The development of late-Holocene farmed landscapes

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The Development of Late Holocene Farmed Landscapes: Analysis of Insect Assemblages using a Multi-period Dataset

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Abstract

Global agricultural intensification and expansion has led to the spread of a fairly cosmopolitan insect fauna associated with arable land and pasture. Studies of modern expansion and intensification of agriculture have shown profound effects in terms of declines in biodiversity, with implications for current nature conservation. However, modern entomological studies of farmland faunas do not consider if such effects occurred over a longer period of time or are merely a modern phenomenon. We examine the substantial British archaeoentomological dataset for the development of beetle (Coleoptera) faunas in a range of intensively farmed archaeological landscapes dating from the Late Neolithic through to the early Medieval period (*c*. 24,000 cal. BC – AD 900). The archaeological beetle fauna typically consisted of generalist species which still dominate modern farmland. Our analysis indicates that there is an essentially stable 'core group' of taxa that repeatedly occur regardless of period, location or the specific nature of the archaeological feature involved. On the basis of this result, we argue that the effects of the expansion of intensive farming on insect faunas seen in the modern world is a continuation of a longer pattern. We suggest that this is an example of human econiche replacement and ecosystem engineering. The approach taken here is applicable elsewhere in the world and we offer suggestions for future British and international research strategies.

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Introduction

We live in a world where agricultural production, and consequently farmed landscapes, are expanding rapidly at the expense of natural 'wild' landscapes resulting in largescale loss of global biodiversity (e.g. Tilman, 1999, Foley et al. 2005; Tscharntke et al., 2005; Deininger and Byerlee, 2011; Zabel et al., 2014). The effects of modern agricultural intensification and expansion seems to be particularly dramatic and are presenting major issues for both agricultural production itself and also for nature conservation (e.g. Touhasca 1993, Holland and Reynolds 2003, Hutton and Giller 2003, Purtauf et al. 2005,). This decline in insect faunas as a result of farming is often portrayed as an essentially modern phenomenon rapidly approaching an 'ecological cliff edge' (Tilman 1999, Foley et al. 2005, Deninninger and Byerlee 2011;). However, there is little apparent understanding of how these effects may have operated over a longer timescale than that normally considered by ecologists (Ellis et al., 2013).

Many regions of the world currently do not have sufficient archaeoentomological data to address this issue; however, in Britain several decades of archaeoentomological research is available. Early work in southern Britain by Osborne (1978) and Robinson (1978, 1981a) described a number of Iron Age and Roman agricultural faunas which were dominated by a range of dung beetles, predatory ground beetles, click beetles and chafers. Both Robinson and Osborne noted the obvious contrast between these later prehistoric and Roman beetle faunas associated with farmed landscapes as compared with the woodland beetle faunas that dominate sites from the preceding, largely pre-agrarian, Mesolithic and Neolithic periods. Osborne (1978) suggested that post-Iron Age faunas indicated the presence of open grasslands, dominated by grazing animals and arable fields, and described this as 'culture-steppe'. In a later series of review papers, Robinson (e.g. 1983, 2000, 2003, 2013a, 2013b) outlined temporal changes in the insect faunas from a number of sites in the upper and lower Thames Valley. In particular, he observed a pattern such that many faunas from the Early Iron Age (c. 800 BC) onwards increasingly include taxa indicative of progressive woodland clearance and the development of pastureland, grassland and arable fields. Kenward (2009) also has produced similar results for the north of Britain.

These early studies often do not explicitly explore a number of issues surrounding the ecology, nature, origins and development of 'farmland beetle faunas'. More recently, as a result of developer-funded archaeology, many other archaeological sites associated with ditched and/or farmed landscapes have become available for study. The archaeoentomological data from these sites cover a wider range of archaeological periods, regions and deposit types, and most have a strong chronological dating programme.

This paper presents an analysis of the current dataset of archaeological Coleoptera (beetle) faunas from farmed landscapes (both arable and pastoral) dating between the Late Neolithic to Medieval (*c*. 2,4000 cal. BC – 900 AD) period in Britain. This analysis was undertaken to explore the following research questions:

1) What is the archaeological fauna recovered from farmed landscape? How does this compare to modern insect faunas from this habitat?
2) What is the ecology of the taxa that belong to this fauna?
3) To what extent do these faunas vary across periods, locations and by type of archaeological context? What other factors may account for any variation?
4) When did this fauna first appear in the archaeological record? What are the potential origins of this fauna and how quickly does it come to dominate in this changing landscape? What are the implications of this?

This paper also outlines a number of potential research directions for the study of insect faunas from archaeological farmland which are applicable worldwide.

Archaeological background

The insect faunas considered come from 30 rural archaeological sites encompassing the British Neolithic (c. 4000–2200BC), Bronze Age (c. 2200-800 BC), Iron Age (800 BC – AD 47), Roman (AD 47 – 410) and early medieval periods (c. AD 900). Where sites are multiperiod, they have been divided into separate archaeological periods giving a total of 39 separate 'chronological entities'. The location, dating, site type, details of publication and the number of samples analysed from the individual sites are presented in Table 1 and Figure 1. Where available, radiocarbon determinations for the sites mentioned are given in Table 1 and have been standardised and calibrated using the OxCAL programme (Reimer et al., 2013 OxCAL V.4.3, 2017; Bronk Ramsey 2009). Other chronology is based on archaeological finds or stratigraphic association.

Over the last 40 years our understanding of the development of the rural archaeological landscape of southern and central Britain has greatly changed. 'Co-axial ditched field systems' developed from around 1600 BC in upland areas; such as, Dartmoor, Cumbria and the Pennines, and also in lower-lying areas such as Wessex, the North and South Downs, the Midlands and substantial areas of the Thames Valley (e.g. Fleming, 1988, 2007; Yates, 1999, 2007; Johnston, 2005; Chadwick, 2013; English, 2013). Earlier field systems have been primarily linked to stock rearing (Fleming, 1987; Yates, 1999; 2007; Fyfe et al., 2008, 2015). Ditched landscapes rapidly expanded in the Iron Age (*c.* 800 – 0 cal. BC) and the mid–Romano-British period (c. 100 – 200 cal. BC). These ditched field systems typically took the form of 'strip fields', 'brick fields' or 'ladder enclosures' and represent mixed farming landscapes incorporating arable fields, drove roads, waterholes and wells, the latter associated with livestock rearing (Riley, 1980; Taylor, 2007; Yates, 2007; Fyfe et al., 2008, 2015; Chadwick, 2013).

The development of such ditched agricultural landscapes at this period has often been attributed to an increase in agricultural production by a 'top down' autocratic authority responding to population rise and climatic downturn (i.e. Bradley, 1980; Fleming, 1987). However, alteration in landscape often is not synchronous with periods of dramatic climate change (Fyfe et al, 2015) and may relate to changing ideas of ownership and land tenure in response to social intensification and the production, exchange and consumption of elite materials (i.e. Brück, 2000; Johnston, 2005; Yates, 2007; Chadwick, 2013). The development of ditched farmlands appears to have coincided with a series of major changes to the British landscape (Huntley and Birks, 1983; Bell and Walker, 2005). Recent large-scale surveys of environmental archaeology by Dark (2006) and Fyfe and colleagues (2015) indicate that widespread clearance of woodland occurred in central and Southern England from around 1400–1200 BC, with a peak in clearance at around 500–200 BC. This loosely coincided with the onset of clay alluviation in most river systems, possibly in response to agricultural intensification (i.e. Macklin and Lewin, 2003; Macklin et al., 2005).

Data collection and Analysis

Sampling

Bulk samples of sediment were recovered from the sites listed in Table 1 during excavation from a range of archaeological features (mainly ditch, pit and well fills). Typically, the sample weight and volume ranged between 5–10 kg and 3–10 litres of sediment.

Basic identification and quantification

The bulk samples were prepared using the standard method of paraffin floatation outlined by Kenward and colleagues (1980). Waterlogged insect remains were sorted and identified under a low-power binocular microscope at magnifications between x15 and x45 by a number of different specialists (indicated in Table 1). Where achievable, the insect remains were identified to species level, often by direct comparison to specimens in reference collections. The nomenclature used in this paper follows Duff (2012) for the beetles and Stace (2010) for plants. The number of samples available per site varied from 1 to 22. The scores for the samples from each site have been amalgamated to generate a combined Minimum Number of Individuals (MNI) for each taxon. The full dataset consisted of 34,678 individuals, representing 932 taxa.

Analysis

The degree of variation in the faunas over time, location and archaeological feature was analysed in the following ways:

Ranked occurrence tables: These were constructed for each of the main archaeological periods and were based on the MNI for each taxon. This analysis allowed the comparison between the most common taxa in each archaeological period and against modern faunas.

Functional group analysis: Taxa have been allocated to functional groups where possible (see Hill 2015) and the relative proportions of these groupings were calculated. This analysis was undertaken to assess the extent to which the ecology of the faunas might differ between sites and periods.

This approach is a revision of both Robinson's (1981a, 1983) 'landscape' and Kenward and Hall's (1995) synanthropic (associated with human activity) groupings. The functional group codes are displayed in Table 2. Ecological information comes from the Bugs CEP database (Buckland and Buckland 2006), Koch (1989, 1992) and the authors' field experience.

The aquatic and waterside ecological groupings are calculated as a percentage of the overall MNI for each 'chronological entity'. The percentages of terrestrial ecological groupings are calculated once the aquatic taxa have been removed from the NMI. In order to examine the extent of synanthropy (association with human settlement) shown by the faunas, two other summary statistics have been calculated for the terrestrial fauna:

1) The proportion of 'house fauna' recovered (a suite of beetles that have a particular affinity for human habitation and settlement – see Hall and Kenward, 1990; Smith, 2012a)

2) The Synanthropic Value (SV) has been calculated for the terrestrial fauna. In this statistic 'strongly' synanthropic species (*S*) carry more value (or weight) than 'typical'

(T) or weakly 'facultative' (F) species (Hall & Kenward 1990, Kenward, 1997; Hill, 2015) using this formula: $SV = F + (2 \text{ x } T) + (3 \text{ x } S)$

Similarity coefficients and Statistical ordination: The degree of similarity of the faunas was assessed using Sørensen's similarity coefficient (Sørensen, 1948). This coefficient was chosen because it gives more weight to multiple occurrences and less weight to outliers, and its reciprocal is equivalent to Bray-Curtis distance (McCune and Grace, 2002; Borcard et al., 2011). The coefficient was calculated based on presence / absence of taxa.

A statistical ordination was carried out using non-metric multidimensional scaling (nMDS) within the 'R' statistical package (R Core Team, 2013). In terms of exploring community ecology data nMDS is generally considered to be an effective and passive ordination method. The ordination here is based on the proportions of the terrestrial functional group with aquatics and 'uncoded' taxa removed for all 39 'chronological entities'. We chose to restrict the nMDS analysis to the functional groups to determine if the faunas recovered are distinct or clustered according to their ecology and to prevent any 'superabundant' or rare species unduly influencing the ordination (e.g. Smith 1991, 2012a, 2013a, Hill 2015).

Results

Defining the beetle fauna of archaeological farmed landscapes

The ranked occurrence of taxa in each archaeological period is presented in Table 3. The ecology of the main species recovered is summarised in table Table 4. The relative proportions of functional groups recovered by archaeological site are presented in Figures 2 and 3 and by archaeological period in Figure 4.

The insect faunas from archaeological farmed landscapes appear to be dominated by a relatively narrow and repetitive range of terrestrial beetle taxa. Dung beetles, account for between 15%–40% of the terrestrial taxa, with 5%–10% belonging to the genus *Aphodius* (Figures 3 and 4). *Aphodius contaminatus, A. granarius, A. sphacelatus, A. prodromus, A. rufipes* and *A. fimetarius* are particularly common. *Geotrupes* spp., *Onthophagus fracticornis* and *O. joannae* also occur in some numbers, particularly in the Neolithic and Bronze Age material.

A large proportion of species (20%–40%) are associated with open and disturbed ground (Figure 4). Often this includes a range of predatory ground and rove beetles (e.g. *Bembidion spp., Calathus melanocephalus, C. fuscipes, Trechus quadristriatus, T. obtusus, Stenus spp., Amara spp. Xantholinus linearis, Rugilus spp., Philonthus spp, Harpalus rufipes* are particularly common). Phytophages associated with plants of disturbed ground are important (e.g. the weevil *Nedyus* (*Cidnorhinus) quadrimaculatus,* associated almost exclusively with stinging nettle (*Urtica dioica* L), and 'flea beetles' such as *Chaetocnema concinna*, *Phyllotreta* spp. and *Longitarsus* spp.). Other phytophage taxa, such as, *Mecinus pyraster*, *Mecinus (Gymnetron) pascuorum*, *Sitona* spp., *Rhinoncus* spp. *Gastrophysa* spp. and *Apion* spp., are associated with plants common in pasture. The 'click beetles' *Agrypnus murinus, Agriotes* spp*., Athous haemorrhoidalis* and the 'chafers'

Phyllopertha horticola, Melolontha melolontha and *Hoplia philanthus* also occur commonly in grassland. The larvae of click beetles and chafers can be pests of arable crops; but as Robinson (1983) pointed out, they are only a serious problem in newly ploughed fields from former grassland.

Beyond this core group of recurrent species, there is a long tail of individual taxa that occur in small numbers, often only at one or two sites. These beetles probably represent small populations of individuals associated with isolated patches of 'wild' or weedy ground which will vary with local conditions. In addition, taphonomic effects can bring insects into archaeological deposits from some distance (Kenward, 1975, 1978).

Water beetles usually account for between 10%–40% of the individual assemblages but achieved 60%–70% of all taxa at several locations (Figure 2). The aquatic fauna is dominated by three taxa (*Ochthebius minimus, Hydraena testacea* and small *Helophorus* spp.), which are indicative of slow-flowing, vegetated and often temporary waterbodies. *Colymbetes fuscus*, *Agabus bipustulatus*, various *Hydroporus* species and a range of Hydrophilidae are associated with this environment as well. Given that many of these faunas come from archaeological ditches or waterholes, the presence of significant numbers of water beetles is not surprising.

Several phytophage species also are associated with aquatic environments and watersides. *Tanysphyrus lemnae* is associated with duckweeds (*Lemna* spp.), *Notaris acridulus* with reed sweet grass (*Glyceria maxima* (Hartm.) Holmb.), *Plateumaris braccata* with water reed (*Phragmites australis* (Cav.) Trin. ex Streud.) and *Donacia crassipes* with water lilies (*Nymphaea alba* L. and *Nuphar* spp.). Surprisingly many of the ditches from this survey did not yield large numbers of these waterside phytophages (functional groups MA and MFC – Figure 3), suggesting they were periodically maintained and cleared of vegetation, perhaps indeed by grazing. The Late Roman sites of Balby Carr and East Carr in the northern Trent Valley do, however, contain high proportions of these taxa, but these ditch systems appear to have been affected by rising water tables which lead to the development of carr (Knight et al., 2004).

Comparing modern and past beetle faunas from farmland

There is extensive modern literature on several families of Coleoptera from farmland, since beetles have potential economic importance as pests or predators. These studies often concentrate on issues concerning resource partitioning, predator-prey relationships and response to different cultivation practices. They also tend to be restricted to a limited number of beetle families (Carabidae Staphylinidae, Scarabaeidae and some phytophage leaf beetles and weevils), rather than considering the fauna in its entirety (one exception is Robinson's (1983) survey of a variety of agricultural landscapes near Oxford undertaken for comparison with archaeological faunas). A ranked order list of taxa from a number of these modern studies is presented in Table 5. One limit to direct comparison between archaeological and modern coleopterous faunas is that they are sampled in very different ways (e.g. pitfall trapping vs. sediment sampling) and can represent very different time intervals (often one season for modern work as opposed to an unknown number of years or decades for the accumulation of archaeological deposits – Smith, 2017; Smith et al., 2010, 2014).

Despite these issues, there is a remarkable similarity between insect faunas from farmed landscapes regardless of whether they are modern or from archaeological sites (compare Tables 3 and 5). Both modern and ancient faunas include the same range of xerophilous predatory ground and rove beetles from arable land and a similar range of dung beetles and phytophage weevils in grasslands. This implies that the 'farmland fauna' has been essentially stable in Britain for two and a half millennia.

Variation in the faunas between sites by period

The similarity of the ranked occurrence of taxa (Table 3), the proportions of functional groups recovered when plotted chronologically (Figures 3 and 4) and the close clustering of the nMDS when displayed by period (Figure 5) suggest remarkable consistency for the majority of fauna associated with farmed landscapes over time.

However, two components of the 'farmland fauna', to an extent, change over time:

1) There is a relative decline in species associated with animal dung and grassland between the Late Iron Age and the Romano-British period (see Figures 3 and 4). During the Bronze and Early Iron Age half of sites (8 out of 16) have dung beetle values exceeding 20%. This declines to a third of all sites (6 out of 19 sites) in the Late Iron Age and Romano-British periods.

2) The values for 'house fauna', and the Synanthropic Values remain consistently low at these sites throughout all periods (see Figure 3 and Figure 4), with the exception of the Romano-British ditch deposits from Northfleet, Kent, Perry Oaks, Berkshire and St. Loyes, Oxfordshire, where synanthropes and grain pests are quite common.

Variation in the faunas between sites by deposit and site type

In order to explore whether deposit type was an important factor in shaping this data the nMDS ordination was replotted with deposit types labelled (see Figure 6). No obvious clustering or separation of deposits is seen, suggesting that the insect fauna is ubiquitous, regardless of the type of archaeological feature it comes from.

The only clear distinction identified by the nMDS ordination is the presence of a strong gradient for the wet-loving taxa (MA and MFC fauna) towards the lower left-hand side of the plot. This suggests that the greatest variation between faunas was largely determined by moisture. The two sites that most strongly indicate the influence of wet-loving taxa are Balby Carr and East Carr which were mentioned above.

It could be argued that this survey of faunas results in such similarity because it concentrates on ditched farmland sites and ignores other landscapes. As a result, it may overemphasise the dominance of this suite of beetles and, indeed, this type of farmland landscape which exists in Britain from the Late Bronze Age onwards. However, a number of archaeological insect faunas from other landscapes have been recovered for this period, for example, the woodlands and heathlands of the Humberhead levels (Buckland, 1979; Whitehouse, 2000, 2004), the swamps and carrs of the Somerset Levels (e.g. Girling, 1977, 1979, 1982, 1985) and the floodplain of the Trent river (Smith and Howard, 2004; Greenwood and Smith, 2005). Crucially, all of these sites have insect faunas distinctly different in character from the farmland faunas discussed here and that they come from a range of landscapes that would not favour agricultural production in the first place.

Another form of variation?

The construction of matrices based on similarity coefficients using only presence-absence of taxa between faunas (see Figure 7) was undertaken to understand any variations by period and site type. In addition, this explored whether any presence of 'metacommunity level' regional variations (*sensu* Gilpin and Hanski, 1991; Hanski, 1998; Leibold et al., 2004) could be established. These plots indicate that there is little similarity between faunas (most of the plot has light shading, which indicates little or no similarity). This seems contradictory compared to the results outlined above. However, the use of only presence-absence in the analysis is probably significant. The presence of the very long 'tail' of less abundant, 'rare' and local species at the sites probably has a greater impact on the ordination than frequently occurring taxa which are limited to a comparatively narrow range. This is a problem already identified for this kind of ordination when used on occupation-site faunas by Carrott and Kenward (2001) and overcome with considerable success by excluding such rare taxa (or 'outliers').

Once the sites are organised by statistical similarity rather than by chronology (the right-hand plot in Figure 7), there does appear to be a pattern. Most of the sites from the Midlands and the Lower Thames Valley plot towards the top half of the diagram, those from the Upper Thames Valley plot in the middle and lower right, and a small group of other Midland sites plots at the bottom right. This could indicate weak regional variations (*sensu* Leibold et al., 2004; Brooks et al., 2008) or the effects of local 'mass effects' such as field size, heterogeneity of the landscape and the presence or absence of wild areas (e.g. Brooks et al. 2008).

However, this pattern also could be caused by a less edifying effect. The faunas appear to group by which archaeoentomologist studied them (the specialists have been named on Figure 7). In this case the analysis may be picking up on quite minor differences in the way in which the various archaeoentomologists have identified insect fragments and/or how precisely these are recorded. For example, the Helodidae (Scirtidae) has been classified in a number of different ways by specialists. This ranges from the conservative 'Helodidae Gen. et sp. indet.', through '?*Cyphon* sp.' to the possibly overoptimistic '*Cyphon pubescens* (F.)'. It is worth noting that one advantage of basing the nMDA analysis on ecological groupings, rather than the individual taxa, is it helps to negate this exact problem (e.g. Kenward 1978, Kenward and Hall 1995).

Discussion

Stability and change in the 'farmland' beetle fauna

The results presented above clearly indicate that once agricultural landscapes developed, the majority of the insect fauna associated with them remained very stable, consistent and resilient over a considerable period of time reaching up to late medieval/pre-modern times.

The decline in the relative proportion of 'dung beetles' in the later Iron Age and the Roman periods merits further discussion. Robinson (2013a) also has suggested that there is a shift from *Onthophagus*-dominated faunas to *Aphodius*-dominated dung communities at the same time. Using specific proportions of dung beetles to estimate proportions of landcover can be problematic (Smith et al., 2010, 2014) but this decline in dung beetles probably indicates that grazing and pasture were less dominant in the landscape from *c.* 400 - 200 BC onwards. Some (Fyfe et al., 2008, 2013; Trondman et al., 2015) have argued that there is evidence in the British pollen records for a change from predominantly pastoral economy towards mixed and arable farming at the same time. Van der Veen and O'Connor (1998) also suggest that the British landscape becomes predominantly arable during the warming effect of the 'Roman climatic optimum'.

It could be argued that in terms of deposit types and depositional environments, we are comparing apples with oranges. The majority of the Bronze and Early Iron Age samples are from relatively shallow features such as ditches and 'waterholes'; whereas the Later Iron Age and Romano-British samples derive from deeper features, such as pits or wells. Wells and pits often are thought to act as 'pitfall' traps and collect insect faunas from a wider geographical area than shallower features (e.g. Hall et al. 1980; Kenward et al., 1986; Smith and Kenward, 2013). However, the nMDA analysis in Figure 6, where the sites are plotted together independently of feature type, suggests the relative depth of context is not actually a factor; therefore, a change in land use remains the most sensible explanation.

The increase in the proportions of synanthropic faunas at some Roman sites can be explained more easily. These deposits may have formed particularly close to settlement or, more likely, incorporated dumped settlement waste that contained numerous synanthropes and grain pests.

The ecology of the 'farmland' fauna recovered

This analysis has demonstrated that there is a very distinct 'farmland fauna' associated with archaeological agricultural landscapes. Many of the common species in this 'farmland fauna' such as the carabids and staphylinids, are fast moving, mobile ground-based predators which feed on small insects, snails and slugs and effectively exploit disturbed and temporary habitats. Modern ecological studies of these taxa describe them as being eurytopic and essentially opportunistic (e.g. Turin, 2000, Luff, 2002; Brooks et al., 2008; Betrand et al., 2016). Other species, such as the dung beetles and many of the phytophage taxa, also are adapted to exploit suitable temporary patches of habitat as they occur. Many of the species, especially the ground beetles, are to some degree xerophilous (Lindroth, 1974; Luff, 2007) and favour open environments with some disturbance. The species concerned, whether they are water beetles, ground beetles, phytophages or dung beetles, are all typically associated with the early stages of ecological successions (Brooks et al., 2008, Tonhasca, 1993, Turin, 2000). What is apparent from our analysis is that through continuous human agency (uninterrupted farming in this case) what essentially is a short-lived, opportunistic fauna has had its longevity extended by millennia due to the stable and continuous generation of this farmland environment.

Many of the beetle species encountered in farmland, both in the archaeological record and today, also appear to have high dispersal and breeding rates (the so called 'R' reproductive strategy) which enables them to rapidly distribute themselves across the landscape and quickly build up large populations. This R-strategy is seen as particularly important for species that take advantage of the early stages of successions in fragmented landscapes, where resources often are short-lived and separated by long distances (De Vries et al., 1996; Ribera et al., 2001; Bonsall and Hastings, 2004; Woodcock et al., 2010, 2014; Brooks et al., 2008; Betrand, 2016).

Possible origins of the 'farmland' in Britain

The nature and ecology of the Later Holocene 'farmland fauna' are quite distinct from earlier insect communities dating to the Early and Middle Holocene (c. 9500 – 4000 cal. BC) which are dominated by numerous species associated with long-lived *urwald* woodland (e.g. Smith and Whitehouse, 2005; Whitehouse and Smith, 2010). These woodland faunas are ecologically complex, have many trophic levels and contain a wide range of highly specialised species which probably follow the so-called 'K' reproductive strategy (low dispersal and breeding rates). Conversely, the 'farmland fauna' identified here is relatively simple with shallow trophic levels, is eurytopic-dominated, and follows a clear 'R' strategy. This replacement of a 'natural' fauna by a 'farmland' fauna, from the Neolithic onwards, seems to have been very rapid where it happened (i.e. there are no faunas that could be regarded as transitional) and this process appears to have occurred repeatedly in different regions of Britain at several points in time. The earliest occurrence of the 'farmland fauna' seems to be at the late Neolithic sites of Silbury Hill, Wessex (2550–2535 cal BC) and Etton, Cambridgeshire (3725–3210 cal. BC). Despite their relatively early date these sites already contain most aspects of the 'farmland fauna'. However, both sites are associated with landscapes that were cleared of forest very early (c. 2600 cal. BC) as compared to other parts of Britain, where clearance generally occurred from 1600 cal. BC onwards (Allen, 1997, 2000; Bell and Walker, 2005; Fyfe et al., 2015). Whether such early clearance of the Wessex Downs or the Cambridge Fen resulted from factors such as thin soils preventing reforestation, the development of a predominantly pastoral economy, or was related to cultural factors surrounding monument building and ritual use is not clear (Thomas, 1999, 2013; French et al., 2007, 2012; Wilkinson and Straker, 2008). However, these sites do demonstrate that the 'farmland fauna' was present in lowland Britain from the late Neolithic onwards and, presumably, had the potential to develop wherever woodland was cleared.

Most of the taxa which later become associated with archaeological farmland probably existed naturally within a range of small, localised ecological niches (niche in this instance being the place, function and ecological requirements of an individual insect) as part of the Early Holocene woodland habitat (habitat being the wide environment in which this insect can occur). Andersen (2000) and Buckland (2005) suggest that species typical of dry anthropogenic habitats, such as farmland or heathland, were originally steppe species which recolonised open landscapes at the end of last glaciation. As woodland returned during the Early Holocene, they became associated with temporary glades and open areas. These glades could have resulted from storm damage, forest fires, river bank erosion, beavers and/or actions of grazing animals (e.g. Coles and Orme, 1988; Vera, 2000; Coles, 2006). Large herbivores may have a particular significance in maintaining openings in the canopy (Vera 2000). There has been considerable argument recently over the physical extent of such woodland clearings in the Early and Mid-Holocene woodland (e.g. Vera, 2000; Mitchel, 2005). Additionally, a number of recent studies using estimates of landscape cover based on regional pollen proportions has indicated that open areas may have occurred more often than previously thought in

Britain during the Early and Mid-Holocene (Fyfe et al., 2013, 2015, Trondman et al., 2015, Woodbridge et al., 2014). Ecologically, any Coleoptera associated with these glades would have to be able to exploit these spatially and temporally limited open environments before woodland regeneration occurred. They would exhibit many of the same forms of ecological adaptation we have described above for the ‘farmland fauna’ itself. A substantial part of the beetle ‘farmland fauna’ has actually been recovered, albeit in small numbers, from a range of Early and Mid-Holocene woodland faunas (Buckland and Buckland, 2006).

It was only with large scale woodland clearance and the development of extensive farmed landscapes from the Middle Iron Age onwards that these small limited niches in woodland begin to coalesce into the larger anthropogenic habitat of open farmland and pasture. For the ‘farmland fauna’ beetles, it is their ability to exploit open, dry and disturbed landscapes that allows them to become dominant. This is a ‘ragbag’ of a fauna, which probably never existed together in nature prior to this point. They have not changed the niches they use in essence but have come together as a fauna to exploit a new habitat made through human agency. The ecological history and origins of the synanthropic fauna from archaeological settlement is also similar, with taxa that previously did not occur together in nature coexisting in the new habitat provided by human habitation (Kenward and Allison 1995).

It is possible; however, that some of the species associated with open farmland may have dispersed alongside Neolithic farming practices as they spread across Europe. This is probably the case for some field pests, such as the bruchid ‘pea weevils’ and some leaf beetles. A similar origin also has been suggested for most of the pests of stored grain (see Smith and Kenward 2011).

Conclusions and implications

Implications for modern agricultural expansion and the development of insect faunas and biodiversity

The archaeoentomological story described here – a decline in insect biodiversity, the growing dominance of eurytopic species, and a shallowing of trophic levels as agricultural landscapes developed – has clear echoes in the modern world. A number of studies have examined the effect of modern agricultural intensification on insect faunas (e.g. Firbank et al., 2008; Brooks et al., 2008; Bertrand et al., 2016). These suggest that the loss of wild areas, increased cultivation, development of monocultures, decline of fallow crops, and rapid crop rotation all reduce the number and diversity of beetles present in the modern landscape (Brooks et al., 2008, Fournier and Loreau, 1999; Pettit and Usher, 1998; Bertrand et al., 2016, Purtauf et al., 2005, Woodcock et al., 2014). Woodcock and colleagues (2008, 2010) have indicated that overgrazing, loss of surrounding ‘wild’ areas, decline of traditional grazing techniques and hay cutting times all can have a devastating effect on beetle diversity in grasslands. Crucially, this leads to a decline in plant diversity, a resulting drop in phytophage species richness and then a drop in the quantity and diversity of predatory beetles (Brooks et al., 2008; Dombos 2001; Lagerlöf et al., 2002; Purtauf et al., 2005). Recently, Hutton and Giller (2003) have shown that intensification and ‘improvement’ of pasture can lead to a rapid decline in the number and variety of dung beetles.

One of the major implications of the archaeoentomological study presented here is that the modern decline in insect biodiversity and the shallowing of trophic levels resulting from modern intensive agriculture is not a new phenomenon; it is part of a continuum of effects with deep temporal roots that stretch back to at least 3,500 years in Britain. The main differences between the past and present are merely a matter of the scale and perhaps the speed of the effect. Presumably this process may span a much longer period in other parts of the world, such as the Fertile Crescent of the Near East or the 'rice bowl' of China, where there is longer agrarian history leading back to at least 9,500 BC (Ellis et al., 2013).

Is this an example of Human niche creation?

'Niche creation' is a relatively new concept in evolutionary biology; it suggests that organisms have the capacity to modify their environments so they can influence their own and other species evolution, ecology and distribution (Jones et al., 1994, 1997; Laland et al., 1996, 1999, 2000, 2001; Kendal et al. 2011). Humans are undoubtedly efficient 'niche creators', for example the shaping of Pleistocene (Sterelny, 2011; Boivin et al., 2016), agricultural (Rowley-Conwy and Layton, 2011; Gerbault et al., 2011; Smith, DB 2011), and urban landscapes (Boivin et al., 2016). Intentional human 'niche creation', or in this case 'habitat creation', can pronouncedly affect the distribution of other animals and plants. For the insects concerned, there were obvious winners and losers. The creation of farmed landscapes is profoundly destructive for '*urwaldrelikt'* specialists such as *Prosomis mandibularis,* but beneficial for open ground generalists, such as *Pterostichus melanarius*.

Implications for further study

As is the case in every large survey of data, many issues raised here are in need of further investigation. One obvious flaw is the shortage of insect faunas related to farmland from the Neolithic, Saxon and Medieval periods in Britain. The lack of suitable Neolithic sites, in part, relates to an absence of evidence for large-scale agriculture or grazing outside a limited number of locations (Moffett et al., 1989; Thomas, 1999, 2013; Richmond, 1999; Bell and Walker, 2005; Stevens and Fuller, 2012). The shortage of rural archaeoentomological faunas from the Saxon and Medieval periods is partially explained by present archaeological research priorities, which tend only to prioritise the excavation of prehistoric field systems. Gathering more archaeoentomological data associated with agriculture from historic periods should be a national priority in Britain. The present dataset is also largely biased towards the south and midlands of England and again identifies the urgent need for archaeoentomological sampling of farmland environments to occur in other regions of Britain as a national priority.

We also, with some reason, have assumed that the adaptation of Coleoptera from the '*urwald'* woodland biome to culture-steppe was rapid, but this can only be tested on sites which span the transition itself.

The rarity of comparable archaeological studies beyond Britain has restricted this analysis to a limited geographical area. It is likely that preservation of insect faunas will be rare in many areas but similar work should be undertaken in other parts of the world where possible. It would be fascinating to try to establish how insect faunas are affected by the development and spread of farming from the 8th millennium BC onwards in the Near East and continental Europe. Examining how the insect faunas of North America developed in response to farming, whether first nation maize-based agriculture, or European introduced agrarian practices, also would be fascinating.

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Figures and Tables

Figure 1: Location map for the archaeological sites in this survey

Figure 2. The relative proportions of the broader aquatic, wetland and terrestrial functional groups

Figure 3: The relative proportions of the terrestrial functional groups for the archaeological sites

Figure 4. The relative proportions of functional groups (dung, foul material, open and woodland) and synanthropic groups by archaeological period

Figure 5: nMDS analysis for of the taxa from each individual 'chronological entity' by archaeological period (see key for details of each archaeological period)

Figure 6: nMDS analysis for of the taxa from each individual 'chronological entity' by archaeological feature (see key for details of each archaeological feature)

Figure 7: Dissimilarity matrices. On a simple score of presence/ absence, sites' faunas are largely dissimilar to each other (i.e. large tail of less common species heavily influential). However, those sites that are similar cluster to a large extent according to the person carrying out the analysis.

Table 1. Location, dating, feature type and reference for the archaeological sites included in this survey

Table 2. Functional groups used in this analysis (based on Hill 2015)

Table 3: Rank order and % MNI for the 29 most frequently recovered Coleoptera by period for the sites in this survey. Note that some taxa (*Chaetocnema concinna*, *Aphodius sphacelatus*, *A. fimetarius*, *Megasternum 'boletophagum',* here rendered as *'concinnum'*, *Hydrobius fuscipes*, *Anotylus sculpturatus* and *Carpelimus bilineatus*) have been split since these sites were recorded

Table 4. Summary table of the insects thought to be particularly important in archaeological farms by ecological groupings and then by taxonomic order

Table 5. Beetles typically recorded in modern ecological surveys from arable, grassland and pasture (taxa ordered by frequency)

Table 1. Location, dating, feature type and reference for the archaeological sites included in this survey

Site	Number of samples	Type of feature	Radiocarbon or *estimated* calendar dates	Period	Reference
Etton, Cambridgeshire	11	base of enclosure ditch of Causeway Camp	3725-3670 to 3310-3210 cal. BC	Early Neolithic	Robinson, 1998
Silbury Hill,Wiltshire	7	old ground surface and peat stack below mound	2550 – 2535 cal BC	Mid to late Neolithic	Robinson, 1997
Wilsford Shaft, Wiltshire	1	base of shaft / well below Bronze Age barrow	1470– 1290 cal BC	Early Bronze Age	Osborne, 1969
Terminal 5 Heathrow, Greater London (Bronze Age),	22	ditches and waterholes	ca. 1650 – 900 BC	Mid to late Bronze Age	Tetlow, 2010
Perry Oaks (terminal 5) Heathrow, Greater London (Bronze Age)	6	Bronze Age pits and waterholes	1450 – 1210 cal BC and 1380 – 1040 Cal BC	Bronze Age	Robinson, 2006
Hillfarence, Somerset	5	field ditch and pit	1450-1130 cal BC	Mid to late Bronze Age	Smith and Tetlow, 2007
Horton Quarry 71808 Berkshire	2	waterholes	*ca. 1200 – 700 BC*	Mid to late Bronze Age	Smith, 2014a
Kingsmead Horton Quarry (BA), Berkshire	13	waterholes	*ca. 1200 – 700 BC*	Mid to late Bronze Age	Smith, 2009
Imperial Sports Ground), Greater London (Bronze Age)	3	waterhole	1210-910 cal. BC	Mid to late Bronze Age	Smith, 2015a
Anslow's Cottages, Burghfield, Berkshire	5	fluvial succession	Single date of 91-431 cal. BC	Mid to late Bronze Age	Robinson, 1992
Terminal 5 Heathrow (Late Bronze Age - Iron Age)	26	ditches and waterholes	One sample 1690-1500 cal BC. 25 dated 1500-50 Cal BC	Iron Age	Tetlow, 2010
Whitemoor Haye, Staffordshire	1	series of recuts of terminal end of ring ditch	ca. 500 – 200 BC	Mid Iron Age	Smith, 2002
Kingsmead Horton Quarry, Berkshire (Late Bronze Age – Iron Age)	5	ditches and waterholes	ca. 1000 – 0 BC	Late Bronze Age - Iron Age	Smith, 2009
Enderby, Leicestershire	8	waterholes and pit features	*200 – 00 BC?* Estimated dates from archaeology	Late Iron Age	Hill, 2016
Olympic Park, Greater London.	10	ditches	750-260 cal. BC	Mid to late Iron Age	Smith, 2012b
Tattershall Thorpe, Linconshire	15	Iron Age enclosure ditch	*ca. 770-200 BC* based on archaeology	Mid to late Iron Age	Chowne et al., 1986
Fisherwick, Staffordshire	3	enclosure ditch	380 ca.BC – 70 cal AD	Late Iron Age	Osborne, 1979
Minges Ditches, Oxfordshire	12	enclosure ditches	390-40 cal. BC	Late Iron Age	Robinson, 1993
Farmoor, Oxfordshire (Iron Age)	6	Iron Age sumps and gullies	382 cal. BC-76 cal. AD	Late Iron Age	Robinson, 1979
Little Paxton, Cambridgeshire	10	waterholes, brickfield ditches	*80 – 250 AD* dated by pottery	Late First century to mid third century	Smith, 2011a
Lockington, Derbyshire, waterholes	2	waterholes	Estimated period dates from archaeology	'Roman'	Smith, 2012c

Site	Number of samples	Type of feature	Radiocarbon or *estimated* calendar dates	Period	Reference
Imperial Sports Ground, Greater London (Roman)	2	wells	240-510 cal. AD	Roman	Smith, 2015a
Brickets Wood Bund, Hertfordshire	3	waterholes	*Estimated period dates from archaeology*	'Roman'	Smith, 2013b
Perry Oaks (Terminal 5) Heathrow, Greater London (Roman)	4	waterholes	*c100-250 AD and c 200 -300 AD* based on archaeology	Roman	Robinson, 2006
Kingsmead Horton Quarry (Roman)	5	waterholes or pits		Roman	Smith, 2009
Terminal 5 Heathrow (Roman)	5	ditches and waterholes	One date of 170cal BC to 220 AD. Other features estimated from archaeology	Early to late Roman	Tetlow, 2010
St. Loyes College, Exeter	4	military wells (dumped stabling material)	*60 – 100 AD* estimated dates from archaeology	Early Roman	Smith, 2011c
Northfleet Roman Villa, Kent	8	well and cistern	*80 – 120 AD* estimated dates from archaeology	Early Roman	Smith, 2011b
Balby Carr, Catesby Buisness Park, South Yorkshire	4	brickfield Roman ditch system	*100 – 130 AD* estimated dates from archaeology	Early Roman	Smith and Tetlow 1997
Grange Park, Well. Courteenhall, Northamptonshire	1	Roman timber lined well	*50 -450 AD* estimated dates from pottery in fill deposit	2nd century	Smith, 2006
Daventry Rail Frieght Terminal (Covert Farm)	3	waterhole	c. 150 – 225 AD based on pottery assemblage	Mid 2nd to mid third century	Smith, 2015b
Cambridge north West 13, Cambridgeshire	4	three wells	100 BC – 250 AD? Estimated dates from archaeology	Late Iron Age to mid Roman?	Smith, 2014b
Farmoor, Oxfordshire (Roman)	7	Roman wells	ca. 150 – 350 AD	Mid to late Roman (dated by pottery)	Robinson, 1979
Appleford, Oxfordshire	4	Roman wells and waterholes	200 – 400 AD Estimated dates from archaeology and pottery	Mid to late Roman	Robinson, 1981b
East Carr, Mattersey, Nottinghamshire	10	sub rectangular Roman field systems	361 cal. BC to 252 cal. AD but *200 – 300 AD* Estimated dates from archaeology	Mid late Roman	Smith 1997
Cambridge North West 12, Cambridgeshire	4	three timber lined wells	200 – 450 AD estimated dates from archaeology and pottery	2nd, 3rd and 4th century	Smith, 2014b
Salford Priors, Warwickshire	4	ditch associated with villa	300 – 450 AD estimated dates from archaeology	3rd or 4th century	Smith and Langham, 2000
Barton Court Farm, Oxfordshire	6	ditches and other features	c. 350 – 500 AD estimated dates from archaeology	Late Roman to early Saxon	Robinson et al., 1984
Terminal 5 Heathrow (Medieval)	1	ditch	1200 – 1600 AD estimated from archaeology	Medieval	Tetlow, 2010

Radiocarbon dates calibrated using OXCAL and are to 95% probability (2 sigma). Where several dates exist from different features at the site these have been combined to give an extended age range.

Table 2. Functional groups used in this analysis (based on Hill 2015)

	Functional Group	Code	Definition
True Aquatics	Aquatic	**A**	Beetles which spend the majority of their adult life in water. *Not included in terrestrial sum.*
Wetland & Waterside taxa	Riparian	**R**	Hygrophilous taxa, littoral, usually in the bare waterlogged soils besides water. Also associated with emergent vegetation. *Included in terrestrial sum*.
	Marsh and Aquatic Plants	**MA**	Chrysomelidae and Curculionidae species which feed exclusively on marsh and aquatic plants. *Included in terrestrial sum*.
	Marsh, Fen and Carr	**MFC**	Hygrophilous, and often eurytopic taxa, found across a variety of semi-aquatic environments, such as marsh, swamp, fen, and floodplains. *Included in terrestrial sum*.
Generalists	Foul Material	**FM**	Species living on various types of foul (decaying) organic material. Sometimes, but in most cases not exclusively synanthropic. Foul material includes dung, but these taxa are not dung specialists. *Included in terrestrial sum*.
Open landscapes	Dung	**DUNG**	Taxa strongly associated with the faeces of herbivores. *Included in terrestrial sum*.
	Open and Disturbed	**OD**	Taxa found in open and vegetated, or disturbed and relatively bare conditions, wet or dry (but not strictly 'wetlands'). *Included in terrestrial sum*.
Woodland associates	Edge of, or Light, Woodland	**ELW**	Species which show strong preference to forest margins, forest-steppe, copses/felled trees within woodlands, open or pasture woods, pine heaths, hedgerows, single or sun-exposed trees (e.g. certain Elateridae), or whose larval and adult stage alternate between open spaces and forest (e.g. certain Cerambycidae). *Included in terrestrial sum*.
	Woodlands and Trees	**WT**	Includes the Coleoptera which feed on wood in varying stages of decay, leaves, fruit, and bark and live wood, fungal feeders and predators strictly associated with woodland. Except where a taxon can be defined within **ELW**. *Included in terrestrial sum*.
Uncoded or Ubiquitous		**u**	Taxa to which none of the other FGs can be applied owing to either lack of taxonomic resolution or ubiquity. *Not included in terrestrial sum.*

Table 3: Rank order and % MNI for the 29 most frequently recovered Coleoptera by period for the sites in this survey. Note that some taxa (*Chaetocnema concinna*, *Aphodius sphacelatus*, *A. fimetarius*, *Megasternum 'boletophagum'*, here rendered as *'concinnum'*, *Hydrobius fuscipes*, *Anotylus sculpturatus* and *Carpelimus bilineatus*) have been split since these sites were recorded. The second column lists the rank occurrence scores for the entire archaeological dataset, regardless of archaeological period, followed by the percentage of individuals as part of the whole fauna for each taxon.

Rank order	Total for all periods	%MNI	Neolithic faunas	%MNI	Bronze age	%MNI	Iron age	%MNI	Romano-British	%MNI	Post Roman	%MNI
	39 sites in total		2 sites in period		8 sites in period		9 sites in period		18 sites in period		2 sites in period	
1	*Aphodius* spp.	7.4	*Megasternum concinnum* (Marsh.)	10.1	*Aphodius* spp.	8.9	*Aphodius* spp.	10.6	*Aphodius* spp.	5.1	*Helophorus brevipalpis* Bedel	8.4
2	*Ochthebius* spp.	3.2	*Ochthebius* spp.	7.1	*Geotrupes* spp.	6.7	*Helophorus brevipalpis* Bedel	4.7	*Ochthebius* spp.	3.7	*Platystethus* spp.	8.2
3	*Helophorus* spp.	2.7	*Aphodius* spp.	6.5	*Onthophagus fracticornis* (Preyssl.)	4.7	*Cercyon* spp.	4.0	*Helophorus* spp.	3.7	*Aphodius* spp.	4.5
4	*Apion* spp.	2.4	*Stenus* spp.	4.3	*Calathus melanocephalus* (L.)	4.7	*Ochthebius minimus* (F.)	2.8	*Latridius minutus* (group)	2.6	*Meligethes* spp.	3.6
5	*Megasternum concinnum* (Marsh.)	2.2	*Apion* spp.	4.3	*Calathus fuscipes* (Goeze)	2.8	*Apion* spp.	2.8	*Apion* spp.	2.4	*Apion* spp.	3.2
6	*Cercyon* spp.	2.1	*Helophorus* spp.	3.5	*Onthophagus joannae* (Goljan)	2.6	*Phyllopertha horticola* (L.)	2.6	*Megasternum concinnum* (Marsh.)	1.9	*Latridius minutus* (group)	2.8
7	*Latridius minutus* (group)	1.9	*Xantholinus linearis* (Ol.)/*longiventris* Heer	2.0	*Ochthebius* spp.	1.9	*Ochthebius* spp.	2.5	*Anotylus sculpturatus* (Grav.)	1.8	Ceutorhynchinae indet.	2.6
8	*Helophorus brevipalpis* Bedel	1.8	*Calathus melanocephalus* (L.)	1.9	Aleocharinae indet.	1.8	*Platystethus cornutus* (Grav.)	2.0	Aleocharinae indet.	1.8	*Longitarsus* spp.	2.4
9	*Anotylus sculpturatus* Grav.	1.4	*Ochthebius minimus* (F.)	1.9	*Helophorus* spp.	1.7	*Megasternum concinnum* (Marsh.)	1.9	*Cercyon* spp.	1.7	*Helophorus grandis* (Ill.)	2.4
10	*Geotrupes* spp.	1.4	Aleocharinae indet.	1.7	*Phyllotreta* spp.	1.5	*Helophorus* spp.	1.8	*Philonthus* spp.	1.5	*Phyllotreta vittula* (Redt).	2.2
11	*Ochthebius minimus* (F.)	1.4	*Aphodius granarius* (L.)	1.4	*Hydraena testacea* Curt.	1.3	*Latridius minutus* (group)	1.8	*Platystethus cornutus* (Grav.)	1.3	*Oxyomus sylvestris* (Scop.)	1.9
12	Aleocharinae indet.	1.4	*Calathus fuscipes* (Goeze)	1.2	*Anobium punctatum* (Geer)	1.3	*Chaetocnema concinna* (Marsh.)	1.6	*Platystethus arenarius* (Fourcr.)	1.3	*Phyllotreta nigripes* (F.)	1.9
13	*Platystethus cornutus* (Grav.)	1.3	*Tachyporus* spp.	1.2	*Megasternum concinnum* (Marsh.)	1.2	*Aphodius contaminatus* (Hbst.)	1.4	*Lesteva longelytrata* (Goeze)	1.3	*Megasternum* (Marsh.)	1.5
14	*Philonthus* spp.	1.2	*Phyllopertha horticola* (L.)	1.2	*Apion* spp.	1.2	*Anotylus sculpturatus* (Grav.)	1.4	*Amara* spp.	1.2	Corticariinae indet.	1.5
15	*Calathus melanocephalus* (L.)	1.2	*Barynotus obscurus* (F.)	1.2	*Phyllopertha horticola* (L.)	1.2	*Tanysphyrus lemnae* (Payk.)	1.3	*Anobium punctatum* (Geer)	1.2	*Cercyon* spp.	1.3

Rank order	Total for all periods	%MNI	Neolithic faunas	%MNI	Bronze age	%MNI	Iron age	%MNI	Romano-British	%MNI	Post Roman	
16	*Chaetocnema concinna* (Marsh.)	1.2	*Rugilus* spp.	1.2	*Ptinus fur* (L.)	1.0	*Carpelimus bilineatus* (Steph).	1.1	*Oxyomus sylvestris* (Scop.)	1.1	*Chaetocnema concinna* (Marsh.)	1.3
17	*Phyllopertha horticola* (L.)	1.1	*Philonthus* spp.	1.2	*Anotylus sculpturatus* (Grav.)	1.0	*Trechus obtusus* Er./*quadristriatus* (Schr.)	1.1	*Phyllotreta* spp.	1.1	*Hydrobius fuscipes* (L.)	1.3
18	*Stenus* spp.	1.1	*Agrypnus murinus* (L.)	1.2	*Stenus* spp.	1.0	*Hydrobius fuscipes* (L.)	1.0	*Anotylus rugosus* (F.)	1.1	*Tachyporus* spp.	1.3
19	*Anobium punctatum* (Geer)	1	*Longitarsus* spp.	1.2	*Chaetocnema concinna* (Marsh.)	0.9	*Aphodius sphacelatus* (Panz.)	1.0	*Aphodius contaminatus* (Hbst.)	1.1	Cryptophagidae indet.	1.3
20	*Calathus fuscipes* (Goeze)	1	*Mecinus pyraster* (Hbst.)	1.2	*Aphodius granarius* (L.)	0.9	*Bembidion* spp.	1.0	*Stenus* spp.	1.1	*Tachinus* spp.	1.1
21	*Aphodius contaminatus* (Hbst.)	0.9	*Geotrupes* spp.	1.1	*Longitarsus* spp.	0.8	*Philonthus* spp.	0.9	*Chaetocnema concinna* (Marsham)	1.0	*Geotrupes* spp.	0.9
22	*Phyllotreta* spp.	0.9	*Gabrius* spp.	1.0	*Limnebius* spp.	0.8	*A. prodromus* Brahm/*sphacelatus* (Panzer)	0.9	*Xantholinus* spp.	1.0	*Anotylus rugosus* (F.)	0.9
23	*Longitarsus* spp.	0.9	*Hydrothassa glabra* (Hbst.)	1.0	*Xantholinus linearis* (Ol.)/*longiventris* Heer	0.8	*Anobium punctatum* (Geer)	0.9	*Anotylus nitidulus* (Grav.)	0.9	*Trechus obtusus* Er./*quadristriatus* (Schr.)	0.9
24	*Oxyomus sylvestris* (Scop.)	0.9	*Tachinus* spp.	0.9	*Mecinus pyraster* (Hbst.)	0.8	*Anotylus rugosus* (F.)	0.8	Corticariinae indet.	0.9	*Atomaria* spp.	0.9
25	*Anotylus rugosus* (F.)	0.9	*Quedius* spp.	0.9	*Philonthus* spp.	0.8	*Longitarsus* spp.	0.7	*Brachypterus urticae* (F.)	0.9	*Aphodius rufipes* (Geer)	0.9
26	*Amara* spp.	0.8	*Anotylus rugosus* (F.)	0.8	*Oxyomus sylvestris* (Scop.)	0.8	*Aphodius fimetarius* (L.)	0.7	*Longitarsus* spp.	0.9	*Aspidapion aeneum* (F.)	0.9
27	*Lesteva longoelytrata* (Goeze)	0.8	*Atomaria* spp.	0.8	*Brachypterus urticae* (F.)	0.7	Scirtidae indet.	0.7	*Bembidion* spp.	0.9	*Phyllotreta atra* (F.)	0.9
28	*Platystethus arenarius* (Fourcr.)	0.8	*Onthophagus joannae* (Goljan)	0.8	*Chaetocnema* spp.	0.7	*Aphodius prodromus* (Brahm)	0.7	*Ochthebius minimus* (Group)	0.9	*Ochthebius* spp.	0.7
29	*Onthophagus fracticornis* (Preyssl.)	0.8	*Phyllobius* spp.	0.8	*Latridius minutus* (group)	0.7	*Limnebius* spp.	0.6	*Ptinus fur* (L.)	0.8	*Philonthus* spp.	0.7

Table 4 Summary table of the insects thought to be particularly important in archaeological farms by ecological groupings and then by taxonomic order based on Table 3 and the authors' previous experience.

PART OF FAUNA	SPECIES	ECOLOGICAL NOTES
TYPICAL GROUND BEETLES	*Notiophilus biguttatus, Nebria brevicollis, Loricera pilicornis, Clivina fossor, Trechus quadristriatus, T. obtusus, Pterostichus madidus, P. melanarius, Anchomenus (Agonum) dorsalis, Amara spp., Harpalus affinis, Harpalus rufipes, Calathus fuscipes, Calathus melanocephalus, Syntomus truncatellus. Dromius linearis*	A range of 'generalist' predators favoured by open and often disturbed ground. This may be ploughed fields or grassland. *C. fossor* seems to be typical of soft damp ground, *S. truncatellus* and *D. linearis* of open sandy ground.
TYPICAL OF GRASSLANDS	Range of Elateridae 'click beetles' Typically various *Agriotes* spp. and *Athous haemorrhoidalis.* The 'Garden Chafer' *Phyllopertha horticola*, the 'cockchafer' *Melolontha melolontha* and 'the Welsh Chafer' *Hoplia philanthus*.	These species tend to be typical of old grassland, where they feed on the roots of grasses.
PLANT FEEDERS	***<u>Grassland and meadow</u>*** *Gastrophysa polygoni, G. viridula, Apion frumentarium, Perapion violaceum, P. hydrolapathi* (on docks) *Sitona lepidus, S. suturalis, S. humeralis, Hypera* spp. (Clover) *Coelositona cambricus, S. waterhousei* (birds foot trefoil) *Oxystoma craccae, O. cerdo, O. pomonae* (Vetches) *Cleonis piger (thistles)* ***<u>Disturbed ground and wasteland</u>*** *Aspidapion aeneum* (common mallow) *Rhinoncus pericarpius, Rhinoncus castor* (Docks) *Ceutorhynchus contractus* (poppies and mignonettes) *Ceutorhynchus erysimi* (Shepard's purse) *Brachypterus urticae, Parethelcus (Ceutorhychus) pollinarius, Nedyus quadrimaculatus* (stinging nettle) *Mecinus pyraster, M. (Gymnetron) labile, M. (Gymnetron) pascuorum* (lanceolate plantain)	There is substantial overlap between the species which occur in grassland and meadow and those in disturbed ground. All these species feed on plants typical of grassland. Often they are carried into settlement in cut hay (Kenward and Hall, 1997).
NEAR TO DAMP AREAS AND MUDDY GROUND	*Lesteva longoelytrata, Carpelimus 'bilineatus', Anotylus nitidulus, Platystethus cornutus*	These species are typical of open, wet and disturbed ground both in agricultural land and within settlements. They may often be associated with areas of trampled or poached ground around waterholes and channels, but this may be overly simplistic.
DUNG BEETLES	*Sphaeridium scarabaeoides, S. lunatum, Cercyon impressus, Cercyon haemorrhoidalis Cercyon melanocephalus, Cercyon unipunctatus, Platystethus arenarius Geotrupes spp., Onthophagus spp., Aphodius fossor, Aphodius rufipes, Aphodius luridus, A. contaminatus, A. sphacelatus, A. prodromus, A. porcus, A. fimetarius, A. ater, A. granarius* etc.	This is a selection of the most common of a wide range of species associated with herbivore dung. Several other species are recovered, some of which from the Bronze and Iron Ages are rare at the present day (Robinson, 2013b). Several are also thought to be capable of breeding in wet waste materials around human settlement (Kenward *et al*., 2004). These dung associates can be very numerous in some sites where they can account for up to 40% – 60% of the terrestrial fauna, suggesting nearby grazing or pasture.
TREES	Various woodborers - *Anobium punctatum, Grynobius planus, Lyctus linearis, Phloeotribus rhododactylus, Hylesinus (Leperisinus) varius, Hylesinus toranio (oleiperda),* (ash). Phytophages - *Andrion (Sitona) regensteinense* (broom and gorse), *Rhynchites* spp. s. lat. (rosaceous shrubs such as blackthorn, hawthorn and bramble), *Rhynchaenus* spp. (leaf miners), *Curculio* spp. (nut weevils)	Most archaeological sites from agricultural ditches and rural landscapes contain very few of these taxa.

Table 5. Beetles typically recorded in modern ecological surveys from arable, grassland and pasture (taxa ordered by frequency).

Habitat type	Reference	Sampling method	Families	Species in order of occurrence
Arable land				
Arable lands in Scotland	Blake et al. , 2003	Pitfall trapping	Carabidae	*Nebria brevicollis, Loricera pilicornis, Pterostichus strenuus, Amara familiaris, Anchomenus dorsalis, Synuchus* spp. *Amara apricaria*
Middle of open crop fields in Southern England	Fournier and Loreau, 1999	Pitfall trapping	Carabidae	*Pterostichus melanarius* and *Trechus obtusus* favoured, *Bembidion obtusus, Notiophilus biguttatus, Nebria brevicollis Badister sodalis* also present
Mixed arable land on floodplain of river Trent	Greenwood *et al.*, 1991	Pitfall trapping	Carabidae and Staphylinidae	*N. brevicollis, Pterostichus madidus, Anchomenus dorsalis, Amara familiaris, Bembidion obtusum, Drusilla caniculata.*
Ploughed land in Sussex, England	Holland and Reynolds, 2003	Pitfall trapping	Carabidae	*Nebria brevicollis, Anotylus* spp., *Harpalus rufipes, Pterostichus madidus, Harpalus affinus, Trechus quadristriatus, P. melanarius, Calathus fuscipes, Amara* spp., *Bembidion obtusum, Xantholinus* spp, *Notiophilus biguttatus* and *Poecilus cupreus.*
Ploughed fields in northern Germany	Kroos and Schaefer, 1998	Pitfall trapping	Staphylinidae	*Tachyporus hypnorum, Anotylus inustus, Lesteva longoelytrata, Philonthus fuscipennis, Ocypus nitens, Omalium caesum, Philonthus rotundicollis* and *Coprophilus striatulus*
Arable land, Binsley Lane and South Hinksey, Oxford	Robinson, 1983	Pitfalls and sweep-netting	Whole fauna	**Pitfall trapping**_*Harpalus rufipes, Tachinus rufipes, Pterostichus melanarius, Amara similata,* Aleocharinae gen. & spp. indet., *Anchomenus dorsalis, Ceutorhynchus typhae, Enicmus transversus, Tachyporus solutus.* **Sweep-netting**_*Ceutorhynchus floralis, Phyllotreta* spp., *Meligethes* spp.
Grassland, meadow and pasture				
Large number of undisturbed grassland sites across UK	Eyre et al., 2003	Pitfall trapping	Carabidae	Dominated by *Abax parallelepipedus, Pterostichus niger and Platynus assimilis;* dry grassland also with *Calathus fuscipes, Amara aenea, Harpalus rufipes.* Damper grassland with *Bembidion obtusum, Harpalus affinus, Dromius melanocephalus.*
Series of coastal grasslands	Luff, 1989	Pitfall traping	Carabidae	*Badister bipustulatus, Amara aenea, A. communis. A. tibialis, Syntomus foveatus*
Mesotrophic Grasslands in Scotland	Blake et al., 2003	Pitfall trapping	Carabidae	*Notiophilus biguttatus, Bembidion lampros, Anchomenus dorsalis, B. guttula, B. lampros, B. aeneum*
Grassland on floodplain of River Trent	Greenwood et al., 1991	Pitfall trapping	Carabidae and Staphylinidae	*Nebria brevicollis, Bembidion aeneum, B. guttula, Philonthus cognatus Aleochara bipustula.*
Mesotrophic meadowland Sussex	Woodcock et al., 2008	Suction collection	Chrysomelidae and Curculionidae	*Longitarsus pratensis, L. luridus, Sitona lepidus, S. lineatus, L. melanocephalus, Trichosirocalus troglodytes, Protapion fulvipes,Sphaeroderma rubidum, Ischnopterapion loti, Protapion assimile.*

Habitat type	Reference	Sampling method	Families	Species in order of occurrence
Calcareous and five mesotrophic grassland sites in southern England	Woodcock et al., 2010	Suction collection	Chrysomelidae and Curculionidae	**Calcareous grassland** *Longitarsus pratensis, Sitona lineatus, L. luridus, Trachyphloeus alternans, L. parvulus, Catapion pubesens, S. hispudulus, L. atricillus, Protapion dichroum, C. seniculus.* **Mesotrophic grassland** *L. pratensis, P. trifolii, P. fulvipes, L. melanocephalus, Sitona lepidus, S. lineatus, P. assimile, L. atricillus, S. hispidulus, P. apricans*
Hay meadow, Pixey mead, Oxford	Robinson, 1983	Pitfalling and sweep netting	Whole fauna	**Pit fall trapping** *Pterostichus versicolor, Peocilus cupreus, Amara communis, Oedostethus quadripustulatus, Pterostichus melanarius, Longitarus luridus, Bembidion gilvipes, Clivina fossor, Harpalus rufipes, Agriotes obscurus.* **Sweep netting** *Protapion trifolii, Cantharis nigra, Cantharis rufa.*
Grazed Pasture, Port Meadow, Oxford	Robinson , 1983	Pitfalls and sweep netting	Whole fauna	**Pitfall trapping** *Philonthus cognatus, Loricera pilicornis, Bembidion guttula, Tachinus signatus, Aleocharinae gen and spp, indet. Notaris acridulus, Helophorus brevipalpis, Bembidion properans, B. lunulatum, Philonthus laminatus, Aphodius fossor*
Grazed pasture in Southern Ireland	Hutton and Giller, 2003	Baited pitfall traps	Scarabaeidae, Hyrophilidae and Histeridae 'dung beetles'	*Aphodius prodromus, A. sphacelatus, A. ater, A. rufipes, A. depressus, Sphaeridium lunatum, S.scarabaeoides* and *Margarinotus ventralis* accounted for 95% of variation

Figure 1: Location of the archaeological sites used in this survey

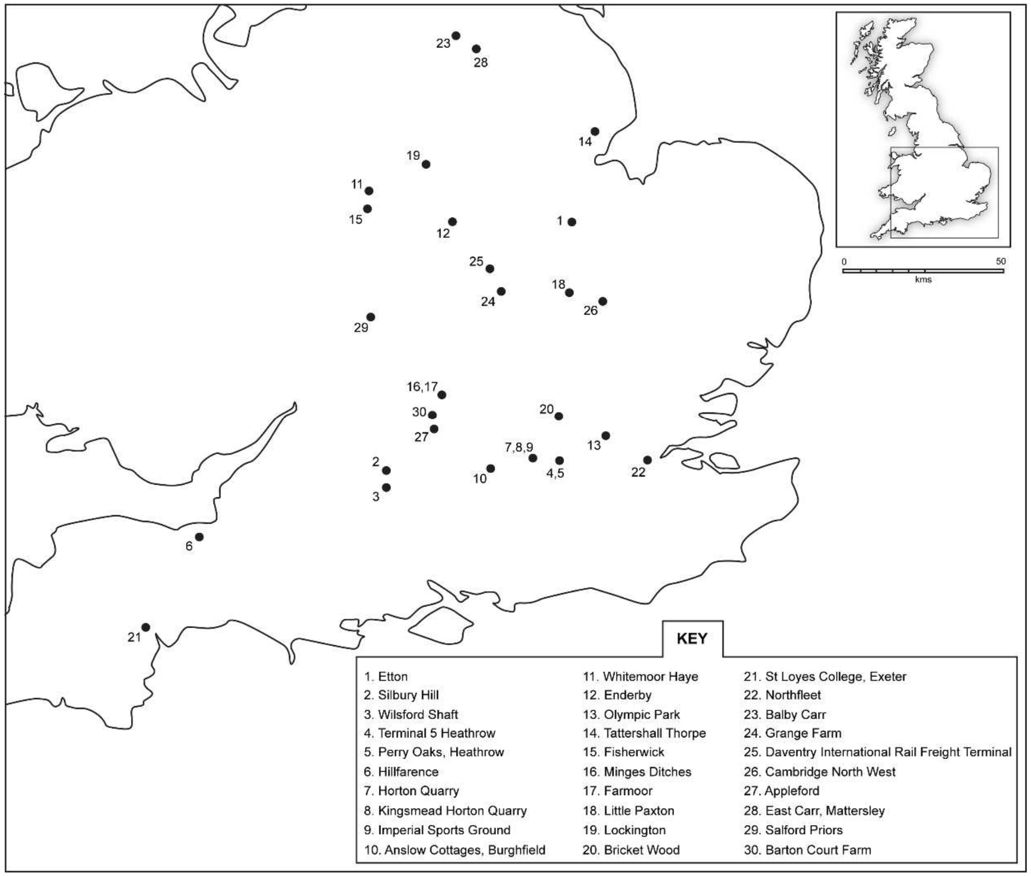


Figure 2: The relative proportions of the broader aquatic, wetland and terrestrial functional group for each site in chronological order (N – Neolithic, BA – Bronze Age, IA – Iron age, RB – Romano British, S – Saxon, M – Medieval).

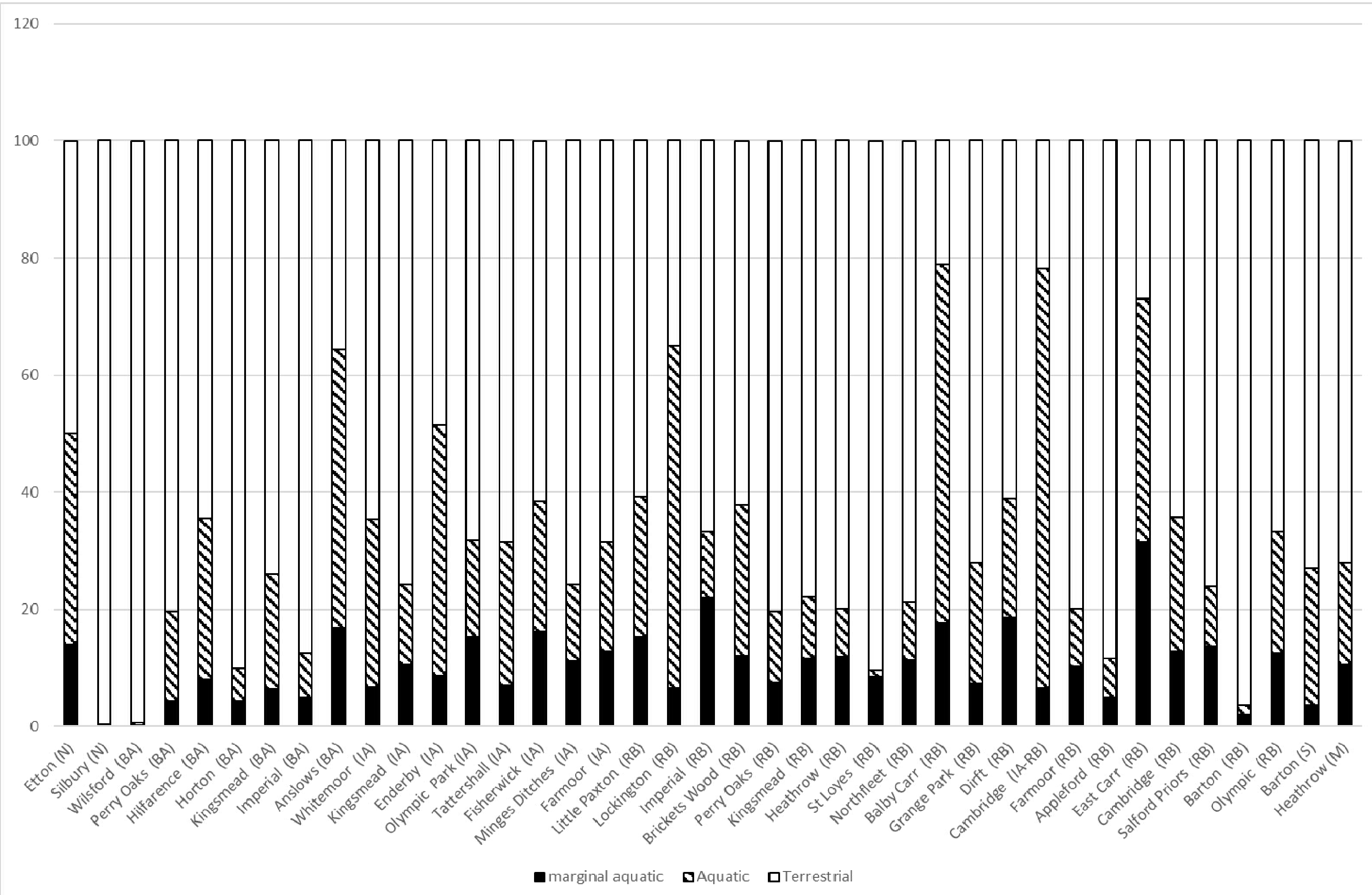


Figure 3: The relative proportions of the terrestrial functional groups by site in chrological order (N – Neolithic, BA – Bronze Age, IA – Iron age, RB – Romano British, S – Saxon, M – Medieval).

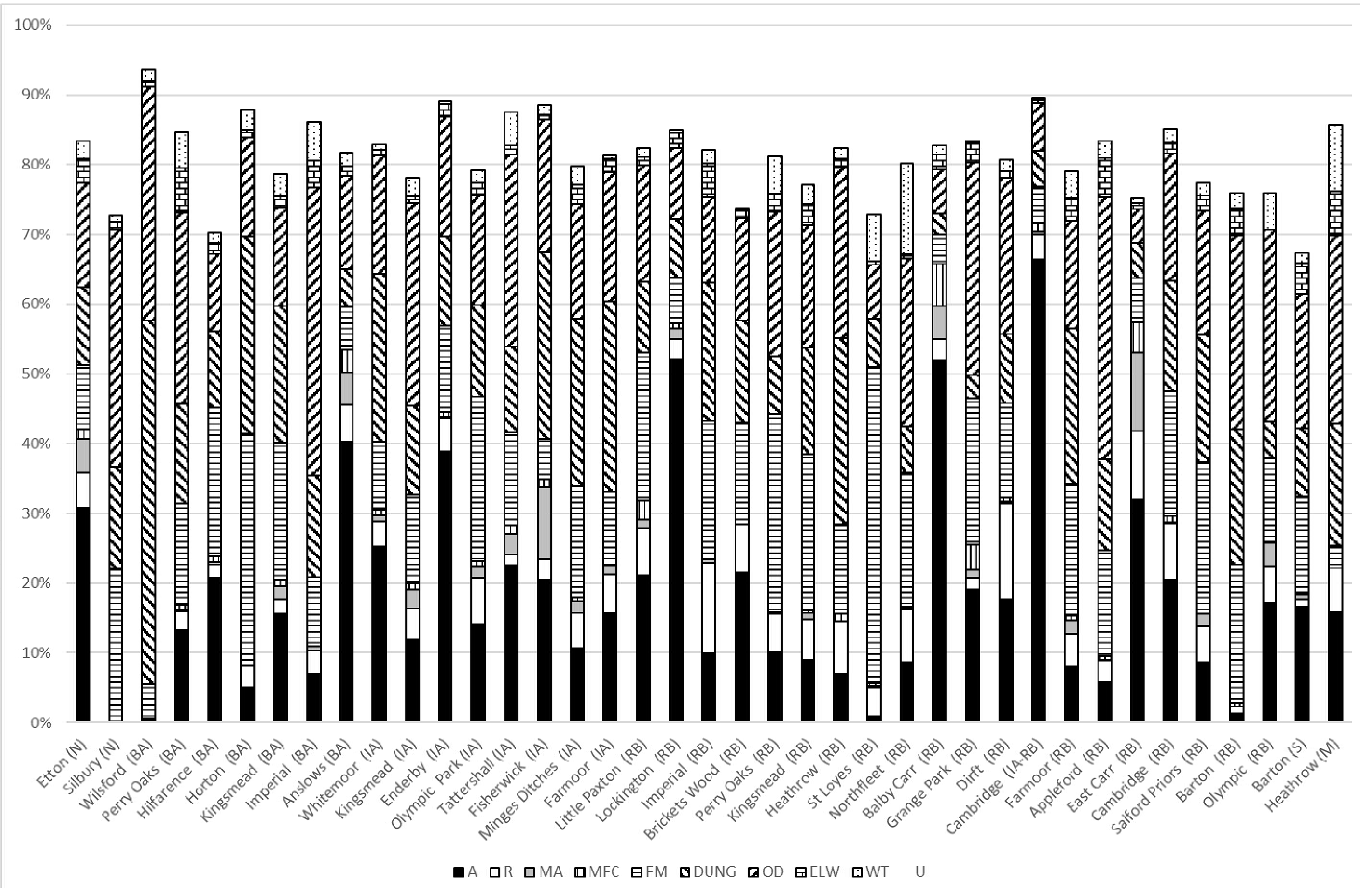


Figure 4: The relative proportions of functional groups (dung, foul material, open and woodland) and synthropic groups by archaeological period using box and whisker plots to indicate the range and mean for each functional group. Outliers have the same numbers as are given for the sites in Figure 1. The number of sites in each archaeological period is indicated below the middle row of the diagrammes.

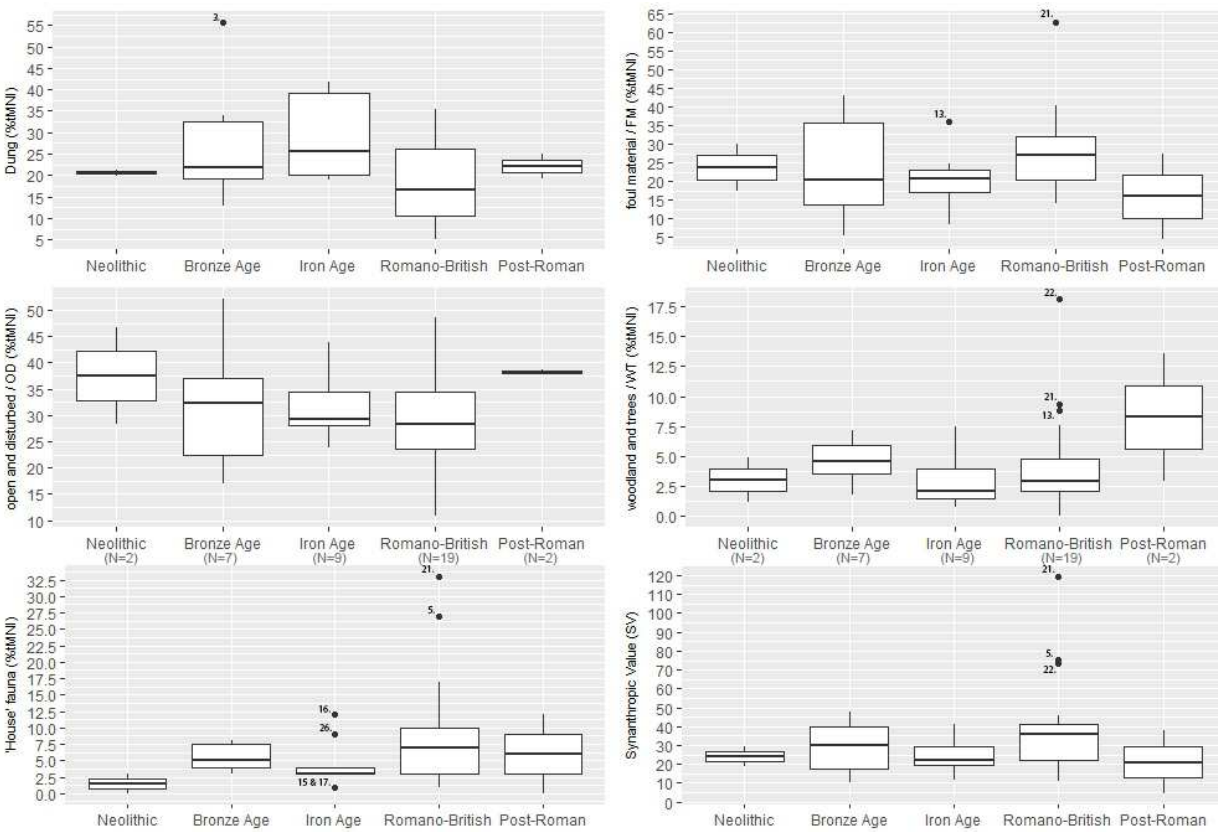


Figure 5: nMDS analysis for of the taxa from each individual ‘chronological entity’ by archaeological period (see key for details of each archaeological period)

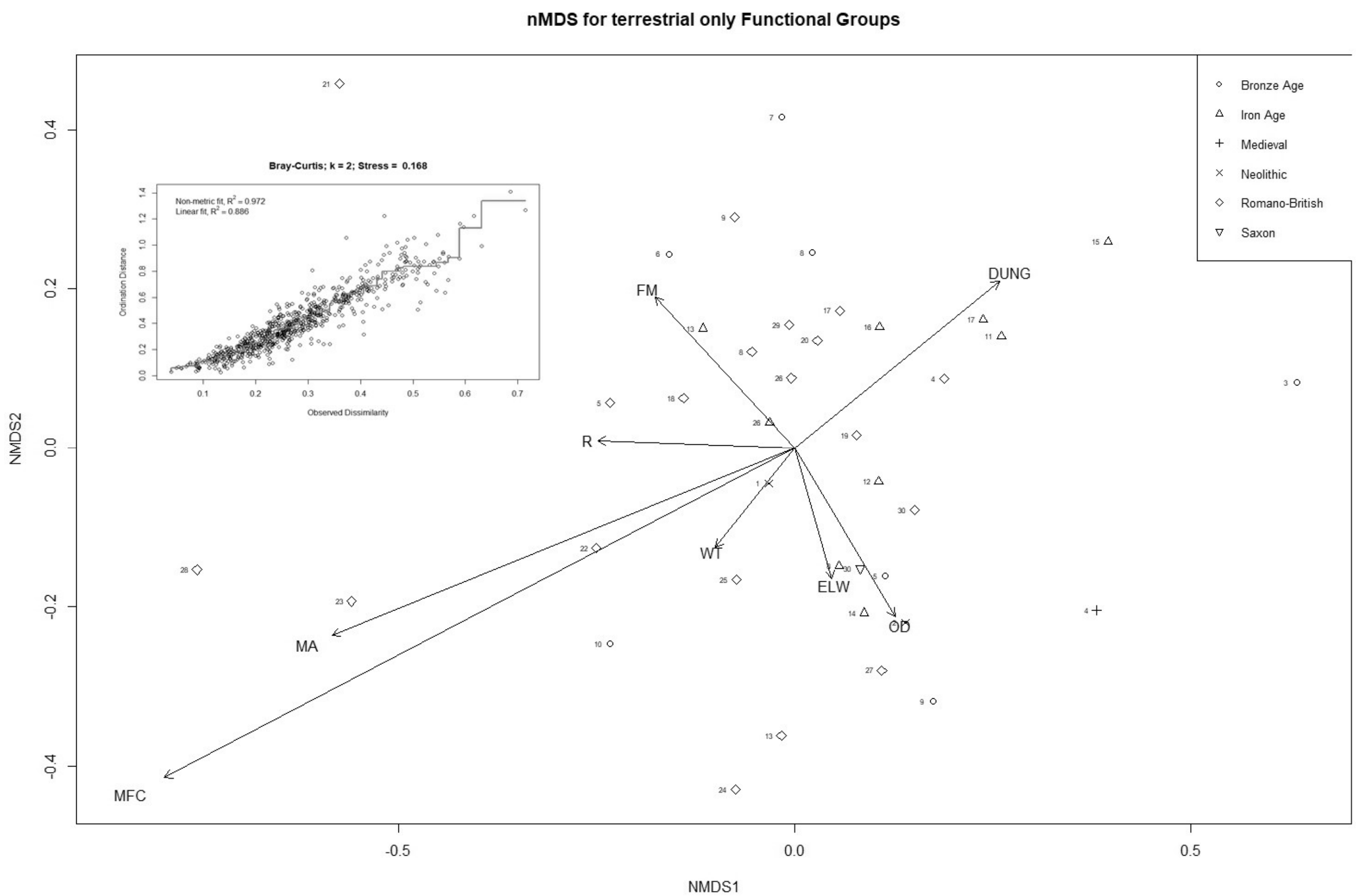


Figure 6: nMDS analysis for of the taxa from each individual 'chronological entity' by archaeological feature (see key for details of each archaeological feature)

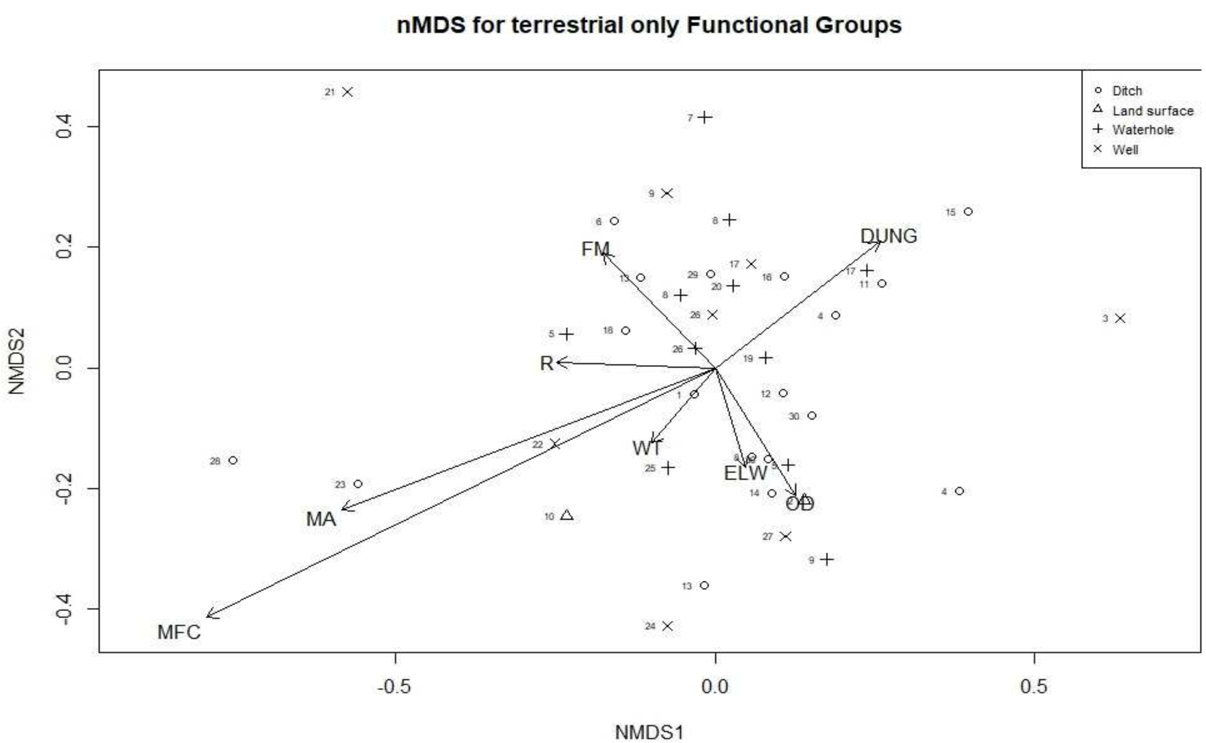
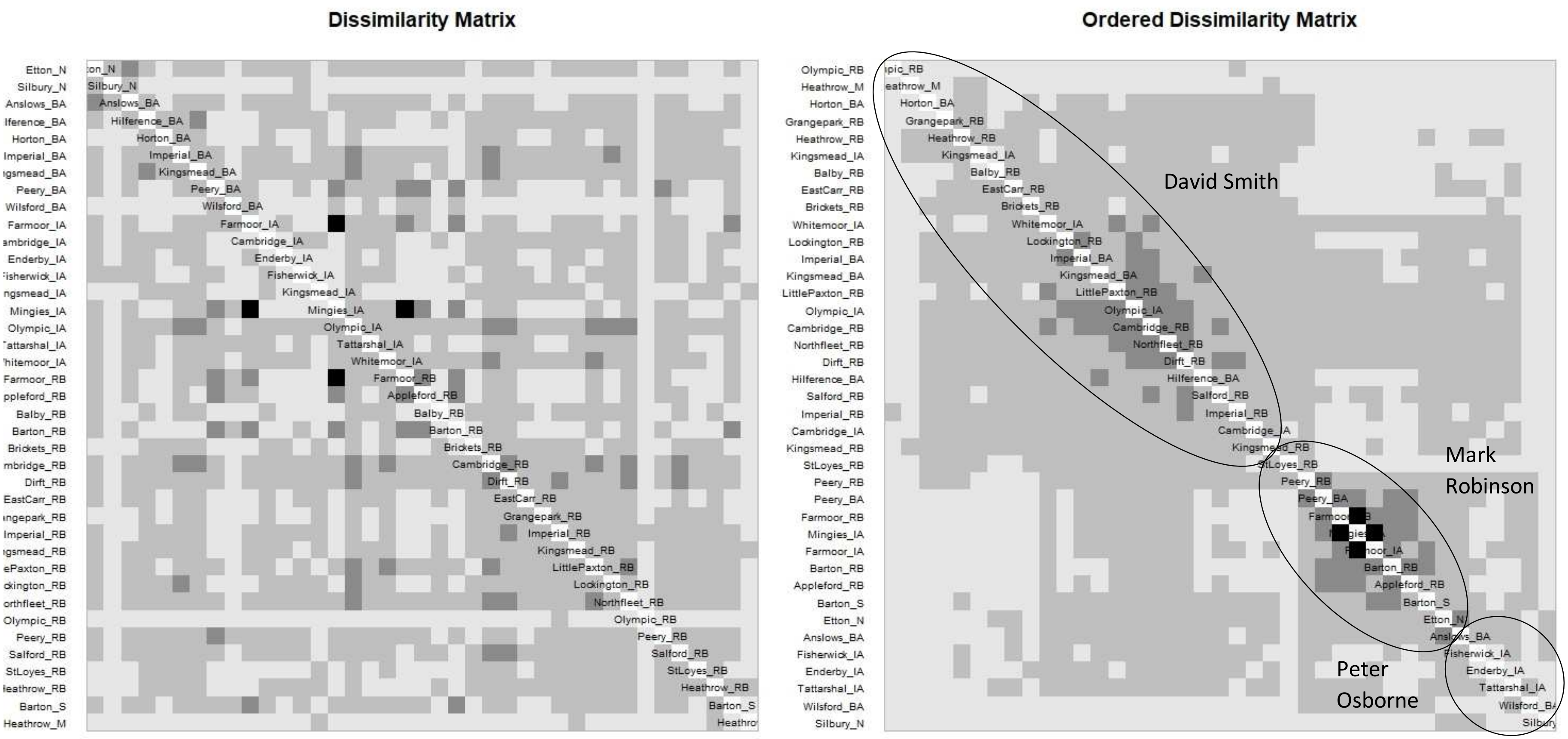


Figure 7: Dissimilarity matrices for the insect faunas from the sites examined based on simple score of presence/absence. The left-hand diagram presents the sites ordered alphabetically by period. The right-hand diagram re-orders the sites by the degree to which their archaeoentomological faunas are similar, regardless of period; assemblages with similar faunas plot closer together. Results are presented as a heat map of the similarity matrix with blocks indicating the highest degree of similarity.



Figures and Tables

Figure 1: Location map for the archaeological sites in this survey

Figure 2. The relative proportions of the broader aquatic, wetland and terrestrial functional groups

Figure 3: The relative proportions of the terrestrial functional groups for the archaeological sites

Figure 4. The relative proportions of functional groups (dung, foul material, open and woodland) and synanthropic groups by archaeological period

Figure 5: nMDS analysis for of the taxa from each individual 'chronological entity' by archaeological period (see key for details of each archaeological period)

Figure 6: nMDS analysis for of the taxa from each individual 'chronological entity' by archaeological feature (see key for details of each archaeological feature)

Figure 7: Dissimilarity matrices. On a simple score of presence/ absence, sites' faunas are largely dissimilar to each other (i.e. large tail of less common species heavily influential). However, those sites that are similar cluster to a large extent according to the person carrying out the analysis.

Table 1. Location, dating, feature type and reference for the archaeological sites included in this survey

Table 2. Functional groups used in this analysis (based on Hill 2015)

Table 3: Rank order and % MNI for the 29 most frequently recovered Coleoptera by period for the sites in this survey. Note that some taxa (*Chaetocnema concinna*, *Aphodius sphacelatus*, *A. fimetarius*, *Megasternum 'boletophagum',* here rendered as *'concinnum'*, *Hydrobius fuscipes*, *Anotylus sculpturatus* and *Carpelimus bilineatus*) have been split since these sites were recorded

Table 4. Summary table of the insects thought to be particularly important in archaeological farms by ecological groupings and then by taxonomic order

Table 5. Beetles typically recorded in modern ecological surveys from arable, grassland and pasture (taxa ordered by frequency)

Table 1. Location, dating, feature type and reference for the archaeological sites included in this survey

Site	Number of samples	Type of feature	Radiocarbon or *estimated* calendar dates	Period	Reference
Etton, Cambridgeshire	11	base of enclosure ditch of Causeway Camp	3725-3670 to 3310-3210 cal. BC	Early Neolithic	Robinson, 1998
Silbury Hill,Wiltshire	7	old ground surface and peat stack below mound	2550 – 2535 cal BC	Mid to late Neolithic	Robinson, 1997
Wilsford Shaft, Wiltshire	1	base of shaft / well below Bronze Age barrow	1470– 1290 cal BC	Early Bronze Age	Osborne, 1969
Terminal 5 Heathrow, Greater London (Bronze Age),	22	ditches and waterholes	ca. 1650 – 900 BC	Mid to late Bronze Age	Tetlow, 2010
Perry Oaks (terminal 5) Heathrow, Greater London (Bronze Age)	6	Bronze Age pits and waterholes	1450 – 1210 cal BC and 1380 – 1040 Cal BC	Bronze Age	Robinson, 2006
Hillfarence, Somerset	5	field ditch and pit	1450-1130 cal BC	Mid to late Bronze Age	Smith and Tetlow, 2007
Horton Quarry 71808 Berkshire	2	waterholes	*ca. 1200 – 700 BC*	Mid to late Bronze Age	Smith, 2014a
Kingsmead Horton Quarry (BA), Berkshire	13	waterholes	*ca. 1200 – 700 BC*	Mid to late Bronze Age	Smith, 2009
Imperial Sports Ground), Greater London (Bronze Age)	3	waterhole	1210-910 cal. BC	Mid to late Bronze Age	Smith, 2015a
Anslow's Cottages, Burghfield, Berkshire	5	fluvial succession	Single date of 91-431 cal. BC	Mid to late Bronze Age	Robinson, 1992
Terminal 5 Heathrow (Late Bronze Age - Iron Age)	26	ditches and waterholes	One sample 1690-1500 cal BC. 25 dated 1500-50 Cal BC	Iron Age	Tetlow, 2010
Whitemoor Haye, Staffordshire	1	series of recuts of terminal end of ring ditch	ca. 500 – 200 BC	Mid Iron Age	Smith, 2002
Kingsmead Horton Quarry, Berkshire (Late Bronze Age – Iron Age)	5	ditches and waterholes	ca. 1000 – 0 BC	Late Bronze Age - Iron Age	Smith, 2009
Enderby, Leicestershire	8	waterholes and pit features	*200 – 00 BC?* Estimated dates from archaeology	Late Iron Age	Hill, 2016
Olympic Park, Greater London.	10	ditches	750-260 cal. BC	Mid to late Iron Age	Smith, 2012b
Tattershall Thorpe, Linconshire	15	Iron Age enclosure ditch	*ca. 770-200 BC* based on archaeology	Mid to late Iron Age	Chowne et al., 1986
Fisherwick, Staffordshire	3	enclosure ditch	380 ca.BC – 70 cal AD	Late Iron Age	Osborne, 1979
Minges Ditches, Oxfordshire	12	enclosure ditches	390-40 cal. BC	Late Iron Age	Robinson, 1993
Farmoor, Oxfordshire (Iron Age)	6	Iron Age sumps and gullies	382 cal. BC-76 cal. AD	Late Iron Age	Robinson, 1979
Little Paxton, Cambridgeshire	10	waterholes, brickfield ditches	*80 – 250 AD* dated by pottery	Late First century to mid third century	Smith, 2011a
Lockington, Derbyshire, waterholes	2	waterholes	Estimated period dates from archaeology	'Roman'	Smith, 2012c

Site	Number of samples	Type of feature	Radiocarbon or *estimated* calendar dates	Period	Reference
Imperial Sports Ground, Greater London (Roman)	2	wells	240-510 cal. AD	Roman	Smith, 2015a
Brickets Wood Bund, Hertfordshire	3	waterholes	*Estimated period dates from archaeology*	'Roman'	Smith, 2013b
Perry Oaks (Terminal 5) Heathrow, Greater London (Roman)	4	waterholes	*c100-250 AD and c 200 -300 AD* based on archaeology	Roman	Robinson, 2006
Kingsmead Horton Quarry (Roman)	5	waterholes or pits		Roman	Smith, 2009
Terminal 5 Heathrow (Roman)	5	ditches and waterholes	One date of 170cal BC to 220 AD. Other features estimated from archaeology	Early to late Roman	Tetlow, 2010
St. Loyes College, Exeter	4	military wells (dumped stabling material)	*60 – 100 AD* estimated dates from archaeology	Early Roman	Smith, 2011c
Northfleet Roman Villa, Kent	8	well and cistern	*80 – 120 AD* estimated dates from archaeology	Early Roman	Smith, 2011b
Balby Carr, Catesby Buisness Park, South Yorkshire	4	brickfield Roman ditch system	*100 – 130 AD* estimated dates from archaeology	Early Roman	Smith and Tetlow 1997
Grange Park, Well. Courteenhall, Northamptonshire	1	Roman timber lined well	*50 -450 AD* estimated dates from pottery in fill deposit	2nd century	Smith, 2006
Daventry Rail Frieght Terminal (Covert Farm)	3	waterhole	c. 150 – 225 AD based on pottery assemblage	Mid 2nd to mid third century	Smith, 2015b
Cambridge north West 13, Cambridgeshire	4	three wells	100 BC – 250 AD? Estimated dates from archaeology	Late Iron Age to mid Roman?	Smith, 2014b
Farmoor, Oxfordshire (Roman)	7	Roman wells	ca. 150 – 350 AD	Mid to late Roman (dated by pottery)	Robinson, 1979
Appleford, Oxfordshire	4	Roman wells and waterholes	200 – 400 AD Estimated dates from archaeology and pottery	Mid to late Roman	Robinson, 1981b
East Carr, Mattersey, Nottinghamshire	10	sub rectangular Roman field systems	361 cal. BC to 252 cal. AD but *200 – 300 AD* Estimated dates from archaeology	Mid late Roman	Smith 1997
Cambridge North West 12, Cambridgeshire	4	three timber lined wells	200 – 450 AD estimated dates from archaeology and pottery	2nd, 3rd and 4th century	Smith, 2014b
Salford Priors, Warwickshire	4	ditch associated with villa	300 – 450 AD estimated dates from archaeology	3rd or 4th century	Smith and Langham, 2000
Barton Court Farm, Oxfordshire	6	ditches and other features	c. 350 – 500 AD estimated dates from archaeology	Late Roman to early Saxon	Robinson et al., 1984
Terminal 5 Heathrow (Medieval)	1	ditch	1200 – 1600 AD estimated from archaeology	Medieval	Tetlow, 2010

Radiocarbon dates calibrated using OXCAL and are to 95% probability (2 sigma). Where several dates exist from different features at the site these have been combined to give an extended age range.

Table 2. Functional groups used in this analysis (based on Hill 2015)

	Functional Group	Code	Definition
True Aquatics	Aquatic	**A**	Beetles which spend the majority of their adult life in water. *Not included in terrestrial sum.*
Wetland & Waterside taxa	Riparian	**R**	Hygrophilous taxa, littoral, usually in the bare waterlogged soils besides water. Also associated with emergent vegetation. *Included in terrestrial sum*.
Wetland & Waterside taxa	Marsh and Aquatic Plants	**MA**	Chrysomelidae and Curculionidae species which feed exclusively on marsh and aquatic plants. *Included in terrestrial sum*.
Wetland & Waterside taxa	Marsh, Fen and Carr	**MFC**	Hygrophilous, and often eurytopic taxa, found across a variety of semi-aquatic environments, such as marsh, swamp, fen, and floodplains. *Included in terrestrial sum*.
Generalists	Foul Material	**FM**	Species living on various types of foul (decaying) organic material. Sometimes, but in most cases not exclusively synanthropic. Foul material includes dung, but these taxa are not dung specialists. *Included in terrestrial sum*.
Open landscapes	Dung	**DUNG**	Taxa strongly associated with the faeces of herbivores. *Included in terrestrial sum*.
Open landscapes	Open and Disturbed	**OD**	Taxa found in open and vegetated, or disturbed and relatively bare conditions, wet or dry (but not strictly 'wetlands'). *Included in terrestrial sum*.
Woodland associates	Edge of, or Light, Woodland	**ELW**	Species which show strong preference to forest margins, forest-steppe, copses/felled trees within woodlands, open or pasture woods, pine heaths, hedgerows, single or sun-exposed trees (e.g. certain Elateridae), or whose larval and adult stage alternate between open spaces and forest (e.g. certain Cerambycidae). *Included in terrestrial sum*.
Woodland associates	Woodlands and Trees	**WT**	Includes the Coleoptera which feed on wood in varying stages of decay, leaves, fruit, and bark and live wood, fungal feeders and predators strictly associated with woodland. Except where a taxon can be defined within **ELW**. *Included in terrestrial sum*.
Uncoded or Ubiquitous		**u**	Taxa to which none of the other FGs can be applied owing to either lack of taxonomic resolution or ubiquity. *Not included in terrestrial sum.*

Table 3: Rank order and % MNI for the 29 most frequently recovered Coleoptera by period for the sites in this survey. Note that some taxa (*Chaetocnema concinna, Aphodius sphacelatus, A. fimetarius, Megasternum 'boletophagum',* here rendered as *'concinnum', Hydrobius fuscipes, Anotylus sculpturatus* and *Carpelimus bilineatus*) have been split since these sites were recorded. The second column lists the rank occurrence scores for the entire archaeological dataset, regardless of archaeological period, followed by the percentage of individuals as part of the whole fauna for each taxon.

Rank order	Total for all periods	%MNI	Neolithic faunas	%MNI	Bronze age	%MNI	Iron age	%MNI	Romano-British	%MNI	Post Roman	%MNI
	39 sites in total		2 sites in period		8 sites in period		9 sites in period		18 sites in period		2 sites in period	
1	*Aphodius* spp.	7.4	*Megasternum concinnum* (Marsh.)	10.1	*Aphodius* spp.	8.9	*Aphodius* spp.	10.6	*Aphodius* spp.	5.1	*Helophorus brevipalpis* Bedel	8.4
2	*Ochthebius* spp.	3.2	*Ochthebius* spp.	7.1	*Geotrupes* spp.	6.7	*Helophorus brevipalpis* Bedel	4.7	*Ochthebius* spp.	3.7	*Platystethus* spp.	8.2
3	*Helophorus* spp.	2.7	*Aphodius* spp.	6.5	*Onthophagus fracticornis* (Preyssl.)	4.7	*Cercyon* spp.	4.0	*Helophorus* spp.	3.7	*Aphodius* spp.	4.5
4	*Apion* spp.	2.4	*Stenus* spp.	4.3	*Calathus melanocephalus* (L.)	4.7	*Ochthebius minimus* (F.)	2.8	*Latridius minutus* (group)	2.6	*Meligethes* spp.	3.6
5	*Megasternum concinnum* (Marsh.)	2.2	*Apion* spp.	4.3	*Calathus fuscipes* (Goeze)	2.8	*Apion* spp.	2.8	*Apion* spp.	2.4	*Apion* spp.	3.2
6	*Cercyon* spp.	2.1	*Helophorus* spp.	3.5	*Onthophagus joannae* (Goljan)	2.6	*Phyllopertha horticola* (L.)	2.6	*Megasternum concinnum* (Marsh.)	1.9	*Latridius minutus* (group)	2.8
7	*Latridius minutus* (group)	1.9	*Xantholinus linearis* (Ol.)/*longiventris* Heer	2.0	*Ochthebius* spp.	1.9	*Ochthebius* spp.	2.5	*Anotylus sculpturatus* (Grav.)	1.8	Ceutorhynchinae indet.	2.6
8	*Helophorus brevipalpis* Bedel	1.8	*Calathus melanocephalus* (L.)	1.9	Aleocharinae indet.	1.8	*Platystethus cornutus* (Grav.)	2.0	Aleocharinae indet.	1.8	*Longitarsus* spp.	2.4
9	*Anotylus sculpturatus* Grav.	1.4	*Ochthebius minimus* (F.)	1.9	*Helophorus* spp.	1.7	*Megasternum concinnum* (Marsh.)	1.9	*Cercyon* spp.	1.7	*Helophorus grandis* (Ill.)	2.4
10	*Geotrupes* spp.	1.4	Aleocharinae indet.	1.7	*Phyllotreta* spp.	1.5	*Helophorus* spp.	1.8	*Philonthus* spp.	1.5	*Phyllotreta vittula* (Redt).	2.2
11	*Ochthebius minimus* (F.)	1.4	*Aphodius granarius* (L.)	1.4	*Hydraena testacea* Curt.	1.3	*Latridius minutus* (group)	1.8	*Platystethus cornutus* (Grav.)	1.3	*Oxyomus sylvestris* (Scop.)	1.9
12	Aleocharinae indet.	1.4	*Calathus fuscipes* (Goeze)	1.2	*Anobium punctatum* (Geer)	1.3	*Chaetocnema concinna* (Marsh.)	1.6	*Platystethus arenarius* (Fourcr.)	1.3	*Phyllotreta nigripes* (F.)	1.9
13	*Platystethus cornutus* (Grav.)	1.3	*Tachyporus* spp.	1.2	*Megasternum concinnum* (Marsh.)	1.2	*Aphodius contaminatus* (Hbst.)	1.4	*Lesteva longelytrata* (Goeze)	1.3	*Megasternum* (Marsh.)	1.5
14	*Philonthus* spp.	1.2	*Phyllopertha horticola* (L.)	1.2	*Apion* spp.	1.2	*Anotylus sculpturatus* (Grav.)	1.4	*Amara* spp.	1.2	Corticariinae indet.	1.5
15	*Calathus melanocephalus* (L.)	1.2	*Barynotus obscurus* (F.)	1.2	*Phyllopertha horticola* (L.)	1.2	*Tanysphyrus lemnae* (Payk.)	1.3	*Anobium punctatum* (Geer)	1.2	*Cercyon* spp.	1.3

Rank order	Total for all periods	%MNI	Neolithic faunas	%MNI	Bronze age	%MNI	Iron age	%MNI	Romano-British	%MNI	Post Roman	
16	*Chaetocnema concinna* (Marsh.)	1.2	*Rugilus* spp.	1.2	*Ptinus fur* (L.)	1.0	*Carpelimus bilineatus* (Steph).	1.1	*Oxyomus sylvestris* (Scop.)	1.1	*Chaetocnema concinna* (Marsh.)	1.3
17	*Phyllopertha horticola* (L.)	1.1	*Philonthus* spp.	1.2	*Anotylus sculpturatus* (Grav.)	1.0	*Trechus obtusus* Er./*quadristriatus* (Schr.)	1.1	*Phyllotreta* spp.	1.1	*Hydrobius fuscipes* (L.)	1.3
18	*Stenus* spp.	1.1	*Agrypnus murinus* (L.)	1.2	*Stenus* spp.	1.0	*Hydrobius fuscipes* (L.)	1.0	*Anotylus rugosus* (F.)	1.1	*Tachyporus* spp.	1.3
19	*Anobium punctatum* (Geer)	1	*Longitarsus* spp.	1.2	*Chaetocnema concinna* (Marsh.)	0.9	*Aphodius sphacelatus* (Panz.)	1.0	*Aphodius contaminatus* (Hbst.)	1.1	Cryptophagidae indet.	1.3
20	*Calathus fuscipes* (Goeze)	1	*Mecinus pyraster* (Hbst.)	1.2	*Aphodius granarius* (L.)	0.9	*Bembidion* spp.	1.0	*Stenus* spp.	1.1	*Tachinus* spp.	1.1
21	*Aphodius contaminatus* (Hbst.)	0.9	*Geotrupes* spp.	1.1	*Longitarsus* spp.	0.8	*Philonthus* spp.	0.9	*Chaetocnema concinna* (Marsham)	1.0	*Geotrupes* spp.	0.9
22	*Phyllotreta* spp.	0.9	*Gabrius* spp.	1.0	*Limnebius* spp.	0.8	*A. prodromus* Brahm/*sphacelatus* (Panzer)	0.9	*Xantholinus* spp.	1.0	*Anotylus rugosus* (F.)	0.9
23	*Longitarsus* spp.	0.9	*Hydrothassa glabra* (Hbst.)	1.0	*Xantholinus linearis* (Ol.)/*longiventris* Heer	0.8	*Anobium punctatum* (Geer)	0.9	*Anotylus nitidulus* (Grav.)	0.9	*Trechus obtusus* Er./*quadristriatus* (Schr.)	0.9
24	*Oxyomus sylvestris* (Scop.)	0.9	*Tachinus* spp.	0.9	*Mecinus pyraster* (Hbst.)	0.8	*Anotylus rugosus* (F.)	0.8	Corticariinae indet.	0.9	*Atomaria* spp.	0.9
25	*Anotylus rugosus* (F.)	0.9	*Quedius* spp.	0.9	*Philonthus* spp.	0.8	*Longitarsus* spp.	0.7	*Brachypterus urticae* (F.)	0.9	*Aphodius rufipes* (Geer)	0.9
26	*Amara* spp.	0.8	*Anotylus rugosus* (F.)	0.8	*Oxyomus sylvestris* (Scop.)	0.8	*Aphodius fimetarius* (L.)	0.7	*Longitarsus* spp.	0.9	*Aspidapion aeneum* (F.)	0.9
27	*Lesteva longoelytrata* (Goeze)	0.8	*Atomaria* spp.	0.8	*Brachypterus urticae* (F.)	0.7	Scirtidae indet.	0.7	*Bembidion* spp.	0.9	*Phyllotreta atra* (F.)	0.9
28	*Platystethus arenarius* (Fourcr.)	0.8	*Onthophagus joannae* (Goljan)	0.8	*Chaetocnema* spp.	0.7	*Aphodius prodromus* (Brahm)	0.7	*Ochthebius minimus* (Group)	0.9	*Ochthebius* spp.	0.7
29	*Onthophagus fracticornis* (Preyssl.)	0.8	*Phyllobius* spp.	0.8	*Latridius minutus* (group)	0.7	*Limnebius* spp.	0.6	*Ptinus fur* (L.)	0.8	*Philonthus* spp.	0.7

Table 4 Summary table of the insects thought to be particularly important in archaeological farms by ecological groupings and then by taxonomic order based on Table 3 and the authors' previous experience.

PART OF FAUNA	SPECIES	ECOLOGICAL NOTES
TYPICAL GROUND BEETLES	*Notiophilus biguttatus, Nebria brevicollis, Loricera pilicornis, Clivina fossor, Trechus quadristriatus, T. obtusus, Pterostichus madidus, P. melanarius, Anchomenus (Agonum) dorsalis, Amara spp., Harpalus affinis, Harpalus rufipes, Calathus fuscipes, Calathus melanocephalus, Syntomus truncatellus. Dromius linearis*	A range of 'generalist' predators favoured by open and often disturbed ground. This may be ploughed fields or grassland. *C. fossor* seems to be typical of soft damp ground, *S. truncatellus* and *D. linearis* of open sandy ground.
TYPICAL OF GRASSLANDS	Range of Elateridae 'click beetles' Typically various *Agriotes* spp. and *Athous haemorrhoidalis.* The 'Garden Chafer' *Phyllopertha horticola*, the 'cockchafer' *Melolontha melolontha* and 'the Welsh Chafer' *Hoplia philanthus*.	These species tend to be typical of old grassland, where they feed on the roots of grasses.
PLANT FEEDERS	***Grassland and meadow*** *Gastrophysa polygoni, G. viridula, Apion frumentarium, Perapion violaceum, P. hydrolapathi* (on docks) *Sitona lepidus, S. suturalis, S. humeralis, Hypera* spp. (Clover) *Coelositona cambricus, S. waterhousei* (birds foot trefoil) *Oxystoma craccae, O. cerdo, O. pomonae* (Vetches) *Cleonis piger (thistles)* ***Disturbed ground and wasteland*** *Aspidapion aeneum* (common mallow) *Rhinoncus pericarpius, Rhinoncus castor* (Docks) *Ceutorhynchus contractus* (poppies and mignonettes) *Ceutorhynchus erysimi* (Shepard's purse) *Brachypterus urticae, Parethelcus (Ceutorhychus) pollinarius, Nedyus quadrimaculatus* (stinging nettle) *Mecinus pyraster, M. (Gymnetron) labile, M. (Gymnetron) pascuorum* (lanceolate plantain)	There is substantial overlap between the species which occur in grassland and meadow and those in disturbed ground. All these species feed on plants typical of grassland. Often they are carried into settlement in cut hay (Kenward and Hall, 1997).
NEAR TO DAMP AREAS AND MUDDY GROUND	*Lesteva longoelytrata, Carpelimus 'bilineatus', Anotylus nitidulus, Platystethus cornutus*	These species are typical of open, wet and disturbed ground both in agricultural land and within settlements. They may often be associated with areas of trampled or poached ground around waterholes and channels, but this may be overly simplistic.
DUNG BEETLES	*Sphaeridium scarabaeoides, S. lunatum, Cercyon impressus, Cercyon haemorrhoidalis Cercyon melanocephalus, Cercyon unipunctatus, Platystethus arenarius Geotrupes spp., Onthophagus spp., Aphodius fossor, Aphodius rufipes, Aphodius luridus, A. contaminatus, A. sphacelatus, A. prodromus, A. porcus, A. fimetarius, A. ater, A. granarius* etc.	This is a selection of the most common of a wide range of species associated with herbivore dung. Several other species are recovered, some of which from the Bronze and Iron Ages are rare at the present day (Robinson, 2013b). Several are also thought to be capable of breeding in wet waste materials around human settlement (Kenward *et al*., 2004). These dung associates can be very numerous in some sites where they can account for up to 40% – 60% of the terrestrial fauna, suggesting nearby grazing or pasture.

TREES	Various woodborers - *Anobium punctatum, Grynobius planus, Lyctus linearis*, *Phloeotribus rhododactylus*, *Hylesinus* (*Leperisinus) varius, Hylesinus toranio (oleiperda),* (ash). Phytophages - *Andrion (Sitona) regensteinense* (broom and gorse), *Rhynchites* spp. s. lat. (rosaceous shrubs such as blackthorn, hawthorn and bramble), *Rhynchaenus* spp. (leaf miners), *Curculio* spp. (nut weevils)	Most archaeological sites from agricultural ditches and rural landscapes contain very few of these taxa.

Table 5. Beetles typically recorded in modern ecological surveys from arable, grassland and pasture (taxa ordered by frequency).

Habitat type	Reference	Sampling method	Families	Species in order of occurrence
Arable land				
Arable lands in Scotland	Blake et al. , 2003	Pitfall trapping	Carabidae	*Nebria brevicollis, Loricera pilicornis, Pterostichus strenuus, Amara familiaris, Anchomenus dorsalis, Synuchus* spp. *Amara apricaria*
Middle of open crop fields in Southern England	Fournier and Loreau, 1999	Pitfall trapping	Carabidae	*Pterostichus melanarius* and *Trechus obtusus* favoured, *Bembidion obtusus, Notiophilus biguttatus, Nebria brevicollis Badister sodalis* also present
Mixed arable land on floodplain of river Trent	Greenwood *et al.*, 1991	Pitfall trapping	Carabidae and Staphylinidae	*N. brevicollis, Pterostichus madidus, Anchomenus dorsalis, Amara familiaris, Bembidion obtusum, Drusilla caniculata.*
Ploughed land in Sussex, England	Holland and Reynolds, 2003	Pitfall trapping	Carabidae	*Nebria brevicollis, Anotylus* spp., *Harpalus rufipes, Pterostichus madidus, Harpalus affinus, Trechus quadristriatus, P. melanarius, Calathus fuscipes, Amara* spp., *Bembidion obtusum, Xantholinus* spp, *Notiophilus biguttatus and Poecilus cupreus.*
Ploughed fields in northern Germany	Kroos and Schaefer, 1998	Pitfall trapping	Staphylinidae	*Tachyporus hypnorum, Anotylus inustus, Lesteva longoelytrata, Philonthus fuscipennis, Ocypus nitens, Omalium caesum, Philonthus rotundicollis* and *Coprophilus striatulus*
Arable land, Binsley Lane and South Hinksey, Oxford	Robinson, 1983	Pitfalls and sweep-netting	Whole fauna	**Pitfall trapping**_*Harpalus rufipes, Tachinus rufipes, Pterostichus melanarius, Amara similata,* Aleocharinae gen. & spp. indet., *Anchomenus dorsalis, Ceutorhynchus typhae, Enicmus transversus, Tachyporus solutus.* **Sweep-netting**_*Ceutorhynchus floralis, Phyllotreta* spp., *Meligethes* spp.
Grassland, meadow and pasture				
Large number of undisturbed grassland sites across UK	Eyre et al., 2003	Pitfall trapping	Carabidae	Dominated by *Abax parallelepipedus, Pterostichus niger and Platynus assimilis;* dry grassland also with *Calathus fuscipes, Amara aenea, Harpalus rufipes.* Damper grassland with *Bembidion obtusum, Harpalus affinus, Dromius melanocephalus.*
Series of coastal grasslands	Luff, 1989	Pitfall traping	Carabidae	*Badister bipustulatus, Amara aenea, A. communis. A. tibialis, Syntomus foveatus*
Mesotrophic Grasslands in Scotland	Blake et al., 2003	Pitfall trapping	Carabidae	*Notiophilus biguttatus, Bembidion lampros, Anchomenus dorsalis, B. guttula, B. lampros, B. aeneum*
Grassland on floodplain of River Trent	Greenwood et al., 1991	Pitfall trapping	Carabidae and Staphylinidae	*Nebria brevicollis, Bembidion aeneum, B. guttula, Philonthus cognatus Aleochara bipustula.*
Mesotrophic meadowland Sussex	Woodcock et al., 2008	Suction collection	Chrysomelidae and Curculionidae	*Longitarsus pratensis, L. luridus, Sitona lepidus, S. lineatus, L. melanocephalus, Trichosirocalus troglodytes, Protapion fulvipes,Sphaeroderma rubidum, Ischnopterapion loti, Protapion assimile.*

Habitat type	Reference	Sampling method	Families	Species in order of occurrence
Calcareous and five mesotrophic grassland sites in southern England	Woodcock et al., 2010	Suction collection	Chrysomelidae and Curculionidae	**Calcareous grassland** *Longitarsus pratensis, Sitona lineatus, L. luridus, Trachyphloeus alternans, L. parvulus, Catapion pubesens, S. hispudulus, L. atricillus, Protapion dichroum, C. seniculus.* **Mesotrophic grassland** *L. pratensis, P. trifolii, P. fulvipes, L. melanocephalus, Sitona lepidus, S. lineatus, P. assimile, L. atricillus, S. hispidulus, P. apricans*
Hay meadow, Pixey mead, Oxford	Robinson, 1983	Pitfalling and sweep netting	Whole fauna	**Pit fall trapping** *Pterostichus versicolor, Peocilus cupreus, Amara communis, Oedostethus quadripustulatus, Pterostichus melanarius, Longitarus luridus, Bembidion gilvipes, Clivina fossor, Harpalus rufipes, Agriotes obscurus.* **Sweep netting** *Protapion trifolii, Cantharis nigra, Cantharis rufa.*
Grazed Pasture, Port Meadow, Oxford	Robinson , 1983	Pitfalls and sweep netting	Whole fauna	**Pitfall trapping** *Philonthus cognatus, Loricera pilicornis, Bembidion guttula, Tachinus signatus, Aleocharinae gen and spp, indet. Notaris acridulus, Helophorus brevipalpis, Bembidion properans, B. lunulatum, Philonthus laminatus, Aphodius fossor*
Grazed pasture in Southern Ireland	Hutton and Giller, 2003	Baited pitfall traps	Scarabaeidae, Hyrophilidae and Histeridae 'dung beetles'	*Aphodius prodromus, A. sphacelatus, A. ater, A. rufipes, A. depressus, Sphaeridium lunatum, S.scarabaeoides* and *Margarinotus ventralis* accounted for 95% of variation

Figure 1: Location of the archaeological sites used in this survey

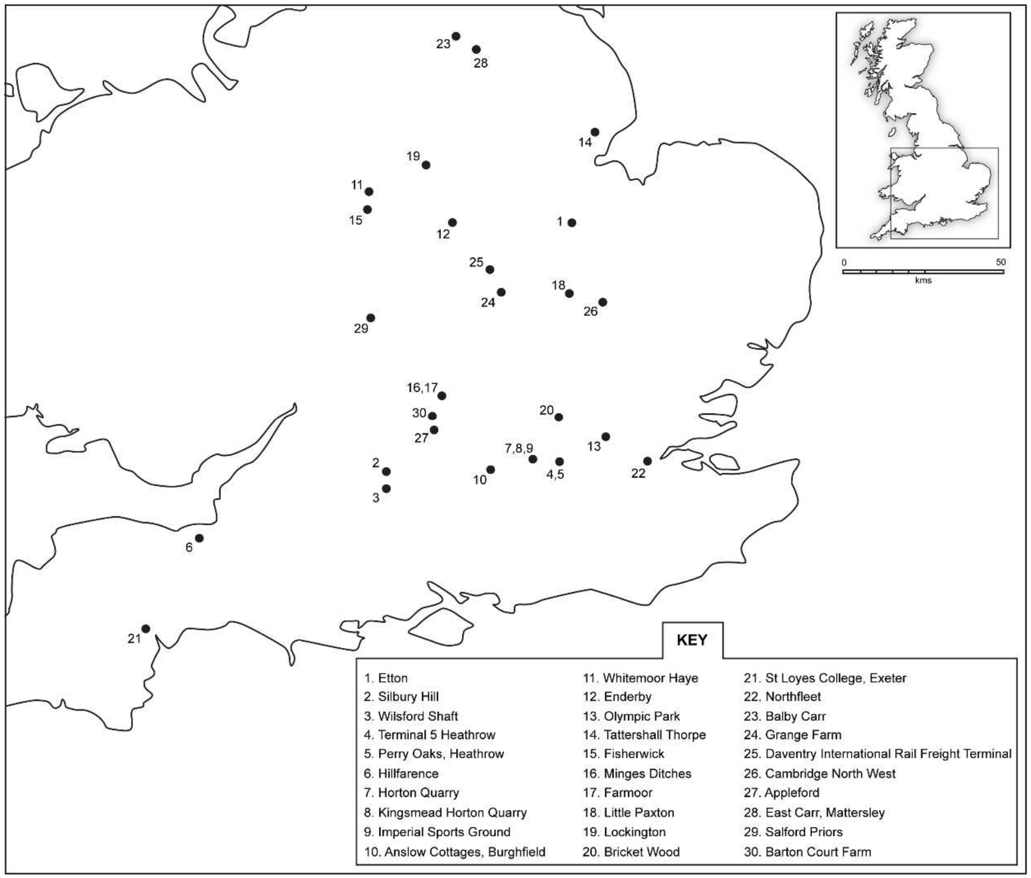


Figure 2: The relative proportions of the broader aquatic, wetland and terrestrial functional group for each site in chronological order (N – Neolithic, BA – Bronze Age, IA – Iron age, RB – Romano British, S – Saxon, M – Medieval).

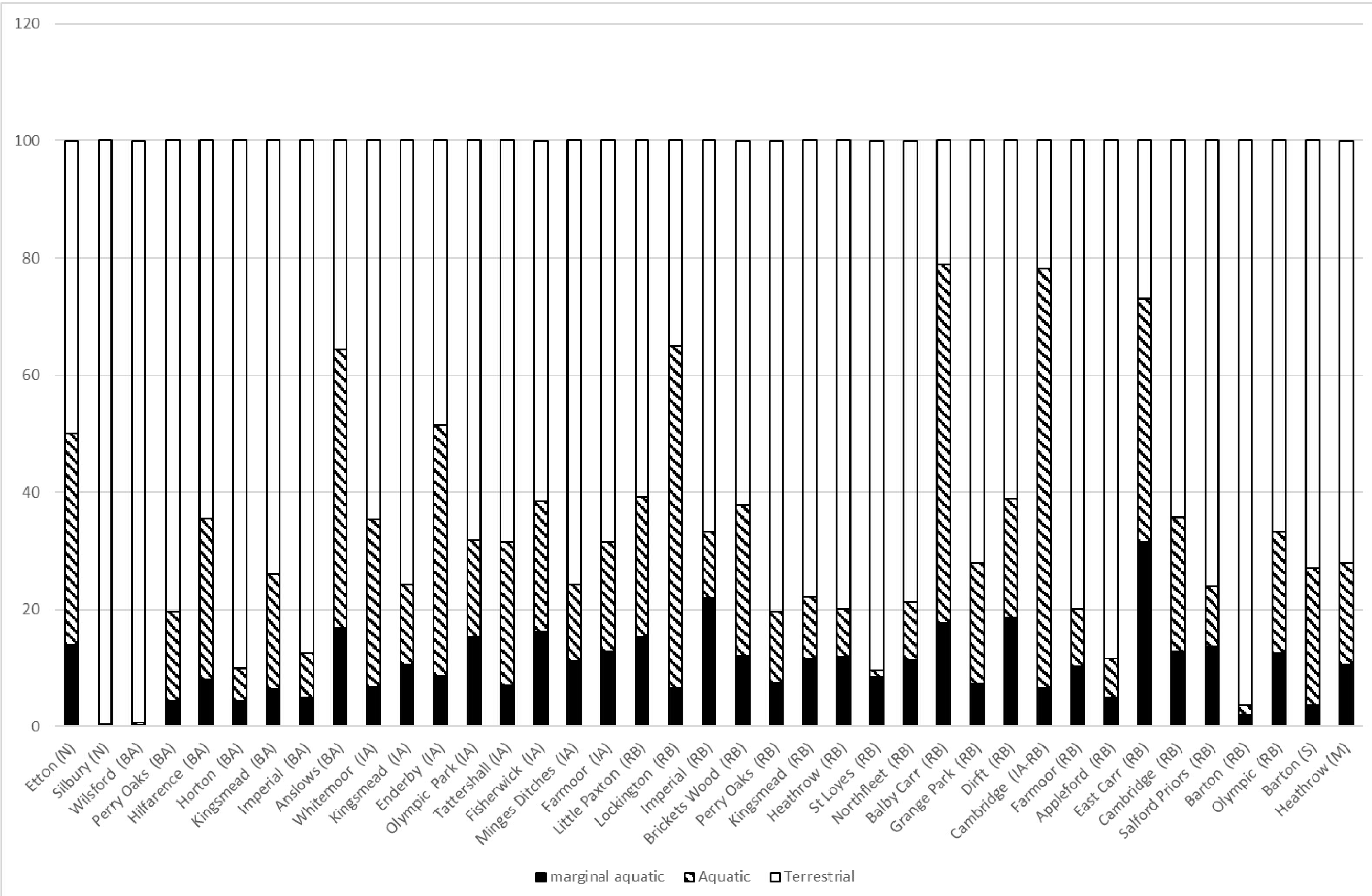


Figure 3: The relative proportions of the terrestrial functional groups by site in chrological order (N – Neolithic, BA – Bronze Age, IA – Iron age, RB – Romano British, S – Saxon, M – Medieval).

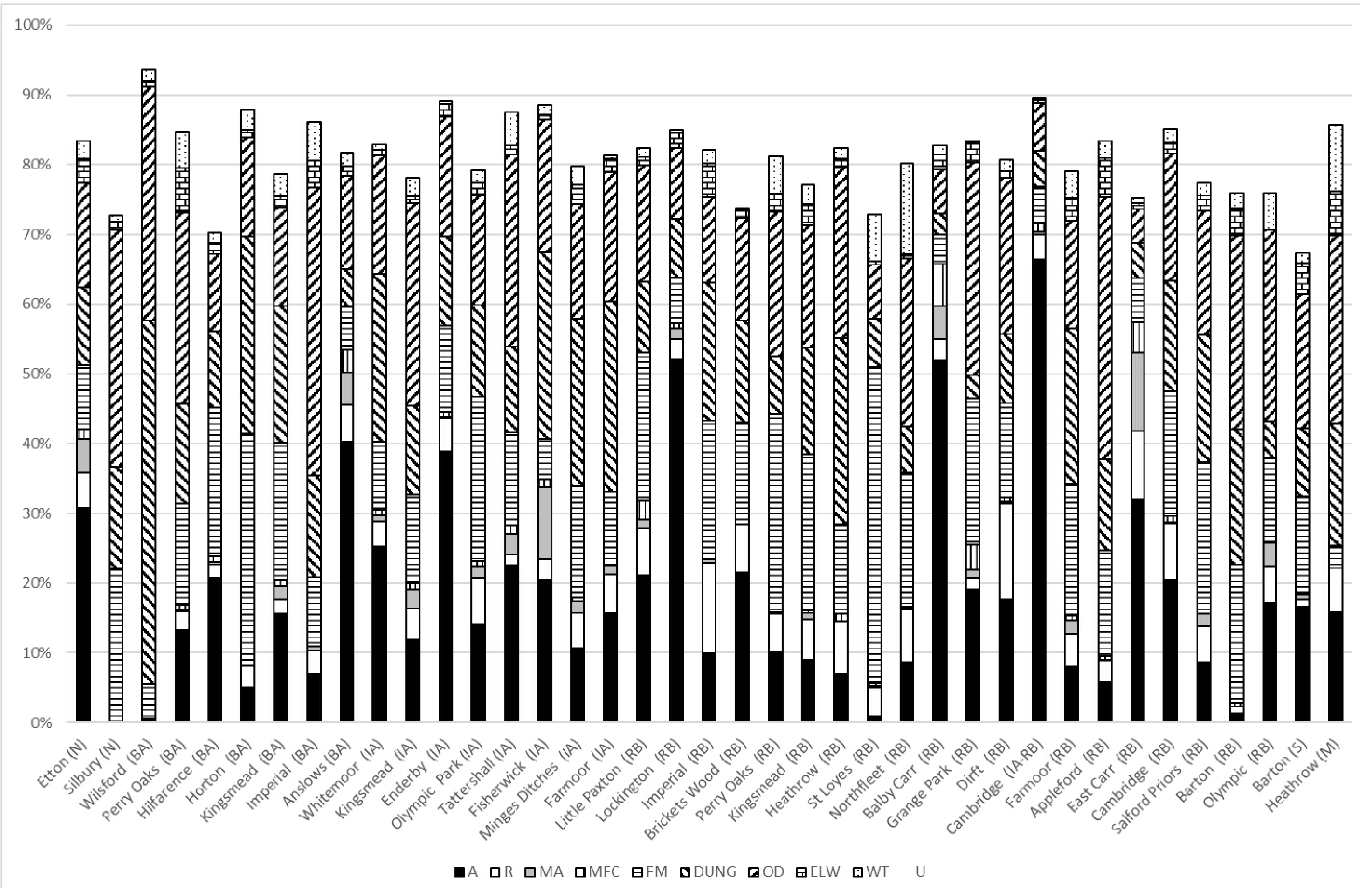


Figure 4: The relative proportions of functional groups (dung, foul material, open and woodland) and synthropic groups by archaeological period using box and whisker plots to indicate the range and mean for each functional group. Outliers have the same numbers as are given for the sites in Figure 1. The number of sites in each archaeological period is indicated below the middle row of the diagrammes.

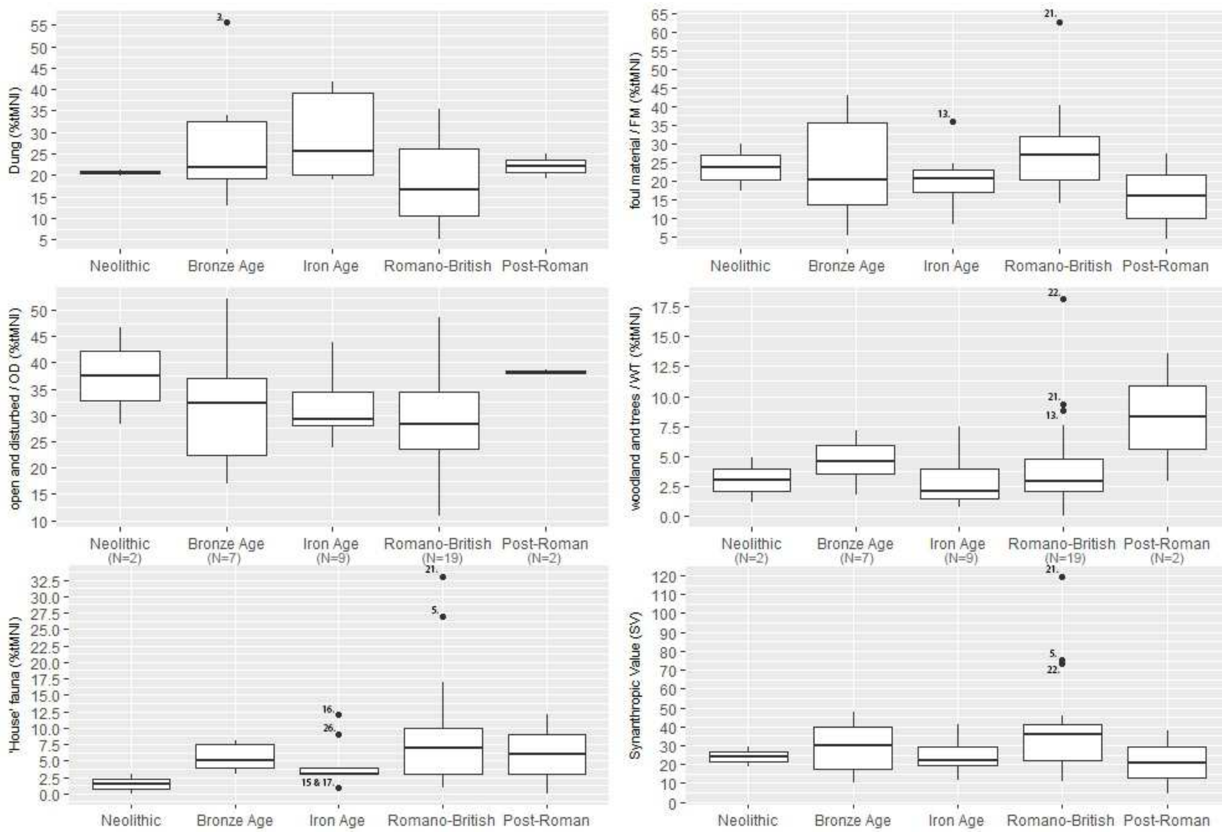


Figure 5: nMDS analysis for of the taxa from each individual ‘chronological entity’ by archaeological period (see key for details of each archaeological period)

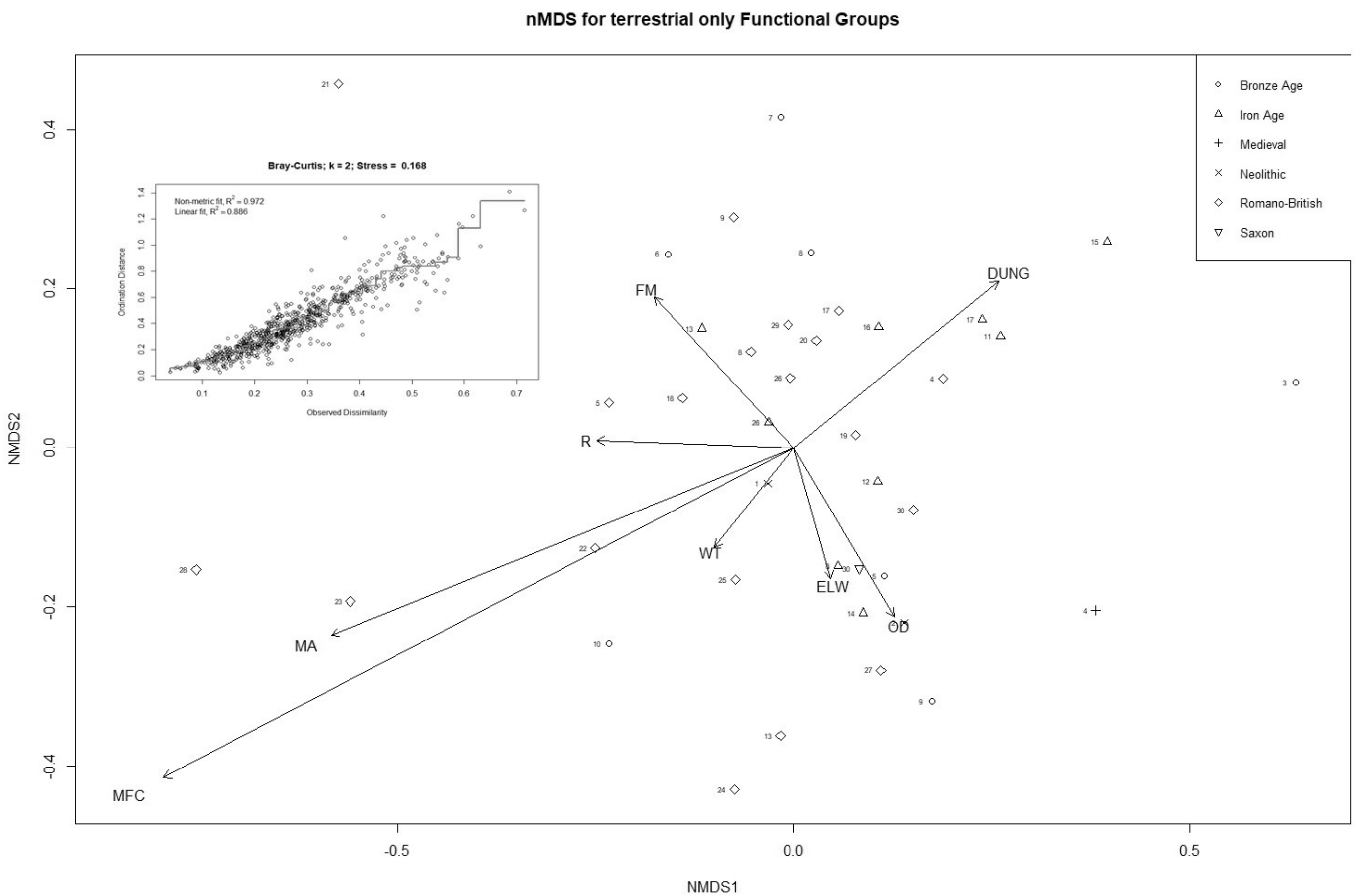


Figure 6: nMDS analysis for of the taxa from each individual 'chronological entity' by archaeological feature (see key for details of each archaeological feature)

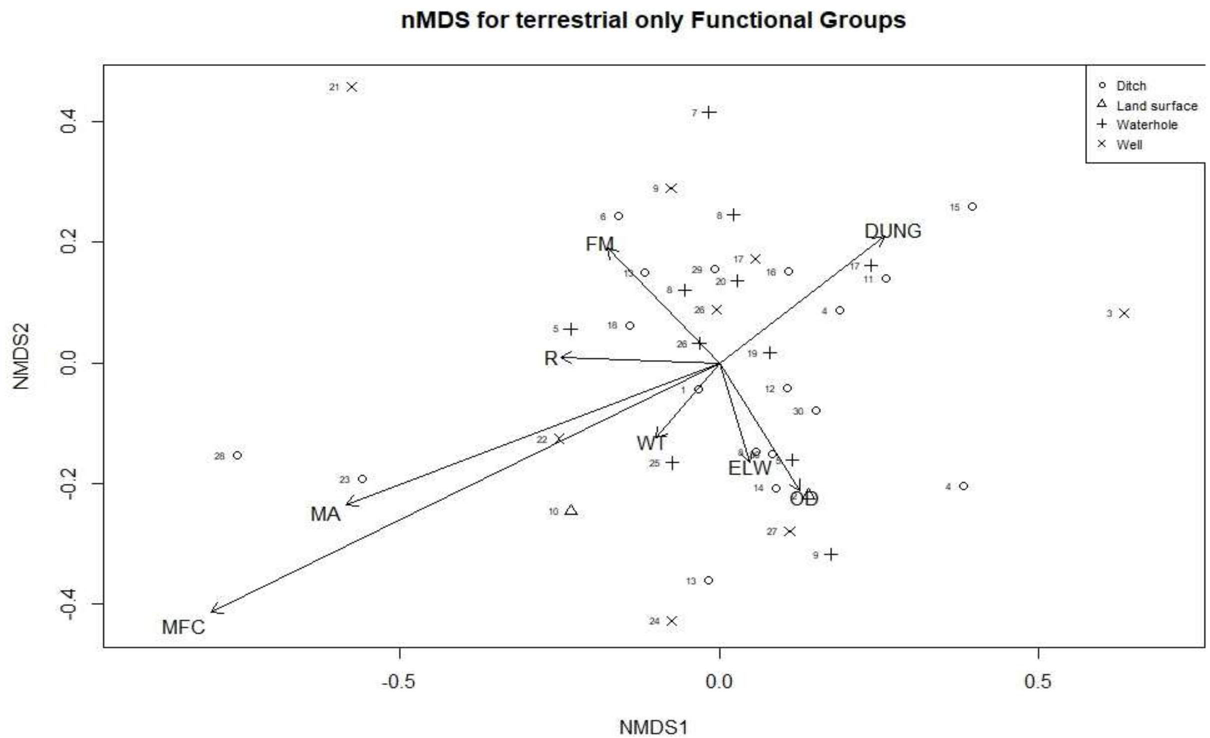


Figure 7: Dissimilarity matrices for the insect faunas from the sites examined based on simple score of presence/absence. The left-hand diagram presents the sites ordered alphabetically by period. The right-hand diagram re-orders the sites by the degree to which their archaeoentomological faunas are similar, regardless of period; assemblages with similar faunas plot closer together. Results are presented as a heat map of the similarity matrix with blocks indicating the highest degree of similarity.