

Title

Archaeology and agriculture: plants, people and past land-use

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Highlights

1. Ancient plant remains hold information on past subsistence strategies and land-use
2. Recent advances in the field of archaeobotany have broadened the range of techniques by which ancient plant remains can be studied
3. Archaeobotanical investigations show a diverse range of ancient farming practices and innovative solutions to social and natural pressures
4. Descriptions of ancient land-use could be integrated into models of human-environment interactions, enabling a more accurate understanding of the impacts of past practices with potential lessons for the future

Abstract

As a specialised branch of archaeology requiring specific field and laboratory methodologies, the contributions of archaeobotany have often been overlooked by the ecological research community. Developments in the fields of botany, chemistry and ancient DNA analyses have greatly increased the potential for archaeobotany to contribute to topical questions concerning the Anthropocene and landscape transformations. We review archaeobotany's role in identifying and describing past arable land-use. Analytical techniques are illustrated with examples at both local and regional scales, demonstrating how archaeobotany can provide unique details on the wide array of past subsistence and land-use strategies. These data and their potential should be better recognised as important information, which could underpin models seeking to evaluate or predict the effects of socio-environmental interactions.

Main text

Archaeology and Land-Use

Human food procurement has been shaping the Earth's landscapes and ecosystems since before the dawn of agriculture. Throughout the history of farming, food procurement has been both the product and support of increasing human populations, and represents one of the biggest drivers of the Anthropocene and the transformation of virgin habitats [1,2]. Transformation of the biosphere is a topic of growing significance [3], as is the recognition of the role that land use, and land-use change, has had on degrading terrestrial and marine ecosystems [4]. Much focus has been placed on the consequences of the "great acceleration" from AD 1950, and the industrialisation before it [5], underpinned by well-documented data. Nevertheless, the density and distribution of the archaeological record demonstrate that environmental transformations began several millennia before this point [6]. Examination of such longer-term environmental degradations demands knowledge of land-use systems for which the archaeological record remains an underexploited resource.

Models of how humans have interacted and transformed their environments have been developed based on theoretical approaches [eg. niche construction, diet breadth/optimal foraging and historical ecology: 7-9]. The integration of plant macro-remains as direct evidence of land use is an exception [eg.10,11]. Instead, earth system models that seek to describe the climatic and ecological impact of past agricultural systems, tend to rely on anthropogenic land cover change (ALCC) scenarios that integrate data on technology and land suitability for agriculture (eg.KK10: [12]; Hyde: [13]). Such approaches are limited as they generally assume a linear relationship between human population and land-cover, and lack consensus [14,15]. Analyses of fossil pollen records combined with human population fluctuations have demonstrated complex relationships between land-cover, population and food production, suggesting that how land is used has a greater affect upon the environment than the size of the population *per se* [16,17,18]. Recent projects are beginning to demonstrate the value of archaeological data in mapping land-use patterns, and illustrate a consensus to make such data available to a broader scientific community [15,19]. To better enable the integration of archaeological data into earth system models, the LandCover6K working group have devised a classification of land-use types based on peoples' uses of the land [15]. Archaeobotany can provide useful insights into the different forms of land 'uses' by studying the plant remnants of such activities [20].

Archaeobotanical Evidence

Ancient plant remains are found as microscopic and macroscopic elements [Box 1]. Pollen, though an excellent proxy for vegetation cover, only preserves in anoxic, waterlogged mediums (ideally lake and peat sediments). Conversely, charred grains/seeds and wood preserve in most conditions and are therefore much more abundant than pollen. The former, when recovered from archaeological contexts, are the outcome of human action and are associated with land use [Box 1]. They can contextualise land-cover changes identified through palynology (pollen analysis), especially as effects of geography and climate can become entangled with those from anthropogenic

influences when palynology is applied at broad spatial scales [16,21]. Charred wood represents the selection of wood for fuel and building material, and can be very informative on past vegetation cover and woodland management, particularly in the absence of pollen evidence [22; eg.23]. Agricultural land-use is best recognised through the crops and arable weeds lost or discarded during processing activities. We therefore focus on the analytical techniques applied to charred crops and weeds through which information on ancient agriculture can be obtained (Table 1). This information falls into two broad categories. First, the range of crops (including fodder crops) utilised and their evolutionary history can be identified, and distinguished from collected and traded plant foods. Second, land management strategies, such as fix-plot versus **shifting cultivation** (see glossary), **intensive versus extensive regimes** and crop-rotation systems, can be defined. Although the techniques are applicable to all charred crops and weeds, regardless of geography and archaeological period, the examples provided are mostly drawn from Britain and Europe where these approaches have been more common, particularly on Neolithic remains. Advances are being made in other regions where interest in archaeobotany is rising, and we hope that this review will encourage further developments. We refer to all plant domesticates produced for food as crops, and their companion wild plants as weeds. The term ‘seed’ is used for structures known botanically as diaspores, drupes or nutlets.

Table 1: Summary table of analytical techniques applicable to plant macrofossil data (excluding charcoal), and the information gained on land-use

Analytical technique	Evidence for land-use	Key references
CROPS AND GATHERED EDIBLE TAXA		
Presence/Absence	Introduction of crops and farming practices Development of farming regime, including monocultures and specialised production Developments in the extent of land-use Trade/exchange and the accumulation of surplus Location of finds can reveal social status, symbolism and conspicuous consumption	24-29, 84, 95, 104, 105
Summed probability of radiocarbon dates	Used as a proxy for identifying changes in subsistence practices, namely a temporal shift from cultivation to gathering	101-103, 108, 110
DNA from ancient and extant species	Recognising domestication Tracing pathways of agriculture and the evolution of adaptive traits to changes in latitude, temperature and seasonality Development of land-races	33, 34, 40-42
Growing degree-days	Suitability of crops to latitude and temperature may explain failures in, and the tempo of, agricultural expansions	42, 111
Morphometrics	Recognising domestication Recognising land-races and sub-species	43, 45, 46
Strontium isotopes	Geological provenance of crops Trade/exchange/taxation and social implications	48, 49
Nitrogen isotopes	Identifying soil fertility levels during a crop's growth Elevated levels may indicate the addition of fertiliser, suggestive of intensive farming practices	51, 52, 56
Carbon isotopes	Identifying soil moisture levels during a crop's growth Identifying cycles of aridity and irrigation	53, 56, 57
ARABLE WEEDS		
Autoecology – pH and soil texture	Identifying soil pH and location of cultivated soils	62, 65, 66, 68
Autoecology – moisture levels	Identifying hydrological conditions, be they man-made or natural	62, 65, 66, 68
Autoecology – nutrient levels	Identifying soil fertility levels Recognising management of soil fertility	62, 65, 66, 68, 70, 71
Autoecology – life cycle	Recognising shifting from open, permanent field cultivation Identifying levels of disturbance and cultivation intensity	62, 65, 66, 68
Autoecology - germination	Identifying agricultural cycles and crop rotation	62, 65, 66, 68, 70
Autoecology – flowering time and duration	Identifying germination time and levels of disturbance	62, 65, 66, 70, 71, 73
Autoecology – seed bank and dormancy	Identifying levels of disturbance, such as the introduction of deeper ploughing methods, and sowing regimes	62, 65, 66, 68, 94
FIBS – physiological attributes that are an adaptive response to specific ecological conditions	The method is most commonly used to identify levels of cultivation intensity through the combined analyses of adaptive traits	69, 70, 72, 74, 76

Crops – reshaping the land

Mapping cultivation

The type and frequency of crop remains can hint at the extent of land used for arable production [24]. Large-scale studies using the presence of taxa on archaeological sites have described the first spread of agriculture and subsequent developments in cultivation practices (Box 2) [eg.25-29]. Careful excavation, sampling and radiocarbon dating minimise the risk of over interpreting intrusive plant remains. A good example is millet (*Panicum miliaceum* L.), which a recent radiocarbon dating programme has shown was not a European crop before the 2nd millennium BC despite the regular occurrence of seeds in earlier contexts [28]. Additionally, finds of rare and exotic taxa may be indicative of trade rather than local cultivation, at least for those species that were not naturalised like foreign fruits [eg.30]. Macrofossils recovered from rural sites away from trade routes are likely to represent local cultivation, as are seeds of plants grown for their roots or leaves [31]. The frequency and abundance of crop remains are important to gauge the scale of production and relative importance of taxa. Not all farming communities were completely dependent upon domesticated crops, using both arable land and wild resources to various degrees. This is particularly relevant during the initial spread of farming when gathering may have been as important as cultivation (Box 2). The implications for land-use are important, as the range, abundance and frequency of cultivars can indicate how much land was used for arable production and how it was organised [cf.32].

Genetic evidence

Genetic data are becoming increasingly valuable in explaining the biological mechanisms behind the domestication and spread of both cereal and non-cereal crops [see reviews by 33,34; eg.35-37]. Although genetic extraction and replication has advanced significantly in recent years, ancient DNA is rare in charred plant remains, and ancient cultivation pathways are usually deduced from extant **landraces** of crops through **phylogeography** [33,38]. Detecting the evolution of genetic sequences

can reveal how adaptations to new environments, of natural and/or anthropogenic design, influenced the rate and direction of farming migrations and the developments of unique landraces [39-41]. One line of research in genetics and archaeobotany has been to explore the biological adaptations necessary for crops being moved into different climatic zones [eg.36,37]. The timing of a plant's developmental stages, such as germination and flowering, are controlled by genes triggered by climatic constraints [42]. A species' suitability to a climate can be measured by its **growing degree-days (GDD)**, reflecting a species' genetic adaptation to climatic variables (Box 3). The expansion of farming across multiple climatic zones is partly due to mutations in these genes which enabled crops to grow successfully in climates very different to those in which they were domesticated [see review by 34].

Morphometrics

Climate, soils and environmental conditions affect the growth of plants by providing essential elements in variable quantities, whilst cultivation practices impose selective pressures. The domestication of grain crops altered the shape and size of their seeds, and the thickness of their coats [43,44]. Morphometrics, the measurement of seed size and shape, is used to identify domestication, individual species and the evolution of landraces [eg.43,45], thereby contributing to understanding the development and spread of arable agriculture. This approach has been successful in detecting the pre-domestication cultivation of fruits, such as the beginnings of viticulture in the Aegean [46], and the natural and anthropogenic effects upon the evolution of crop varieties [47].

Stable isotopes

While still a relatively new scientific development, stable isotopes from charred plant macro-remains are increasingly used to infer agricultural intensity, and offer exciting prospects for the study of arable production and land-use. Strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) provide a geographical signature and can be used to assess grain provenance [48,49]. Elevated soil nitrogen due to

enrichment (usually attributed to manuring) raises nitrogen isotope ($\delta^{15}\text{N}$) values in cereal grains, offering insights into land management strategies [eg.50-52]. Cycles of aridity and associated agricultural productivity can be investigated via carbon isotope ($\delta^{13}\text{C}$) values [eg.52,53]. Isotopic levels reflect elemental uptake during the growth and development of individual species, which is affected by physiological processes (like the photosynthetic pathway) and environmental conditions [53-55]. For example, experiments have shown that the uptake of ^{15}N and ^{13}C is influenced by soil moisture, particularly in millets, making interpretations difficult from areas with poorly understood rainfall patterns [51,55]. Difficulties therefore arise when establishing crop-specific baselines from which isotopic signals of charred ancient crops can be evaluated. Despite these caveats, stable nitrogen and carbon isotopic levels have been successfully interpreted from cereal grains [see reviews by 56,57]. Analysis of the Sr isotopic signature of charred first millennium AD grains from southern Sweden, indicated that c.20% had not grown locally despite the rich agricultural soils [58]. Grain may have been brought as religious offerings, tithes from surrounding farms or to sell, which serves as a reminder that imposing a type or area of land-use per unit of habitation is overly simplistic.

Weeds – working the land

Arable weeds are of great interpretative value as they hold information on the habitat conditions and husbandry regimes under which crops were grown (Fig. 1). Such studies are commonly based on three main approaches: Ellenberg numbers, ecological and biological traits of individual taxa and functional attributes of modern taxa and their ecological significances (FIBS – Functional Interpretation of Botanical Surveys).

Ellenberg numbers offer an **autoecological** approach by attributing an indicator value to a species' tolerance to ecological conditions (such as temperature, light availability and soil humidity), based on field observations. Indicator values are a numerical score assigned to a species according to its

frequency in a particular environmental setting. Plant communities, or syntaxa, are then classified by the average score of its individual members [59,60]. The study of plant associations can define ecological conditions and monitor environmental changes that may have long-term effects on wider biodiversity. However, this approach is problematic in archaeology as plant sociological groupings are sensitive to anthropogenic as well as natural influences, and many plants have a broad ecological amplitude [61-63]. Additionally, the range and abundance of weeds in ancient fields will have been filtered by processing activities, taphonomy and preservation conditions, leaving only a sub-sample of the original to be interpreted [63-65]. Problems of uniformitarianism and equifinality can be minimised by using genetically set characteristics, such as life cycle, reproductive strategy and pH tolerance, which can indicate likely ecological conditions of ancient arable fields. For example, sheep's sorrel's (*Rumex acetosella* L.) tolerance of acidic environments might be taken to indicate a low soil pH and henbane's (*Hyoscyamus niger* L.) prevalence in rich soils is used to indicate good soil fertility [66]. Nevertheless, numerous weeds tolerate a broad range of conditions and are therefore of little interpretative value, whilst others are specific to certain conditions depending on geography. For example, primrose (*Primula vulgaris* Huds.) is a woodland plant in eastern England, but is often found on grassy banks in the north and west, exhibiting different tolerances to shade [67]. FIBS offers a more robust approach by using physiological attributes that are a measure of a plant's adaptation to specific environments [66,68]. The application of FIBS in archaeobotany thereby enables specific past ecological variables to be defined through the measurable physiological adaptations of modern species [51,69-72]. Functional attributes have been recorded from modern weed floras across NW Europe, the Mediterranean and the Near East [69-75]. Apart from flowering data, which is best sourced from local floras, the use of combined attribute measurements seems to be applicable across broad geographical areas, at least within those mentioned above [76].

Results of ecological analyses are more robust when based on large assemblages recovered from extensive sampling strategies [77,78], and when associations between weeds and cereal processing stages are robust [64,79,Box 1]. A variety of ecological conditions of archaeological significance can be eluded from weeds.

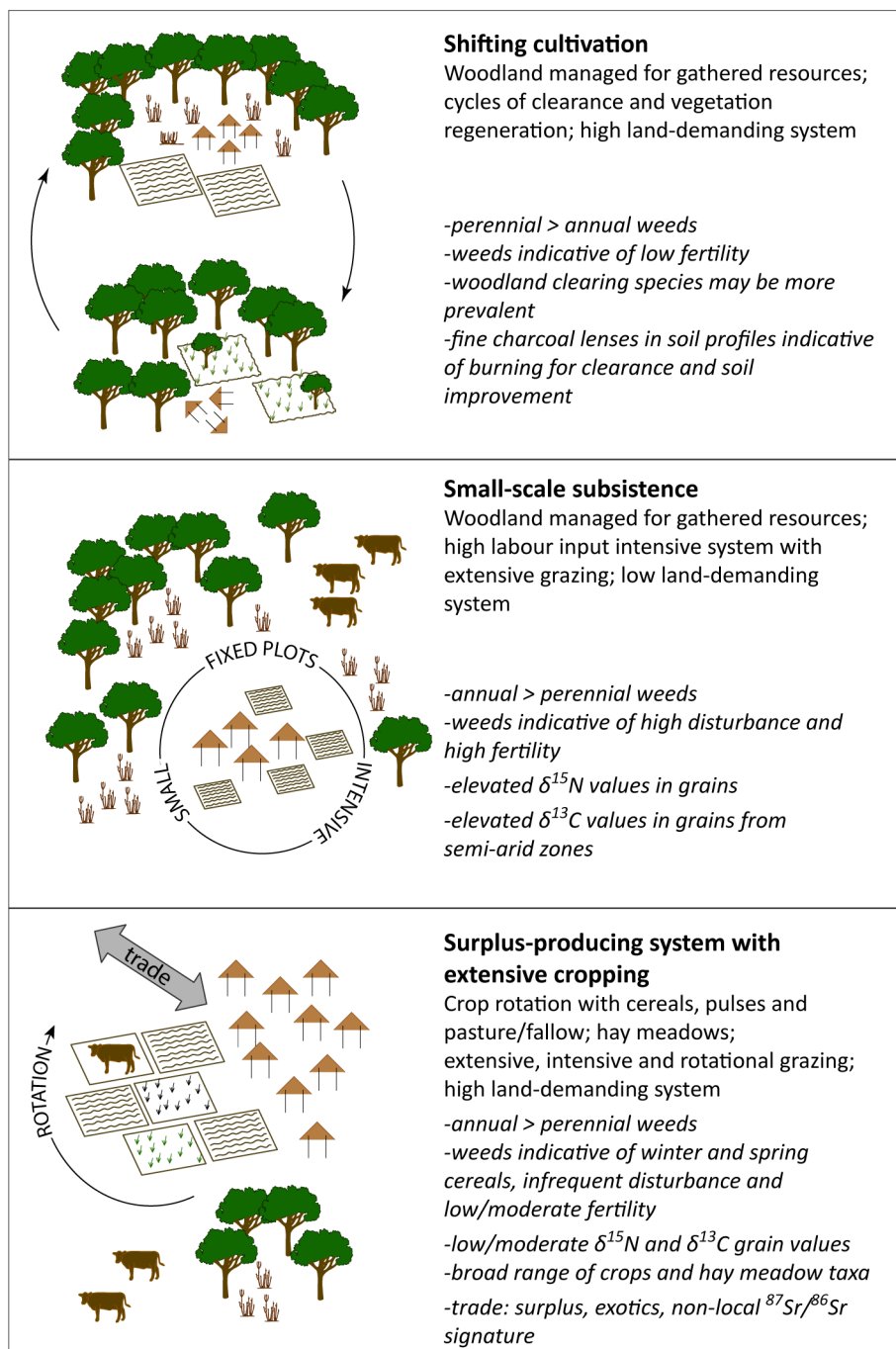


Figure 1: Different land use models identified within the archaeological record. The character of land use is described for each, along with the nature of the archaeobotanical evidence (in italics).

Soil preferences

The geological location of arable fields and their edaphic conditions can be established through the soil pH, moisture level, nutrient requirements and soil texture preferences of weeds, providing information on the organisation of the landscape and the labour investments dedicated to cultivation (Box 3).

To take an influential example, Jones' [80] seminal work on the large stores of spelt wheat from Danebury hillfort (UK) indicated that, during the second half of the first millennium BC, wheat was grown in both damp valley bottoms and drier, calcareous soils. Isotopic analyses on grains have corroborated this interpretation [81]. Isotopes from animal bones suggest herds were also brought in from the wider landscape, where they grazed across varying ecozones beyond those of their home sites [82]. Multiple arable environmental contexts were also interpreted from the numerous weeds found at Battlesbury Bowl (UK), another Iron Age hillfort on the southern chalk uplands [83]. These hillfort assemblages reflect a level of social cohesion and organisation not witnessed before the first millennium BC, and indicate an increased political, or at least communal, control over land during the Middle Iron Age in southern Britain [84]. Indeed a rise in the range of arable weeds between the Bronze and Iron Ages indicates changing attitudes towards land-use, instigated and reinforced by the increase in land under cultivation [85]. It also illustrates how weeds had far greater ecological plasticity than crops enabling them to adapt to new cultivation regimes. A survey of charred plant macro-remains and fossil pollen in SW Germany showed that many weeds of calcareous soils were more common with a wider distribution than today [86]. Rather than indicate a change in bedrock, the propensity of these species during the medieval period was probably due to the development of shallow topsoils where they could thrive without competition, as a result of extensive arable cultivation. Soil improvements and changes in land-use during the 18th century led to the demise of many of these species [86].

The Neolithic settlement of Vaihingen (Germany) was continuously occupied from c.5500-5050 cal. BC, and expanded over c.6 ha. Its extensive excavations and systematic sampling over a period of ten years have transformed our understanding of the subsistence practices of one of the earliest farming groups in Europe known as the Linearbandkeramik (LBK). The first European farming systems were initially described as slash-and-burn cultivation through natural forests [87], but over forty years of archaeobotanical investigations have rejected these hypotheses. At Vaihingen, arable plots were fixed and cultivated over prolonged periods, echoing the lifespan of longhouses with which they appear to have been associated. Archaeological research suggests that LBK longhouses represent individual households or 'clans' who probably owned their own pieces of land. During the Flomborn period (middle Early Neolithic) differences in the location and intensity of cultivation are evident between different 'clans'. Weeds tolerant of high disturbance and basic soils were common in assemblages from 'clans' A and D, whilst 'clan' C worked soils of intermediate pH less intensively. These differences were evident over several occupation phases, indicating established, long-term social stratifications that affected the location and quality of fields [88].

Germination and flowering habit

The germination season of weeds is a commonly-used trait to establish whether autumn or spring sowing was practised, although it is important to remember that the arable field is not a natural construct; ploughing, weeding and manuring can induce germination at different times to those recorded in local floras [65]. Germination season can also be gained from flowering onset and duration [73], and three recent UK archaeological studies have used this information to define sowing seasons as well as the degree of disturbance caused by weeding, ploughing and tilling – i.e. the intensity of cultivation [89-91]. Using the flowering cycles of weeds, McKerracher [90] suggests that wheat was generally sown during the autumn in the Anglo-Saxon period, but that in particularly wet areas, spring-sown barley was likely favoured. Hamerow and colleagues [91] use a combination of techniques (FIBS, weed autoecology and stable isotopes) to identify an extensive

arable regime in which rye, oat and free-threshing wheat were grown in rotation during the 10th-13th century AD at Stratford (UK). Barley was grown separately on more enriched soils. These findings help to contextualise the open field systems more broadly known from the late first/early second millennium AD in Europe.

The intensity of disturbance can also be reconstructed from the flowering habit of weeds. Species that can flower early and for a brief period are likely to develop seeds before the destructive spring plough, and so should be more common in autumn-sown crops [73]. Similarly, late flowering plants are more likely in spring-sown crops and will be better represented in late summer/autumn harvests [73]. Species with a long flowering period tend to have a prolonged germination season, allowing the species to 'survive' disturbance events. The longer the time frame over which an annual can reach maturity to fructify, the higher the chances it will have to reproduce within the annual crop cycle without being removed through disturbances such as hoeing, tilling or ploughing. In a study on the functional ecological attributes of weeds associated with disturbance, it was found that plants with long flowering periods that regenerate from seeds (both annuals and perennials) were associated with agricultural regimes that included a fallow year, where disturbance can be unpredictable and intensive [70]. Perennials with shallow regenerative root systems (hemicryptophytes) were also found to be at a competitive advantage in disturbed habitats [70,71]. These perennials are likely to be found in damp environments (naturally or through irrigation) as vegetative reproduction requires damp conditions [69]. Most perennials, however, usually take several years to develop and so need relatively undisturbed environments. They have been associated with shifting cultivation in which cleared plots receive a low-level of disturbance [92,93]. As perennials are unlikely to set seed in the first year, a high proportion of perennials would suggest shallow cultivation or limited disturbance over a consecutive number of years, either through shifting cultivation or an extensive form of farming [92]. A predominance of 'annual'

perennials (i.e. those that can regenerate seasonally by seed and/or vegetatively) could be representative of an intensive system with shallow disturbance in which weeds are not uprooted.

Seed bank and dormancy

Seed bank, dormancy and the conditions that trigger germination are important factors affecting why certain plants respond better than others to particular human ecological settings [66]. Weeds with transient seed-banks and simple dormancy (i.e. expedient germination) will be quickly eliminated unless they are re-sown with the crop. Species with more persistent seed-banks and complex dormancy may not germinate annually and would have been harder to eliminate without herbicides. The introduction of the mouldboard plough during the Late Iron Age/Early Roman period in western Europe is reflected by an increase in weeds of persistent seed-banks and complex dormancy [94]. Stronger iron ploughs also made it possible to expand cultivation onto heavier soils, which is reflected in the surge of weeds from damp, clay-rich soils like stinking chamomile (*Anthemis cotula* L.) [89]. These changes in land-use associated with technological developments included the cultivation of larger areas under extensive regimes [31].

Managing wild resources

We have focused on food production through cultivation and its implications for land-use, but the procurement of wild food resources also forms an important part of how humans have transformed environments, and a brief note on the subject is added here. Archaeobotanical research on the Jomon period (c.14000-300 BC, Japan) has shown how subsistence was primarily based on the management of wild resources with some cultivation of barnyard grass (*Echinochloa crus-galli* P. Beauv.) and the lacquer tree (*Toxicodendron vernicifluum* (Stokes) F.A. Barkley) [9]. Natural environments were managed to encourage particular species, thereby altering land-cover and biodiversity. This example of ‘wild’ anthropogenic habitats is not unique, and evidence for similar practices has been found from across the globe [eg.95,96].

Concluding Remarks: prospects and potential of Archaeobotany to study land use

The study of land use and human agency is complex and multi-faceted. Archaeobotany offers a tool by which direct evidence for land use can be analysed and integrated into models of various scales, creating a more accurate framework through which to understand the legacy of past subsistence strategies. Different agricultural regimes have different ecological outcomes, making archaeobotanical contributions to the study of socio-environmental interactions essential. Results are strengthened when different analytical techniques are applied to the same assemblages, and when interpreted in light of outcomes from other archaeological evidence and associated disciplines. Questions about the relationships between past land-use, land-cover, palynological diversity and ecological novelty (see Outstanding Questions), can be tested through the integration of multi-disciplinary datasets from the archaeological and palaeoecological sciences. Interdisciplinary approaches must define future research aiming to determine the role of past human land use in shaping emerging landscapes and biodiversity patterns.

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Supplementary materials

Box 1 – Preservation of Archaeobotanical Remains

Archaeobotany is the study of ancient plant remains within the field of archaeology. Though remains are recovered within an archaeological framework, their analyses and interpretation draw upon botany, chemistry and other natural sciences. The discipline is therefore strongly influenced by developments in these fields, as is evident from the analytical approaches described in the main text. Plant remains range from the microscopic (eg. starch grains, **phytoliths** and pollen) to the macroscopic (eg. wood, roots/tubers/rhizomes, grains/seeds and whole plants). Being organic, plant remains only survive when exposed to extreme conditions, including dessication and oxygen-free mediums like waterlogged sediments. In archaeological deposits, the most common form of plant preservation is through carbonisation. This process is not dependant upon climatic or environmental conditions but rather human action, which can be investigated through the charred outcomes. The selective preservational bias is therefore towards plants more regularly used by humans but extends to those whose processing requires a source of heat (eg. hulled wheat requiring parching to remove finer chaff), and to plant parts rich in lignin or carbohydrates [97,98]. The latter, such as wood and seeds, are more likely to retain an identifiable form when their organic matter is transformed into inert carbon. Consequently, the vast majority of archaeobotanical assemblages are composed of charred wood, grains and seeds reflective of routine fires and crop-processing activities [98]. The latter generate crop products, by-products and/or seeds of arable weeds, all of which may be intentionally or accidentally burnt. However, seeds from other sources may also be present and erroneously included into weed ecology analyses, such as seeds from manure burnt for fuel, medicinal plants, and plants used in construction and furnishings. Additionally, the distinction between crop and weed is not always evident as some ‘weeds’ may have been tolerated, occasionally leading to newly domesticated crops. An example is the domestication of erect polygonum (*Polygonum erectum* L.) in eastern North America during the second millennium BC. This lost crop was first considered an arable weed but recent morphometric analyses have shown

changes in seed size and seed coat characteristics concomitant with domestication [99]. Iron Age (c.300-1600 AD) plant remains from eastern Africa constitute another example, where frequent seeds of the wild grasses *Brachiaria* sp., *Echinochloa* sp., and *Panicum* sp. suggest these may have been food rather than weeds, raising questions on the role of wild plants in early farming communities [100].

Box 2 – Tracing Agriculture through its Crops

A study in 2012 used the summed probability of radiocarbon dates from grains and hazel nutshells as a proxy indicator for the success and failure of Neolithic arable agriculture across the British Isles [101,102]. A surge in settlements at the start of the 4th millennium BC signal the beginnings of farming in Britain [103]. Although records of arable weeds are rare, the overall predominance of annual over perennial weeds and their open, disturbed ground habitat preferences, indicates that farmers did not practise shifting cultivation, but focused on fixed plots [104-106]. This evidence is corroborated by nitrogen stable isotopes from grains at Lismore Fields (UK), which suggest that the intensive cultivation of small, fixed ‘garden’ plots evidenced in central Europe was also common in the British Isles [50,106]. However, at around 3600 cal. BC, trends in the radiocarbon dates on cereal grains show a sharp decline across the British Isles. The number of dates on hazel nutshells also declines but not as steeply, suggesting that gathered nuts continued to be used whilst the cultivation of cereals appears to have stopped altogether in some regions [101,102]. A similar pattern is evident for the Neolithic in Ireland, though the replacement of cultivation by gathering is far from evident, as the quantity of wild plant foods is not seen to increase [105]. The drop in cereal grains during the Neolithic has long been noticed by archaeobotanists [107,108], even though animal domesticates, and in particular cattle, continued to be an important dietary element [103]. A transition from mainly fixed, agricultural communities to mobile pastoralists, relying predominantly upon wild plants and cattle is therefore likely, at least in England, Wales and Ireland [101]. Stevens and Fuller’s study [101,102] has its critiques [*cf.* 104,106,109], yet additional dates have strengthened the original signals, and the same patterns of land use and abandonment are indicated

by both pollen records and human population levels [16,103,110]. Another study based on presence/absence data compared the relative proportions of Neolithic wheat and barley from across northern Europe, including the British Isles, and used an autoecological approach on the arable weeds [26]. It concluded that an increased presence of barley and weeds tolerant of poor soils indicate that soil deterioration was a major cause towards the collapse of arable agriculture during the later Neolithic.

Box 3 – Agricultural Adaptations to Climatic Shifts

Climate is often thought to have been a deterministic factor in the choice and successful cultivation of crops. In south-eastern Tibet declines in temperature following the 4.2ka (c.2200-2100 BC) event coincide with the abandonment of settlements and the introduction of new farming practices. A model on changing crop niches has now demonstrated how a colder climate made it impossible for farmers to grow their traditional crops of broomcorn and foxtail millets. Habitation of the Tibetan Plateau only resumed after the introduction of two non-native crops, wheat and barley, better suited to low temperatures [111]. However, a change in diet has not always been the inevitable solution. Research in Thailand shows surprising and innovative responses to aridification during the Iron Age, illustrating how changes in societal structures and farming practices enabled rice, the main dietary staple, to be retained [112]. Palaeoclimatic records suggest changes in the Monsoon strengths and patterns leading to a drier climate in Thailand during its Iron Age. Conversely, weeds of rice show an increase in wetland species, indicating a gradual replacement of dry- (rain-fed) to wet- (paddy fields) rice cultivation between the Bronze and Iron Ages. Moats/reservoirs were constructed around Late Iron Age settlements, during which time wet-rice cultivation became the predominant form of production. This suggests that water management was partly prompted by the need for surplus grain to feed and trade with emerging cities during a time of unpredictable climate. Paleoclimatic reconstructions cannot always provide precise measurements, particularly for precipitation levels which are one of the key delimiting factors for cultivation in arid and semi-arid environments. At Tell Tawila in northern Syria, Jarl and colleagues [113] applied a multi-proxy

approach on the archaeobotanical remains to investigate how subsistence strategies were adjusted to cope with aridification during c.5850-4000 BC. Carbon isotope values from cereal grains indicate water stress around 4000 BC, which coincides with increasing numbers of edible wild grasses in the assemblages, whilst charcoal analyses show a surge in scrubby species better adapted to drought. The three different lines of evidence point to aridification in the Late Chalcolithic period and a heavier reliance on wild resources (also visible in the zooarchaeological record) as an adaptive mechanism [113]. These examples serve to illustrate the diverse and innovative stratagems humans have developed to survive changing climatic conditions, and how a multi-proxy approach can provide more robust interpretations.

Outstanding Questions

1. Large national and international datasets of archaeobotanical remains have been assembled over the last decade. These data are not well known and under utilised. How can research frameworks be devised to encourage collaboration between archaeologists and archaeobotanists with other palaeoenvironmental and ecological research teams interested in refining predictive models of land use and their environmental consequences?
2. How can plant macro-remains (indicative of land-use) and pollen (indicative of land-cover) datasets be analysed collectively to strengthen our understanding of human agency in leading landscape transformations?
3. The use and management of wild resources has had a transformative effect across the globe since at least the Palaeolithic. Once defined, can specific examples of the management of wild resources help refine descriptions of niche construction and ecological novelty?
4. The growth and abandonment of settlements can be explained by evaluating agricultural practices in light of other environmental and archaeological data. What past land-use activities led to resilient agricultural systems and which land-use practices are linked to more vulnerable ecosystems?

5. How far can macrofossil analytical approaches, particularly the use of isotopes, reveal landscape character, such as openness, suggested by other proxies (pollen and molluscs)?
6. Recent developments in compound-specific isotope analysis is showing promising results for extracting isotopic signatures from individual amino-acids in charred food residues. How can this new line of research help to refine current interpretations of isotopic levels in charred grains/seeds, and might we see spatial differences within targeted archaeological sites between produced and consumed cereals?

Glossary

Autoecology

This approach measures the physiological traits of individual species in relation to ecological conditions. In archaeobotany, this approach is now preferentially used over synecology, which measures the traits of plant communities, biomes or ecosystems.

Growing degree-days (GDD)

A plant's development from emergence to maturity will be triggered above a certain temperature threshold (unique to every plant) and after a defined number of days at a given temperature. GDD are a measure of accumulated heat above a threshold and can be used to predict phenological stages.

Intensive vs extensive cultivation

In archaeobotany, the intensity of cultivation is defined by the amount of labour expended per unit of land for food production. Intensive regimes are characterised by small, 'garden' plots that receive high levels of labour (weeding, manuring, irrigating, etc). Large, extended fields that receive relatively little labour (less weeding/disturbance, no manuring) are known as extensive cultivation and are usually associated with larger settlements where a few farmers are expected to feed a large population.

Landrace

A plant that is historically grown in an area using traditional methods, having never undergone any formal crop improvement. A landrace is locally adapted, unique and usually genetically diverse.

Phylogeography

Phylogeography is an analytical framework through which the genealogical relationship of genes within a species, or between very closely related species, can be established and correlated with their spatial distribution. The biogeographical history of lineages can therefore be traced.

Phytoliths

Microscopic silica structures that form within and between plant cells. Some are diagnostic to family, genus or species, and can sometimes be associated with a specific area of a plant, such as the leaves or stems.

Seed bank

When seeds are shed onto the ground they form a seed bank. Plants can be classified according to four seed bank types [66]:

5. Transient seed bank - seeds germinate shortly after being shed and do not survive until the next season
6. Semi-transient seed bank - seeds can overwinter and germinate in the spring
7. Mostly transient - seeds will mostly germinate shortly after being shed though some will persist in the seed bank
8. Persistent seed bank - seeds will survive for at least one year before germinating

Shifting cultivation

In shifting or slash-and-burn cultivation, parcels of land are cleared of natural vegetation, often by burning, and cultivated for a few years until soil fertility declines. Cultivation then shifts to new land, letting the previous area regenerate. Shifting cultivation has traditionally been used in the tropics where woodland regeneration is fast.