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The development of arable cultivation in the south-east of England and its relationship with vegetation cover: A honeymoon period for biodiversity?

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Abstract

The onset of prehistoric farming brought unprecedented changes to landscapes and their biodiversity. Past biodiversity patterns are broadly understood for different parts of Europe, and demonstrate trajectories that have been linked to prehistoric and historic demographic transitions, and associated land-use practices. To our knowledge, this paper is the first attempt to directly link evidence of agricultural practice from the archaeological record to biodiversity patterns. Records of fossil pollen are used to estimate plant and landscape diversity patterns, and novel approaches are employed to analyse 1194 harmonised archaeobotanical samples (plant macrofossil remains) spanning the prehistoric and Roman periods, from southern England. We demonstrate changes in the use of crops and gathered edible plants and non-linear trends in cultivation practices. Whilst, overall, cereal production is characterised by ever larger and extensive regimes, different trajectories are evident for most of early prehistory, the Middle Iron Age and the Late Roman period. Comparisons with the Shannon diversity of fossil pollen records from the same region suggest a positive relationship between developing agricultural regimes and landscape scale biodiversity during the prehistoric period. The Roman period represents a tipping point in the relationship between expanding agriculture and pollen diversity, with declining pollen diversity evident in the records from the region.

Keywords

archaeobotany, biodiversity, British prehistory, land use and land cover, Late-Holocene, palaeoecology, Southeast England

Introduction

Biodiversity is inextricably linked to landscape type and stability. Climate change, human population densities and farming have been major forces, impacting on observable early Holocene levels of biodiversity (Giesecke et al., 2019; Redford and Richter, 1999). The latter two factors are interdependent as larger populations necessarily require increased food production, although it has been shown that population growth does not have a predictable, linear impact on vegetation diversity (Woodbridge et al., 2021). How land was used for food production, and the different time scales involved in species regeneration, need to be considered when interpreting the effects of land use (Watts et al., 2020). Climate change is known to have influenced livelihoods and stages of climatic shifts in prehistory have been linked to population 'booms' and "'busts', adaptations in farming practices, and changes in land cover (Bevan et al., 2017; Woodbridge et al., 2014). The Birks et al. (2016) conceptual model on trends in biodiversity during the Holocene in north-west Europe describes how, within fertile soils, woodland clearance for farming had a positive effect on biodiversity through the creation of new habitats. This beneficial effect lasted until a tipping point was reached, after which continued woodland clearance/land use had a detrimental impact upon biodiversity (see also Woodbridge et al., 2021, Figure 1). It remains unclear when the tipping point was reached, and whether this was within prehistory (e.g. with the development of spatiallyextensive enclosures (cf. Løvschal, 2020)) or as a consequence of the rapid onset of mechanised agriculture in the past 200 years (Ellis, 2019).

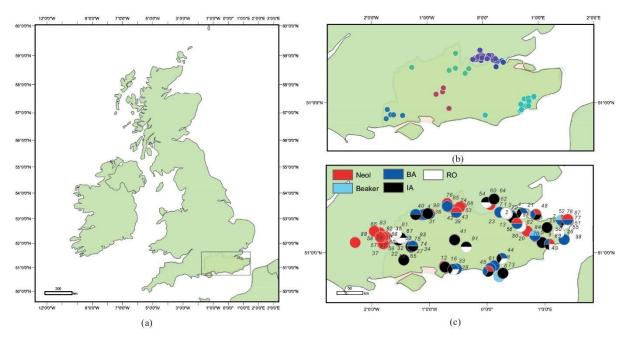


Figure 1. The study area in southern England (a), the location of off-site pollen cores (b, colours represent site groups) and on-site archaeobotanical samples (c) used in this study. Site numbers refer to Table 1. References to the pollen cores are listed in the Supplemental Information, Table SM3, available online.

From the onset of farming across Britain and Ireland at c. 4000 BC, vegetation cover has gradually, though not continuously, become more open (Fyfe et al., 2013, 2015; Trondman et al., 2015). A

similar pattern is evident in the diversity and evenness of fossil pollen (as a proxy for vegetation change) from southern England, which show a continued increase in diversity between the Bronze Age and the Roman period (Woodbridge et al., 2021, Figure 4). Entomological remains from archaeological sites also indicate changes in habitats through time (Smith et al., 2019, 2020). The presence of synanthropic insect species in Britain increased during early prehistory and taxa associated with pastoral activities were common during the Bronze and Iron Ages. Changes in insect taxa are also associated with the Romanisation of Britain, such as new grain pests indicating denser human settlements and increased agricultural production (Smith et al., 2019, 2020).

In this paper we explore how arable production, evidenced from remains of crops, seeds and fruits, changed from its onset in the Neolithic to the Late Roman period and whether such changes coincide with diversity trends inferred from fossil pollen records. Amalgamating data by archaeological period allows general trends in farming practices to be explored and compared to contemporary off-site fossil pollen records. With the aid of multivariate analyses and the ecological signatures of arable weeds, trends in farming practices are identified. Whilst these are common approaches in archaeobotany (de Vareilles et al., 2021), we are not aware of direct comparisons with fossil pollen records, or studies that attempt to explain how land use drove biodiversity over long time scales. This research therefore represents a novel and important contribution to how we understand the relationship between land use, land cover and biodiversity. The research area covers the region of southern England south of the Thames, from Kent in the south-east as far west as the Stonehenge and Avebury World Heritage Site (Figure 1). This area contains some of the earliest farming sites in Britain and all periods are well represented in the archaeobotanical record. Whilst acknowledging that cause and effect between climate, farming practices and biodiversity are complex and convoluted, the integration of two archaeological and palaeoecological strands of evidence represents a fundamental and important step to demonstrate, for the first time, how a better understanding of land-use practices can contribute towards explaining changes in land cover and biodiversity.

The development of agriculture in southern England

The introduction of farming in Britain and Ireland instigated localised and small-scale deforestation of deciduous woodlands (Fyfe et al., 2013; Woodbridge et al., 2014). Land-cover changes correspond well to the summed probability distribution (SPD) of radiocarbon dates, which suggest a demographic incline during the Early Neolithic (ENEOL) (Bevan et al., 2017, Figure 1; Shennan et al., 2013, Figure 3). Indeed, the correlation between the arrival of farmers and the decline in deciduous woodland has been shown to be statistically significant (Racimo et al., 2020; see also Marquer et al., 2017). The restricted range of Neolithic arable weeds, predominantly annuals, point to permanent plots more than shifting cultivation (e.g. Jones and Rowley-Conwy, 2007). Isotopic analyses on cereal grains from six sites across England and Wales suggest both manured (site in Derbyshire: Bogaard et al., 2013) and non-manured (sites in Wales: Treasure et al., 2019) cultivation was practised.

A dramatic change in agricultural practice across most of Britain and Ireland is evident from the start of the Middle Neolithic (MNEOL, c. 3300 BC). Pollen records point to a regeneration of deciduous woodland (Treasure et al., 2019; Whitehouse et al., 2014) with an associated decline in vegetation diversity. Trends in the SPD of dates on cereal grains show a sharp decline across England, contrasting with dates on hazelnut (Corylus avellana) shells, suggesting that gathered nuts continued to be used whilst the cultivation of cereals was greatly reduced, and even stopped altogether in some regions, such as in southern England (Bevan et al., 2017; Stevens and Fuller, 2012, 2015; see also Bishop,

2015). The rarity of cereals in later Neolithic assemblages has long been recognised (e.g. Brown, 2007; Jones, 1980; Moffett et al., 1989; Robinson, 2000), even though animal domesticates, particularly cattle, continued to be farmed (Serjeantson, 2011). A transition from mainly fixed, agricultural communities to a reduced population of mobile pastoralists is therefore likely (Rowley-Conwy et al., 2020; Worley et al., 2019). The shift away from arable farming and decline in human demographics may have been triggered by unstable, colder and wetter climatic conditions (Bevan et al., 2017; Stevens and Fuller, 2015; Whitehouse et al., 2014) and potentially new crop pests and diseases (Antolín and Schäfer, 2020; Dark and Gent, 2001). A deterioration in soil quality has also been suggested, as a focus on a narrow range of cultigens may have led to soil depletion and harvest failures (Colledge et al., 2019; Shennan et al., 2013).

The Beaker period is marked by a new influx of people of central European ancestry by around 2400 BC (Olalde et al., 2018). Changes in material culture, such as the introduction of Bell Beaker pottery, and settlement patterns attest to a shift in lifestyles (Bradley, 2019: Chapter 4). Little is known of Beaker subsistence strategies although a study of the isotopic signatures in human bone suggests a diet high in terrestrial animal (Parker Pearson et al., 2016). The Beaker period is marked by the expansion of Neolithic monuments, requiring a greater gathering of labour and organisation than previously seen (Gibson, 2020).

The resurgence in arable agriculture at around 1600 BC has been termed the Middle Bronze Age (MBA) agricultural revolution (Stevens and Fuller, 2012), and is associated with renewed and repeated migrations from the European continent (Patterson et al., 2022). Fossil pollen records indicate a sharp decrease in woodland cover (Woodbridge et al., 2014), coinciding with the development of field systems and drove-ways (Bradley et al., 2016; Yates, 2007). Enclosures used for both crops and herds, on a seasonal rotation system, would have encouraged disturbance-tolerant weeds. Indeed, the increase in grassland perennials during the Late Bronze Age (LBA) is indicative of the cultivation of fields previously under pasture (Stevens and Fuller, 2018: 31). The Bronze Age in southern Britain sees a rise in sheep at the expense of cattle (Hambleton, 2008: 56), and the addition of spelt wheat (Triticum spelta) and pulses. Spelt is higher yielding than emmer (T. dicoccum) and better adapted to harsher growing conditions; its adoption from the MBA may reflect a change to more extensive arable cultivation (Lambrick and Robinson, 2009: 258; Van der Veen, 1995: 342; Van der Veen, 2016: 301-302; van der Veen and Palmer, 1997). Agricultural intensification is also evident from tools and features, such as granaries, wells and waterholes, enabling permanent settlements away from main waterways and increasing habitat diversity (Bradley et al., 2016; Yates, 2007). Insects chart a change from mostly wooded early prehistoric landscapes to open ground for pasture and fodder production from the MBA (Smith et al., 2019, 2020).

Britain became more insular during the LBA, with limited archaeological and palaeogenomic evidence for foreign contacts (Cunliffe, 2013; Patterson et al., 2022). A population decline (Bevan et al., 2017) would have led to reduced arable production and the abandonment of settlements/fields. In southern England, the Middle Iron Age (MIA) is a period of significant social change, with the emergence of multivallate hillforts encompassing a greater catchment area, indicating a level of social cohesion and organisation not witnessed in the preceding era (Jones, 1985; Jones et al., 2008; Jones, 1996). Hillforts were abandoned by the Late Iron Age (LIA) and a change in land use is once again visible with the scattering of settlements and new agricultural developments (Cunliffe, 1987, 2013).

The Iron Age weed spectrum shows little diversity, suggesting that agricultural regimes became increasingly influenced by market forces or a standardisation in crops and agricultural tools (Campbell, 2017; Carruthers and Hunter Dowse, 2019: 55). Frequent wild oat and brome grass

(Bromus secalinus/hordeaceus) may have been an accepted addition to the crop (Knörzer, 1967; Zech-Matterne et al., 2021), whilst ryegrass (Lolium perenne) might have been an early fodder crop around Danebury (Campbell, 2000; see also Lodwick, 2017). Other common weeds include small grasses, vetches/tares, cleavers and clover types (clover, medicks, trefoil), and are suggestive of the use of grass fallow in a rotation regime (Carruthers and Hunter Dowse, 2019: 55). They are indicative of a full annual agricultural regime, with crops sown in both autumn (spelt wheat) and spring (barley (Hordeum vulgare), pea (Pisum sativum) and possibly oat (Avena sativa)) (Campbell, 2000; Campbell and Straker, 2003).

Agriculture during the Roman period is characterised by large-scale, extensive regimes focused on spelt wheat (Allen and Lodwick, 2017; Campbell, 2017; Lodwick et al., 2021). Production was scaled-up to feed a growing population, within and beyond Britain (Allen and Lodwick, 2017; Orengo and Livarda, 2016; Van der Veen, 2016). An increase in horticulture and imports makes it difficult to separate locally grown from imported plant foods (Van der Veen, 2014). Developments in ploughing technology, evident from tools and new weed taxa, allowed the expansion of cultivation onto heavier soils (Allen and Lodwick, 2017; Jones, 2009; Stevens and Fuller, 2018: 33).

During the fall of the Roman Empire a reduction in arable production is traditionally associated with a population decline in Britain, though the dynamics between agricultural production and the changing political and social spheres remains elusive (Van Der Veen, 2022). The starkest contrast between Romano-British and Saxon cereal production is the almost complete replacement of spelt for free-threshing wheat (McKerracher, 2018; Van Der Veen, 2022). The latter (T. aestivum/durum/turgidum) is usually considered a crop-contaminant in Roman samples, though its cultivation may have begun as small-scale productions to produce more refined, white bread for the elite (Van Der Veen, 2022: 324–326).

Materials and methods

Archaeobotanical dataset

Neolithic to rural Romano-British sites with records of archaeobotanical plant macrofossils (cereal grains and chaff, pulses, fruits, nuts and seeds of wild plants) were selected from the research area. Data collection was focused on records available online which are biased towards large-scale development projects, such as the Channel Tunnel Rail Link (Figure 1). As early prehistoric samples tend to be sparser, greater focus was spent finding records from these periods. All plant macrofossils were registered by site in ArboDat 2016 English Version © (Kreuz and Schäfer, 2002), a Microsoft Access database which associates each taxon with its plant part (e.g. seed, spikelet, awn), level of identification (genus, species, cf. species), preservation (charred, waterlogged, mineralised), sample volume and flotation mesh size. Each site record has a unique ArboDat reference code (Table 1): these data will be made open access through the Archaeological Data Service. A dataset of 1718 archaeobotanical samples from 110 sites was collated.

Table 1: Archaeological sites shown in Figure 1.

Site ID	Site name	ArboDat code	easting	northing	Period	Reference
						Le Hégarat,
1	A2 Activity Park	HE-AdV86	566133	170175	LBA, EIA, MIA	2017
2	A2 Pepperhill-Cobham	HE-AdV58	555652	172311	EIA, MIA, LIA, ERO	Smith, 2012
3	A2/A282 Improvement Scheme	HE-AdV61	555652	172311	MBA, LBA, MIA, LIA, LRO	Smith, 2011
						Arthur and
4	Aldermaston Wharf	HE-AdV132	460584	168092	LBA	Paradine 1980
5	Beechbrook Wood	HE-AdV99	598500	145600	Beaker, LBA, MIA, ERO	Giorgi, 2006
6	Belle Tout 68-69	HE-AdV66	555700	95600	Beaker	Arthur, 1970
7	Bigberry 78-80	HE-AdV137	612000	157000	LIA	Jones, 1983
9	Black Patch Bower Road	HE-AdV136 HE-AdV107	549500 605946	108600 138812	LBA ERO, MRO, LRO	Hinton, 1982 Stevens, 2006
3	Bowel Road	TIL-AUVIO7	003340	130012	LKO, WKO, LKO	Pelling et al.,
10	Broadstairs	HE-AdV76	637000	167700	ENEOL, MBA, LIA	2008
11	Chilbolton 86	HE-AdV135	439100	139700	Beaker	Green, 1990
					ENEOL, LNEOL, EBA,	Hinton, 2006
12	Claypit Lane, Westhampnett	HE-AdV74	488400	106600	MBA, LBA	
13	Cobham Golf Course	HE-AdV129	568330	169550	MBA, LBA	Davies, 2006
						Carruthers,
14	Coneybury Anomaly	HE-AdV109	413420	141689	ENEOL, LNEOL	1990
15						Carruthers,
4.6	Coneybury Henge	HE-AdV108	413420	141689	Beaker, EBA	1990
16	Copse Farm	HE-AdV138	489460	105510	LIA	Hinton, 1985
17	Cottington Hill (cemetery)	HE-AdV54	633845	164106	LRO	Stevens, 2009
18 19	Cottington Rd, Thanet Crowder Terrace (Oram's Arbour)	HE-AdV51 HE-AdV70	634011 447595	164328 129450	MNEOL Beaker	Stevens, 2009 Green, 2004
20	Cuxton	HE-AdV117	570743	166619	EIA	Davies, 2006
21	Damhead Creek Power Station	HE-AdV87	581140	172802	MBA, LIA, MRO, LRO	Hinton, 2017
22	Danebury 78 (hillfort)	HE-AdV77	432500	137500	EIA, MIA, LIA	Jones, 1984
23	Dartford Football Club	HE-AdV62	555140	173240	ERO	Pelling, 2011
						Robinson,
24	Dorney	HE-RP27	492881	178047	ENEOL	2000
	Dunkirt Barn, Danebury Environs					Campbell,
25	Project	HE-AdV34	431400	141900	MRO, LRO	2008
					ENEOL, LBA, MIA, LIA,	Hunter, 2015
26	East Kent Access Rd	HE-AdV113	633584	163813	ERO, MRO, LRO	
27				400000		Carruthers,
27 28	Easton Lane, 76-77 Eden Park (Toddington Nurseries)	HE-AdV78 HE-AdV123	448000	129000	Beaker, MIA	1989 Pelling, 2012
28	Eden Park (Toddington Nurseries)	HE-AUV123	503520	103565	MBA	Carruthers,
29	Ellington School	HE-RP2	637166	165332.5	ENEOL	2021
30	Eyhorne Street Hollingbourne	HE-AdV128	583600	154302	LNEOL, Beaker	Davies, 2006
	,				,	Jones and
						Rowley-
31	Field Farm	HE-RP4	463226	168612	EBA	Conwy, 2007
	Flint Farm, Danebury Environs					Campbell,
32	Project	HE-AdV32	435000	140500	EIA	2008
33	Ford Airfield	HE-AdV111	499426	103067	LBA, LIA, ERO	Hinton, 2004
24	Fullerton, Danebury Environs	HE V4//33	127157	140105	LPO	Campbell, 2008
34	Project Grateley South, Danebury	HE-AdV33	437457	140105	LRO	Campbell,
35	Environs Project	HE-AdV31	427600	141000	LIA, ERO, LRO	2008
33	Environs Project	TIE AUVSI	427000	141000	LIA, LIO, LIO	Campbell,
36	Green Park 95	HE-AdV104	469700	169600	LNEOL, MBA LBA	2004.
			1			Powel and
						Dinwiddy,
37	Greentrees School	HE-RP12	415160	132620	Beaker, MNEOL	2016
38	Guston Roundabout	HE-AdV114	633190	143450	LBA	Pelling, 2002a
		115 A D.(155		47765-	LNEOL, MNEOL, EBA,	Stevens, 2015
39	Harlington ICSG and RMC	HE-AdV120	508267	177935	MBA, ERO, MRO, LRO	Committee
40	Hartshill Conso	HE-V9//80	/52100	169500	I BA FIA	Carruthers, 2004
40	Hartshill Copse Hascombe Camp	HE-AdV130	453100	168500	LBA, EIA	
41	пазсопіре Сапір	HE-AdV139	500500	138600	ENEOL, Beaker, MBA,	Murphy, 1979 Carruthers,
42	Heathrow T5	HE-AdV102	505028	175827	LBA, MIA, LIA, MRO, LRO	2010
				175294	ENEOL, LNEOL	2010
43	Horton Quarry (Kingsmead)	I HF-AdV174				
43	Horton Quarry (Kingsmead) Isle of Grain- Shorne Gas	HE-AdV124	501683	173234	LIVEOL, LIVEOL	
43	1	HE-AdV124 HE-AdV88	558620	117550	LBA, LIA, ERO, LRO	

46	King's Barrow Ridge	HE-RP17	413598	142168	MNEOL, LNEOL	Carruthers, 1990
47	King's Gate, Amesbury	HE-RP13	416550	140070	MNEOL, LNEOL, Beaker	
48	Kingsborough – prehistoric	HE-AdV100	597757	172093	ENEOL, LBA, MIA	
49	Little Stock Farm	HE-AdV116	606646	138531	EIA, LIA	Stevens, 2006
50	Manston Rd, Ramsgate,	HE-AdV56	636175	165500	MBA, LBA	Hinton, 2009
51	Manston Rd1, Ramsgate	HE-AdV89	636169	165755	LBA	
52	Monkton Road, Minster	HE-AdV119	630580	164625	EBA	
53	New Road (Oram's Arbour)	HE-AdV71	447800	129900	MIA	
54	Newnham	HE-RP1	542500	182000	ENEOL	
						Carruthers,
55	Nonington	HE-AdV92	626892	151707	ERO	2011
56	Northumberland Bottom	HE-AdV103	563000	171500	ERO, LRO	
57	Old Dairy	HE-RP14	416200	142000	MNEOL	
58	Old Sarum Airfield	HE-RP15	415460	133087	MNEOL	
59	Old Sarum Spur	HE-RP16	413319	133124	MNEOL	
60	Olympic Park	HE-AdV84	538000	184500	MIA, ERO	
00	Olympic Fark	TIE AUVO4	330000	104300	ENEOL, EBA, MBA, LBA,	
61	Peacehaven, Lewes	HE-AdV60	542030	101600	MIA	
62	Princes Road, Dartford	HE-AdV75	554100	173200	MBA	Pelling, 2003
63	Prospect Park	HE-RP9	505990	178191	LNEOL	Hinton, 1996
	Redbridge	HE-AdV24	546830			HIIItoli, 1990
64	ŭ			188810	EIA	
65	Regents Park	HE-AdV64	439200	113600	EIA	
			440000	446400	511501	Carruthers,
66	Robin Hood's Ball	HE-RP25	410300	146100	ENEOL	1990
c=	Rowbury Farm, Danebury		405046	440055	514 4414 550	Campbell,
67	Environs Project	HE-AdV36	435346	140066	EIA, MIA, ERO	2008
68	Runnymede 78	HE-AdV126	501800	171800	MNEOL, LBA	
					ENEOL, EBA, MBA, LBA,	Stevens, 2006
69	Saltwood Tunnel	HE-AdV115	615750	136900	MIA, LRO	
70	Sandway Road	HE-AdV97	587975	151642	MNEOL	Giorgi, 2006
71	Springhead Sanctuary	HE-AdV68	561800	172750	LIA, ERO, MRO	
						Campbell,
72	Springhead, 1994 Pipeline	HE-AdV67	561819	172339	ERO	1998
73	St Anne's Hill	HE-AdV85	560268	99800	LIA	Hinton, 2016
74	Staple Gardens (Oram's Arbour)	HE-AdV69	447745	129809	EIA, MIA	
75	Sussex St (Oram's Arbour)	HE-AdV72	447820	129870	MIA	
76	Taplow Hillfort	HE-AdV65	490700	182300	ENEOL, EBA, LBA	
	Thanet Area 16, Weatherlees &					
77	Ebbsfleet, Kent	HE-AdV52	633330	163000	LBA, LIA, ERO	
					ENEOL, LNEOL, Beaker,	Carruthers,
78	Thanet Earth	HE-AdV91	628900	166700	EBA, MBA, MIA	2019
79	The Beehive	HE-RP22	414359	133338	MNEOL	
80	The Portway	HE-RP23	414278	133022	MNEOL	
	Thruxton Villa, Danebury					Summers et
81	Environs Project	HE-AdV37	429818	146199	MRO	al., 2008
82	Thurnham Roman Villa	HE-AdV59	579954	157111	ERO, MRO, LRO	
83	Tilshead nursery school	HE-RP18	403510	148100	MNEOL	
84	Tutt Hill	HE-AdV98	597520	146600	Beaker, MBA	Giorgi, 2006
85	Weir Bank Stud Farm	HE-AdV118	490950	178900	MBA	
86	West Amesbury Farm	HE-RP21	414030	141390	MNEOL, LNEOL	
87	Westwood Cross	HE-AdV125	636300	167600	ENEOL, MBA, LBA	1
88	White Horse Stone	HE-AdV127	575300	160410	ENEOL, LNEOL, MBA	Giorgi, 2006
00	The control of the co		3.3300	200110		Jones and
						Rowley-
89	Whitesheet Hill	HE-RP19	380300	134600	ENEOL	Conwy, 2007
90	Wickhams Field	HE-AdV131	467500	169700	EIA	CONTWY, 2007
91						+
JТ	Wickhurst Green	HE-AdV90	514800	130300	MIA, ERO	Carruthers,
	Wilsford Down	HE-RP26	410800	140800	ENEOL	1990
92		I DE-NE/D	1 4 10500	1400UU	LINEUL	1 1770

To explore changes in land use from the ENEOL to the Late Roman period (LRO), the complete archaeobotanical dataset was filtered to remove:

- •waterlogged plant macroremains (carbonised, mineralised and silicified remains were retained. The latter two make up <5% of total counts and presence by period, and all species are also present in a carbonised state);
- •taxa that are unlikely to represent edible plants or arable weeds, such as trees and shrubs with non-edible fruits, heather and ferns;
- •unquantifiable plant parts, such as awns, glume fragments, culms, thorns and non-tuberous roots (edible roots of pignut (Conopodium majus) and roots of false oat grass (Arrhenatherum elatius) were retained though the former were found to be rare);
- •indeterminate remains and taxa identified to cf. family (e.g. cf. Ranunculaceae) (Chenopodiaceae/Caryophyllaceae and Polygonaceae/Cyperaceae were retained);
- •items not dated to the early, middle or late span of an archaeological period, either directly or by association. Dates and periods follow Historic England's Period List, FISH terminology (Updated March 2022: http://www.heritage-standards.org.uk/chronology/). Radiocarbon dates are listed in Supplemental Table SM1, available online.

The filtering process resulted in archaeobotanical data from 1194 samples (93 sites; Figure 1 and Table 1). In order to further harmonise the data, taxa identified to possible species (e.g. Apium cf. nodiflorum) were recorded as species. Identifications to possible genus were either retained at genus level or recorded to family level, depending on seed morphology and ecological grouping. For example, cf. Rubus was recorded as Rubus because all British species grow under similar conditions, are edible and are distinct from other Rosaceae seeds, whereas cf. Danthonia was recorded as Poaceae since small grass seeds are difficult to separate taxonomically. The mode value of 10 L was used as a conservative estimate for missing sample volumes (flotation samples from archaeological deposits). Only for the Early Roman Period (ERO) did estimated volumes make up >10% of the total volume (14.5%). Although crop densities per period may have been artificially increased, using the mode value of 10 L makes it unlikely that the actual densities differ substantially (Table 2).

Table 2. Summary data of plant macrofossils by archaeological period. Counts are taxa present in \geqslant 5% (<5%) of samples per period (for the EBA and the weeds of the Beaker period (n) is the number of taxa in only one sample); estimated sample volumes are included in the total volume.

Archaeological Period	Nº Sites	Nº Samples	Total vol. (L)	Density (items/l)	Nº crops	Nº gathered edibles	Nº possible weed taxa*/[seeds]
ENEOL	19	122	3243	6.7	4 (3)	3 (3)	9 (18) / [515]
M/LNEOL	22	146	3803	7.5	2 (4)	1 (5)	9 (14) / [191]
Beaker	12	51	752	1.8	2 (2)	2 (3)	4 (7) / [31]
EBA	9	18	362	1.8	3 (2)	2 (1)	1 (16) / [61]
MBA	18	124	2484	10	6 (1)	1 (8)	26 (38) / [6942]
LBA	25	190	3459	16.9	7 (2)	2 (4)	25 (68) / [15956]
EIA	13	56	1231	17.3	6 (1)	2 (1)	40 (36) / [4120]
MIA	19	76	2481	3.8	5 (3)	1 (3)	29 (54) / [3482]
LIA	17	76	1411	200.4	6 (1)	1 (3)	45 (25) / [4467]
ERO	18	168	2608	299.5	5 (3)	4 (4)	35 (63) / [37034]
MRO	9	65	1236	263	6 (1)	4 (4)	40 (34) / [16620]
LRO	14	89	1271	71.3	6 (2)	1 (4)	33 (51) / [6875]
ENEOL	19	122	3243	6.7	4 (3)	3 (3)	9 (18) / [515]
M/LNEOL	22	146	3803	7.5	2 (4)	1 (5)	9 (14) / [191]
Beaker	12	51	752	1.8	2 (2)	2 (3)	4 (7) / [31]

The number of samples and of identified archaeobotanical remains varies considerably between contemporary sites as well as archaeological periods (Table 2). Inconsistencies also exist in the recording of contextual provenance, with many reports containing poorly defined or missing information. To mitigate against these biases when comparing archaeological periods, all data were amalgamated by period regardless of context and all analyses were produced using presence/absence data, except for Figure 2. Transforming count data to a binary format (i.e. presence/absence) enabled the inclusion of estimated as well as unusually large counts and avoids apparent differences between periods based on seed count, which can reflect the scale of cereal processing and the use/discard of processing waste (Fuller et al., 2014). Presence/absence data also reduces potential biases towards particular arable weeds and their associated ecological conditions; taxa may be more numerous in assemblages because they produce more seeds or because they are retained with crops until the last stages of processing, and are therefore more likely to become burnt as settlement waste (Hillman, 1984).

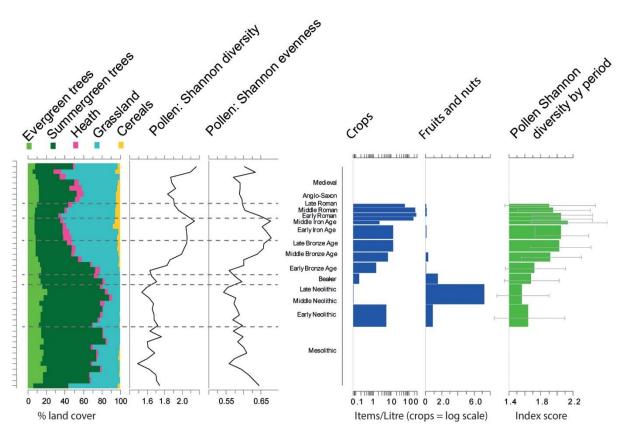


Figure 2. (a) quantified land cover, (each division in the REVEALS and pollen diversity represents a 200 year time step from 11,000 BC to present); (b) density of crops and gathered fruits and nuts (items per litre of deposit) alongside the Shannon diversity of fossil pollen by archaeological period. Although LIA data is represented in the bar chart, space was lacking for a label. Note that the chart for crops uses a logarithmic scale whereas the one for fruits and nuts does not as they occur in much lower densities.

Figure 2b uses whole counts of plant macroremains and sample volumes to illustrate changes in assemblage concentrations by period. Although changes in assemblage densities reflect changes in settlement patterns and the organisation of crop processing/use, they are also associated with the

growth of populations and are here used as a crude measure for the scale of production. The density of assemblages is plotted against the trend in pollen diversity (Shannon index), further explained in Section 3.2. The relationships between trends were tested using Spearman's Rank, which shows a positive correlation between pollen diversity and concentrations of crop remains (Spearman's rho = 0.6 and r2 = 0.5, p < 0.005).

Data analysesSeveral approaches were used to explore the archaeobotanical dataset for patterns of changing land use. As the number of samples varies between archaeological periods, we tested the relationship between plant taxa richness and the number and volume of samples. Both correlations are moderate, with Spearman's Rho centred around 0.6 and r2 around 0.3 (p < 0.0005 in both cases). Similar results are found when the correlations are calculated by individual time periods, except for the Beaker and Early Bronze Age (EBA) where correlations are weak (Rho = 0.3/0.2 respectively, p = 0.3). The latter confirms that the distribution and recovery of Beaker and EBA archaeobotanical finds are unpredictable, making it even more important to sample sites from these periods intensively. Despite variations in site types and sampling strategies, taxa richness is comparable between other periods, validating comparisons made below.

The presence of crops and gathered edible plants per sample was plotted for all archaeological periods, to illustrate the changing use of plant foods through time (Figure 3). The internal structure of the dataset was explored using hierarchical cluster analysis (HCA) (Murtagh and Legendre, 2014; Ward, 1963), performed in the 'Vegan' R package (Oksanen et al., 2020), after small samples and rare taxa had been removed, that is, samples with fewer than 30 items (before the transformation to presence/absence data) and taxa occurring in fewer than 2% of samples (n = 24). Excluding small samples affected the early prehistoric periods most strongly, removing two-thirds to three quarters of the Middle/Late Neolithic (M/LNEOL), Beaker and EBA samples. HCA groups samples by similarity of composition and visual inspection of outputs. Experimentation with grouping levels suggested that six clusters adequately represent relationships of dissimilarity between different groups. This technique is more commonly used in the field of palynology (e.g. Woodbridge et al., 2018), but has the advantage of allowing the taxonomic composition of each cluster to be explored as well as a taxon's frequency within the cluster group assigned to each sample. Taxa that occurred in >50% of samples within a cluster are here described as 'common' (Table 3).

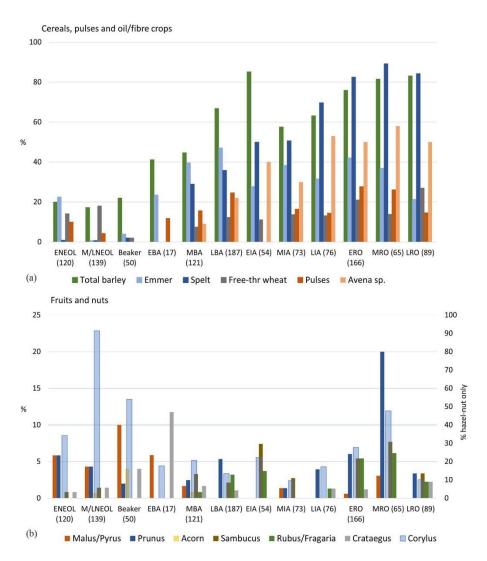


Figure 3. The ubiquity of crops (a), fruits and nuts (b) by archaeological period. Only taxa present in >5% of samples in at least one period are represented. Avena sp. may include undomesticated grains; pulses includes Lens culinaris, Pisum sativum, Vicia faba and large Fabaceae; berry includes Rubus spp.; Prunus includes Prunus spp., and acorn all Quercus spp.

Table 3. Results of the hierarchical cluster analysis by six clusters, showing taxa present in \geq 50% of samples within each cluster (see text for Latin binomials).

Clusters (samples predominantly from)	Common Taxa (in >50% samples)	Nº of other taxa
1 (early prehistory)	Hazelnut	15
	Hulled barley grain, bromes, cleavers,	
2 (Iron Age)	indeterminate wild grasses	48
	Emmer/spelt grain and chaff, emmer chaff, spelt	
3 (Bronze Age with some Iron Age, mostly MIA, and Roman)	chaff, indeterminate wild legumes	44
4 (Middle Bronze Age, Early to Middle Iron Age and Late		
Roman, with some Late Bronze Age and Late Iron Age to	Emmer/spelt chaff, spelt chaff, indeterminate	
Middle Roman)	wheat grains, indeterminate wild grasses	62
5 (Middle/Late Neolithic)	Hazelnut	0
	Hulled barley grain, emmer/spelt grain and chaff,	
	spelt chaff, indeterminate cereal grain,	
	indeterminate oat grain, ryegrass, corn gromwell,	
	curly dock (Rumex crispus), indeterminate wild	
6 (Late Iron Age to Middle Roman)	legumes, hazelnut	55

Ecological analysesSeeds of herbaceous wild plants are here analysed as arable weeds. Whilst some may represent species that were eaten or used (as leaves, roots, etc), their presence as charred seeds associated with cereal grains/chaff suggests they grew in arable fields. An autoecological approach (Ellenberg, 1988; Ellenberg et al., 1991), based on modern field observations of individual species' tolerances to environmental conditions, was adopted (see de Vareilles et al., 2021 for a critique of different ecological approaches on archaeobotanical material). Ellenberg numbers have been adjusted for British plants (Bunce et al., 1999; Hill et al., 1999, 2000), and are used to record species' preferences for soil nitrogen (2-3 = low, 4-5 = intermediate, 6-7 = high, 8-9 very high fertility) and light intensity (6 = shade to well lit, 7 = mostly well lit, 8 = ample light) (Figure 5b and e). Figure 5a, c and d illustrate species' life form (annual or perennial), flowering habit of annual plants, and preference to light or heavy soils (Fitter and Peat, 1994; Stroh et al., 2020). The onset and duration of flowering in annuals is associated with both season of germination and a plant's tolerance to disturbance (Bogaard et al., 1999, 2001; Hodgson and Grime, 1990). Plants that flower early are more likely to develop in autumn-sown crops, growing in time with the crop. Similarly, plants that germinate and flower late are at a competitive advantage in spring-sown crops, where they avoid competition from autumn-germinating plants and the spring plough. Some annuals flower repeatedly throughout the year as an adaptation to disturbance, and duration of flowering time can therefore be used as an indication of disturbance frequency. Figure 5c translates flowering habit to season of germination and disturbance levels following Bogaard et al. (2001). Ubiquity charts in Figure 5 are calculated using presence/absence data for traits, not the number of taxa or seeds. Relevant taxa within a given sample (i.e. all those with a score for a particular ecological/biological trait) are reduced to a single occurrence by trait score. The number of samples is that for which there is information on a given trait. Ubiquity scores by archaeological period are therefore a measure of the frequency of presence of a particular characteristic within an assemblage for an ecological/biological trait. The measured characteristics are listed in Supplemental Table SM2, available online.

Fossil pollen data

The fossil pollen datasets used in this study include 106 datasets from the south-east of England (Woodbridge et al., 2021; in review) (Supplemental Table SM3, available online). Pollen records (Fyfe et al., 2013; Leydet, 2007; Trondman et al., 2015) from individual coring sites have been taxonomically harmonised and summed into 200-year time windows (Woodbridge et al., 2023). Shannon diversity indices derived from the pollen datasets, which reflect both taxa richness and evenness, are presented in Figure 2. Quantified land cover was reconstructed from a subset of 98 sites suitable for the application of the REVEALS (Regional Estimates of Vegetation Abundance from Large Sites) approach (Fyfe et al., 2013; Githumbi et al., 2022; Marquer et al., 2014; Sugita, 2007). This approach uses information about the productivity of different plants, the dispersal behaviour (fall speed) of different pollen types, and site type (lake or peatland/bog) and size to quantify land cover using pollen count data. To produce estimates of regional vegetation using the REVEALS model, pollen sites need to be grouped together. This grouping is based on site type, site size, proximity to other pollen sites, and landscape characteristics. The grouping resulted in five sub-regions in SE England, which are illustrated in Figure 1b (see Woodbridge et al., 2023, for further details). A pairwise Wilcox test for non-normally distributed data was used to test the differences between pollen diversity scores by archaeological period. All comparison periods were shown to be statistically significantly different with a p-value below 0.05.

Results

Land cover, pollen diversity and scale of cultivation

The concentrations of crops and edible fruits/nuts represent an approximation of the scales of cultivation and gathering activities between periods (Figure 2). The overall relationship between densities of crop assemblages and pollen Shannon diversity is positive and statistically significant. An increase in cultivation correlates with increased vegetation diversity. The bar chart suggests that this relationship is strongest during Early Prehistory.

Compared to the Mesolithic, the ENEOL is marked by a decrease in forest cover (Figure 2a). A decline in crop density and increase in the presence of gathered fruits/nuts after the introduction of agriculture is evident for the Middle/Late Neolithic (Figure 2b). Whilst this change may represent a shift in human behaviour and depositional activities, it coincides with a slight decline in pollen diversity and increase in forest cover (Figure 2a), suggesting a change in landscape use and reduction in arable activity. Crop density then increases from the Beaker period, with a significant increase in the LIA and Roman period. The REVEALS model (Figure 2a) illustrates how the proportion of grassland and cereal land cover increased relative to forest cover when farming was introduced and as the scale of cultivation increased from the MBA to the Middle Roman period (MRO). A decline in crop density is seen in the MIA, despite a continued increase in pollen diversity, and again, marginally, during the LRO. The positive correlation between crop density and pollen diversity appears to change during the LIA when there is a decline in pollen diversity which continues into the LRO.

The impact that the production/management of wild resources had on the landscape and its biodiversity cannot be measured through our dataset. Similarly, the effect of individual crop species is not known. However, the evident growth in the representation and density of crop assemblages from the MBA to the Roman period, and its association with increased areas of land under cultivation, is reflected in changing vegetation cover and diversity.

The representation of crops and edible fruits and nuts

The frequency of data suggests that emmer and barley were the predominant crops of the Early Neolithic (Figure 3 and Table 2). Naked barley (H. vulgare var. nudum) is present but infrequent and absent from later periods, as is the pattern across Britain and Europe (Lister and Jones, 2013). The decrease in cereal remains in the M/LNEOL and Beaker periods coincides with a marked increase in gathered hazelnuts and apples/pears (Malus/Pyrus). The few crops seen in the data from M/LNEOL and Beaker periods are largely free-threshing wheat and pulses, which when dated (from site 43 and others not included) have consistently returned later dates (Pelling et al., 2015); great care is needed when interpreting early prehistoric crop data. The earliest British record of spelt is from Monkton Road (site 52) where glume bases, associated with fragments of Celtic bean (Vicia faba), were dated to the end of the EBA (1896–1690 cal BC, Martin et al., 2012). Spelt replaced emmer as the predominant wheat in the region by the Early Iron Age (EIA), and spelt and hulled barley (H. vulgare) became the main crops in Britain during later prehistory and the Roman period. Barley is tolerant of poorer growing conditions, both edaphic and climatic, and was an important animal feed (Rhiel, 2019). Whether these factors affected the changing representation of barley relative to the wheats cannot be fully explored here.

Free-threshing wheat is most frequent in Neolithic (n = 193, 3% of all wheats) and Roman (n = 398, 0.04% of all wheats) samples, although the number of remains are low. Rare grains and chaff of tetraploid free-threshing wheat from Thanet Earth (site 78) were radiocarbon dated to 3940–3660 cal. BC (Carruthers, 2019), though free-threshing wheat grains from other Neolithic sites have returned later dates (Pelling et al., 2015). The richest assemblage was recorded from Late Roman Grateley (site 35), consisting of 121 free-threshing wheat grains but only three rachises, amongst thousands of barley and spelt remains. The dataset corroborates current evidence suggesting that free-threshing wheat was not a common crop in Britain before the Anglo-Saxon period (McKerracher, 2018). Cultivated oat (Avena sativa) is poorly represented, its highest occurrence being in the Middle and Late Iron Age (in 3% of samples). However, in the absence of diagnostic chaff, domesticated oats are difficult to identify and may be under-represented in Iron Age and Roman samples, where oat caryopses recorded only to genus (Avena sp.) are present in 40–58% of samples.

Trends in ubiquity suggest an overall temporal increase in the range and presence of crops across sites (Figure 3a), and mirror the increase in the density of assemblages. Exceptions to these trends are evident for the M/LNEOL, Beaker, MIA and the LRO. Compared to the EIA, the MIA sees a marked drop in the ubiquity of barley but an increase in that of emmer and pulses. The decline in the ubiquity of crops is less marked for the LRO: a decline is visible for emmer, spelt and pulses though the score for free-threshing wheat increases. Minor crops are not shown on the chart but are intermittently present from the ENEOL (flax – Linum usitatissimum) and more consistently from the EBA (opium poppy – Papaver somniferum) or MBA (brassicas – Brassica nigra/oleraceae/rapa), sometimes in substantial numbers.

Early prehistoric finds of cultivated pulses (see Figure 3 for taxa in this category) should be viewed with caution as all directly dated finds from Neolithic contexts pertain to later periods (Pelling et al., 2015; Stevens and Fuller, 2012; Treasure and Church, 2017). Celtic beans first appear during the EBA, becoming more prolific along the south coast and spreading inland from the MBA onwards (Treasure and Church, 2017). The absence of pulses in the dataset from EIA samples is surprising, but reminiscent of a national pattern: pulses and flax were not universally grown during the Iron Age, perhaps reflecting regional cultivation of pulses in areas of poorer soils and the growth of fodder crops (De Carle, 2014: 160; Treasure and Church, 2017: 120). The frequency of pulses increases during the Roman period, when the only secure find of lentil (Lens culinaris) is recorded (site 71), although potentially imported. The drop in the ubiquity of pulses during the LRO may reflect a decline in trade rather than/as well as cultivation.

Fruits and nuts are assumed to be wild in the early prehistoric period, when the data is dominated by hazelnut shell, but include cultivated and imported varieties by the LIA and Roman period, when Prunus numbers greatly increase. There is an opposite trend in decreased fruits and nuts related to increased cereal finds through time, with the exception of the MRO when both cereal production and (orchard) fruits are high.

Hierarchical cluster analysis

Hierarchical cluster analysis (HCA) separated the archaeobotanical samples into six clusters with some clear temporal trends (Figure 4 and Table 3). Clusters 1 and 5 are predominantly composed of early prehistoric samples, whilst cluster 6 contains LIA, ERO and MRO samples. Clusters 2, 3 and 4 suggest later prehistoric samples can be separated into three distinct groups. Cluster 5 is composed

of almost half of the M/LNEOL samples and is made up entirely of hazelnut. Hazelnut is also common in cluster 1 where cereals, fruits and nuts also occur, but only four arable weed taxa (Galium aparine, Fallopia convolvulus, Rumex sp. and wild legumes). In contrast clusters 2, 3, 4 and 6 are influenced by cereal remains and each contain over 30 weed taxa. While the number of Beaker and EBA samples is very low and may not be representative, the inclusion of 20% of EBA samples in clusters 2 and 3 is consistent with a renewed emphasis on cereal cultivation. M/LNEOL, Beaker and EBA samples are excluded from further ecological analyses below owing to the very low representation of possible arable weeds and the low correlation between the number and volume of samples, and taxa richness.

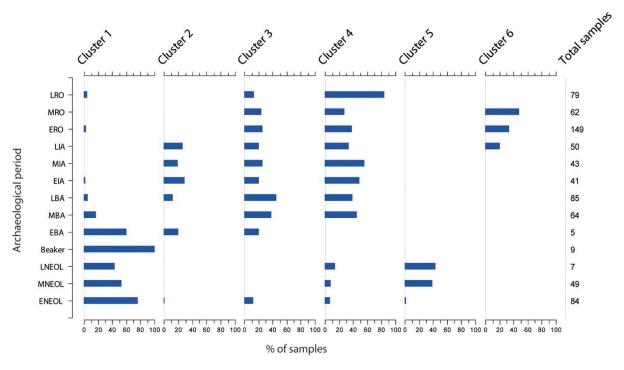


Figure 4. The Hierarchical Cluster Analysis classification of archaeobotanical samples into six clusters.

Clusters 3 and 4 include the majority of MBA to LRO samples. These clusters have similar compositions with spelt and/or emmer chaff present in >50% of samples (Table 3). The main difference between the clusters seems to be the presence of emmer, which is less frequent in cluster 4 where IA and Romano-British samples predominate. Both clusters also contain other crops and 32 weed taxa each, including stinking chamomile (Anthemis cotula, an indicator of clay soils), but corncockle (Agrostemma githago) is only present in cluster 4; both species are anthropochores associated with the expansion of cultivation in the Romano-British period (Preston et al., 2004; Stevens and Fuller, 2018). Spelt and emmer grains and chaff are also present in cluster 2, but in fewer than 50% of samples, so are not a defining characteristic.

Cluster 2, which includes EBA, LBA and IA samples, is characterised by hulled barley grain, cleavers (Galium aparine), brome and indeterminate wild grass seeds. Barley is also dominant in cluster 6, but in association with oats and ryegrass, rather than brome, as well as corn gromwell (Lithospermum arvense) which is indicative of light sandy soils, contrasting with the stinking chamomile and hulled wheats in clusters 3 and 4. The different weed flora between clusters 2 and 6 could indicate a

development in the cultivation of barley through the Iron Age and Roman periods (cf. Campbell and Straker, 2003). In addition to cereal remains, cluster 6 also contains fruits and nuts, reflecting the rise in horticulture and exotics during the Roman period (cf. Van der Veen, 2014).

Table 2, which lists the number of weed taxa by archaeological period, further helps to understand the classification of samples into clusters. The low representation of ENEOL weeds conforms to the small, low-density assemblages common for that period, and may relate to the practice of intensive cultivation that included careful weeding. The very low representation of weeds in the M/LNEOL, Beaker and EBA periods aligns with the poor representation of crops, though the low number of sites and processed volume of sediments for the Beaker and EBA make comparisons difficult. The MBA sees a significant increase in the representation of weeds and the overall density of samples, demonstrating increased emphasis on arable cultivation. This trend peaks in the LBA which, after the ERO, has the highest range of taxa (n = 93). The relatively low quantity of weed seeds, despite a high number of taxa (n = 83) in the MIA, and the low overall density of samples, is unexpected. The same is true for the LRO where there is a drop in the density of samples, despite a comparable volume and number of taxa to the other Roman periods.

Biological and ecological traits

In the previous sections, we have demonstrated that pollen diversity is affected by the scale of cultivation, that is, the amount of land under cultivation (Figure 5). In this section, we analyse the weed floras to gain a better understanding of agrarian practices.

Life form. Three life forms were detected: annuals, plants that can act as both annuals and hemicryptophyte perennials, and hemicryptophyte perennials (perennials that propagate from stoloniferous or rhizomatous roots and benefit from shallow ploughing/disturbance (Bogaard et al., 1999; Jones et al., 2000)) (Figure 5a). True perennials (plants that take more than a year to grow from seed and regenerate from the same root stock) are not present in any period suggesting that even the ENEOL assemblages are from well-established fields rather than recently cleared vegetation (Bogaard, 2002; Rösch et al., 2002). It is also possible that newly established fields were dutifully weeded of perennials and annuals alike, such that the few ENEOL weed taxa, most of which are twining, reflect weeding and harvesting techniques. The proportional difference between annuals and hemicryptophyte perennials is similar during the prehistoric and LRO phases, averaging at 25%. This may be an indication of disturbance as well as hand weeding; although shallow cultivation associated with the scratch plough (symmetrical arc that cuts a shallow furrow without inverting the soil) in early prehistory would have encouraged hemicryptophyte perennials, an intensive approach to weeding would have removed visible roots. The difference between life-forms is smallest during the ERO and MRO; perennial roots split and scattered by the plough may not have been removed, enabling them to regrow and seed.

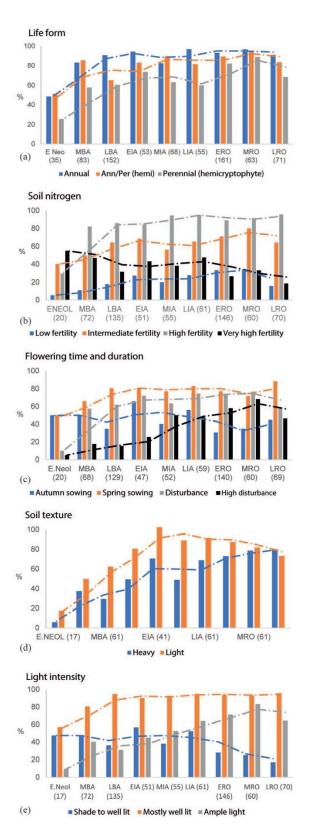


Figure 5. The ubiquity of measured characteristics by archaeological period, for five biological/ecological traits. 'Disturbance' includes plants that flower for no more than 3 months, those that flower for 4 or more months are in the 'high disturbance' category. Beaker and EBA samples are not representative (see Section 2.1.3). The ubiquity is calculated on the number of samples for which data on a particular trait are available. (a) Life form, (b) soil nitrogen, (c) flowering time and duration, (d) soil texture, and (e) light intensity.

Soil nitrogen: The ENEOL is the only period where weeds favouring very high fertility are the most ubiquitous, which concurs with the intensively managed (i.e. manured) fields deduced from cereal grain isotopic analyses from Lismore Fields, Derbyshire (Bogaard et al., 2013) (Figure 5b). Indicators of high fertility remain high in all phases but weeds tolerant of low fertility gradually increase into the MRO. Soil fertility seems not to have been maintained in all arable fields, though a more intensive approach to manuring may have been adopted during the LRO. These results corroborate isotopic analyses performed on charred cereal grains from Stanwick (Northamptonshire), that indicate a decline in soil fertility from the MBA to the Roman period (Lodwick et al., 2021). Another, not incompatible, explanation for the decline in the ratio of nitrophile to nitrophobe weeds during Late Prehistory could be an increase in autumn sowing (Stevens, 2011c). Experiments at Rothampsted (Hertfordshire) have shown that soil nitrogen levels are highest in the spring but tend to decrease rapidly if not maintained, suggesting that a gradual change in fertility indicators may not be due to soil exhaustion (Stevens, 2011c), although little is known of the cumulative effects of different forms of soil management (e.g. crop rotation, green manure, fallow periods, fresh/dried manure).

Flowering onset and duration: Autumn and spring sowing appear to have been practiced in all phases. However, there may be a bias towards spring sowing indicators in enriched soils, where spring weeds would be encouraged (Jones et al., 2000), an effect which could have been particularly strong in the ENEOL (Figure 5c). Another bias towards spring sowing indicators generated by the possible uneven representation of cereal processing products and by-products is possible. Small seeds, more consistently represented in crop-processing by-products (threshing and sieving waste), tend to be from nitrophile spring-germinating weeds (Bogaard et al., 2005; Jones, 1992). Caution is therefore needed in interpreting season of sowing, particularly as crop processing waste is better represented through time (see Section 4.3, Table 3). Taxa tolerant of disturbance, through tilling, weeding, ploughing and/or grazing animals, increase through time up to the LRO. This signal is reflected in the increased proportion of hemicryptophyte perennials (Figure 5a). High levels of disturbance are usually associated with small-scale, intensive cultivation rather than the large-scale, extensive regimes described for the Roman period (Allen and Lodwick, 2017). However, Figure 5a and c may be depicting the development of agricultural tools and changes to labour assigned to collecting weeds. Deeper ploughing from the LIA, enabled by iron ploughs and animal traction, would have favoured weeds tolerant of more intrusive disturbance. Although ubiquity scores are reduced in the LRO, the ratio between disturbance and high disturbance indicators remains comparable throughout the Roman period.

Soil texture: While light, free-draining soil indicators are present in all periods, plants of heavy soils are also ubiquitous, either pointing to the cultivation of clay-rich soils or the inadvertent change in soil texture through prolonged shallow ploughing which can increase clay concentrations (Jones, 1981: 111) (Figure 5d). The difference in the ratio of heavy to light soil indicators starts to decline in the LIA and is reversed in the LRO. This trend corroborates finds of stinking chamomile from the LIA, commonly used to indicate expansion of cultivation onto heavier soils (Allen and Lodwick, 2017; Lodwick et al., 2018: 809).

Light intensity: The increased proportion of weeds favouring ample sunlight coincides with an increasingly deforested landscape evident from fossil pollen (Figures 2a and 5e). These arable weeds

may indicate a trend towards larger arable fields that, by the nature of their size, were less shaded by surrounding vegetation. In contrast, the arable plots of the ENEOL are noticeably more enclosed.

Discussion

Using presence/absence plant macroremain data and amalgamating all contexts per period into single assemblages has enabled general temporal trends in land-use to be explored without biases incurred from context, settlement types, and habitation densities. Calculating density of crop assemblages by archaeological period provides an indication of changes in the scale of production, and therefore area of land under cultivation as well as land for infrastructure required to process, store and trade crops. Density trends through time compare well to the summed probability distribution of radiocarbon dates (SPD) for southern England, used as a proxy for fluctuations in population densities (Bevan et al., 2017, Figure 2a). The statistically significant positive correlation between the density of crop assemblages and pollen diversity demonstrates that cultivation contributed to land cover change in prehistory and the Roman period. Previous research has demonstrated that increases in population do not, on their own, explain changes in vegetation diversity; how land was used is a crucial factor (Woodbridge et al., 2021).

Early prehistory

The ENEOL dataset could indicate fixed farming regimes, including the intensive cultivation (high energy input per unit of land) of relatively small fields (Bogaard et al., 2013; Jones and Bogaard, 2017). Nevertheless, these interpretations are based on a restricted range of arable weeds. This is clearly demonstrated by the HCA which grouped ENEOL samples into cluster 1 where only four weed taxa are present. Pollen diversity and grassland vegetation increases after the end of the Mesolithic, suggesting that the onset of farming had a positive effect on landscape diversity, marking the onset of a honeymoon period between agricultural land use and biodiversity. A mosaic-type landscape of more open and closed vegetation will have promoted small-scale niches and ecological novelty (cf. Woodbridge et al., 2023).

The proposed abandonment of cereal cultivation in southern England during the M/LNEOL is supported by the dataset. The ubiquity and number of hazelnut remains clearly predominate, whilst the interpretation of cereals and pulses is complicated by the likelihood of intrusive materials (Pelling et al., 2015). Further work is required to explain the low occurrences of other edible wild plants relative to hazelnuts, large deposits of which are likely to be associated with particular behavioural activities. Woodland regeneration, presumably resulting from the neglect of arable plots, is associated with a decline in pollen and habitat diversity. Cattle are better adapted to forested landscapes than caprines, which may explain the adoption of a cattle-based mobile pastoralist lifestyle (Serjeantson, 2011; Worley et al., 2019).

Archaeobotanical results for the Beaker period are comparable to those for the preceding M/LNEOL, though the very low number of samples may not be fully representative. Even fewer samples are attributed to the EBA and yet the number and ubiquity of wheat and barley remains are greatly increased. The classification of EBA samples across clusters 1, 2 and 3 suggests a gradual increase in cereal cultivation, as does the surge in pollen diversity, probably associated with population increase through immigration, and cultural changes (Bradley, 2019; Gibson, 2020; Olalde et al., 2018).

The Middle Bronze Age 'agricultural revolution'

The resurgence in arable agriculture at around 1600 BC is clearly demonstrated by the results presented and aligns with decreases in woodland cover and increases in pollen diversity. Results from the analyses mark the MBA as the start in a progression towards larger fields of less intensively grown cereals (less weeding and manuring). Manuring may have occurred more naturally in rotational systems. As fields expanded and the removal of weeds became less efficient, disturbance-tolerant weeds become more evident in the records. The extent to which an enlarged weed flora contributed to the pollen records cannot be ascertained and greater floral diversity would have supported a greater range of insects. The Middle and Late BA see the greatest rise in pollen diversity and may represent the periods of greatest harmony between agrarian practices and biodiversity.

Late prehistory and the Roman period

The suggested Bronze Age population decline (Bevan et al., 2017) is not reflected by the datasets; there is no evidence for a reduction in the scale of production or habitat diversity. The rate of change between periods appears to slow down, perhaps indicating stability in the scale of production until the MIA. The flat shape of the radiocarbon calibration curve covering the Iron Age does make it difficult to assess the length and extent of the population downturn, making it possible that the MIA results reflect this period. The significant decrease in the density of MIA archaeobotanical assemblages is surprising and cannot be explained by lower sample or site numbers (Table 2). It either suggests a change in the depositional activities of crop processing waste (cereal processing and storage may have predominantly occurred in hillforts, but the dataset only includes one MIA hillfort (Danebury: site 22) as most Iron Age hillfort samples are only dated to the Iron Age generally), or a reduction in the production of cereals. Either way, the results suggest that the intensified cereal production indicated for the LIA (Van der Veen and O'Connor, 1998) was not the culmination of a progressive, linear trajectory. Pollen diversity increases slightly in the MIA before reducing continually from the LIA onwards; the gradual reforestation of abandoned settlements and arable fields during a population downturn could result in increased vegetation diversity during the successional stages to woodland.

The Late Iron Age sees a substantial increase in the scale of production and continued extensive cultivation practices (Figures 4 and 5). The probable cultivation of oat is also evident in our results, as is the surge in wild legumes, brome grass and ryegrass, all common taxa in cluster 6 of the HCA. The change in agrarian practices, whereby production became more defined by market forces, may be reflected in the dip in pollen diversity, which is then maintained into the ERO; results suggest that increased and standardised arable production removed some of the diversity present in the prehistoric mosaic of habitats.

Table 2 and Figure 2 show a significant increase in the density of Roman samples, suggesting another surge in arable production. The results corroborate evidence for the expansion of cultivation onto new soils and large-scale, extensive regimes described for the Roman period (Allen and Lodwick, 2017; Campbell, 2017). This appears to precipitate a decline in pollen diversity, suggestive of a reduction in the variation of landscape types, at least in the research area. Throughout prehistory pollen diversity increased with the expansion of agriculture, as forests were cleared for mixed agricultural regimes that encouraged biodiversity (cf. Birks et al., 2016). Results suggest that the tipping point between the expansion of open habitats and the growth of biodiversity may have been

reached by the Roman period. We suggest that the increased scale of arable cultivation during the LIA and Roman period marks a point in British farming history, when, for the first time, the expansion of cultivation had a negative effect on vegetation diversity. The slight increases in the ratio between annuals and perennials and the drop in low fertility indicators in the LRO could suggest a reversal to smaller scale, more intensive cultivation, although this is not matched by a contemporary recovery in levels of pollen diversity (Woodbridge et al., 2023). Broad ecological characteristics established during earlier farming regimes may have persisted for longer.

Conclusion

The use of large-scale archaeobotanical data, over both time and space, and a novel use of HCA, has revealed new details in the development of arable production during the first c. 4500 years of agriculture in southern England. Despite differences in behavioural, depositional and taphonomical trajectories between sites and periods, long-term trends in the use of edible plants and cultivation practices are evident. Previously described phenomena, such as fixed, 'garden'-type cultivation during the ENEOL, the dramatic change in subsistence strategies during the later Neolithic and the significant increase in arable production during the LIA and Roman period, are corroborated. Other results indicate that different strategies for collecting and interpreting archaeobotanical remains from some periods are needed: Beaker and EBA sites require more comprehensive sampling, whilst MIA evidence for cultivation may be concentrated in specific site types. Closer dating of archaeobotanical assemblages is needed to maximise information about temporal developments, particularly during the Iron Age. Additionally, understanding the possible Iron Age cultivation of oat requires new analytical procedures, such as geometric morphometrics, given the lack of diagnostic chaff (Bonhomme et al., 2017; Wallace et al., 2019).

Hierarchical cluster analysis separated the archaeobotanical samples not only by the frequency of cereal remains but also according to the association of different taxa. Neolithic and Beaker samples cluster into two groups: one with only hazelnuts and the other where cereals, but very few weeds, are also present. EBA samples straddle three clusters, showing similarities with cluster 1 but also a new, barley-focused assemblage (see also Figure 3a). Clusters 3 and 4 contain assemblages where glume wheat chaff is present in most samples and seem to mark the shift from emmer to spelt cultivation during the Bronze Age. They also demonstrate that crop processing waste is better represented through time. By contrast, clusters 2 and 6 are dominated by barley, but are differentiated by the presence of brome in cluster 2 and oats and ryegrass in cluster 6, potentially indicating a development in barley cultivation between the Iron Age and Roman periods.

Increased densities of archaeobotanical remains from the Bronze Age to the Roman period are, to some extent, shaped by depositional behaviours related to growing populations, but they also reflect an emphasis on cereal production for a market economy. The surge in the number and range of arable weeds through time reflect a gradual extensification in cultivation and an increase in floral diversity within arable fields. Comparisons with the Shannon diversity of fossil pollen has revealed that arable agriculture influenced changes in landscape types and indicate that early arable farming was not detrimental to biodiversity. Conversely, the onset of farming, increases in crop production and diverse forms of land use practices (varied cropping systems) resulted in elevated levels of biodiversity, reflected by trends in pollen diversity. This honeymoon period for farming and biodiversity was interrupted in the Roman period, when an expanding agricultural economy grew at the expense of biodiversity.

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