUSIONS

This paper represents a first attempt at assessing species representativeness in archaeology-based crop history research. This is relevant to ‘forgotten’, ‘underutilized’ and ‘orphaned’ crops in at least three main ways. First, this study identifies 53 crop species across 45 genera absent from the archaeobotanical record of the Mediterranean, Middle East, the Caucasus, Central Asia and South Asia. This includes 39 genera unrepresented by any species in the archaeobotanical record of this region, despite the pre-1492 cultivation of species from these genera within this region. These may be viewed as ‘orphan’ crops of archaeobotany since they were apparently once cultivated and eaten by the people whom archaeologists study but have not yet made it into the archaeobotanical record of these regions. Some might never be found in archaeobotany for methodological reasons, but others surely will. For archaeobotanists and other scholars of crop history, keeping an eye on the possibilities for future finds can be helpful in the identification process. More generally, an awareness of biases favoring certain species is important for ensuring representativeness and reliable interpretation of crop history research. Although taphonomic sources of bias are well known, we also suggest that broader economic agendas may be indirectly affecting species representativeness in archaeobotany, and almost certainly in archaeogenetics. The observed lower representation of tropical Asian crops in archaeobotany may be a reflection of both taphonomic and economic biases.

Second, this study puts into perspective the numerical significance of global food crops, including some that are referred to as ‘forgotten’ or ‘underutilized’ crops. Much research has discussed ancient crop introduction, exchange and diffusion, often with recourse to the themes of agricultural innovation, globalization, capitalism and inequality. At least within the study region, this research tends to focus on crops that are economically important in global markets

today, leaving behind many other crops. The present study puts these phenomena into perspective by showing that they are based on a small subset of historical crop diversity—a few dozen crop species out of a few hundred. Despite the impression one might get from the research on historical crop diffusion, most crops did not diffuse widely, and we know relatively little about the crop histories of most. In this sense, most food cultivars are ‘forgotten’ crops.

Finally, archaeology-based crop history research broadens the temporal and geographical scale of understanding of the ‘lost’ or ‘forgotten’ crops phenomena, in the traditional sense. Archaeobotanical data on past distributions, economic use and cultural significance of a large set of crop species can be used to chart both expansions and contractions in distribution as well as cultural significance of crops throughout history. This potentially offers a much deeper historical perspective on how some crops might have come to be marginalized and ‘forgotten’. GMM, aDNA and SIA applied to archaeobotanical remains can further inform on genetic and phenotypic diversity over time, as well as growing conditions. Such data can be an asset for agricultural conservation. Although many of these studies have been markedly skewed towards a few key crops, in some cases they may draw attention to, and deepen understanding of, ‘forgotten’ crops (e.g., Kistler & Shapiro, 2011). Archaeobotanical studies can also offer more nuanced understandings of human–plant interactions in diverse environmental and cultural contexts, including agricultural projects that proved unsustainable (e.g., Fuks et al., 2020; White et al., 2014). Thus, archaeology-based crop history research is not only influenced by modern agricultural agendas but could perhaps influence them as well. Certainly, data on historical and ancient crops, their past geographic distributions, domestication status, local significance and infraspecies diversity ought to constitute essential information for assessing policy proposals to reintroduce, expand and promote forgotten crops.

AUTHOR CONTRIBUTIONS

Daniel Fuks designed the research. Daniel Fuks, Frijda Schmidt, Maite I. García-Collado, Margot Besseiche, Neal Payne, Giovanna Bosi, Charlene Bouchaud, Elisabetta Castiglioni, Vladimir Dabrowski, Suembikya Frumin, Dorian Q. Fuller, Roman Hovsepyan, Sureshkumar Muthukumar, Leonor Peña-Chocarro, Guillem Pérez Jordá, Jérôme Ros, Mauro Rottoli, Philippa Ryan, Robert Spengler, Chris J. Stevens, Soultana Maria Valamoti, Ehud Weiss, Michelle Alexander and Muriel Gros-Balthazard contributed data and/or text. Daniel Fuks, Muriel Gros-Balthazard, Michelle Alexander, Frijda Schmidt, Maite I. García-Collado and Margot Besseiche analyzed data and wrote the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the main text and supplementary materials.

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