Frontispiece. Birch leaf roller, *Deporaus betulae* (L.) (Attelabidae)

A phytophagous weevil of birch, alder and hazel, remains of which were recovered from modern woodlands, and death assemblages of Late Bronze Age date at St George's Field, York.

Magnification approximately x 25.

INSECT DEATH ASSEMBLAGES
AND THE INTERPRETATION OF WOODLAND HISTORY:
evidence from the Vale of York

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Abstract

Insect death assemblages (the accumulated remains of insect body parts), preserved in archaeological and natural deposits, have often been used as an aid to interpreting past environments. This thesis assesses the extent to which beetle and bug assemblages can be used in palaeoenvironmental reconstruction, particularly for woodland habitats, using data from both modern and fossil assemblages from the Vale of York.

The study of insect assemblages accumulating in modern woodland habitats suggests that species composition may be used to determine whether an assemblage formed under woodland conditions. However, the taxa present in an assemblage appear to be insufficiently constant to permit further interpretation of woodland structure using statistical methods.

The use of 'ecological groups' to classify species appears to be of value in reducing the complexity of species lists without reducing the interpretative value of the assemblage. The numbers in the broad ecological groups identified could be used to provide a reliable guide to the general ecological conditions under which an assemblage formed.

The tree species present in a woodland were well-represented amongst the host-specific phytophagous insects present in the insect assemblages studied, but certain groups of plants, such as the woodland herbs, were not represented.

Fossil insect assemblages from two sites in the Vale have been studied. It appeared that the Late Bronze Age faunas from St George's Field, York, were laid down in (or near) old woodland rich in woodland insect taxa. However, from deposits dated 180 BC - AD 500 at Thornton, there is little evidence for habitats beyond the local marshland in which the assemblages formed, and none for woodlands. The results of these studies suggest that the depositional environment, and post-depositional conditions can both act as important influences on the nature of preserved death assemblages, and this must be considered when they are used to reconstruct past environments.

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Author's Declaration

All the work contained in this thesis is my own, except for the collection, processing and identification of insects from, some of the assemblages described in Chapter 3. Litter samples from woodlands at Yorkletts, near Whitstable, Kent, and the Wyre Forest, Hereford and Worcester, were collected and processed by H. K. Kenward, who also identified the insect taxa present in the former samples. The invertebrates present in the Wyre Forest sample were identified by the author.

H. K. Kenward also provided species lists for insect death assemblages from roofs in York, Nettlebeds in Yorkshire and Lincolnshire, and decomposer communities in the Vale of York. Some statistics from the Yorkletts assemblages have been published by Kenward (1978), and from the York roof faunas by Kenward (1976 and 1978).

Chapter 1 Introduction

1.1 Woodlands, landuse history and insect death assemblages

Insect death assemblages, preserved by waterlogging (or, less frequently, by desiccation) in Quaternary sediments have been used to interpret both large-scale climatic change and the paleoecology of individual sites (Birks and Birks, 1980). In certain cases, they have been used to provide evidence of past woodland environments (Girling, 1982), but little comparative work has been carried out to assess the value of insects as environmental indicators by using modern assemblages (but see for example, Kenward, 1978, working on modern corollaries of archaeological assemblages, and Robinson, 1983, and Fishpool, 1992, who consider arable and pastoral habitats, and woodlands, respectively).

This project seeks to add to this body of evidence, using the specific example of woodland insect death assemblages from the Vale of York. Woodland was chosen as it has been an important resource from earliest prehistory, and, in some areas, may have been limited in extent and managed since the Neolithic, for example, at Skipsea, Holderness (Gilbertson, 1984). Woodlands also probably represent the 'climax vegetation' of a large part of Britain (Marren, 1990), and so well-developed communities of plants and animals are associated with them. As Evans (1972) states, "one of the prime concerns of environmental archaeology is the way in which agricultural communities have destroyed the ancient forests of these islands and brought about their replacement, through successive stages of landuse, by the predominantly open landscape of today."

The rest of this chapter will set the background for this investigation, describing the physical geography of the Vale of York, and previous studies of its vegetational history and landscape archaeology. Chapter 2 explains the methods used in the development of a scheme for assigning insect species to ecological groups, an essential tool to help reduce the complexity of death assemblages to make their interpretation easier.

In Chapter 3, the results of a study of modern death assemblages accumulating in existing woodlands and non-wooded situations in the Vale of York and beyond are presented. Chapters 4 and 5 are concerned with the investigation of fossil insect and plant assemblages preserved by waterlogging at two very different sites in the Vale. In Chapter 6, the implications of the study of modern assemblages for the interpretation of ancient faunas are discussed, with particular emphasis on their application to questions of woodland history.

1.2 The Vale of York

1.2.i Physical geography and geological background

The Vale of York is low lying and broad, around 40 km across at the point now occupied by the City of York. The eastern boundary of the Vale is formed, in the southern part, by the Cretaceous scarp of the Yorkshire Wolds, and, further north, the Jurassic scarps of the Hambleton Hills (on the western edge of the North York Moors), and the Howardian Hills. In the West, the Vale is bounded by the foothills of the Pennines. To the north and south, the edges of the Vale are less distinct; around Northallerton and Thirsk, the Vale of York narrows (to about 25 km wide), and is named the Vale of Mowbray. This lowland area continues north to the valley of the Tees, and thence to the North Sea. The northern boundary of the Vale of York is usually taken as the ill-defined watershed between the catchments of the Rivers Ouse and Tees (Peel and Palmer, 1955). In the south, the Vale merges with the wetlands of the Humberhead levels, and the lowland area continues southward along the Valley of the Trent (Kent, 1980). By convention, the Rivers Aire and Humber are taken as the southern boundary of the Vale (see Figure 1.1).

The solid geology underlying the Vale is largely made up of Triassic Red Sandstones of the Sherwood sandstone group (Kent, 1980), but this only reaches the surface at Brayton Barf and Holme-on-Spalding Moor, where it forms isolated hills. Over the rest of the Vale it is overlain by thick Quaternary deposits, glacial, lacustrine, or fluvial in nature. In the south, the Vale approaches sea level, and in general, it does not exceed 10-20 m above OD.

The most prominent relief features on the flat Vale are the York and Escrick moraines, crescentic ridges of sand, gravel and till which cross the Vale in an east-west direction south of the City of York (see Figure 1.2). The moraines rise to 22.9 m at Stillingfleet, but are generally lower (Bullock, 1974).

To the south of the moraines, drift deposits (the '25 foot drift') of up to 20 metres of laminated clays were laid down in Lake Humber, which occupied much of the southern part of the Vale of York and the Trent Valley when the Humber was blocked by ice from the North Sea region in the Devensian glaciation. Water from the Vale of Pickering (where ice blocked the Derwent's route to the sea, forming the smaller Lake Pickering) and from the catchment of the Humber flowed into the new lake. As the ice retreated, the lake receded, allowing redistribution of drift and glacial deposits. By about 11000 BP, Lake Humber had drained completely (Gaunt *et al*, 1971). A period of fluvial incision of these glacial deposits appears to have followed, which in turn was halted by marine transgressions from around 7000 BP that emphasised alluviation as a dominant process in the Vale (Gaunt and Tooley, 1974).

At the end of the glaciation, wind action also caused redistribution of earlier deposits. Aeolian (wind-blown) sands, in the form of fossil dunes, dominate the floor of the Vale in the area to the north of York, around Sutton-on-the-Forest and Strensall. These were probably deposited in the Late Glacial period, around 10700-9950 BP (Matthews, 1970), before forest vegetation re-established itself in the Vale. In the historic period, clearance of woodland and, more recently, removal of hedges has led to strong wind erosion of some of these sands (Radley and Simms, 1967).

The Vale of York is drained by the River Ouse and its tributaries, which also drain large areas of the surrounding uplands (over 4660 km^2 in all, Cowper Reed, 1901). The River Ouse (and, until the Norman period, the lower Foss) was probably tidal to York (Fife and Walls, 1973), before canalisation of large parts of the Fosse and lower Ouse, and associated drainage of large areas of the Vale and Humberhead levels, from the seventeenth century onward. Human activity has also influenced alluviation in the Vale, by the practice of 'warping', on the lower Ouse from the mid eighteenth century (Ellis, 1990).

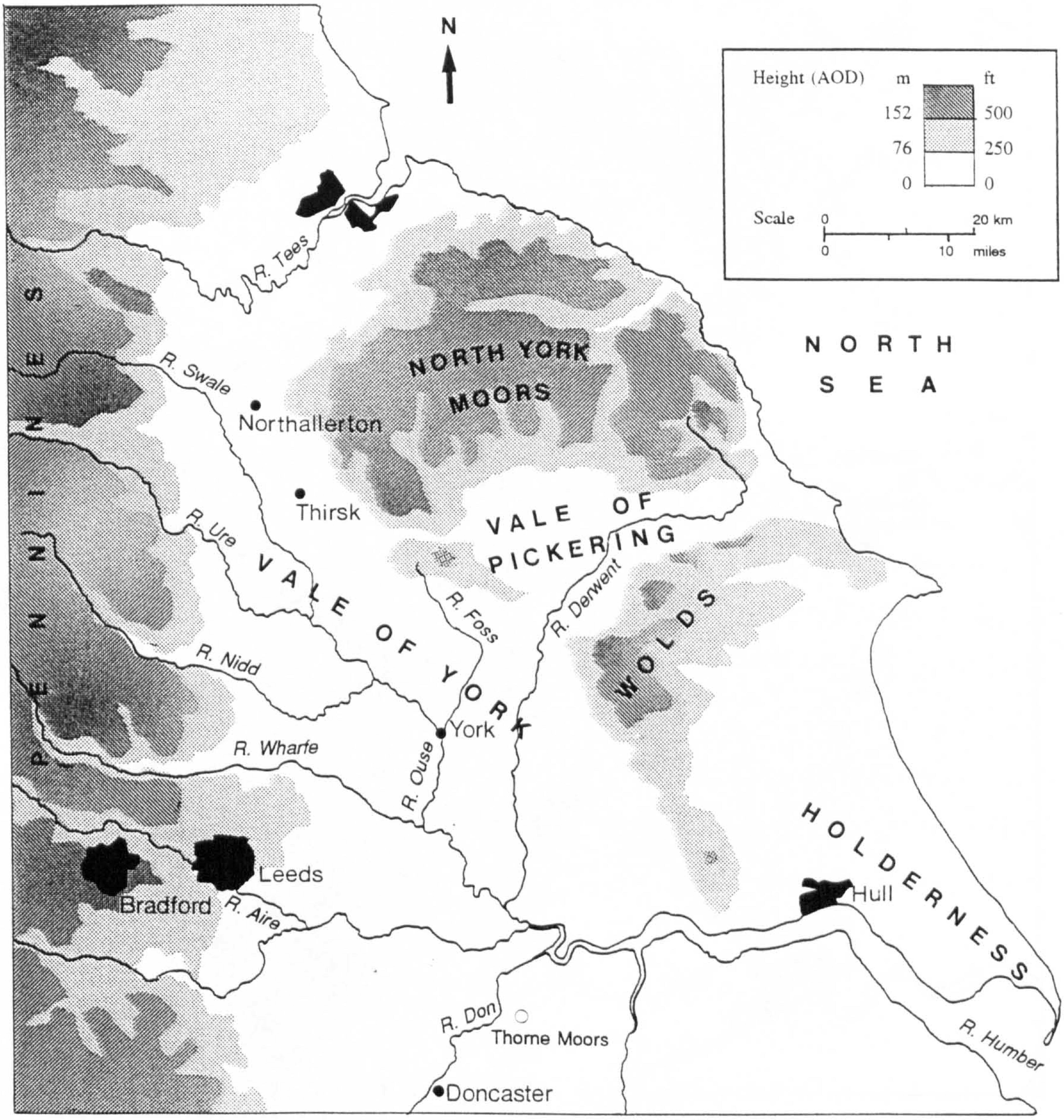


Figure 1.1 The north-east of England, showing the position of the Vale of York and surrounding uplands.

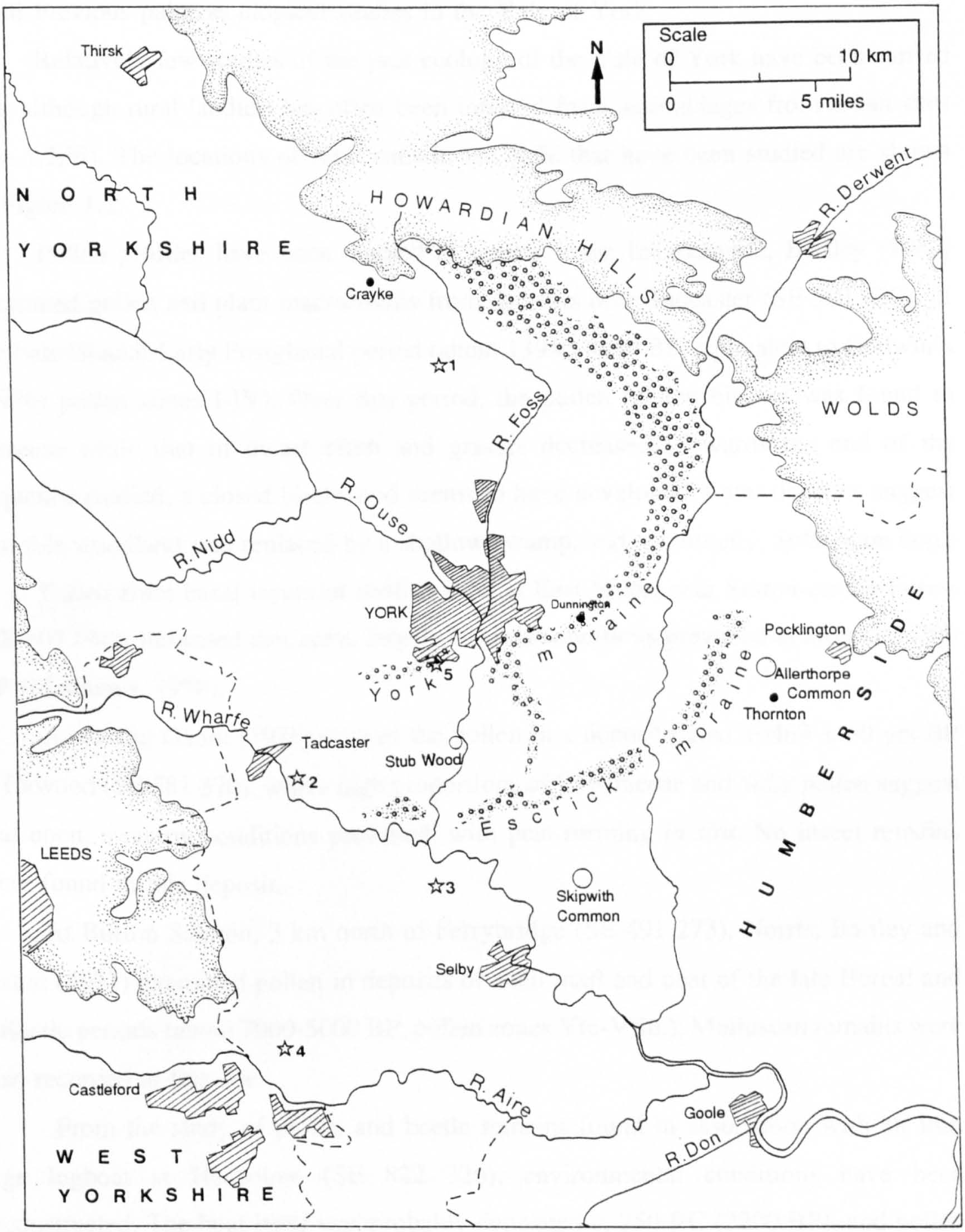


Figure 1.2 The Vale of York

░ Land over 61m (200 ft)   - - - -County boundaries

⁘ Morainic deposition: boulder clay and glacial sands

▨ ● Settlements   ○ Other sites mentioned in the text

☆ Previous palaeoecological studies in the area: **1** Matthews (1970)

2 Bartley (1962) **3** Jones and Gaunt (1976) **4** Norris, Bartley and Gaunt (1971)

5 Askham Bog (see Hall *et al*, 1979)

1.2.ii Previous palaeoecological studies in the Vale of York

Relatively few studies of the past ecology of the Vale of York have been carried out, although rural landuse has often been inferred from assemblages from urban sites (see 1.2.iii). The locations of rural sites in the Vale that have been studied are shown in Figure 1.2.

Pollen profiles have been studied at several sites: for example, Bartley (1962) examined pollen and plant macrofossils from deposits near Tadcaster (SE 501 430), of the Late Glacial-Early Postglacial period (about 13950-8950 BP, equivalent to Godwin's (1956) pollen zones I-IV). Over this period, the pollen of tree birches was found to increase while that of dwarf birch and grasses decreased. Towards the end of the sequence studied, a closed birchwood seems to have developed. Later deposits suggest that this woodland was replaced by a shallow swamp, and, eventually, *Sphagnum* bog.)

Pollen from basal layers of aeolian sand at East Moor, near Sutton-on-the-Forest (SE 607 640), indicated that open, largely treeless conditions prevailed at around 10700 BP (Matthews, 1970).

Jones and Gaunt (1976) studied the pollen in a deposit dated 10469 ± 60 yrs BP at Cawood (SE 581 370), where high proportions of Cyperaceae and *Salix* pollen suggest that open, swampy conditions prevailed, with peat forming *in situ*. No insect remains were found in this deposit.

At Burton Salmon, 3 km north of Ferrybridge (SE 491 273), Norris, Bartley and Gaunt (1971) examined pollen in deposits of shell marl and peat of the late Boreal and Atlantic periods (about 7000-5000 BP, pollen zones VIc-VIIb.). Molluscan remains were also recorded at this site.

From the study of pollen and beetle remains found in association with an Iron Age logboat at Hasholme (SE 822 326), environmental conditions have been reconstructed. The boat itself was probably deposited *c.* 250 BC (2200 BP), and pollen evidence from underlying peat deposits laid down over the period *c.* 4710-540 BC, 6660-2490 BP suggests that the vegetation of the surrounding dry land was dominated by oak woodland (Millett and McGrail, 1987). Occasional peaks of hazel pollen suggest that some form of woodland management, possibly coppicing, was occurring. There is little evidence for agricultural activity in the region from the pollen diagrams. The insect assemblages contained almost no dung beetles, suggesting that livestock, if present, were not abundant.

Further south and west on the Humberhead Levels at Thorne Moors (SE 721 153), the coleopteran remains associated with a Bronze Age feature (about 3000 BP) have been studied (Buckland and Kenward, 1973; Buckland, 1979). The remains of many species no longer found in the Thorne area were identified; several of these are now only found on the continent of Europe. Buckland suggests that climate in the Thorne area may have been more continental in this period than at present, allowing more thermophilous species to survive. Over 25% of the taxa recovered at Thorne were associated with woodland. From the ecological and hostplant preferences of these species today, a landscape dominated by birch/alder fen, with much dead wood (perhaps on oaks suffering dieback caused by a rising water table), and some areas of open water, has been reconstructed.

Turner (1960; 1965) examined pollen profiles from Thorne Moors and inferred a period of extensive clearance of woodland from about 400 BC to 100 AD.

At Cowick, near Snaith, South Humberside (SE 653 205), plant remains (pollen and macrofossils) and insect assemblages (Coleoptera and Trichoptera) have been studied from deposits in the moat of a medieval royal manor house (Hayfield and Grieg, 1989). The coleopteran assemblages were used to suggest that the moat itself was kept clean for the decades immediately following its construction (documented as AD 1323); however, natural succession and additional anthropogenic debris appear to have contributed to its later stagnation. The environment around the site seems to have been open countryside, but with a significant presence of trees: 3.5% of the total number of beetle individuals recovered were of species associated with wood and trees (74% were aquatic species).

At Askham Bog, 5 km south-west of York (SE 570 480), pollen profiles covering the post-glacial period have been studied (summarised in Hall *et al.*, 1971). These show the establishment of forests including limes, *Tilia*, oaks, *Quercus*, and elm, *Ulmus*, before the formation of a raised bog on the site at around 7000 BP. However, the bog appears to have remained a local feature, resulting from small-scale topographic conditions, and forest persisted on the drier land surrounding it. Pollen from the post-Roman period onwards suggests a landscape of arable and pasture-lands, with some woods, coppice and heathland (Kenward *et al*, 1978), but unfortunately provides little information on the distribution or quantities of these various landuses. In the upper peat layers, abundant macrofossils (achenes) of *Cannabis sativa* L. suggest that, in the medieval period, the bog was the site of hemp-retting, the steeping of hemp stems in water to make the fibres suitable for working; Bradshaw *et al.*, 1981.

Around the Vale of York, sites in the Yorkshire Wolds, Moors, Pennines, and Vale of Pickering have been studied. The extent of palaeoenvironmental evidence in these areas is generally greater than that available for the Vale of York, and it suggests that the influence of man on the landscape was felt much earlier than on the Vale. In the Yorkshire Wolds, pollen from Willow Garth (from a deposit covering the period c.9500 BP-present, with discontinuities around 7980-4300 BP and 3300-2200 BP) was studied by Bush (1988). Here, tree birches dominate the pollen diagram around 9400 BP, but the expected succession to other forest tree species such as oak and lime does not occur. The abundance of pollen of grassland herbs, along with the occurrence of insects characteristic of open grassland, such as *Phyllopertha horticola* (L.), indicate that the vegetation in the vicinity was already being dramatically influenced by man in the early Mesolithic period.

Pollen and plant macrofossils from peat deposits on the North York Moors and its adjacent lowlands have been identified by various workers (see reviews by Jones *et al.*, 1979, and Simmons *et al.*, 1982). These suggest that the 'wildwood' of the early Flandrian was modified by man from at least the late Mesolithic onward (from around 10400 BP).

In studies of pollen profiles from the central Pennines at Nidderdale, Tinsley (1975) identified three major periods of woodland clearance, associated with the Beaker Folk of the Bronze Age (from around 3950 BP), the Romano-British (from around 2200 BP), and Cistercian institutions (granted large areas of land in the area, around 800 BP).

1.2.iii Environmental archaeology of urban sites in York

In contrast to the relatively poorly studied rural Vale of York, environmental evidence from the city itself (and, to a lesser extent, other nearby settlements, for example, Beverley: see Hall and Kenward, 1980; McKenna, 1991) is abundant. York's history of nearly two thousand years of more or less continual occupation as an urban site, and the accumulation of deep almost anoxic waterlogged deposits with good preservation of fossil material, have made the city ideal for environmental archaeological studies (O'Connor *et al.*, 1984). Environmental reports on a number of sites have been published, from deposits of pre-Roman to late medieval date.

Pre-Roman

Buried soil from a site at Skeldergate (Hall, Kenward and Williams, 1980) contained plant macrofossils and insect remains indicative of open pastureland, with plants including *Plantago major* L., *Ranunculus* Section *Ranunculus*, *Polygonum* spp., and with *Aphodius* spp. the dominant beetle. However, some woodland or tree-associated species were recorded, including the scolytid beetle *Dryocoetinus villosus* (Fabricius), usually found on large old oaks, and seeds of the woodland herb *Moehringia trinervia* (L.) Clairv.

Roman

Evidence from the Roman period (*c.* 71-400 AD, or 1879-1550 BP) has been recovered from several sites, including 1st-2nd century AD warehouses in Coney Street (Kenward and Williams, 1979), where large assemblages of grain pests such as *Oryzaephilus surinamensis* (L.), *Cryptolestes ferrugineus* (Stephens) and *Sitophilus granarius* (L.), were found, along with charred grain and the seeds of arable weeds. Other sites of this period include a 2nd-3rd century AD (1850-1550 BP) timber-lined well in the Bedern (Kenward *et al.*, 1986), and deposits from the vicinity of the Roman Colonia (24-30 Tanner Row and 5 Rougier Street) (Hall and Kenward, 1990). At the Bedern site, assemblages were dominated by grassland species, with plant macrofossils including grasses, *Linum catharticum* L., *Prunella vulgaris* L., and *Trifolium* flowers and pods. The insect remains included dung beetles (*Aphodius* spp.), and phytophages such as *Gymnetron pascuorum* (Gyllenhal) (hostplant plantains, *Plantago* spp.), and *Chaetocnema concinna* (Marsham) (hostplants *Rumex* and *Polygonum* spp.). The deposits at the Tanner Row and Rougier Street sites spanned a greater period and showed a gradual change in ecology, from open vegetation of grassland and disturbed ground (with insects including the weevils *Apion* and *Sitona* spp.), to more intensive urban landuse, with abundant grain pests, and organic layers indicating the stabling of horses.

Roman deposits have also been studied from the fill of a well in Skeldergate (Hall *et al.*, 1980), built in the 2nd century AD (1850-1750 BP), but probably backfilled from the 4th century AD onward. This yielded a rich flora and fauna, indicative of disturbed conditions (and including plants such as *Juncus* spp., *Rumex* spp. and *Stellaria media* (L.) Vill.), and distinctive groups of stored product beetles, probably dumped in the well with stored grain, and peatland species, imported with blocks of turf or peat.

Insects from a Roman sewer system in Church Street (Buckland, 1976) were of species tolerant of fairly foul conditions, but included stored-product pests.

Anglo-Scandinavian

Deposits of Anglo-Scandinavian date (from around 850-1068 AD, 1100-882 BP) include those from 6-8 Pavement (mid 9th-late 11th century AD), where pollen spectra were dominated by grass and cereal types. Plant macrofossils mainly belonged to 'disturbed ground' species, and the beetle and bug assemblages were dominated by synanthropic and decaying-matter species (Hall *et al.*, 1983). All the large constructional timbers identified were oak, with alder (*Alnus glutinosa* (L.) Gaertner), ash (*Fraxinus excelsior* L.) and hazel (*Corylus avellana* L.), important for the production of posts. Smaller wood elements and wattle were generally hazel, with some willow (*Salix* spp.), and smaller numbers of various other taxa (Addyman, 1991). Hazel was also an important constituent of wattle at Coppergate (Hall, 1984), where the age-distribution of wattle elements suggests that coppicing may have been practised over at least part of the Anglo-Scandinavian period.

At the General Accident (24-30 Tanner Row) and Rougier Street sites, the few late Anglo-Scandinavian period samples (11th and 12th centuries AD), included a rich weed flora (Hall and Kenward, 1990). Pit fills in the Bedern area, including one dated at 780 ± 80 AD, contained remains of plants of disturbed ground and grassland, and marsh/foul-matter insects which suggest that earlier (Roman) intensive occupation of the site had ceased (Kenward *et al.*, 1986).

The most intensively studied Anglo-Scandinavian deposits from urban York are those from 16-22 Coppergate (Kenward and Hall, in prep.). Here, plant macrofossils, invertebrate remains and bone were recovered from deposits representing the earliest

Anglo-Scandinavian date to c.975 AD (975 BP). In pit fills from one tenement (Tenement B), of early Anglo-Scandinavian date, distinctive groups of woodland plants and insects were recovered, including the woodland mosses *Thuidium tamariscinum* (Hedw.) Br. Eur., *Neckera complanata* (Hedw.) Hüb., *Mnium hornum* Hedw., and *Eurhynchium striatum* (Hedw.) Schimp. Vascular plants represented included *Oxalis acetosella* L., *Ceratocapnos (Corydalis) claviculata* (L.) and *Stellaria holostea* L. Woodland insects recovered in these samples include *Deporaus betulae* (L.) and *Platypus cylindrus* (Fabricius), possibly imported with the mosses. Timbers at this site were again chiefly oak, but alder was also an important component of the assemblages (Hall, 1982). Bone assemblages from various Anglo-Scandinavian sites commonly contained wetland bird species, suggesting that there were areas of wet pasture or floodmeadow in sufficient proximity to the city to act as a source of wildfowl and waders (O'Connor, 1986b).

Medieval

Twelfth - thirteenth century contexts from the General Accident and Rougier Street site yielded mainly evidence of human faecal material, with some other organic deposition, and a few grain pests (Hall and Kenward, 1990). At the Bedern, deposits of medieval and post-medieval date contained insect assemblages rich in 'house fauna' (Hall, Kenward and Robertson, 1993a-c). Generally, 'domestic' insects (eg. *Anobium punctatum* (Degeer) and *Tipnus unicolor* (Piller & Mitterpacher)) become more important than the 'dung' and 'foul-matter' species found in Anglo-Scandinavian deposits (O'Connor *et al.*, 1984).

Insect and plant assemblages from deposits in the city have been used as evidence of the change in urban living conditions over time. The general preponderance of grain pests and near absence of a foul matter fauna in Roman deposits contrasts greatly with those of Anglo-Scandinavian date, where stored grain insects are virtually unknown, but insects of rotting vegetation are abundant, suggesting a major change in waste disposal and food storage regimes in the city. At some sites, such as the General Accident and Rougier Street sites, deposits spanning the post-Roman period seem to indicate a drastic reduction in the intensiveness of urban occupation at this time (Hall and Kenward, 1990). In the medieval period, assemblages more closely resemble those of early twentieth century towns, with representatives of today's synanthropic species becoming important.

Evidence for woodland in the environs of York from this material must remain vague, however. Although it seems unlikely that, for example, woodland mosses imported into the city in the Anglo-Scandinavian period (Kenward and Hall, in prep.) would have been carried far, large quantities of the clubmoss *Diphasiastrum complanatum* (L.) Holub appear to have been imported, probably from Scandinavia, for use in dyeing processes at this time, so the long-distance transport of plant materials, and concomitant insects, cannot be ruled out. Even if the source was local, organic remains preserved *ex situ* in urban deposits can give little information on the availability of woodland resources around the city. Higher value products, such as timber, are more likely to have been transported considerable distances. For example, in the medieval period, timber for the construction of York castle was brought from Dorset (Kaner, pers comm.). By 1641, softwoods were regularly imported into the East Riding port of Hull to compensate for the lack of local timber (Best, 1641, reprinted 1857).

1.3 Other evidence available for the reconstruction of past woodland extent and management

1.3.i General

In addition to the evidence from environmental remains such as that outlined above, several further sources of data on the extent and use of woodland resources exist, and these are summarised by Rackham (1980), and Watkins (1990). They include evidence *in situ*, in the form of archaeological features such as woodbanks delimiting medieval woodlands, ecology of extant woods (for example, the presence of certain 'ancient woodland indicator' species), and individual old trees, which, in the case of coppice stools, or the self-layering small-leaved lime (*Tilia cordata* Miller), may be several hundred years old. *Ex situ* evidence includes timber and woodland products in archaeological sites and ancient buildings (Rackham, 1972), and that provided by documents, maps and place-names.

1.3.ii Other evidence for woods in the Vale of York

At present, the Vale of York is dominated by arable and, to a lesser extent, grassland. Those woods that do remain may occupy the sites of ancient woodland

(Carter, 1989), but many have been extensively altered in recent times, particularly since 1950, by clearfelling and replanting. Archaeological evidence within woods, such as woodbanks, is sparse.

Peterken's (1974) system for the use of plant species as indicators of ancient woodland has been developed for local woods by Gulliver (pers. comm.). The concept of 'indicator species', originally applied to woodland herbs only, has since been developed or discussed for other groups, among them lichens (Harding and Rose, 1986), spiders and pseudoscorpions (see Marren, 1990), and Coleoptera (Harding and Rose, 1986; Garland, 1983). The technique relies on the relatively poor dispersal and colonisation abilities of the indicator species recognised, and the tendency of relict populations to survive even where the habitat has been altered to some extent. The use of such techniques can be valuable, although the information that can be derived on the history of woodlands is limited; for instance, it would appear that 'primary' woodland areas (those with a history of continual forest cover over the past 10000 years) cannot be distinguished from other, ancient woodland sites (those with a history of woodland cover from AD 1600, 350 BP; Day, 1993). The colonising abilities, and hence indicator status, of herb species varies geographically, so that many of the plants suggested as indicators in Lincolnshire by Peterken (1974) differ from those listed by Rackham (1980) for East Anglia, or compiled by Hornby and Rose (quoted in Marren, 1990), for Southern England. The same appears to be true for beetles (Greenslade, 1968). In areas with relatively little woodland, indicator species should be more reliable than in parts of the country where woodland is common (Marren, 1990), but the increased rarity of such species in these areas increases the probability of local extinction. Thus, in the Vale of York, presence of relatively few of the classic 'old woodland indicator' herb species often suggests that a wood is ancient, but, in some sites of known antiquity, recent management practices (especially conifer planting) have reduced this component of the flora. The use of biological indicators would therfore appear to be of limited value in interpreting the history of Vale of York woodlands.

The earliest written records for the area are those of the Domesday book of AD 1086 (864 BP). Although often vague in nature (Wightman, 1964), these reveal that the East Riding as a whole had a particularly low proportion of wooded land (only 4.4%). In the North Riding of Yorkshire, 12% of the land area is recorded as woodland. However, this figure appears to include a large part of the North York Moors, the greater part of which appears, from pollen evidence, to have been treeless by this time. If the Moors are excluded, only 6.1% of the area is recorded as forest (Rackham, 1980). In contrast, around 16% of the land area of the West Riding was wooded. The most well-wooded parts of the Vale were the western fringes, and along the Rivers Derwent and Ouse (Darby and Maxwell, 1962). In comparison with the wealthier Lincolnshire to the south, the Vale of York seems to have been in decline in this period, with low land values and whole settlements abandoned (Knowles, 1990). One of the early Norman kings (William I, II, or Henry I) established the Forest of Galtres to the North of York, primarily as a hunting ground. In 1316 AD, its boundaries, which had contracted somewhat from those of the original Forest, ran from the Walls of York North to Crayke (see Figure 1.2), and bounded to the East and West by the Rivers Foss and Ouse (Cowling, 1967). Within this area, Forest law applied, and permission was needed to make assarts (bringing land into cultivation); although Galtres was probably well-wooded initially (Kenward *et al*, 1978), the term 'Forest' refers to its legal status, rather than its physical appearance. Records of gifts of timbers from the Forest show that at least part of the area was high forest, capable of supplying large oaks for construction (Cowling, 1967). However, much of the landscape may well have been more open, and there were several settlements within the bounds of the Forest, with cultivated land and pasture. By the time the land was legally disafforested in 1630 AD, stocks of deer and timber were still substantial, but much of the land was enclosed for farmland soon after the cessation of Forest law.

Two other Forests, the Forests of Langwith (to the south of the city) and Knaresborough, to the west, on the borders of the Vale, also supplied timber used in the city of York (Kaner, pers. comm.).

In contrast to many areas of Britain, documentary evidence for landuse in the Vale of York in the 11th and 12th centuries AD is good, at least for lands under royal or monastic control (Harrison, 1984). Unfortunately, there is little archaeological evidence from this period, except for that from a few important settlements such as York.

Wightman (1968) has made a study of the documentary sources available for vegetation in the Vale of Pickering *c.* AD 1300 (650 BP), and uses legal, ecclesiastical, royal and manorial records to reconstruct the probable pattern of vegetation at that time. However, these records show a bias towards those lands owned by large landowners, particularly the crown and monastic institutions. Thus royal Forests tend to be well documented, with even small infringements of forest law being recorded. However the histories of private parks and woodlands are less well known, and records of the nature of woodland (e.g. spatial continuity of canopy cover, tree species structure, and rates of deforestation) are poor.

In the early eighteenth century, the Vale had many large, heathy commons (such as that at Holme Moor, which occupied 7000 acres, 2833 ha.). Documentary evidence reveals drainage and enclosure in the eighteenth century (Harris, 1961), but much of the Vale appears to have remained poorly drained into the nineteeth century.

Other documentary evidence exists in the form of maps. The earliest maps likely to provide useful evidence for the landscape historian are estate maps, which were produced from around AD 1580 (Rackham, 1980). The first edition Ordnance Survey maps for the region were surveyed in 1844-1855, and these have been used by the Nature Conservancy Council (now English Nature) as the main source for an inventory of ancient woods in the Harrogate, Hambleton, Selby and York districts (Carter, 1989). This estimates that ancient woodlands of over 2 hectares in extent cover approximately 4707 ha. of the district (1% of the land area), although many of these are on the limestone periphery of the Vale (for example, remnants of the Forest of Knaresborough at Birkham Wood, SE 357 549).

Historical records also exist in the form of herbarium sheets, and other natural history collections. The herbarium of the Yorkshire Museum holds records for the 'ancient woodland indicator' species *Chrysosplenium alternifolium* L. and *Oxalis acetosella* L. from Moreby Hall, Naburn (SE 596 433), in 1928 and 1929, and *Paris quadrifolia* L. from sites at Sand Hutton, and 'near Tillmire, York', in 1883 and 1945. However, the problems involved in the use of indicators in existing woods also hold for such records, compounded by possible uncertainties associated with poor or incomplete documentation.

Overall, archaeological and historical records give little information to suggest early clearance of Vale of York woodlands by man. Permanent settlement would appear to have occurred later here than on the surrounding uplands (see Bush, 1988, and Jones *et al.*, 1979). However, from the Anglo-Scandinavian period onwards, there is evidence that woodlands were managed, possibly indicating scarcity of woodland resources in the face of the demands of the large urban population of York. The timber requirements alone of a large city in this period would have been massive, and would have increased through the early middle ages as larger, timber frame houses replaced earlier structures. By the time of the first records in the 11th century AD, at least the eastern part of the Vale was largely devoid of woodland, and this pattern appears to have held throughout the historic period, so that Humberside is now amongst the least wooded counties in England.

1.4 The use of insect death assemblages in woodland archaeology

'Woodland assemblages' of insects have been identified from a number of ancient archaeological and natural sites in the past. In particular, the older sites studied have yielded faunas rich in woodland-dependent species, some of which have become rare, or are extinct in Britain today. Many of these 'old forest species' or *Urwaldtiere* are saproxylic, feeding on dead and decaying wood in undisturbed habitats. Such niches are now scarce in this country, which has one of the lowest percentages of wooded land in Western Europe: only around 8% of Britain is woodland, whereas, for most other countries in Europe, the figure exceeds 25% (Garland, 1983). A high proportion of the woodland that does exist is intensively managed, in the past particularly for coppice products, now, more frequently, for timber production using alien species.

Thus Girling and Greig (1977), working on material from a site at Hampstead Heath, London, where deposits from 7000-3000 BP (Atlantic - sub-boreal period) were studied, described an 'old forest' fauna, from the oldest deposits at least, with beetles such as *Gastrallus immarginatus* (Müller, P. W. J) (Anobiidae) and *Ernoporus caucasicus* Lindemann (Scolytidae). However, after the period of the elm decline, such taxa become a smaller proportion of the fauna at this site.

Similarly, 'old forest' insects have been recovered from deposits of the sub-boreal period (approximately 5000-3000 BP, from pollen dating) at Worldsend, Shropshire (Osborne, 1972), with species including *Pycnomerus tenebrans* (Ol.) (Colydiidae), and *Porthmidius austriacus* (Sch.) (Elateridae). The latter species is no longer found in Britain, and both feed on rotten wood. At Shustoke, Warwickshire (Kelly and Osborne, 1963), deposits dated at 4830 ± BP by radiocarbon techniques yielded 'Urwaldtiere' including *Pycnomerus tenebrans*, *Rhysodes sulcatus* Fabricius (Rhysodidae), and *Ernoporus caucasicus*. *E. caucasicus* was first identified from Britain as a fossil at this site, but has since been discovered on *Tilia* at Moccas Park, Herefordshire (Allen, 1969), and has been historically present at other sites (Cooter, 1980). At Shustoke, it was found along with pollen and macrofossils of *Tilia cordata* and *T. platyphyllos*, which appear to have been an important part of the tree cover at the site.

Deposits described briefly by Osborne (1978), from Misterton Carr, Nottinghamshire, where the onset of accumulation has been dated at 4330 ± BP, contain in the earliest layers assemblages dominated by deadwood feeders such as *Sinodendron cylindricum* (L.) (Lucaniidae), *Grynobius* and *Anobium* species (Anobiidae), *Melasis buprestoides* (L.) (Eucnemidae) and *Ernoporus caucasicus*.

Duffey (1968) reported a single specimen of the large cerambycid *Cerambyx cerdo* L. (again, no longer present in Britain) from a Cambridgeshire bog oak dated 4000 BP. This has since been supported by a second record, confirming the species' status as a member of Britain's 'Urwald' fauna (Harding and Plant, 1978).

Bronze Age peats have yielded 'old forest' insects, at sites in Yorkshire and on the Somerset Levels. At Thorne Moors, Yorkshire, deposits of *c.* 3000 BP contain species such as *Zimioma grossum* (L.) (Ostomidae) and *Rhysodes sulcatus* (both now absent from the UK) (Buckland, 1979). In Somerset, Girling (1985) identified a fauna including *Pycnomerus tenebrans* and many other dead-wood and woodland insects from a Bronze Age site at Stileway.

However, Buckland (1979) points to potential dangers of using the occurrence of species outside of their present range as ecological indicators, suggesting that their present distribution is likely to be a function of factors other than simply the availability of undisturbed old woodland habitats. Annual temperature regimes are known to have changed over the periods involved in all the above sites, and, in certain cases, may have been more important than habitat loss in the contraction of the range of rare woodland species (Hammond, 1974). In some species, temperature conditions certainly seem to play a part in maintaining restricted ranges; thus the deathwatch beetle, *Xestobium rufovillosum* (Degeer) (Anobiidae), requires high temperatures before it will take to the wing. This could explain its diminishing range and apparently, marginal status in Britain today (Buckland, 1975).

1.5 Aims of this project

In summary, the aims of this project are twofold;

(i) To assess the feasibility of using insect death assemblages to reconstruct woodland history, by studying:

(a) archaeological insect assemblages laid down under different conditions, and, to provide comparanda,

(b) modern insect death assemblages from woodland and non-woodland sites.

(ii) To apply methods developed in (i) to sites in the Vale of York, and act as a basis for further palaeoecological research on sites in the region.

1.6 Nomenclature conventions

Nomenclature of bryophytes (mosses) follows Smith, (1978), and that of vascular plants, Kent (1992).

Insect nomenclature and order of families and genera follows Kloet and Hincks (1964, small orders and Hemiptera; 1972, Lepidoptera; and 1977, Coleoptera), except where there has been a more recent review, such as in the Royal Entomological Society Handbooks for the identification of British Insects. Nomenclature of Coleoptera no longer represented in Britain is as used by Freude, Harde and Lohse (1965-83).

Nomenclature of freshwater molluscs is as used in Macan (1977), terrestrial molluscs as in Kerney (1976).

Regularly used abbreviations are listed in the 'definitions and abbreviations' section, page 163.

Chapter 2 The classification of insects according to their ecology

2.1 Introduction

The classification of insect taxa into groups on the basis of their ecological requirements is particularly difficult, yet is essential for the interpretation of large assemblages of fossil remains from natural or anthropogenic deposits (Robinson, 1981). Various workers in the field of palaeoentomology have arrived at their own classifications, often emphasising certain ecological groups according to the nature of the assemblages and deposits being studied, and the aims of the investigation. Thus the classification arrived at by Girling (1980), and that discussed by Robinson (1981; 1983), stress the importance of the insects of a range of 'semi-natural' habitats such as woodland, fenland and meadow. This reflects the representation of members of these groups in the rural, natural (non-anthropogenic) deposits examined. In contrast, the classifications developed by Osborne (1971), and Kenward (1976; 1978; 1982), for application to insect assemblages from urban archaeological deposits, place more emphasis on the nature of synanthropic and decomposer communities. Kenward (1982) attempts to divide decomposer communities of foul matter from those in dry compost, excluding insects of poorly-represented natural habitats as these probably form part of the 'background fauna' in the deposits studied.

In order to illustrate some of the problems associated with such methods, two beetle groups were chosen, the ground beetles (family Carabidae) and weevils (superfamily Curculionoidea, families Nemonychidae, Anthribidae, Urodontidae, Attelabidae, Apionidae and Curculionidae). For each species in these groups, the major reference works available (listed at the end of this chapter) were scanned and, for those species recorded as associated with woodland to any extent, a code assigned. The code varied according to the weight given to the species' dependence on woodland in the various works consulted, ranging from **(1)** strongly associated with woods, to **(5)** rarely in woods. More detailed notes on the ecology of each species were also taken. Large synthetic works on the groups, such as Freude, Harde and Lohse (1965-83) were used to identify ecological requirements before minor papers scattered in the entomological literature, simply for ease of access to these data. The resulting lists of species associated with woodland are presented in Appendix 3.

2.2 Some problems associated with the ecological coding technique

2.2.i Bias in the available literature

One difficulty immediately apparent in this technique is the uneven nature of the entomological literature relating to different insect groups. Thus the Carabidae is a well studied family of generally large, active beetles which have been intensively studied and collected by coleopterists for over a century. As a result, the corpus of works of reference on this group is large, with volumes devoted to their habits, ecology and biogeography (for example, Thiele, 1977; Forsythe, 1987; Stork, 1990; Lindroth, 1992), as well as several keys to the British and European representatives of the family (e. g. Lindroth, 1976; 1986), which include details of locations and habits of the various species for collectors. In comparison, the weevils are relatively poorly covered; there is a key to the British Orthocerous Weevils (families Nemonychidae, Anthribidae, Urodontidae, Attelabidae and Apionidae) by Morris (1990), which includes descriptions of the ecology and hostplant preferences of the species covered, but the most recent work in English to deal with the superfamily as a whole is by Joy (1932), with limited information beyond diagnostic features. Fowler's (1887) volumes contain some information concerning habits and habitats of the British weevils. For information on weevil ecology, European works such as those of Freude, Harde and Lohse (1981 and 1983), and Hoffman (1958) were, of necessity, relied upon to a greater extent, together with personal communications from Prof. M. G. Morris and other entomologists.

The unevenness of the coverage of different groups in the entomological literature is apparent in families other than those mentioned above; the beetle families Chrysomelidae and Elateridae, for example, though both containing economically important pests as well as many large and obvious species, are very poorly represented in the works on Coleoptera in English. On the other hand, some groups such as the ladybirds (Coleoptera, family Coccinellidae) are well served by the literature (see, for example, Majerus and Kearns, 1986, Pope, 1953).

Where it has been necessary to use reference works on mainland European beetles, rather than literature on the same species in Britain, the reliability of the information obtained must be in question to some extent. Many species retain similar habits over wide geographic ranges: the carabid *Calosoma inquisitor* (L.) is regarded as a predator of caterpillars in oak woodlands in Scandinavia (Palm, 1959; Lindroth, 1986), Central

Europe (Freude, Harde and Lohse, 1965), and Britain (Chrystal, 1948; Harding and Rose, 1986; but see 2.2.iv, below). Penney (1966) found that the ecology of *Nebria brevicollis* (Fabricius) in Scotland was very similar to the ecology of the same species in England, as recorded by other observers, with the breeding season simultaneous across Great Britain. However, in other species, there may be considerable variation in the recorded ecology in different parts of the insect's range. Thus *Pterostichus madidus* (Fabricius), found mainly in woodland in Central Europe, is often encountered in open country and on cultivated soils in the west of Europe (Lindroth, 1986).

Even within Britain, the affinities of individual species may vary geographically. Greenslade (1968) found that the habitats of certain carabid species differed markedly between sites in Silwood Park (Berkshire), and Argyll. Species typical of woodland at Silwood, such as *Carabus problematicus* Herbst., *Cychrus caraboides* (L.), *Nebria brevicollis*, *Pterostichus niger* (Schaller) and *P. madidus*, were common in more open grassland habitats in the Argyll sites. This variation in local distribution may be caused by the difference in climate between the two sites, with the more humid Atlantic climate of Argyll allowing species which are restricted to woodlands in the south-east of England to exploit a wider range of biotopes. Similar effects have been observed among 'woodland indicator species' of plants; *Luzula sylvatica* (Hudson) Gaudin is a 'primary woodland' species in eastern England, but is regularly found outside woods in the west of Britain (Peterken, 1974). Land snails also display comparable ecological variation across their geographic ranges (Boycott, 1934, Evans, 1972).

Microclimate is known to affect the ranges of insects. In a survey of experimental work on 47 carabid species, Thiele (1977) found that the majority (67%) of the 'forest dwelling' species were hygrophilic, compared with only 6% of the species more typical of open field environments. In contrast, 59% of the latter group were xerophilic. Similar effects have been noted in the distribution of molluscs: species confined to, or typical of, East Anglian woodland appear to be hygrophilic (Paul, 1978). Humidity is a particularly important determinant in the distribution of land molluscs, as few species are able to control water loss from the body when active (Evans, 1972), and species confined to damp woods in the south and east of Britain, such as *Ashfordia granulata* (Alder) are often found in a variety of more open habitats in the west and north (Boycott, 1934).

Other environmental factors influencing the local distribution of carabids include temperature (see Dreisig, 1980), and light levels, with 'forest' beetles generally preferring cooler, damper and darker places than species of other habitats. Thus, on a larger scale the more continental climates of Central and Eastern Europe, where much work on beetle ecology has been carried out, might be expected to have the effect of limiting the niches available to insect species, and therefore, the range of habitat types they will inhabit.

Similarly, the extent of habitats available in different parts of a species' range could affect its ecological preferences; in Scandinavia, for instance, Lindroth (1986) records many species as occurring in woods, which British authors do not associate with woodland. *Elaphrus cupreus* Duftschmid is found in '..eutrophic fens in open country as well as in deciduous woodland' in Scandinavia (Lindroth, 1986), but woodland is not mentioned in the habitat descriptions given by Fowler (1887) and Forsythe (1987). This may be due to the relative abundance of forest habitats in Scandinavia when compared with Britain (see Chapter 1). In 1970, approximately 8% of Britain's land area was woodland; Sweden and Norway, in contrast, were 64% and 29% forest, respectively (Peterken, 1981). In both the Hydrophilidae (Coleoptera) and *Aphodius* spp. (Coleoptera, Scarabaeidae), Hanski (1980) found that species occurring in both Finland and England tended to favour more open habitats in Britain, and suggested that this might represent a shift in species ecology to exploit the more abundant open land resource in Britain (although, in the more continental climate of Finland, local environmental factors such as humidity may also play a part in confining some species to woodland habitats).

2.2.ii Mobility

Many insects are capable of dispersal over long distances, and this ability can affect the extent to which reliable ecological codes can be assigned to individual species. For example, the winged adults of *Helophorus* species (Coleoptera, Hydrophilidae) are ready fliers, and form mixed-species swarms which crash-land on reflective surfaces such as cars in summer, sometimes well away from their aquatic habitat (Benham, 1975; Verdcourt, 1983). *Helophorus* spp. frequently occur in terrestrial archaeological death assemblages, apparently as part of the windborne 'background element' (Kenward, 1978). However, species of different habitats differ in their dispersal abilities; Southwood (1962) states that the level of migratory movement in insect species is positively correlated with impermanence of habitat, and carabids of temporary, arable habitats are more frequently trapped in flight than those of more permanent habitats such as heath and woodland (Greenslade and Southwood, 1962). Woodland beetles are generally less able to disperse over unsuitable habitats; the deathwatch, *Xestobium rufovillosum*, for example, is rarely observed to fly in Britain (although British examples are fully winged), and it probably requires high summer temperatures before flight will occur (Buckland, 1975); for most insect species, there is a temperature threshold, below which flight is inhibited, and the level of these thresholds varies between species (Taylor, 1963). One of the factors contributing to the decline of 'old forest beetles' or 'Urwaldtiere' in Britain (Buckland, 1979) may be the insects' inability to respond to fragmentation and loss of their habitat by dispersal.

Evans (1990) suggests that, for carabids at least, although the 'locomotor lifestyle' (ranging from fast-running to burrowing) of a species may have evolved in response to the demands of a particular habitat, once developed, most of these lifestyles prove suitable for a wide range of different habitats. Despite this, the carabid faunas of woodland and grassland sites are distinctive (Maelfait and Desender, 1990) and, in other beetle groups which display a different range of locomotor lifestyles than the Carabidae, it seems likely that there is a greater degree of specialisation to particular habitats.

The mobility of insects allows individual species to utilise different habitats at different stages in their lifecycles, and this can further complicate attempts to classify the ecological requirements of a species. Thus aphids may move between hostplants (see below), and psyllid species (Homoptera, Psylloidea) fall into two major groupings, those that overwinter on their hostplant, and those that migrate to a secondary 'shelter plant'. *Aphalaria* spp. fall into the latter group and move from their true hosts, *Rumex* and *Polygonum* species (mainly in open habitats) to evergreens (e.g. *Pinus* spp.), often in woods and scrub, for the winter period (Hodkinson and White, 1979). The Coleptera (unlike the Hemiptera) undergo complete metamorphosis, with a larval stage morphologically very different from the imago. In extreme cases, such as the wood-boring larvae of some cerambycids or weevils, the larvae are apodous, or virtually apodous (Evans, 1975), while the imagines may be winged and highly mobile. Adult cerambycids are often found feeding on flower heads and leaves some distance from the larval host trees (Duffey, 1952). Such behavioural and developmental adaptations increase the difficulty of assigning species to individual ecological groupings.

To some extent, these problems have been dealt with by placing a single species in more than one ecological grouping, where a species is stenotopic but displays strong affinities for different habitats at different seasons or developmental stages (see 2.6, below). However, the patterns of insect mobility are not always fixed as in predictable migrations, but may be influenced by a range of factors including intra- and interspecific competition, predation and food availability (Dempster, 1968). Such factors emphasise the importance of dealing with the requirements of whole assemblages of species, rather than dwelling on the habits of individual taxa recovered in a sample.

2.2.iii The habitat mosaic

Certain habitat types, such as most modern arable fields, are discrete and clearly defined. However, in the case of others, boundaries are harder to define; an old field being invaded by scrub, for example, will display a gradation of environmental factors across successional stages and contains conditions suitable for insects of a wide range of habitat types in a small space. Thus species of marshland and woodland can both find breeding sites in alder carr. The nature of the habitat mosaic and edge effects further limit the descriptive value of simple ecological coding systems.

2.2.iv Evolutionary change

The habitat requirements of insects appear to be remarkably consistent over long periods of time (Coope, 1991), and, for many species which are now rare in the British Isles, habitat loss (and an inability to adapt to exploit the new habitats being created by human intervention on the landscape) are often cited as the cause of population declines (see, for example, Hyman, 1992).

Certain species have been able to adapt in order to invade newly available habitats; for example, species now seen as synanthropic are known to have existed before the urban landscapes they now inhabit, although the actual ecological changes necessary to allow them to exploit these new environments may have been minor (Kenward and Allison, in press). In the case of land snails, Evans (1972) suggests that the development of synanthropy may be due, not to a change in the species' ecological requirements, but rather in the way those requirements are met. Osborne (1974) records remains of *Calosoma inquisitor*, a predatory carabid today regarded as strongly associated with oakwoods (see section 2.2.i, above), in deposits from Lea Marston, Warwickshire, which were dated (by six radiocarbon dates) at around 9500 BP. Pollen evidence from the site suggested that *Quercus* and other thermophilous trees were absent, although *Salix* and *Betula* spp. were abundant. It appears that the ecological requirements of this species have been capable of some plasticity over the postglacial period, although the extent of adaptation may have been small. The Lea Marston assemblage was laid down in woodland conditions, and it is only in tree species structure that the woodland differed from the present ecological niche of *C. inquisitor.*

Overall, the sparse evidence available suggests that there has been little change in the ecological requirements of insect species in the Pleistocene period. However, when the ecological coding of species is being carried out for the purpose of paleoentomological research, the possibility of significant evolutionary changes over the timescales involved cannot be excluded.

2.3 Hostplants

In certain species it may be possible to use an association with a particular hostplant to reinforce the assignment of that species to a particular ecological group, as the ecological requirements of both the plant and the insect can be taken into account. However, this can only apply to certain phytophagous species. Relatively few of the carabids (37 of 138 species investigated by Lindroth, 1949) take plant foods, and those that do rarely appear to be highly specialised phytophages (exceptions include the cereal ground beetle, *Zabrus tenebrioides* (Goeze), which feeds on the young milky grains of rye, wheat, and barley, but ignores oats, Thiele, 1977).

Even among a largely phytophagous group such as the weevils, the range of hostplants utilised will vary between species. Certain highly specialised insect taxa will be found on only one or two hostplants; for example, *Miaris campanulae* (L.) feeds only on *Campanula rotundifolia* L. and *C. glomerata* L., and does not attack other members of the genus such as *C. trachelium* L. Others (such as many of the short-snouted weevils, *Phyllobius*, *Polydrusus* and *Strophosomus* spp., and most of the root-feeding weevils) feed on a wide range of plants. *Phyllobius pyri* (L.) is found on herbaceous taxa such as *Urtica* spp., as well as a wide range of woody plants, so may indicate one of a variety of habitat types from waste ground and field edges to mature woodland.

Some insects, such as some of the aphids (Homoptera, superfamily Aphidoidea) migrate between hostplants in different habitats; thus the bird cherry aphid

Rhopalosiphum padi (L.) spends autumn to spring on *Prunus padus* L., but feeds on various grasses in the summer (Dixon, 1973). Others, however, utilise the same plant throughout the lifecycle; thus, members of the genus *Sitona* (Coleoptera, Curculionidae) feed on the root nodules of leguminous plants as larvae, and on the aerial parts as adults (although their abundance and ready flight means that some species are often found well away from their hosts; Morris, pers. comm.; Kenward, 1985). Just as the broader ecological requirements of insects may vary over a species' range, the preferred hostplant may change; Allen (1956) reports that the anobiid beetle *Gastrallus immarginatus* (Müller) appears to feed specifically on *Acer campestre* L. at the northern and western edges of its distribution in Britain and Scandinavia, whereas it is not host-specific in Central Europe, and several species of bark beetles attack spruce in the southern part of Denmark and Fennoscandia, and pines in the north of the region (Lekander *et al.*, 1977).

Hostplant-insect relationships are relatively poorly known for some species, and it appears that hostplant selection is capable of modification by experience (Crowson, 1981); this may add further complications to attempts to list insect hostplants. The strength of associations between insect and plant species vary, and the compilation of hostplant lists such as those given in Cooter (1991) will necessarily involve a degree of judgement on the part of the author to decide which species are too polyphagous to be listed, and which associations are 'typical' (Kennedy and Southwood, 1984). As a result, such lists may appear to disagree; thus Hoffman (1958) and Freude, Harde and Lohse (1981) list the hostplant of the weevil *Caenopsis waltoni* (Boheman) as buckshorn plantain, *Plantago coronopus* L.; however, this association is not made by Philp (1991), or Bullock (1992). Further problems with the determination of insect-host relationships are discussed elsewhere (Chapter 3).

2.4 The ecological classification system used

Despite the problems encountered in the attempt to define ecological groups of woodland carabids and weevils, and the reservations outlined above, it was felt that a system of ecological classification was necessary in order to subdivide otherwise unwieldy lists of taxa recovered from sites.

For each species encountered in archaeological or modern assemblages, the entomological literature was consulted as outlined for the carabids and weevils (see above). The main works used are listed at the end of this chapter. The schema used for classification is shown in the diagram below (Figure 2.1). This arrangement broadly follows those of Kenward (1978) and Robinson (1981; 1991), with modifications to reflect the greater degree of detail on the woodland habitats required from these data (as opposed to the emphasis on communities of decomposing matter, and synanthropes found in archaeological deposits).

The five-point coding scheme of strength of association with woodland used in the classification of 'woodland' carabids and weevils (see Appendix 3) can be related to the broader classification schema in Figure 2.1; those species regarded as relatively strongly associated with woodland (graded **1**, and some of those graded **2**) will fall within the group 'woodland'(WOO). Species graded as **2** and **3** are generally 'decomposers/litter dwellers'(LIT), or 'associated with trees'(TRE). Species less strongly associated with woodland (those graded **4** or **5**), are unlikely to fall into any individual one of the groups (unless they are markedly eurytopic, in which case they are coded EUR).

Where an insect species is commonly found in more than one of the habitat types, but still shows clear preferences for a small number of environments (two or three), a code was given for each of these; thus certain species appear more than once in the finished list. However, very few species did not appear to fit within a single ecological group, and, among those taxa coded twice, the two codes were often not exclusive (for example, several litter-dwelling species show a strong preference for woodland or damp habits; the staphylinid beetle *Lesteva longoelytrata* (Goeze) is coded LIT and MAR). The groups to which each species from any of the samples examined were assigned are given in the species lists, Appendices 1 and 2.

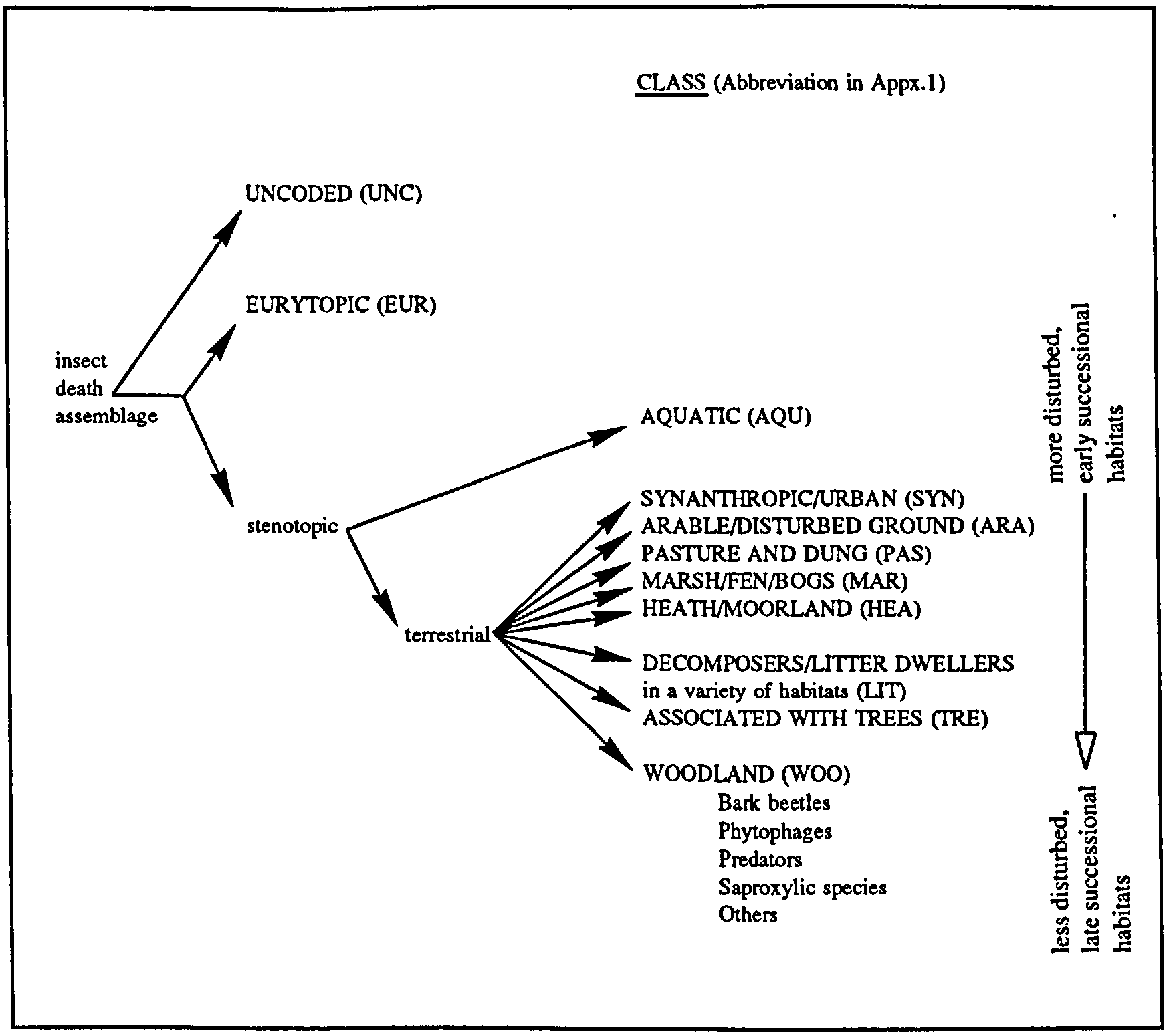


Figure 2.1 Schema for the ecological classification of insects recovered from a death assemblage.

2.4.i Eurytopic Species (EUR)

Species which are regularly recorded in many habitat types, with little apparent selectivity, were assigned to a group of eurytopes. These include common, widely distributed, often polyphagous species such as the carabids *Clivina fossor* (L.) and *Trechus obtusus* Erichson, *Tachyporus* spp. (Staphylinidae; found in litter and climbing among vegetation in habitats ranging from open arable land to woodlands). However, species which are found in many different habitats may still display narrow microhabitat requirements; the staphylinid beetle *Zyras humeralis* (Gravenhorst), for example, is associated with the nests of the ant *Lasius umbratus* (Nylander). In such cases, eurytopic taxa can still be useful in environmental reconstruction.

2.4.ii Aquatics (AQU)

Species spending the majority of their lifecycle underwater, such as the Haliplidae, Noteridae, Dytiscidae, Gyrinidae, most of the Hydrophilidae, and some members of the Sphaeridiinae (Coleoptera), were assigned to this group. Aquatic species may display a considerable degree of habitat specialisation (see Balfour-Browne, 1940-1960, Friday, 1988); thus for example, *Hydroporus incognitus* Sharp (Coleoptera, Dytiscidae), is one species associated in various publications with leaf-litter in woodland ponds. However, it appears that a single water body may provide within it suitable conditions for the survival of several species with differing ecological requirements; thus a modern death assemblage from beside the pond in Stub Wood (Sample SW3) contained both *Hydraena nigrita* Germar ('gravel and stones in rivers, often shaded') and *H. testacea* Curtis ('stagnant water or muddy streams', Friday,1988). Since the aim of this study was to concentrate on woodlands, rather than the aquatic habitat, further subdivision of this group was avoided.

2.4.iii Synanthropic/Urban species (SYN)

This group includes species attacking timber, such as the anobiid beetles, and stored product pests, such as many of the spider beetles (Ptinidae), and many of the Dermestidae (Coleoptera). These are generally of minor importance in natural deposits, although species such as the furniture beetle, *Anobium punctatum* (Degeer), and the deathwatch beetle, *Xestobium rufovillosum*, originally found in woodland habitats, may occur in association with humans.

2.4.iv Arable/Disturbed ground species (ARA)

Includes carabids of open ground (e. g. many *Amara* spp.), crop pests and phytophages of arable weeds (such as some *Ceutorhynchus* spp., *Phyllotreta* spp., and *Meligethes aeneus* (Fabricius)). Arable land habitats often have a characteristic beetle fauna (Robinson, 1983), but many of these species are widely dispersed by flight, and may occur in large numbers some distance from obvious potential habitats.

2.4.v Pasture/Dung species (PAS)

This group contains phytophages of meadowland plants, such as the weevils (many *Sitona* and *Apion* spp.) which feed on clovers, as well as root-feeding elaterids and scarabaeids, and dung beetles (excluding those dependent on sheltered woodland habitats). It is roughly equivalent to Robinson's (1991) groups 'Pasture/dung', '?Meadowland' and 'On roots in grassland'. These species should tend to dominate managed grasslands, but are also often highly mobile, as is the case for the dung beetles *Aphodius* spp., which exploit a temporary, patchy food source as both adults and larvae (Jessop, 1986). This group can therefore be well represented in the background fauna of other habitat types (although, on archaeological sites where stock has obviously been coralled, the proportion of the insect assemblage made up by *Aphodius* may reach 20-25%; Robinson, 1991).

2.4.vi Marsh/Fen species (MAR)

Includes phytophages of aquatic and waterside plants (such as the weevil *Grypus equiseti* (Fabricius), found on *Equisetum palustre* L., and the bugs *Conomelus anceps* (Germar) and *Euconomelus lepidus* (Boheman), which feed on *Juncus* spp.), as well as species of damp, mossy ground and riverbanks (e.g. many of the *Bembidion* species). Many wetland areas represent stages in a succession to truly terrestrial (usually wooded) conditions, and so this group will contain certain taxa which may also be found under woodland conditions.

2.4.vii Heath/Moorland species (HEA)

Mainly phytophages of *Erica* spp. and *Calluna vulgaris* (L.) Hull; for example, the bug *Ulopa reticulata* (Fabricius), and beetles *Lochmaea suturalis* (Thomson), and *Micrelus ericae* (Gyllenhal). It also contains species which develop in the old twigs of heathers (*Acalles ptinoides* (Marsham)), and carabids of open heathy habitats (*Bradycellus ruficollis* (Stephens)).

2.4.viii Decomposers/Litter dwellers (LIT)

This is a large group, mainly made up of saprophagous taxa which occur in a wide variety of habitats, wherever litter accumulates, or fungi, dung or carrion are available. It includes many staphylinids and most of the Lathridiidae (Coleoptera) (placed in a separate ecological group by Robinson, 1981). Some predators, such as the carabid *Notiophilus biguttatus* (Fabricius), are included.

Since the litter microhabitat is important within woods, these species are likely to be a prominent part of woodland assemblages (see, for example, van der Drift, 1959), but may also be found in other undisturbed situations, for example, in marshes, gardens, beneath hedges and scrub.

2.4.ix Species associated with Trees (TRE)

Many of the remarks above also apply to the group of species associated with trees; these are phytophages of tree and shrub species which may be found in woodlands, or other habitats such as hedges, orchards and gardens. Insects which feed on dead wood and bark in a variety of habitats are also included in this group. Many of the species dependent on the hawthorns (*Crataegus* spp.), and other woody Rosaceous plants, and those found on sallows and willows (*Salix* spp.) fall into this group. Again, these insects could be found on their host trees in and around woods, but are not dependent on the environmental conditions within forests for survival.

2.4.x True 'woodland' species (WOO)

This group contains the taxa which appear (from the literature) to depend on wooded areas, and includes species not necessarily directly dependent on trees, such as certain dung beetles. It can be further subdivided as shown in Figure 2.2, according to the feeding habits of each insect. Of these subgroups, the most characteristic of mature woodland are the **Saproxylic** insects (deadwood dwellers, feeding on the wood itself and associated fungi). Elton (1966) suggested that over 20% of all the animal species in a woodland area may be dependent on the presence of dead wood. Harding (1978) identified 195 species of beetle associated with the deadwood habitat in British woodlands, and Garland (1983) used this classification to identify ancient woodland sites in Yorkshire and North Derbyshire. Certain of the species listed by Harding have been able to survive in areas that have lost their historic woodland cover in recent times; the elaterid *Ampedus balteatus* (L.), for example, is abundant on lowland mosses and commons such as Allerthorpe Common, apparently able to use peat, rather than wood, as the larval food. Many saproxylic species, however, appear unable to survive away from long-established woodland. Harding and Rose (1986), also list saproxylic beetle species, particularly those associated with old pasture-woodlands in Britain.

Woodland **phytophages** include the forest-dwelling weevils which feed on trees and woodland herbs (for example, many of the *Phyllobius* and *Polydrusus* spp., *Strophosomus melanogrammus* (Forster); see Appendix 3 and Phillips, 1992). Also, several elaterid species which feed as larvae on the roots of trees, and many sap-sucking Hemiptera species are largely restricted to woodlands. **Bark beetles** (Scolytidae) are often confined to a small number of host tree species. On the basis of the ecology of their favoured hostplants, truly forest dwelling species can be separated from those found largely on hedgerow trees (for example, the elm bark beetles *Scolytus scolytus* (Fabricius) and *S. multistriatus* (Marsham)), which would be placed in the group 'associated with trees'. Woodland **predators** include the carabid *Calosoma inquisitor* (an arboreal species feeding on lepidopteran caterpillars), and the nitidulid beetles *Glischrochilus hortensis* (Fourcroy) and certain *Rhizophagus* spp., which feed on bark beetles as larvae and adults (Chrystal, 1948).

Other insects confined largely to wooded habitats include some of the dung beetles, such as *Aphodius zenkeri* Germar and *A. nemoralis* Erichson, which utilise all types of dung in woodland habitats (Shirt, 1991), species which inhabit the nests of wood ants (*Formica* spp.), and species feeding on fungi (e.g. the Cisidae and Tetratomidae).

As in the case of the larger ecological groupings, attempts to split the woodland group further result in subgroups that will tend to overlap; thus many of the saproxylic species feed on the fungi associated with dead wood, rather than the dead wood itself, although their dependence on fungi is less obvious than in the case of beetles feeding in the fruiting bodies of large bracket fungi, as with many of the Cisidae.

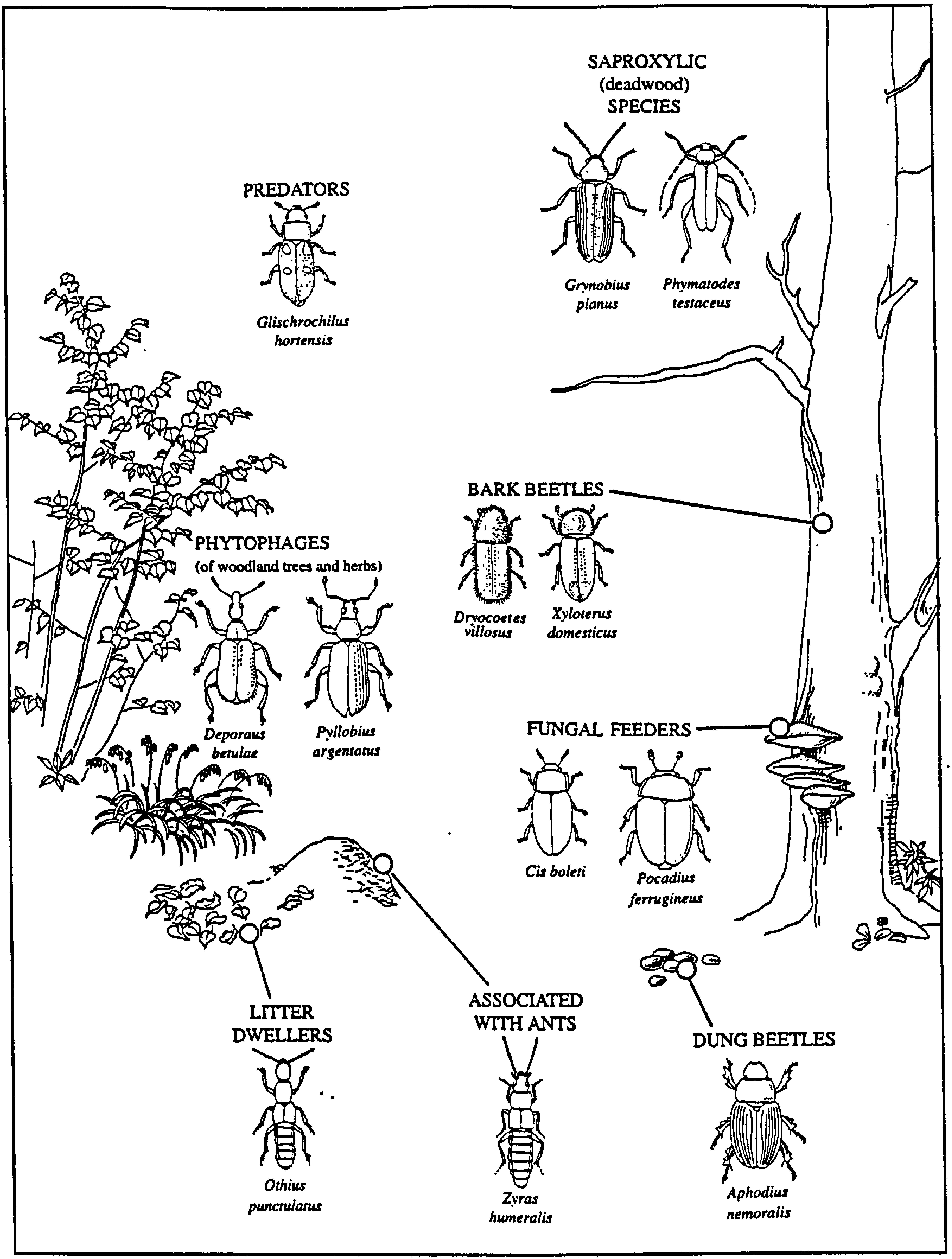


Figure 2.2 Subdivision of the woodland habitat among characteristic beetle groups. (illustrated insects not to scale).

2.4.xi Uncoded species (UNC)

Certain taxa could not be assigned to any of the above ecological groups. These included taxa identified to the level of family or genus, where the species making up these taxonomic groups display a variety of ecological habits; also, individual species whose habits are little-known. In order to avoid confusion, these taxa were assigned to the group 'uncoded'.

The codes which have been assigned to each species are not definitive; this would involve exhaustive literature searches for each species involved, and, in some cases, the weighting of contradictory evidence from different sources. However, if their limitations are kept in mind, and provided excess weight is not placed on the ecological preferences of some individual taxa at the expense of others whose presence may be equally important, they should be useful interpretive tools when dealing with insect assemblages. With use, they can be further refined and adapted. If the ecological groupings of whole assemblages are taken into account, the mis-coding of a few taxa should not greatly affect the overall ecological composition of the fauna.

2.5 A list of the major publications used for the ecological classification of insect species

Cooter, J. *et alii* (3rd edition, 1991). *A Coleopterist's Handbook.* Amateur Entomologist's Society, Feltham.

Forsythe, T. G. (1987). Common Ground Beetles. *Naturalist's Handbook* **8**, Richmond Publishing, Slough.

Friday, L. E. (1988). A key to the adults of British Water Beetles. *Field Studies* **7**, 1-51/*Field Studies Council AIDGAP publication* **189**, Field Studies Council, Preston Montford.

Freude, H., Harde, K. W., and Lohse, G. A. (1965-83). *Die Käfer Mitteleuropas* **1-11.** Goeke and Evers, Krefeld.

Hansen, M. (1987). The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* **18**. E. J. Brill/Scandinavian Science Press, Leiden.

Hansen, V. (1951,52,54). Biller; Rovbiller **1-3**. *Danmarks Fauna* **57, 58, 59**. G. E. C. Gads Forlag, Copenhagen.

Hammond, P. M. (1971). Notes on British Staphylininae 2. On the British Species of

Anotylus Mannerheim, with one species new to Britain. *Entomologist's Monthly Magazine* **107**, 93-111.

Hammond, P. M. (1972). Notes on British Staphylininae 3. The British Species of *Sepedophilus* Gistel. *Entomologist's Monthly Magazine* **108**, 130-165.

Hickin, N. E. (1968). *The Insect Factor in Wood Decay.* Hutchinson and Co, London.

Joy, N. H. (1932, Reprinted 1976). *A Practical Handbook of British Beetles.* Vols **I** & **II**. E. W. Classey, Faringdon.

Koch, K. (1989). *Die Käfer Mitteleuropas; Ökologie* **2**. Goeke and Evers, Krefeld.

Lindroth, C. H. (1986). The Carabidae (Coleoptera) of Fennoscandia and Denmark **1** and **2**. *Fauna Entomologica Scandinavica* vol **15**. E. J. Brill/Scandinavian Science Press, Leiden.

Majerus, M. and Kearns, P. (1989). Ladybirds. *Naturalist's Handbook* **10**, Richmond Publishing, Slough.

Palm, T. (1958). Die Holz- und Rinden-Käfer der Süd und Mittelschwedischen Laubbäume. *Opuscula Entomologica Supplementum* **16**.

R. E. S. L. (1953-1990). *Handbooks for the Identification of British Insects* vols **2** (Hemiptera), **4** and **5** (Coleoptera).

Southwood, T. R. E., and Leston, D. (1959). *Land and Water Bugs of the British Isles.* Warne, London.

Thiele, H-U. (1977). Carabid Beetles in their environments. *Zoophysiology and Ecology* **10**. Springer-Verlag, Berlin.

Chapter 3 Modern insect death assemblages

3.1 Introduction

In order to assess the degree to which data from fossil assemblages reflect the composition of ancient insect communities, and the ecological conditions over the period of deposition, modern death assemblages of beetles and bugs forming in litter in woodland sites were studied.

Three wooded sites in the Vale of York were chosen, to represent the main woodland types presently found in the Vale. In addition, unpublished data collected by H. K. Kenward, listing assemblages from stream deposits in and around a wood at Yorkletts, Kent, were used. The species present in a single assemblage collected from a locality in the Wyre forest, Hereford and Worcester, by HKK were recorded by the present author and also used in the comparison of woodland faunas.

In addition, species lists for insect assemblages in litter samples collected by HKK from various non-woodland sites (compost heaps, nettlebeds, pasture, and virtually abiotic city roofs), mainly from the Vale of York, but with additional data from Lincolnshire, were used. These assemblages provided comparative data for a range of habitats that differ greatly from the woodland sites, both in terms of architecture and plant species composition.

3.2 The modern sites studied

3.2.i Modern Yorkshire woodlands

Insect death assemblages were collected in three modern woodlands in the Vale of York (see Figure 1.2, p.7 for locations). These sites were chosen as representative of the major wooded habitat types in the area: recent conifer plantation, secondary woodland of less than a century's growth on a previously open site, and ancient woodland.

Allerthorpe Common Wood (ACP) (Ordnance Survey National Grid Reference SE 760 479) is a Forestry Commission plantation, dominated by Scots pine (*Pinus sylvestris* L.) planted between 1962 and 1971. Other planted trees present include Corsican pine (*Pinus nigra* Arnold subsp. *laricio* Maire), lodgepole pine (*P. contorta*

Douglas ex Loudon), and hybrid larch (*Larix* x *eurolepis* A. Henry). *Chamaecyparis*, *Picea*, and *Tsuga* spp. have also been planted, although in very small numbers, and the birches *Betula pendula* Roth and *B. pubescens* Ehrh., sallows (*Salix* spp.), oak *Quercus robur* L. and other native trees are present as young self-sown trees, particularly along the edges of rides and firebreaks. The area presently under tree cover is approximately 139 hectares. Before afforestation, it supported open, treeless vegetation dominated by heather *Calluna vulgaris* (L.) Hull and the heaths *Erica cinerea* L. and *E. tetralix* L., and part of the common (approximately 10 hectares) remains in this state, managed as a nature reserve by the Yorkshire Wildlife Trust. The soils of the reserve area are sands overlying Keuper Marl, and are podzolised beneath the *Calluna* (Key, 1986). Fields to the north and south of the wood are named as warrens on the Ordnance Survey 1:25 000 map of the area. On the first edition Ordnance Survey map (surveyed 1845-53), three 'warren' names appear in the area immediately surrounding the common, which is itself shown as rough ground with some coniferous trees. It appears that the land has historically been marginal, its soils, largely podzols with occasional peaty podzols, and some other soil types based on aeolian sands (Bullock, 1974), unsuitable for cultivation. However, today the surrounding area is largely under intensive arable management.

Dunnington Rabbit Warren Wood (DRW) (SE 678 502) is an area of regenerating woodland on a site that was used as a warren, and recorded as open ground on the first edition Ordnance Survey map. The site was heathland until at least the 1930s, although wooded by 1960 (Purdy, 1976). The remains of a wide, hedge-topped bank system relating to this former land use are visible on the eastern edge of the extant wood. Vegetation today is dominated by the birches *Betula pendula* and *B. pubescens*, and oak *Quercus robur*. The woodland fits group W16 (Quercus-Betula-Deschampsia woodland, *Q.robur* subcommunity) of the National Vegetation Classification (NVC) (Rodwell, 1991). Alder (*Alnus glutinosa* (L.)), Scots pine, rowan (*Sorbus aucuparia* L.), aspen (*Populus tremula* L.), holly (*Ilex aquifolium* L.) and hawthorn (*Crataegus monogyna* Jacq.) are present, but rare (rowan as small seedlings, possibly bird-sown from garden sources). *Rhododendron ponticum* L. is common, but the field layer is generally species-poor, with only *Deschampsia cespitosa* (L.), *Dryopteris dilatata* (Hoffm.) A. Gray, *Galium saxatile* L. and *Rhododendron* seedlings in the area studied (see Table 3.4). *Calluna vulgaris* and *Pteridium aquilinum* (L.) Kuhn form an important part of the community in more open areas, and *Rubus fruticosus* agg. is locally dominant, especially towards the woodland edge. Soils underlying the wood are largely heavily leached sandy podzols, of the Holme Moor/Everingham Complex (Matthews, 1971).

Although obviously a recent, secondary woodland, the site has been recorded on the Invertebrate Site Register of the N.C.C. (now English Nature) as of potential importance to invertebrates (Key, 1986). The notable beetles recorded here include *Synchita humeralis* (Fabricius) (Colydiidae), a species associated with woodland and found under bark and in fungi such as *Daldinia concentrica* (Fries) Cesati & de Notaris on birch. *S. humeralis* is uncommon in Britain, its status recorded as 'Notable b' (probably occurring in 31-100 10km squares of the National Grid) by Hyman (1992). Other noteworthy invertebrates include *Cypha pulicarius* (Erichson) (Staphylinidae) and Lepidoptera including the purple hairstreak butterfly *Quercusia quercus* (L.) and the noctuid moths *Enargia paleacea* (Esper) and *Bena prasinana* (L.) (Sutton and Beaumont, 1989). *Q. quercus* is a woodland species feeding on *Quercus* spp., scarce in Northern England. *E. paleacea*, a species normally associated with mature birchwoods (Skinner, 1984) were recorded as larvae on aspen. *B. prasinana* is a more widespread species of oak woodlands (South, 1961), the larvae feeding on oaks (and occasionally birch).

Many of the birches in Rabbit Warren wood have reached maturity and an abundance of sapling and seedling oaks in parts of the wood suggest that succession to a woodland type closer to that of NVC W10 (*Quercus robur-Pteridium aquilinum-Rubus fruticosus* woodland), an important form in much of the Vale of York woods today, may be continuing. However, Rodwell (1991) points out that W16, although a sub-climax community, can attain stability under certain conditions and may stabilise or even promote the formation of podzolised soils that favour it over other woodland types.

Stub Wood, Acaster Malbis (SE 587 433) is regarded as an 'ancient woodland site' (having had tree cover for at least 400 years) and is recorded in the N.C.C. Provisional Inventory of Ancient Woodland (Harrogate, Hambleton, Selby and York districts) (Carter, 1989). Evidence for its antiquity comes from its presence on the first edition Ordnance Survey map of the area and its rich flora, including classic 'ancient woodland indicator species' such as *Anemone nemorosa* L., *Hyacinthoides non-scripta* (L.) Chouard ex Rothm., *Oxalis acetosella* L., *Primula vulgaris* Hudson, *Stellaria nemorum* L. and *Viola riviniana* Reichb. (Rackham, 1980; Peterken, 1981). The value of such plant species in the determination of woodland history varies geographically, and their presence is governed by a number of factors such as shade, disturbance, and the history of a site (Day, 1993) (see Chapters 1 and 2 for a further discussion of the problems associated with the use of 'indicator species' for woodland). However, R. L. Gulliver (pers. comm.) regards *Hyacinthoides non-scripta* and *Oxalis acetosella* as 'moderate colonisers', *Anemone nemorosa* and *Primula vulgaris* as 'less good colonisers', and *Stellaria nemorum* as a true 'ancient woodland indicator species' in North Yorkshire. *Corylus avellana* L. (hazel), a 'less common shrub' (a weak indicator of ancient woods), was also abundant at Stub Wood. This assemblage of woodland species strongly suggests that the wood is relatively undisturbed; the low rates of colonisation of all these species argues for continuity of woodland conditions over a long period.

Stub Wood fits NVC type W10 (*Quercus robur-Pteridium aquilinum-Rubus fruticosus* woodland) (Rodwell, 1991), one of the most common woodland types on base-poor soils in lowland England. Its abundant hazel implies that past management included coppicing, and the name 'stub' probably derives from the Old English (Anglo-Scandinavian) 'stubb' (tree stump) (Smith, 1956). This name may be applied to old coppice woodland. Although less affected by recent woodland management practices than many ancient sites on the Vale of York, Stub Wood was disturbed by construction of tracks, bomb storage facilities and other buildings associated with the adjacent wartime airfield. More recently, there has been some planting of ornamental exotic species such as *Acer platanoides* L., *Chamaecyparis lawsoniana* (A. Murray) Parl., *Pinus* and *Prunus* spp. However, the wood remains one of the least disturbed old woodlands in the York area.

The insect communities of Stub Wood have been little studied; however, collecting by a group from the Yorkshire Naturalists' Union in 1985 revealed a group of typical 'woodland' species, some uncommon in Northern England, including *Zeugophora subspinosa* (Fabricius) (Chrysomelidae), associated with aspen in woods, *Rynchites nanus* (Paykull) (Attelabidae), *Byturus ochraceus* (Scriba) (Byturidae), and *Rhizophagus perforatus* Erichson (Rhizophagidae). The bugs *Scolopostethus grandis* Horváth and *Sehirus bicolor* (L.) (pied shieldbug) were also identified (Ely, 1986). *S. grandis* is a mainly southern, lowland species found in litter in woods and hedges; the pied shieldbug is also largely a woodland species, rare in the north (Southwood and Leston, 1959).

3.2.ii Woodland assemblages from outside the Vale of York

Assemblages collected by H. K. Kenward from woodlands in Kent and Hereford & Worcester were also studied, and their species lists use for comparison with those from Yorkshire sites.

Yorkletts, Kent (YKU, YKM1-5 and YKD) (grid square TR 09 62). Between October 1971 and June 1972, samples of silt and litter were collected at three points in a small stream at Coombe Wood, Yorkletts, near Whitstable, Kent. A single sample was taken upstream of the woodland (YKU), where the stream flows through open pasture. Five samples (YKM1-5) were collected from marginal banks of silt, within the oak woodland. One sample (YKD) was collected downstream of the wood in an area of marshy grazing land. The woodland in this area is dominated by *Quercus* spp. and *Carpinus betulus* L., with some elms (*Ulmus* spp.), and ash (*Fraxinus excelsior*). The ground flora is locally rich (where sufficient light penetrates the canopy), including such species as the bluebell *Hyacinthoides non-scripta*, yellow archangel *Lamiastrum galeobdolon* (L.) Ehrend. & Polatschek, and dog's mercury *Mercurialis perennis* L., listed by some authors (e.g. Rackham, 1980) as 'ancient woodland indicator' herbs. Insect assemblages from these samples were studied by HKK; the species lists produced were treated as described below for those from modern Yorkshire woods. Some of the remains had been retained, and some of these re-examined by the present author. The definitions of a small number of taxa were altered from the original lists to fit the database structure (described below).

Wyre Forest, Hereford and Worcester (WYS) (SO 752 758). A single sample was collected from a stream in the Wyre Forest in January 1971, by HKK. The Wyre Forest is regarded as the largest surviving area of ancient woodland in England, consisting of 2834 ha of woodland (Gibbons, 1993). Of this, 600 ha. forms a National Nature Reserve. Deer hunting was important in the area from the Norman period, and it became a Royal Forest in 1461. Disafforestation occurred before the mid-16th century AD, but it appears that management then favoured the coppicing of oaks and hazel for fuelwood. The fauna of the area is relatively well known (Hickin, 1971), and includes saproxylic species such as the cerambycid beetles *Strangalia maculata* (Poda), and *S. nigra* (L.) (a notable and declining species, according to Hyman, 1992), *Judolia cerambyciformis* (Schrank), *Stenocorus meridionalis* (L.) and *Rhagium mordax* (Degeer).

3.2.iii Non-woodland death assemblages

Compost death assemblages (COM1-3). Species lists derived by H. K. Kenward, from three samples taken in July 1981, were used. COM1 was an assemblage in foul, wet vegetation from an extensive (approx. 1 ha) area of composting leaf litter and garden refuse, at least six years old, at Heslington, York (SE 623 503). COM 3 was from a small, well-rotted compost heap in the same area, and comprised well decayed, earthy material. COM3 was rick-bottom refuse from a hay barn at Oldstead Grange, North Yorkshire (SE 534 793). This material was hard, dry and compacted, probably representing several years of accumulation. COM3 was the driest of these three samples, COM1 the wettest. At each of these locations, a single kilogram subsample was taken and processed as described below (section 3.4).

Nettlebeds (NTB 1-8). Eight samples of deposits from nettlebeds, or beside isolated plants of *Urtica dioica* L., in a variety of locations, were taken by H. K. Kenward in 1977 and 1978 (see Table 3.1, below). For each sample, subsamples of 1kg material were processed as described in section 3.4.

Table 3.1 Modern Nettlebed samples.

Sample	Location (OS NGR)	Description of sample & site
NTB1	Heslington, York (SE 621 503)	Soil, beneath sparse nettles on waste ground.
NTB2	Heslington, York (SE 629 509)	Soil, beneath sparse nettles on waste ground.
NTB3	Lincolnshire (TF 190 314)	Silt, with sparse nettles at edge of Forty-foot drain.
NTB4	Heslington, York (SE 625 503)	Sandy soil, from nettlebed (about 45 cm wide, several m long) beside footpath.
NTB5	Murton, York (SE 652 529)	Silt, from ditch with sparse nettles on banks.
NTB6	Nr. Holtby, York (SE 647 541)	Soil, beneath sparse nettles on roadside bank.
NTB7	Murton, York (SE 652 529)	Silt, from alder/willow carr 2m from NTB5.
NTB8	Murton, York (SE 652 529)	Decaying plant matter (compost & rubbish) with a stand of nettles growing through it.

Roof assemblages from York (RFF1-4). Four samples of litter from roof gutters in the city of York (grid square SE 5951) were taken by H. K. Kenward in 1974. RFF1, RFF2, and RFF3 were from a single roof system in Micklegate, York, 3-4 metres above ground level, and RFF4 from roofs over 10 m above ground. All the roofs were essentially devoid of potential habitats for insects, and the assemblages must therefore be composed entirely of 'background' elements. Statistics from these assemblages have been published by Kenward (1976, 1978).

Pasture assemblages (WGF1 & WGF2). Two samples were taken by HKK at Walmgate Stray, York (SE 617 506), in December 1983. WGF1 comprised turf and soil from an area where dung had been well worked into the soil, WGF2 material where fresh cow dung was still present at the surface. Walmgate Stray is an area of old rough grassland, unimproved but with a relatively low diversity of plants, and grazed by cattle, to the south of York. For each sample, a 1 kg subsample was taken in the laboratory and processed.

3.3 Field investigations of modern Yorkshire woodlands

In each of the modern Yorkshire woodlands studied, leaf litter samples were taken from points within a homogenous block of woodland, 20 x 30 m or more in size (or, in the case of site SW3, at an identifiable feature within the wood). In each woodland, the vegetation of this block was described. The presence or absence, mean height, and percentage ground cover of each of the vegetation layers (tree canopy, shrub, field and ground layers) were recorded. Species present in the canopy layer were recorded, and a measure of their abundance estimated, using the 'Domin' scale described by Rodwell (1991), with the following categories;

Domin **10** (91-100% cover)
9 (76-90% cover)
8 (51-75% cover)
7 (34-50% cover)
6 (26-33% cover)
5 (11-25% cover)
4 (4-11% cover)
3 (<4%, many individuals)
2 (<4%, several individuals)
1 (<4%, few individuals).

The location of the five litter samples taken from the block were decided using random number tables. At each sample point, the field and ground vegetation layers were recorded using a Domin scale (see above), in a 4 x 4 m quadrat. The amount of dead wood in the quadrat, and on surrounding trees, was scored, and the depth of the litter layer recorded. Characteristics of the vegetation cover at each site are shown in Tables 3.2-3.11. For each sampling point, a large bag of litter (approximately 2-3 kg) was taken.

The Allerthorpe Common (ACP) samples were taken from beneath a block (approximately 20 x 30 m) of lodgepole pine planted in 1965. The trees had not been thinned recently and much of the area was in deep shade, except for one small patch (about 2 x 2 m) beneath a gap in the canopy, where *Deschampsia* sp., *Calluna vulgaris*, and a few plants of *Erica tetralix* L., survived in the field layer. There was no shrub layer present (see Tables 3.2 and 3.3). None of the samples were less than 150 metres from the woodland edge.

Table 3.2 Vegetation layers in Allerthorpe Common Woods (trees and shrubs recorded within a 20 x 30 m quadrat, field and ground layers = mean of five 4 x 4m. quadrats).

Vegetation layer	**Tree**	**Shrub**	**Field**	**Ground**
Mean height (cm)	1500	-	40	<0.5
Percentage cover	99	0	3	5

Table 3.3 Field and ground layers, litter and dead wood at sample points, Allerthorpe Common Woods (each quadrat = 4 x 4 m). Tree canopy over each quadrat was either lodgepole (lp) or Scots pine (sp). - = absent.

Sample	**Field/Ground layers (domin)**	**Dead wood**	**Litter depth (cm)**	**Tree cover**
ACP 1	few, dead *Calluna vulgaris* (1)	-	6	lp
ACP 2	dead *Calluna vulgaris* (3) mosses (4)	-	4	sp
ACP 3	-	-	5-6	lp
ACP 4	dead *Erica* sp. (1)	-	7	lp
ACP 5	-	-	10	lp

The tree canopy within the 20 x 30 m quadrat was dominated by lodgepole pine (Domin = 10), with few Scots pine (Domin = 2). Although dead wood was absent on the forest floor, there was much standing dead wood in the dead lower branches of the unthinned pines. Most of these limbs were, however, fairly small (<5 cm diameter), providing a poor habitat for the larger deadwood invertebrates of woodland habitats.

At Dunnington Rabbit Warren Wood, samples were taken beneath a canopy of birch and oak, in a 50 x 50 m block of woodland (see Tables 3.4 and 3.5).

Table 3.4 Vegetation layers at Dunnington Rabbit Warren Wood (trees and shrubs recorded within a 50 x 50 m quadrat, field and ground layers = mean of five 4 x 4m quadrats).

Vegetation layer	Tree	Shrub	Field	Ground
Mean height(cm)	1000	250	30	2
Percentage cover	85	20	80	40

Table 3.5 Field and ground layers, litter and dead wood at sample points, Dunnington Rabbit Warren Wood (each quadrat = 4 x 4 m). Tree species forming the canopy over the quadrats were either silver birch (b) or oak (o).

Sample	Field/Ground layers (Domin)	Dead wood	Litter depth (cm)	Tree cover
DRW 1	*Deschampsia cespitosa* (9) *Rhododendron ponticum* (1) *Campylopus pyriformis* (4)	7 pieces > 5cm 2 pieces > 15cm circumference	2	b
DRW 2	*Deschampsia cespitosa* (9) *Rhododendron ponticum* (1) *Campylopus pyriformis* (4) moss indet. (3)	3 pieces > 5cm circumference	1.5	b
DRW 3	*Deschampsia cespitosa* (9) *Galium saxatile* (2) *Dryopteris dilatata* (1) *Rhododendron ponticum* (1) *Hypnum cupressiforme* (4) *Mnium hornum* (4) *Campylopus pyriformis* (3)	11 pieces > 5cm 4 pieces > 15cm circumference	1.5	b
DRW 4	*Deschampsia cespitosa* (5) *Rhododendron ponticum* (9)	1 piece > 5 cm circumference	2.5	b
DRW 5	*Deschampsia cespitosa* (9) *Dryopteris dilatata* (1) *Rhododendron ponticum* (1) *Hypnum cupressiforme* (3) *Campylopus pyriformis* (3)	10 pieces > 5cm 5 pieces > 15 cm circumference	4	o & b

Within Stub Wood, two contrasting sample sites were chosen, SW2 and SW3. SW2 was at the southern edge of the wood. Here, litter was accumulating in the depression of an apparent former woodbank just within the woodland area (3m from the edge of the wood). The canopy was of *Quercus robur* (50% cover in a 15 x 10 m quadrat), and *Betula pendula* (40% cover). Due to the small scale of this feature in contrast to the larger homogenous blocks of woodland chosen for sampling in the other woods studied, five samples were taken but the vegetation only recorded for three 4 x 4 m quadrats (see Table 3.7, below).

Site SW3 was deeper within the wood (around 500 metres from the nearest edge), at a site where a pond had been dug. Samples were taken from the thin and sparse litter layer, and upcast from the excavation of the pond, in a damp area. The canopy was light (only around 50% cover, made up of old *Betula pendula* trees). The shrub layer was absent, although dense stands of *Rhododendron* occurred within a few metres of the pond. The light, open conditions in this area therefore encouraged a diverse community of herbs associated with woodland, shaded and waterside habitats to flourish (see Table 3.10).

Table 3.6 Vegetation layers at Stub Wood, woodbank site (SW2) (trees and shrubs recorded within a 15 x 10 m quadrat, field and ground layers = mean of three 4 x 4m quadrats).

Vegetation layer	**Tree**	**Shrub**	**Field**	**Ground**
Mean height(cm)	1500	250	20	2
Percentage cover	90	25	30	5-10

Table 3.7 Field and ground layers in sample quadrats, site SW2

(each quadrat = 4 x 4 m).

Species	Domin value for species in sample		
	SW2 i	SW2 ii	SW2 iii
Lonicera periclymenum	4	4	5
Festuca rubra	4	4	4
Carex sp.	3	4	1
Oxalis acetosella	3	4	-
Rubus fruticosus agg.	3	3	1
Hyacinthoides non-scripta	4	1	1
Stellaria holostea	4	-	1
Holcus mollis	5	-	-
Dryopteris dilatata	1	1	3
Anemone nemorosa	-	2	-
Pteridium aquilinum	-	2	-
Dryopteris filix-mas	-	2	-
Galium saxatile	-	-	1
Mnium hornum	4	4	-

Table 3.8 Dead wood and litter in sample quadrats, site SW2

	SW2 i	SW2 ii	SW2 iii
Dead wood (pieces):			
> 5 cm circumference	10	15	10
> 15 cm circumference	-	-	2
Litter depth (cm)	2	1.5	1.5

Table 3.9 Vegetation layers at Stub Wood, pond site (SW3)

(trees and shrubs recorded within a 10 x 5 m quadrat, field and ground layers = mean of three 4 x 4m quadrats).

Vegetation layer	**Tree**	**Shrub**	**Field**	**Ground**
Mean height(cm)	1500	-	5-10	1
Percentage cover	50-60	-	90	<5

Table 3.10 Field and ground layers in sample quadrats, site SW3.

Species	Domin value of species in sample		
	SW3 i	SW3 ii	SW3 iii
Holcus mollis	8	7	8
Ranunculus repens	3	4	5
Rumex obtusifolius	1	4	5
Urtica dioica	1	3	5
Juncus effusus	4	4	-
Myosotis sp.	4	4	-
Lolium perenne	3	-	4
Chamerion angustifolium	2	1	3
Rubus fruticosus agg.	3	2	1
Digitalis purpurea	4	1	-
Stachys sylvatica	-	1	4
Moehringia trinervia	2	1	1
Festuca rubra	3	-	-
Taraxacum sp.	2	1	-
Ajuga reptans	-	1	1
Cirsium arvense	-	1	1
Cirsium vulgare	1	-	1
Heracleum sphondylium	1	-	1
Acer pseudoplatanus	1	-	-
Anthriscus sylvestris	1	-	-
Arctium sp.	-	1	-
Betula pendula	-	1	1
Caltha palustris	-	-	1
Cirsium palustre	-	-	1
Ceratocapnos claviculata	-	1	-
Prunella vulgaris	-	1	-
Taxus baccata	1	-	-
Brachythecium rutabulum	4	-	-
Hypnum sp.	-	-	4
Atrichum undulatum	3	-	-
Campylopus pyriformis	1	-	-

Table 3.11 Dead wood and litter in sample quadrats, site SW3

(each quadrat = 4 x 4 m).

	SW3 i	SW3 ii	SW3 iii
Dead wood (pieces):			
> 5 cm circumference	-	1	-
> 15 cm circumference	-	-	-
Litter depth (cm)	< 1	< 1	< 1

3.4 Laboratory methods

At each of the modern Yorkshire woodland sites, random samples consisting of several kilograms of litter, were taken. At the time of sampling, pH of litter and underlying soil were recorded. A slurry of the litter or soil and 0.01M calcium chloride solution was made up, allowed to stand for 5 minutes, and then mixed again. The use of calcium chloride solution overcomes the variations in soil pH which occur with changes in the concentration of salts. It tends to reduce the pH values recorded (using distilled water tends to increase pH values) (Allen, 1974). pH was taken using a hand-held pH meter. Water content of the litter was found by drying 100g subsamples in an oven at 50°C for 48 hours (see Table 3.12).

Table 3.12 Values for pH and water content of soil and litter layers for modern Yorkshire woodland sites.

	Mean soil pH ± SE	Mean litter pH ± SE	Mean soil water content (g per 100g wet weight) ± SE	Mean litter water content (g per 100g wet weight) ± SE
ACP	3.0 ± 0.09	3.3 ± 0.12	13.4 ± 0.74	66.6 ± 1.25
DRW	4.3 ± 0.05	3.6 ± 0.11	2.5 ± 0.28	66.9 ± 0.82
SW2	4.6 ± 0.09	5.9 ± 0.10	64.0 ± 0.50	52.5 ± 2.50
SW3	4.6 ± 0.84	6.2 ± 0.28	41.4 ± 1.49	43.6 ± 11.90

In the laboratory, each litter sample was processed by boiling in sodium carbonate solution, and treated by paraffin flotation, as described in Kenward *et al.* (1980). The litter was highly organic, with many large pieces of intact plant material (as, in all cases except SW3, little mixing with the underlying mineral soil had occurred). This meant that very large flots were produced, consisting largely of leaf fragments. Chemical treatment (steeping in acetone, in an attempt to strip plant cuticular waxes) failed to significantly reduce the size of the plant component of the flot, so mechanical separation of the insect and plant remains was achieved to some extent by washing flots through wide mesh (2mm gauge) sieves, which retained large plant fragments without reducing the size of the insect assemblage.

Even so, the remaining fraction (retained in a 300 µm sieve) had to be laboriously hand-sorted to separate plant and animal components.

Once sorted, invertebrate remains were grouped on filter paper and identified, where possible, to species level, using relevant key works, the insect reference collection of the Environmental Archaeology Unit, York (EAU), and museum reference collections at the Natural History Museum, London, the University Museum, Oxford, and the Yorkshire Museum, York. Invertebrates other than Coleoptera and Hemiptera were generally identified to order only. Where beetle and bug remains could be identified to a particular family or genus, and were obviously distinct from other unidentified insects, but could not be assigned a specific name, they were assigned to 'Recognisable Taxonomic Units' (RTUs) or 'morphospecies'. Examples of each RTU distinguished were retained for reference, and possible further identification.

For each taxon identified from an assemblage, the numbers of each body part recovered (head, pronotum, left and right elytra, etc.) were recorded, and, from these data, the minimum number of individuals (MNI) calculated. A relational database system was constructed, using the Structured Query Language SQL. Such databases allow data contained in separate tables to be linked in queries through the use of *Key attributes* (elements found in both tables) (see Date, 1986, and Lans, 1988). Rules for the construction of such databases are discussed by Tomlinson (1993). In this case, the construction of a relational database allowed data on the numbers of individuals of each species at each site to be stored in a separate table from other information on, for example, ecological or hostplant preferences of the species recovered. This facilitated rapid data retrieval while allowing the data in different tables to be linked when necessary.

Three tables, linked by the full name of each species or taxonomic unit, were constructed as shown in Figure 3.1, below. The table '**taxlist**' contained basic data of

site, sample number, taxon, MNI (field 'indivs'), and 'cert', a field describing the level of certainty which could be attached to an identification, with values 1, 2 or 3.
Where:

1 = 'certain identification, to species level'

2 = 'probable'; the species named is the most likely of a small range of taxa (1-3 species), or, the taxon could only be identified to genus level, where the genus only contained a small number of species.

3 = 'possible'; the taxon could only be identified with certainty as belonging to a particular family, or large genus.

The 'cert' field was used to exclude taxa where identification was less certain, from some calculations (see section 3.5).

The table **'species'** was made up of three attributes of each taxon identified; a numeric, taxonomic code based on the taxonomic order used by Kloet and Hincks (1964 and 1977) (with minor revisions for certain groups, such as the Psylloidea (Hemiptera), since covered by Royal Entomological Society keys and other publications). In addition to taxon name, names of strongly associated hostplants (derived from the lists of Philp, 1991, and Bullock, 1992) were also given.

The table **'codes'** contained, in addition to the 'species' field, a three-letter code describing the preferred habitat of the insect (field 'ecocode'). These codes are described in more detail in Chapter 2. Since each species might be found in one of two or three habitat types, a single taxon could appear more than once in the table 'codes'. However, each taxon could only occur once in the table 'species', and once for each sample from each site, in the table 'taxlist'. The *primary keys* (the field, or combination of fields, acting as a unique identifier for each record in each table) are underlined in Figure 3.1.

The database, once established, could be interrogated using the language SQL (as described by Tomlinson, 1993). 'Select' statements and views were used to generate data files for analysis using the statistical packages MINITAB, SPSS, and SAS.

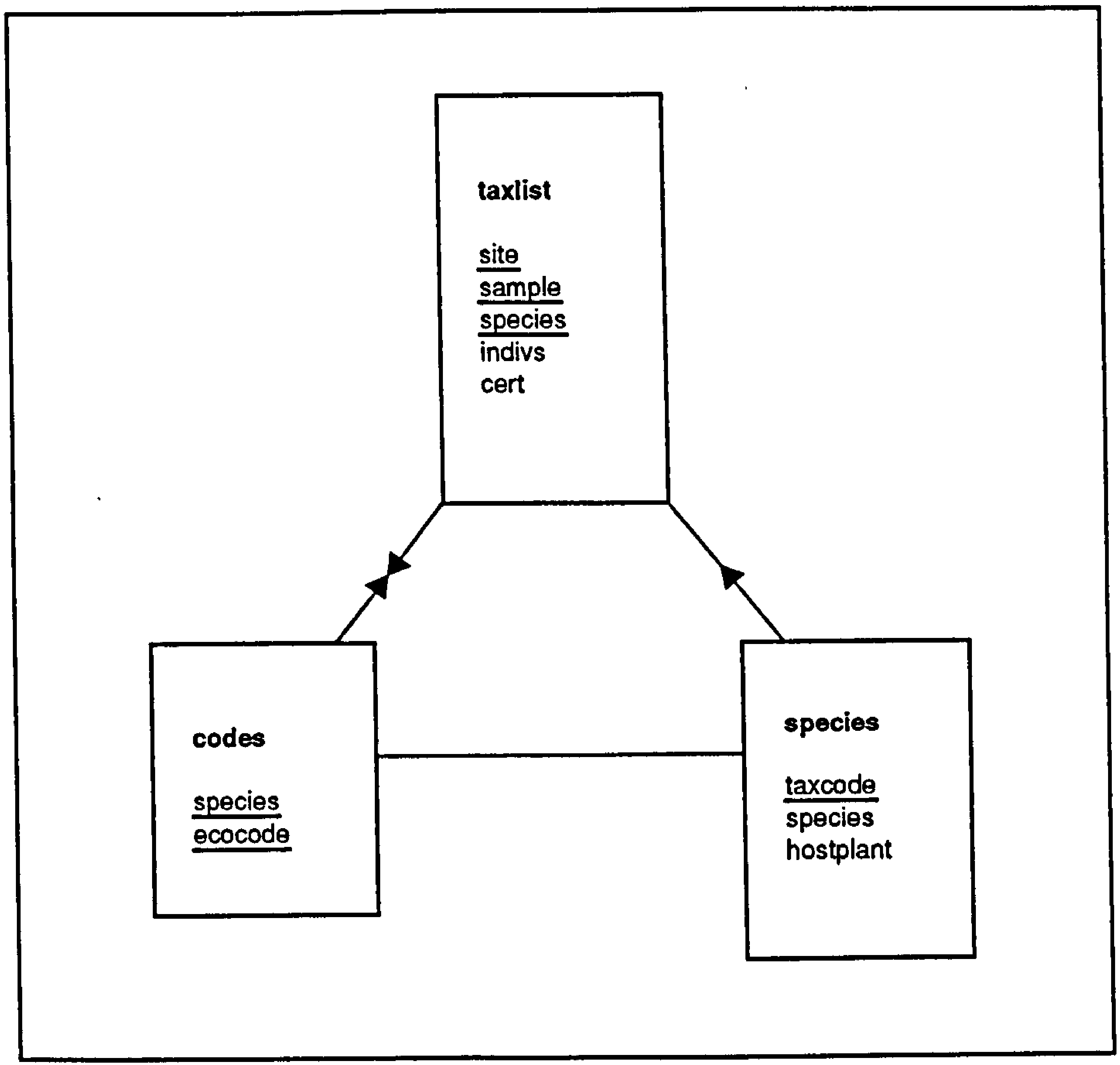


Figure 3.1 Structure of tables making up relational database.
For explanation of field names, see text.
Key to relationships; —— one-to-one —▶— one-to-many
—▶◀— many-to-many

3.5 Results

3.5.i The size and nature of modern assemblages

The species lists produced for each of the modern woodland assemblages were large, with the number of taxa recorded in each sample (S) varying between 33 and 162 (see Figure 3.2, and Table 3.16). In each sample, most of these taxa were represented by a small number of individuals (see section 3.5.ii, below), and therefore attempts were made to reduce the complexity of these lists before analyses were carried out on them. This was achieved by three main methods;

(i) Reduction of the number of taxa being considered (by removing the least abundant).

(ii) The use of ecological classification techniques (see Chapter 2), so that ecological classes rather than individual taxa, were used in analyses.

(iii) The use of statistics descriptive of the assemblage, such as indices of dominance and diversity (see section 3.5.iv).

Multidimensional scaling and discriminant analysis were carried out on truncated lists, which only consisted of the most abundant taxa and therefore excluded the possible over-emphasis of allochthonously derived species occurring as part of the 'background fauna' and rare autochthonous species. One disadvantage of this approach is that it excludes significant indicators of ecological conditions which may be present at low frequencies (for example, in the case of large insects, where populations may be small). Discriminant analysis was carried out on lists of the taxa represented by more than five individuals overall.

The proportions of the whole assemblage falling into each of the ecological groups defined in Chapter 2 are shown in section 3.5.iii, below. This technique allows taxa present at low densities to be taken into account, but they are not weighted according to their perceived value in reconstruction of the environment; such a weighting would have to take into account factors such as the degree of faithfulness of the taxon to its habitat and the extent to which taxa are dispersed into unsuitable areas.

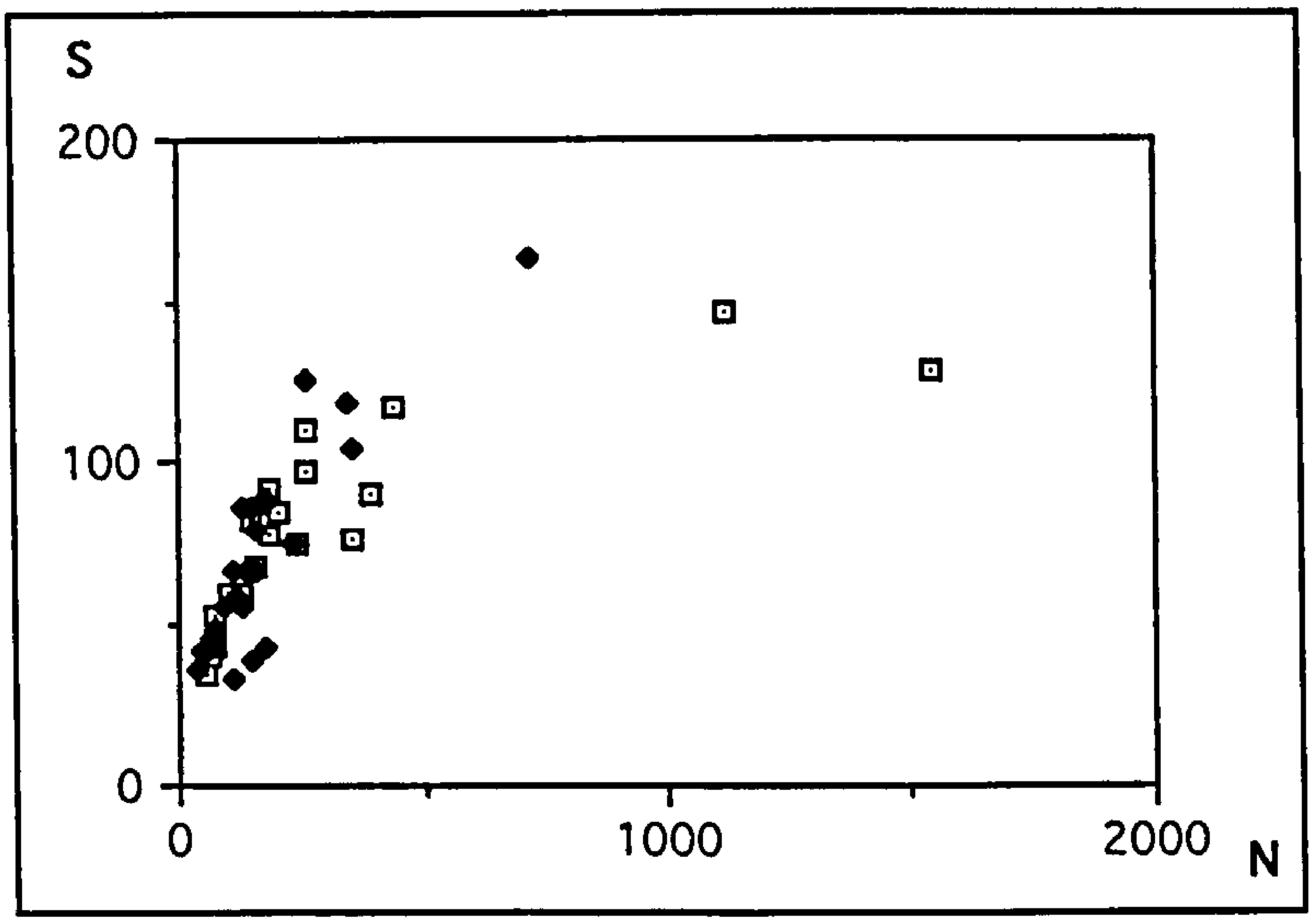


Figure 3.2 The size of modern assemblages, in terms of number of taxa (S) and number of individuals (N).
◆ woodland ▫ non-woodland sites.

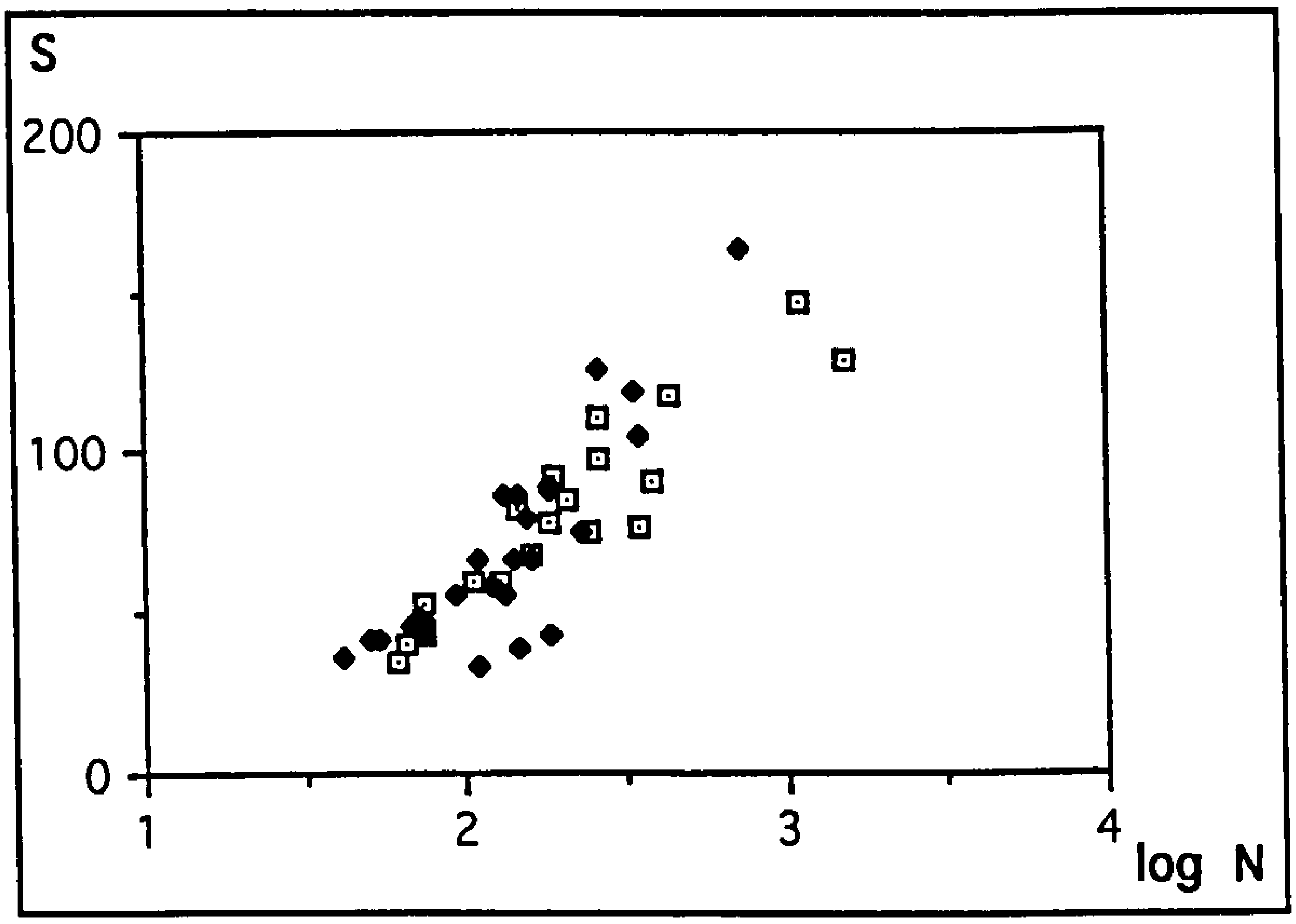


Figure 3.3 S plotted against the logarithm of N for all modern assemblages.

The largest assemblages from modern woodlands are those from site SW2 (all over 160 individuals), and the smallest are those from the same woodland, site SW3 (all under 70 individuals). Since all the samples taken from modern woodlands were of similar weight, the variation in assemblage size probably reflects the nature of the deposit and conditions of preservation of insect remains. Site SW3, though beside a pond, was the driest of the four deposits, with the smallest accumulation of litter (the samples taken were largely mineral soil). Samples from SW2, however, consisted of large quantities of damp litter from a ditch, where undisturbed accumulation could occur, and conditions favoured short-term preservation of insect fragments.

In the smaller assemblages, the number of taxa recovered increases with the number of individuals in the assemblage. However, in the three largest samples (SW2/1, RFF4, and COM3, with 721, 1121, and 1540 individuals respectively), this linear relationship no longer seems to hold; it appears that all the insect taxa likely to be found have been sampled in these large assemblages.

3.5.ii The species composition of modern woodland death assemblages

(a) *Multidimensional scaling*

In order to judge the degree of similarity of species lists from the four modern Yorkshire woodland sites, a matrix of Phi-squared proximity measures was produced using the data analysis package SPSS on the VAX mainframe computer at the University of York. The Phi-squared measure ϕ^2 was obtained from the frequency counts for each species in each sample. For two cases, x and y,

$$\phi^2(x,y)=\sqrt{\frac{\dfrac{\Sigma_i(x_i-E(x_i))^2}{E(x_i)}+\dfrac{\Sigma_i(y_i-E(y_i))^2}{E(y_i)}}{N}}$$

(Norušis/SPSS, 1990).

Where x_i, y_i are the frequencies of species *i* in samples x and y, and E is the value expected (assuming independence of x and y).

ϕ^2 is a measure of dissimilarity giving values independent of total frequencies of x and y, and was therefore suitable for use in this case where the absolute frequencies of species in the samples varied widely (see above). In order to avoid undue weight being given to the rare species, whose occurrence in a sample is likely to be a result of stochastic processes, only the frequencies of the 246 taxa of greatest abundance overall were used (those having total number of individuals >5).

The matrix of ϕ^2 values calculated was used as the basis of metric multidimensional scaling. Figure 3.4 shows a 2-dimensional plot of the calculated Euclidean distances between samples.

The close clustering of the samples from each site, especially ACP, implies that the vectors calculated from ϕ^2 values are similar for the samples within a site. This suggests that the assemblages from the different sites are quite distinctive, although it appears that those from SW3 are less distinct. This may be a result of the relatively small size of these assemblages, both in terms of numbers of individuals and taxa of the top taxa represented; SW3/2 has only 27 individuals, of 20 taxa, SW3/4 only 40 individuals, from 32 of the top 246 taxa. In contrast, the ACP samples have a mean of 133 individuals of 32 taxa, and the DRW samples 98 individuals of 48 taxa each. The relatively small size of the SW3 samples makes them susceptible to bias caused by the chance occurrence of single individuals of any species.

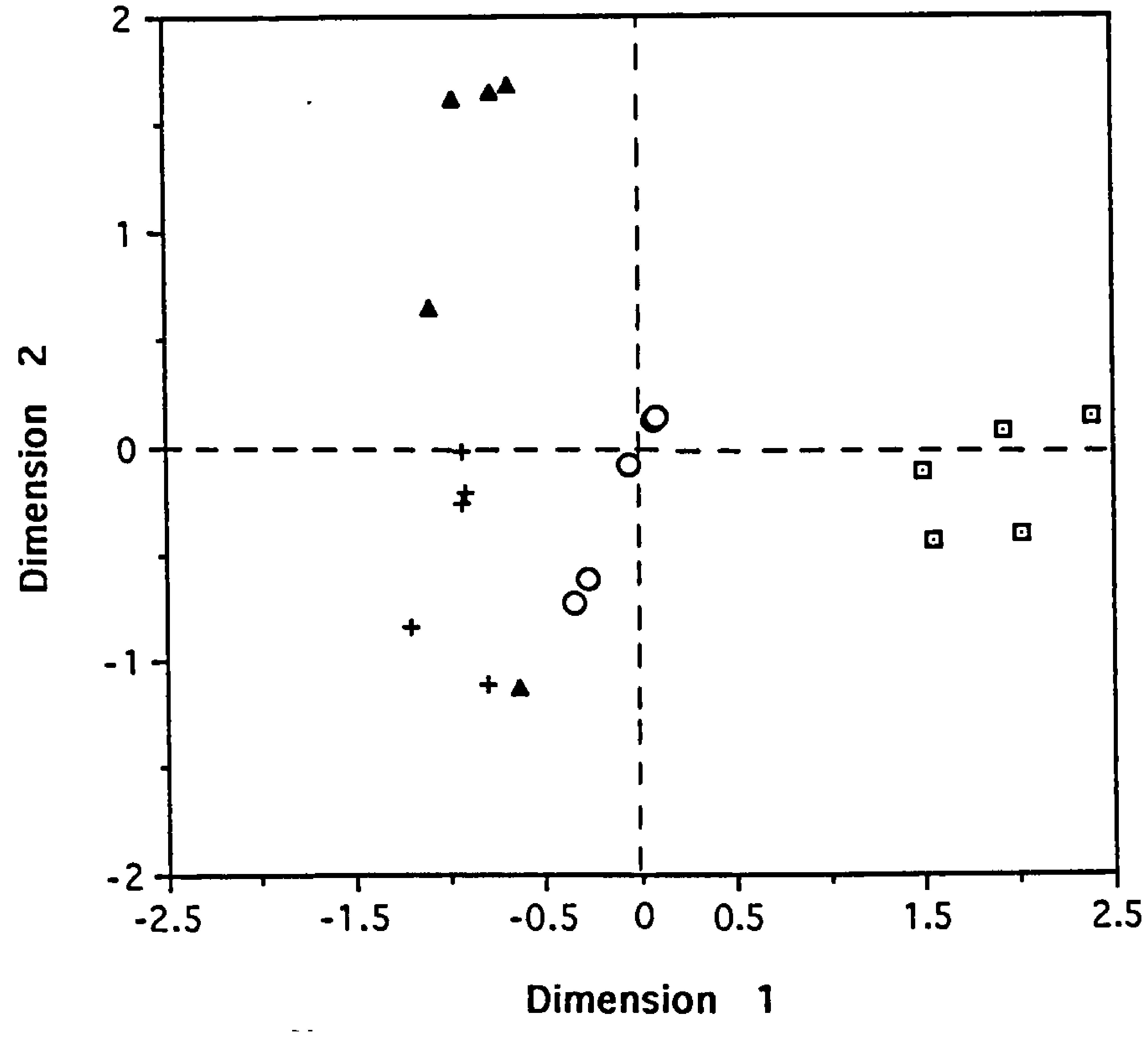


Figure 3.4 Plot of two-dimensional MDS solution, for ϕ^2 dissimilarity data based on lists of species from modern Yorkshire woodland samples.
Site: ▫ ACP ○ DRW + SW2 ▲ SW3

(b) *Most abundant species*

The ten most abundant species in each of the four woodland sites are given in Table 3.13, and those for other situations, non-woodland and woodlands outside the Vale of York, in Tables 3.14 and 3.15. Differences in the assemblages from the different sites are again emphasised in these lists. Certain taxa abundant at one of the sites are absent, or present only in very low numbers, at other sites; thus *Psylla melanoneura* Förster, *Strophingia ericae* (Curtis), *Bradycellus ruficollis* and *Lochmaea suturalis*, all abundant at ACP, were virtually absent from other locations.

Table 3.13 The ten most abundant taxa in death assemblages from each of the four modern Yorkshire woodland sites (summed over five samples in each case). For explanation of ecological coding, see Chapter 2. **n** = total minimum number of individuals in the five samples.

Site ACP

	ecological code	n
Psylla melanoneura	TRE	306
Strophingia ericae	HEA	117
Aphidoidea sp.	UNC	34
Othius myrmecophilus	LIT	15
Bradycellus ruficollis	HEA	13
Lochmaea suturalis	HEA	11
Aridius bifasciatus	LIT	9
Lesteva heeri	LIT	9
Atomaria sp.	UNC	7
Acrotrichis sp.	EUR	7

Site DRW

	ecological code	n
Othius myrmecophilus	LIT	45
Aphidoidea sp.	UNC	29
Anotylus tetracarinatus	LIT	21
Acrotrichis sp.	UNC	17
Drymus brunneus	WOO	16
Ramphus pulicarius	WOO	15
Aleochara sp.1	UNC	14
Phyllobius argentatus	WOO	12
Tachyporus hypnorum	LIT	12
Corticarina fuscula	LIT	12

Site SW2

	ecological code	n
Atomaria sp.1	UNC	126
Othius myrmecophilus	LIT	75
Anotylus tetracarinatus	LIT	73
Aleocharinae sp.1	UNC	70
Stephostethus lardarius	LIT	63
Aleocharinae sp.19	UNC	52
Atomaria sp.	UNC	49
Enicmus transversus or *histrio*	LIT	44
Tachyporus hypnorum	LIT	36
Aleochara sp.1	UNC	35

Site SW3

	ecological code	n
Helophorus sp.	UNC	37
Phyllobius argentatus	WOO	9
Conomelus anceps	MAR	8
Helophorus brevipalpis	AQU	6
Hesperocorixa sp.	AQU	6
Tachyporus hypnorum	EUR	6
Anotylus tetracarinatus	LIT	5
Hydraena testacea	AQU	5
Psylla ambigua	TRE, MAR	4
Hydroporus sp.	AQU	3

Table 3.14 The ten most abundant taxa in death assemblages from some modern non-woodland habitats (summed over *n* samples in each case).

Site NTB (*n* = 8)

	ecological code	**n**
Aleocharinae spp.	UNC	201
Cyphon sp.	UNC	57
Anotylus tetracarinatus	LIT	46
Anotylus rugosus	LIT	45
Brachypterus glaber	PAS	34
Atomaria sp.1	UNC	30
Enicmus sp.	LIT	29
Aridius bifasciatus	LIT	23
Lathridiidae sp.	UNC	23
Lathridiidae sp.1	UNC	22

Site COM (*n* = 4)

	ecological code	**n**
Acrotrichis sp.1	UNC	292
Mycetaea hirta	SYN	199
Acrotrichis sp.2	UNC	195
Cercyon analis	EUR	74
Ptenidium pusillum	LIT	68
Atomaria sp.1	UNC	65
Ptilium sp.	UNC	62
Dienerella sp.	LIT	60
Lathridius minutus gp.	LIT	53
Typhaea stercorea	SYN, LIT	49

Site RFF (*n* = 3)

	ecological code	**n**
Aleocharinae spp.	UNC	231
Atomaria spp.	UNC	154
Atheta sp.	UNC	148
Anotylus tetracarinatus	LIT	138
Corticaria or *Corticarina* sp.	LIT	90
Stephostethus lardarius	LIT	71
Tachyporus chrysomelinus or *hypnorum*	EUR	68
Enicmus sp.	LIT	55
Cryptophagus sp.	UNC	54
Aridius bifasciatus	LIT	38

Table 3.15 The ten most abundant taxa in death assemblages from other modern woodland sites (summed over *n* samples in each case).

Site YKU (*n* = 1)

	ecological code	n
Bembidion lunulatum	MAR	76
Aleocharinae spp.	UNC	34
Platystethus nitens	MAR	32
Helophorus brevipalpis/obscurus	AQU	25
Aridius bifasciatus	LIT	20
Carpelimus sp.	UNC	11
Megasternum obscurum	LIT	11
Anacaena globulus	AQU	8
Anotylus rugosus	LIT	8
Enicmus sp.	LIT	8

Site YKM (*n* = 5)

	ecological code	n
Barypeithes sp.	UNC	71
Barypeithes araneiformis	TRE	64
Hydraena nigrita	AQU	49
Helophorus brevipalpis/obscurus	AQU	42
Barypeithes pellucidus	TRE	40
Enicmus sp.	UNC	33
Aleocharinae spp.	UNC	28
Megasternum obscurum	LIT	24
Athous haemorrhoidalis	TRE	15
Zyras humilis	EUR	15

Site YKD (*n* = 1)

	ecological code	n
Aleocharinae spp.	UNC	15
Helophorus brevipalpis/obscurus	AQU	14
Megasternum obscurum	LIT	11
Aridius bifasciatus	LIT	8
Helophorus sp.	UNC	8
Barypeithes araneiformis	TRE	7
Enicmus sp.	UNC	7
Lesteva longoelytrata	LIT,MAR	7
Carabidae sp.	UNC	6
Bembidion lunulatum	MAR	1

Site WYS (*n* = 1)

	ecological code	n
Barypeithes araneiformis	TRE	17
Helophorus brevipalpis/obscurus	AQU	16
Elmis aenea	AQU	10
Anacaena globulus	AQU	9
Anotylus rugosus	LIT	8
Acalles ptinoides	HEA,WOO	7
Aleocharinae sp.b	UNC	6
Megasternum obscurum	LIT	5
Polydrusus cervinus	WOO	5
Lesteva longoelytrata	LIT,MAR	4

(c) *Discriminant analysis of modern species lists*

Sections (a) and (b), above, suggest a relatively high degree of separation of assemblages from different sites on the basis of species composition of those assemblages. In order to identify a group of species, the frequencies of which may together act as an indicator of habitat type, *discriminant analysis* was carried out on the species lists from modern assemblages. This multivariate statistical technique uses a known classification of cases into groups to construct *discriminant functions* calculated from the values of a number of variates. Using these functions, cases whose group is unknown can then be assigned to a group (Norušis/SPSS, 1990).

In order to reduce the influence of rare taxa, or those which are too rare to be reliable indicators of environmental conditions, only taxa for which the total number of individuals (N) in the modern Yorkshire woodland (ACP, DRW, SW2, SW3), compost (COM), nettlebed (NTB), roof faunas (RFF) and pasture (WGF) sites exceeded certain threshold values were included in discriminant analyses. In the analysis to separate woodland and non-woodland sites, taxa with $N > 5$ were included. In discrimination of woodland types, only taxa for which $N \geq 5$ in the woodland samples were used.

Where the number of variates (in this case, species) approaches or exceeds the number of samples being considered, and the variates are correlated to any extent, the variance-covariance matrix in discriminant analysis becomes unstable (Finney, 1974). It is therefore necessary either to increase greatly the number of samples being considered, or reduce the number of variates. The former solution would be preferable, but impractical, owing to the inherent species richness of insect assemblages. Thus, for these calculations, the species lists were reduced to the most effective predictor variables using *stepwise* discriminant analysis, which proceeds in stages, adding or removing taxa at each step, in order to maximise the Mahalanobis distance between the two closest groups (SPSS, 1990).

Discriminant analysis assumes the underlying distributions of data within each class to be normal. However, the probability of misclassification seems relatively insensitive to many deviations from the normal distribution (Lachenbruch and Goldstein, 1979), and discriminant analysis may be used as a descriptive technique even where this assumption is not met (SAS, 1989).

Discriminant analyses were carried out, attempting to distinguish groups of samples at two distinct levels: **woodland/non-woodland** sites, and **woodland type.**

Woodland/non-woodland

Species lists for sites ACP, DRW, SW2, and SW3 were assigned to the 'woodland', and those for sites COM, NTB, RFF, and WGF to the 'non-woodland' groups. Discriminant analysis was carried out twice; in the first instance, the lists of all taxa where N exceeded 5 (a total of 246 taxa) were used. However, since taxa such as the Aleocharinae may have been recorded differently by MJH and HKK, and since taxa determined with only a low level of certainty can provide little useful ecological information, taxa identified to certainty levels 2 and 3 were excluded from the second analysis, i.e. those where cert = 1 (identification definite) were included. Omitting taxa whose total N ≤ 5 left 119 taxa.

Stepwise discriminant analysis was carried out on these lists using the SPSS statistical package, the most important predictor variables being selected by adding or removing species at each step so as to maximise the Mahalanobis distance between the two closest groups.

Using the reduced species lists produced by this analysis, discriminant analysis was carried out to predict the group membership of stream assemblages from woodland at Yorkletts, Kent, and the Wyre Forest. All these assemblages, except YKU and YKD, were 'woodland' assemblages, and from ancient, deciduous woods most similar to Stub Wood.

Stepwise analysis produced a list of 17 taxa which act as best predictor variables for woodland/non-woodland sites (shown below with their ecological codes):

Tachyporus sp.	(UNC)
Halticinae sp.1	(UNC)
Halticinae sp.	(UNC)
Micropeplus porcatus	(LIT)
Oxytelus laqueatus	(LIT)
Corticaria elongata	(EUR)
Trechus sp.	(UNC)
Anthobium sp.	(UNC)
Carpelimus bilineatus	(EUR)
Brachypterus glaber	(PAS)
Ptenidium sp.	(UNC)
Platystethus arenarius	(PAS)
Tachyporus sp.1	(UNC)
Aleocharinae sp.31	(UNC)
Pselaphidae sp.	(UNC)
Omalium sp.	(LIT)
Ahasverus advena	(LIT & SYN)

When the frequencies of these taxa were used to classify the samples from Yorkletts and Wyre, the following results were obtained:

Placed in group 1 (woodland)	YKU, YKM3, YKM4, YKD, WYS
Placed in group 2 (non-woodland)	YKM1, YKM2, YKM5

Number placed correctly = 3 Number placed incorrectly = 5

When taxa identified to cert = 1 only were considered, 26 species were selected as best predictor variables:

Megasternum obscurum	(LIT)
Bembidion lampros	(ARA & PAS)
Cercyon haemorrhoidalis	(LIT)
Platystethus arenarius	(PAS)
Stilbus testaceus	(PAS)
Carpelimus elongatulus	(PAS)
Loricera pilicornis	(MAR & WOO)
Ceutorhynchus quadridens	(ARA)
Clivina fossor	(EUR)
Habrocerus capillaricornis	(LIT)
Elasmostethus interstinctus	(WOO)
Carpelimus bilineatus	(EUR)
Anthicus formicarius	(EUR)
Pentatoma rufipes	(TRE)
Dalopius marginatus	(WOO)
Meligethes aeneus	(ARA & PAS)
Oxytelus laqueatus	(LIT)
Micropeplus staphylinoides	(LIT)
Leptusa ruficollis	(WOO)
Brachypterus glaber	(PAS)
Aridius nodifer	(LIT)
Drymus brunneus	(WOO)
Aphalaria polygoni	(MAR & PAS)
Tachyporus chrysomelinus	(EUR)
Anotylus rugosus	(LIT)
Anotylus complanatus	(LIT)

The predicted groups for Yorkletts and Wyre samples, based on these species, were:

Placed in group 1 (woodland)	YKM1, YKM2, YKM4
Placed in group 2 (non-woodland)	YKU, YKM3, YKM5, YKD, WYS

Number placed correctly = 5 Number placed incorrectly = 3

The lists of 'best discriminant taxa' produced by stepwise discriminant analysis differ greatly between the analysis when all taxa are considered, and that using only species identified with certainty. Only three species occur on both lists: *Carpelimus bilineatus* Stephens, *Oxytelus laqueatus* (Marsham), and *Platystethus arenarius*

(Fourcroy). Most of the 'best' discriminants in the first analysis are poorly identified taxa to which no ecological codes could be assigned. The second analysis, in which only true species were considered, used a greater number of discriminant taxa, and resulted in a more reliable separation of the Yorkletts and Wyre assemblages as woodland or non-woodland samples.

Woodland type

Discriminant analysis was carried out as described above, using the groups ACP, DRW, SW2 and SW3, on both full species lists (123 taxa in all, including those identified at cert = 1, 2, and 3, but excluding all those where total N for Yorkshire woodland sites < 5), and lists including only those taxa identified with certainty (cert = 1) (65 species). Predicted groups for Yorkletts and Wyre assemblages were found.

Stepwise analysis on the full species lists produced a list of 15 species which acted as best predictor variables:

Othius myrmecophilus	(LIT)
Corticaria elongata	(EUR)
Cyphon sp.	(UNC)
Aleochara sp.	(UNC)
Aleocharinae sp.14	(UNC)
Psylla melanoneura	(TRE)
Ramphus pulicarius	(WOO)
Corticarina sp.	(LIT)
Corticarina fuscula	(LIT)
Elasmostethus interstinctus	(WOO)
Strophosomus melanogrammus	(WOO)
Myrmedobia tenella	(WOO)
Trioza remota	(WOO)
Luperus longicornis	(WOO)
Neuraphes sp.	(UNC)

Yorkletts and Wyre samples were all predicted to belong to the 'DRW' or 'SW3' groups:

Placed in group 2 (DRW)	YKM1, YKD
Placed in group 4 (SW3)	YKU, YKM2-YKM5, WYS

If only taxa where 'cert' = 1 were used, the list of 12 best predictor species was:

Othius myrmecophilus	(LIT)
Corticaria elongata	(EUR)
Megarthrus depressus	(LIT)
Habrocerus capillaricornis	(LIT)
Anotylus rugosus	(LIT)
Psylla melanoneura	(TRE)
Lesteva heeri	(LIT & MAR)
Cortinicara gibbosa	(LIT)
Othius punctulatus	(WOO)
Anotylus sculpturatus	(LIT)
Strophingia ericae adult	(HEA)
Lochmaea suturalis	(HEA)

Yorkletts and Wyre samples were placed in groups thus:

Placed in group 1 (ACP)	YKU, WYS
Placed in group 2 (DRW)	YKM3
Placed in group 3 (SW2)	-
Placed in group 4 (SW3)	YKM1, YKM2, YKM4, YKM5, YKD

It would appear that discriminant analysis is unable to distinguish between woodland and non-woodland sites on the basis of species frequencies. Even using the taxa identified at lower levels of certainty, which often occur in greater numbers, and where there is the greater possibility that the individual methods of classification of taxa by different recorders will emphasise the differences between groups, the ratio of misclassified to correctly classified observations is 5:3. When only taxa identified with certainty to species level are included (in order to minimise the latter error), the ratio improves, becoming 3:5. However, in neither case does there appear to be a significant improvement on the 1:1 ratio which would be expected by chance. The reason for the inclusion of some woodland assemblages from Yorkletts and Wyre with the 'non-woodland' group is unclear. Some of the best predictor species, such as *Drymus brunneus* (Sahlberg) and *Dalopius marginatus* (L.), are relatively abundant, and have fairly strong preferences for woodland habitats. However, others such as the Aleocharinae spp., and *Carpelimus bilineatus* seem less likely to have reliable habitat preferences. The choice of such taxa as predictors would appear to be a result of stochastic distribution effects, or unrecorded differences in the habitats. In the case of Aleocharinae at least, inconsistencies of recording these smaller, more difficult taxa may have played a part; where recording was not uniform between samples, the taxa are likely to be selected as discriminant variables.

3.5.iii Ecological classification of taxa from modern death assemblages.

(a) *Proportion of assemblage in each ecological group*

The species identified in the modern assemblages were assigned to ecological groups based on their habitat preferences, as described in Chapter 2. The ecological groups for the most abundant taxa from various modern sites are given in Tables 3.13-3.15 (above). Figure 3.5 shows the number of taxa and the total number of individuals falling into each of the ecological groups defined, for each of the four Yorkshire woodlands, and non-woodland sites. In most cases, the numbers of taxa in an ecological group seem closely linked to the number of individuals. However, for certain groups, this does not appear to be the case; thus, for site ACP, the woodland, pasture and marshland groups appear to be represented by relatively few individuals, of many taxa. This is also the case for the pasture and marshland groups at site SW2. These probably represent transported components of the assemblages or background fauna, which are carried into assemblages in small numbers. The aquatic group often makes up a significant part of this background fauna (Kenward, 1978), but in these samples (except for site SW3, beside a pond), this group is represented by very small numbers of individuals, of very few taxa. It may be that the assemblages were simply too remote from major sources of aquatic insects to allow their incorporation into the assemblages (see Figure 3.6). The major ecological groups vary slightly between sites, but, except for a large heathland component at site ACP, the most important elements of the fauna appear to be those of local origin. Figure 3.6 shows the proportions of the total number of individuals, N, for each site (all samples from each site summed), in each ecological group (excluding uncoded and eurytopic taxa), with a measure of the distance from the nearest potential source of these insects.

Generally, it appears true that the closer the habitat, the more heavily it is represented in the assemblage. In particular, the 'litter dwelling' component of the fauna is large in every assemblage studied, and these probably represent insects which, in life, are autochthonous to, or found only a short distance from, the accumulating deposit. However, there are certain inconsistencies: heathland (hea) appears over-represented in ACP, whereas the group 'tre' appears under-represented in most woodland samples (but not ACP). In general, most of the assemblage seems likely to originate within a few metres of the point of deposition.

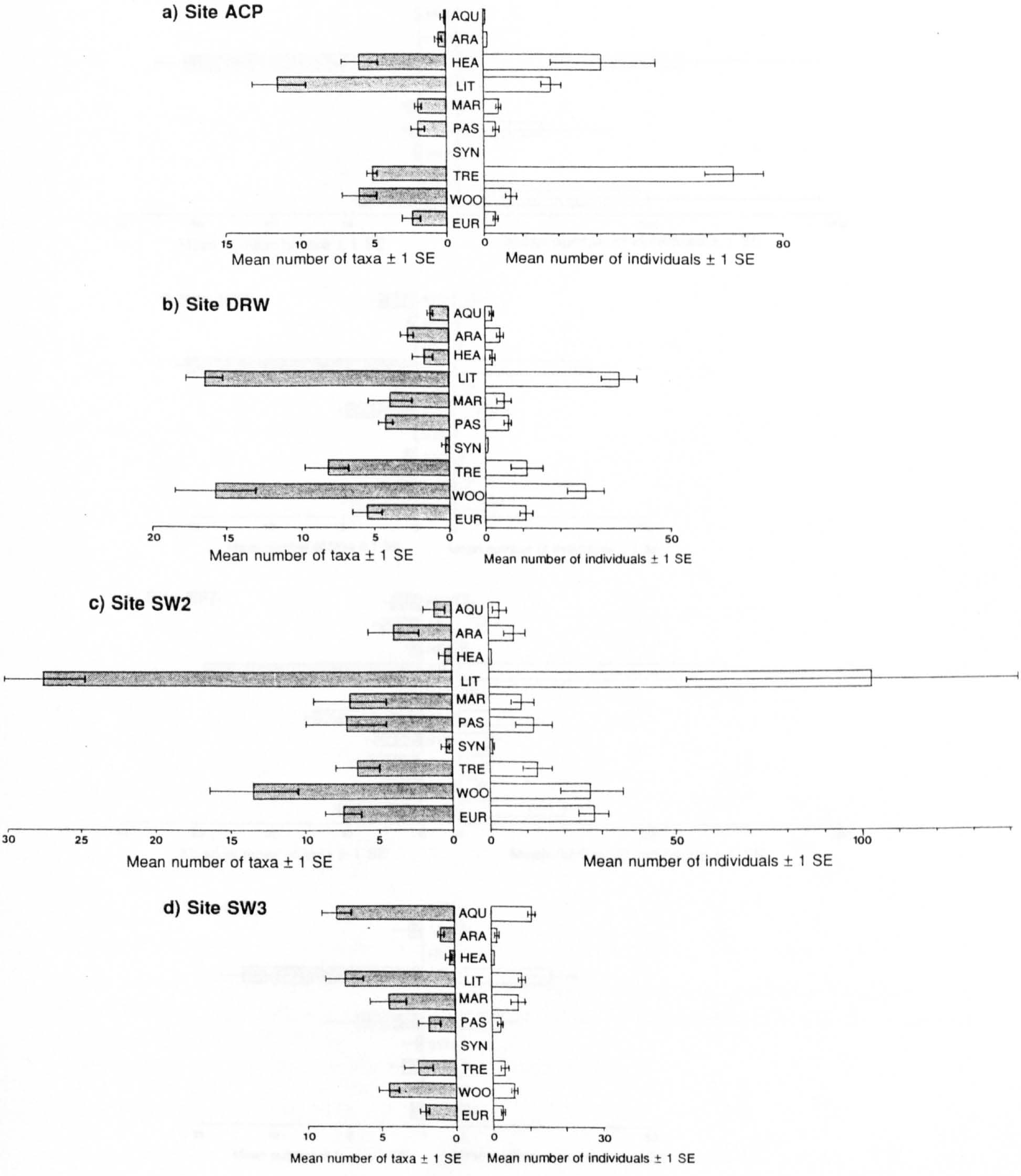
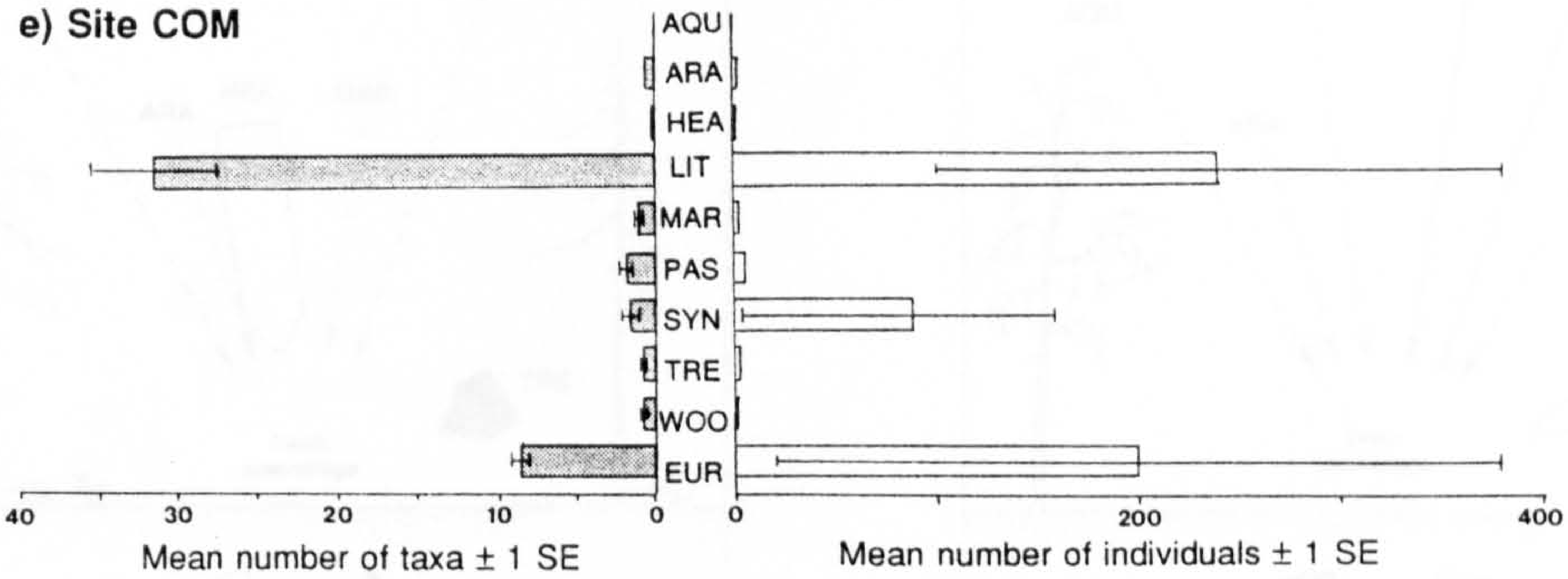
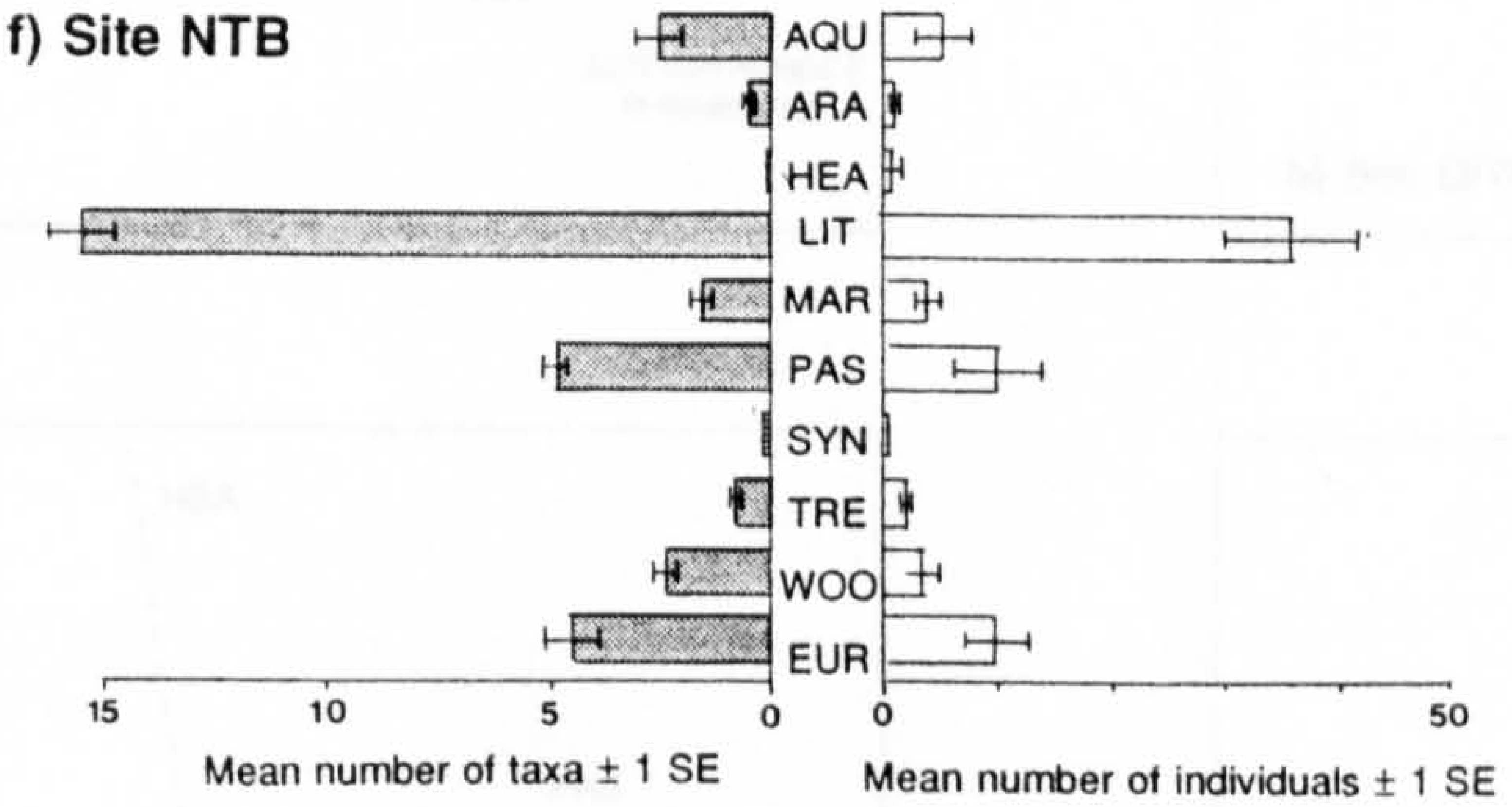


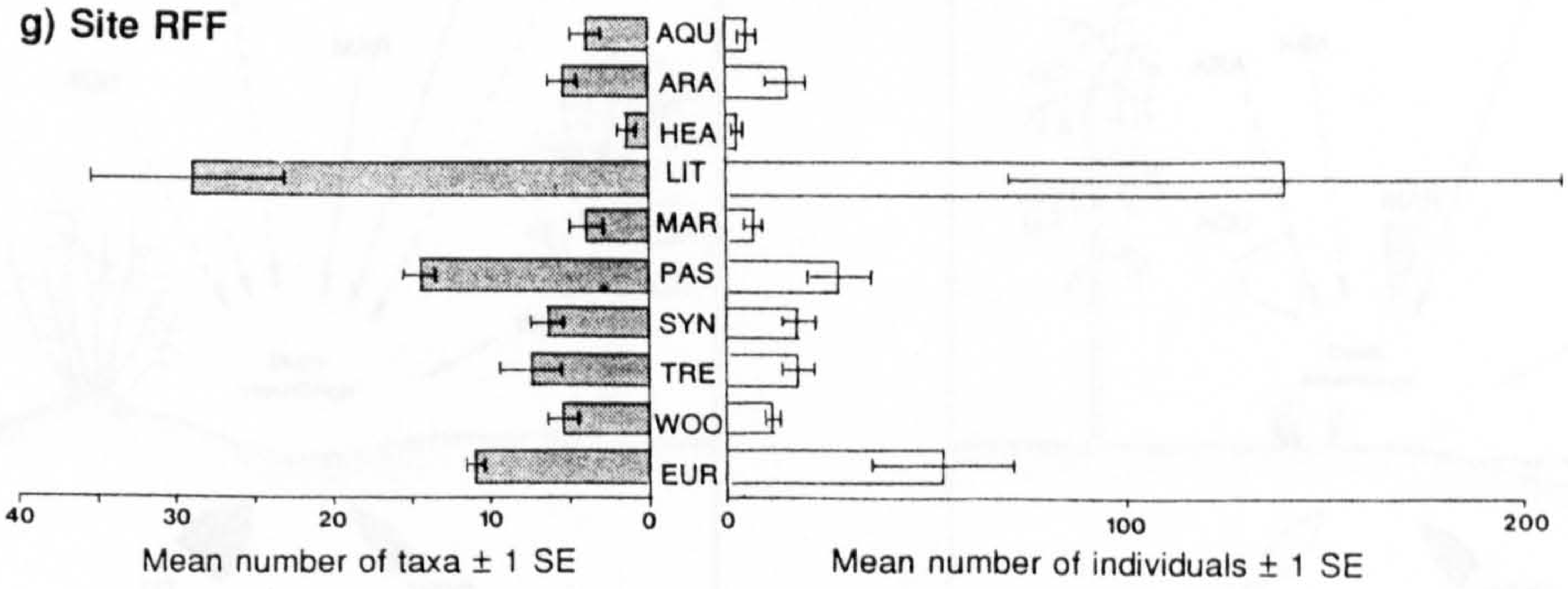
Figure 3.5 a-d Mean number of taxa (S), and number of individuals (N) in each ecological group, ± Standard Deviation (SD), for four modern assemblages from woodland sites.



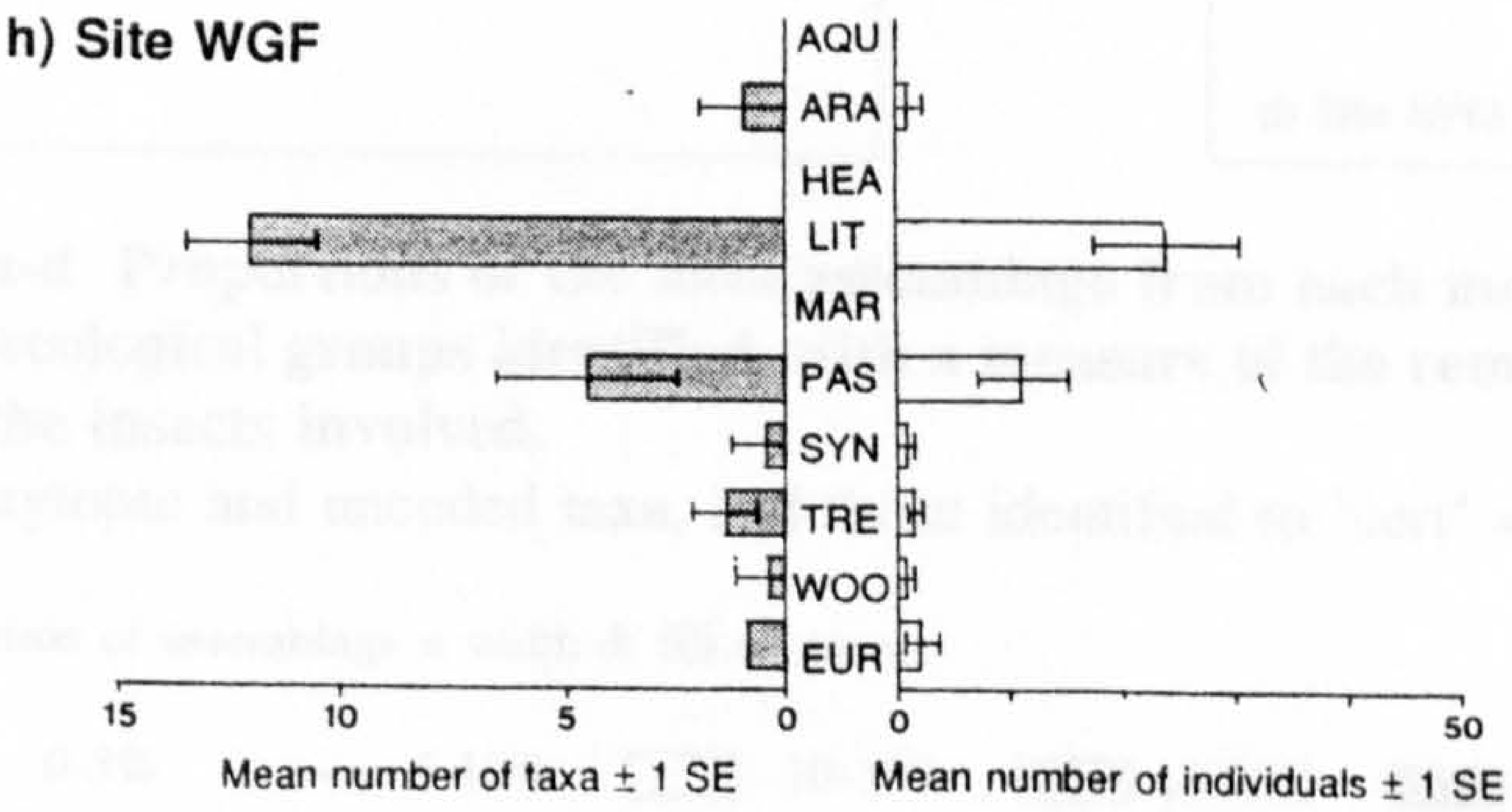
e) Site COM



f) Site NTB



g) Site RFF



h) Site WGF

Figure 3.5 e-h Mean number of taxa (S), and number of individuals (N) in each ecological group, ± SD, for modern assemblages from various sites.

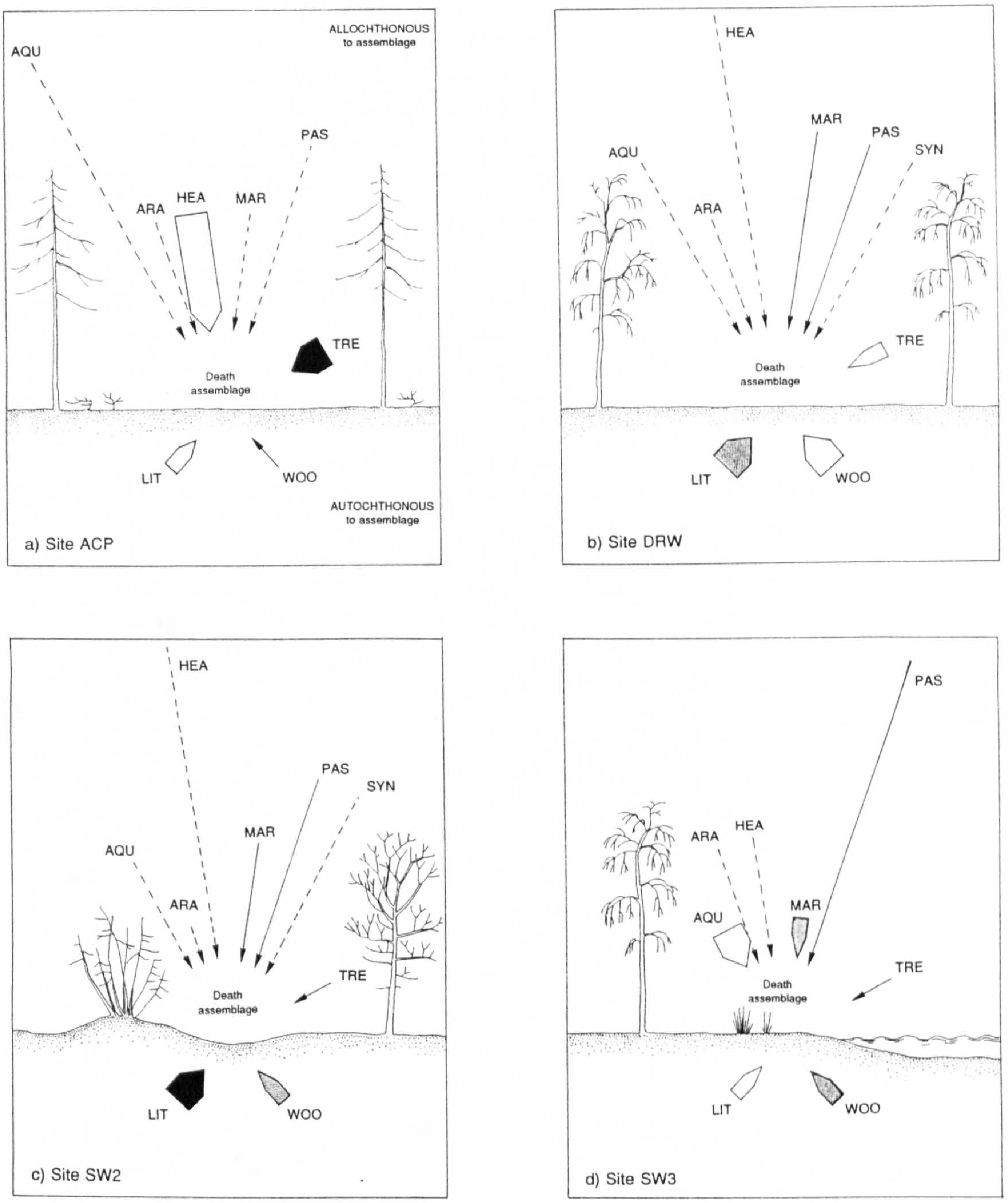


Figure 3.6 a-d Proportions of the total assemblage from each modern Yorkshire woodland site in each of the ecological groups identified, with a measure of the remoteness of the sites from potential sources of the insects involved.

Excludes eurytopic and uncoded taxa, and those identified to 'cert' = 3.

Key; Proportion of assemblage = width & fill of arrow.

- - - - 0-5% —— 5-10% ☐ 10-15% ▨ 15-20% ■ 20-30% ☐ 30-50% ■ >50%

Distance from major area of habitat = length of arrow.

—— 0-10 m.
———— 10-100 m.
—————— 100-500 m.
———————— 500-1000 m.
—————————— 1000 m.+

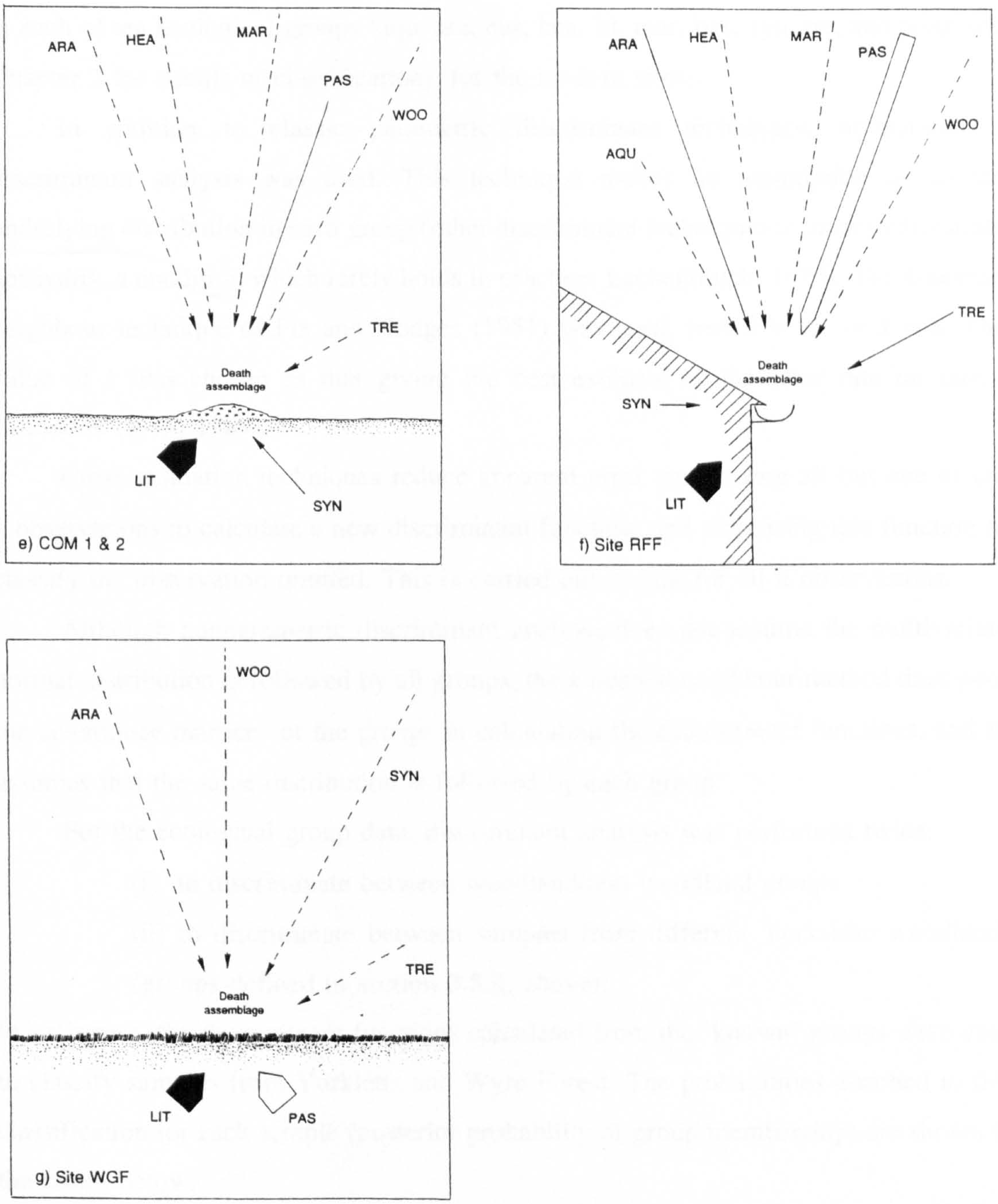


Figure 3.6 e-g Proportions of the total assemblage from other modern sites in each of the ecological groups identified, with a measure of the remoteness of the sites from potential sources of the insects involved.

Excludes eurytopic and uncoded taxa, and those identified to 'cert' = 3.

For explanation of arrows, see previous page.

(b) *Discriminant analysis of numbers in ecological groups*

Discriminant analysis was carried out on the numbers of beetle and bug individuals in each of ten ecological groups (aqu, ara, eur, hea, lit, mar, pas, syn, tre, and woo: see Chapter 2 for details of classification), for the modern sites.

In addition to classic parametric discriminant techniques, nonparametric discriminant analysis was used. This technique makes no assumption as to the underlying distribution in each group (other discriminant techniques assume multivariate normality, a condition which rarely holds in practice; Lachenbruch, 1975). The k-nearest neighbour technique of Fix and Hodges (1951) was used, with $k = 10$, or $k = 8$. The value of k was chosen as that giving the best estimate of the error rate on cross-validation (SAS, 1989).

Cross-validation techniques reduce apparent error rates, using all but one of the n observations to calculate a new discriminant function, and then using this function to classify the observation omitted. This is carried out in turn for all n observations.

Although nonparametric discriminant analysis does not assume the multivariate normal distribution is followed by all groups, the k-nearest neighbour method does pool the covariance matrices of the groups in calculating the discriminant functions, and so assumes that the same distribution is followed by each group.

For the ecological group data, discriminant analysis was performed twice:

(i) to discriminate between woodland/non-woodland groups.

(ii) to discriminate between samples from different Yorkshire woodlands (groups defined in section 3.5.ii, above).

In each case, the discriminant functions calculated from the 'known' groups were used to classify samples from Yorkletts and Wyre Forest. The probabilities attached to this classification for each sample (posterior probability of group membership) are shown in the tables below.

(i) Woodland/Nonwoodland samples

Nonparametric (with $k = 10$) and conventional discriminant analysis produced a similar classification of the 'unknown' samples from Yorkletts and Wyre, although the sample YKD (Yorkletts, downstream) was classified by the latter technique as part of the 'woodland' group, and by the former as part of the 'non-woodland' group. The similarity of results in both parametric and nonparametric techniques for all other samples suggest that the woodland and non-woodland assemblages are highly distinctive in the numbers in each ecological group, and this would appear to be the case (see Figure 3.7).

On cross-validation, seven (of 28) samples were misclassified.

Using nonparametric analysis, the samples from Yorkletts and Wyre were classified as shown below (P = Posterior probability of membership of the most likely group).

Sample	Group	P
YKU	Nonwoodland	0.5405
YKM1	Woodland	0.5604
YKM2	Woodland	0.6648
YKM3	Woodland	0.8844
YKM4	Woodland	0.8844
YKM5	Woodland	0.7727
YKD	Nonwoodland	0.5405
WYS	Woodland	0.6648

(ii) Woodland type

The four woodland sites from Yorkshire were used as groups, as above (3.5.ii, c). Again, nonparametric techniques (with $k = 8$) gave very similar results to conventional analyses, although YKM4, classified in group 1 by conventional analysis, was regarded as equally likely to belong to groups 1 or 4 in nonparametric analysis, and YKM5, classified in group 4 by conventional analysis, was regarded as equally likely to belong to groups 2 or 4 in nonparametric analysis.

On cross-validation, seven (of 28) samples were misclassified.

Using nonparametric analysis, the samples from Yorkletts and Wyre were classified as shown below (P = Posterior probability of membership of the most likely group).

Sample	Group	P
YKU	4 (SW3)	0.625
YKM1	4 (SW3)	0.625
YKM2	4 (SW3)	0.625
YKM3	4 (SW3)	0.625
YKM4	1 (ACP) or 4 (SW3)	0.5 each
YKM5	2 (DRW) or 4 (SW3)	0.5 each
YKD	4 (SW3)	0.625
WYS	4 (SW3)	0.625

The similarity of the results of parametric and nonparametric discriminant analysis in each case suggest that the technique is robust, and that the differences between the groups studied are marked. All the 'unknown' samples were classified correctly as woodland or non-woodland on the basis of discriminant functions calculated from the numbers of individuals in the ecological groups. Even sample YKD, from an open environment but downstream of a large woodland and therefore carrying a woodland component, was identified correctly as a non-woodland site, but with a relatively low posterior probability of membership of the non-woodland group (0.5405). Similarly, YKU, upstream of the same wood, was identified as part of the non-woodland group, but with a relatively low posterior probability of membership of the group.

Figure 3.7 shows the mean percentage of each assemblage from woodland and non-woodland sites in each of the ecological groups identified. For certain ecological groups, the difference appears marked: tree-dependent and woodland insects (groups 'tre' and 'woo') make up a larger proportion of the assemblage in woodland sites, while pasture and synanthropic groups ('pas' and 'syn') are more important in the non-woodland sites. The aquatic group ('aqu') appears more important in woodland situations, but this may be because several of the woodland samples were from beside or within streams and watercourses (for example, the Yorkletts assemblages YKM and YKD), whereas few of the non-woodland sites were close to water. Similarly, the importance of the heathland group 'hea' in the woodland samples is probably a reflection of the dominance of this group in the assemblages from the Allerthorpe Common site (ACP).

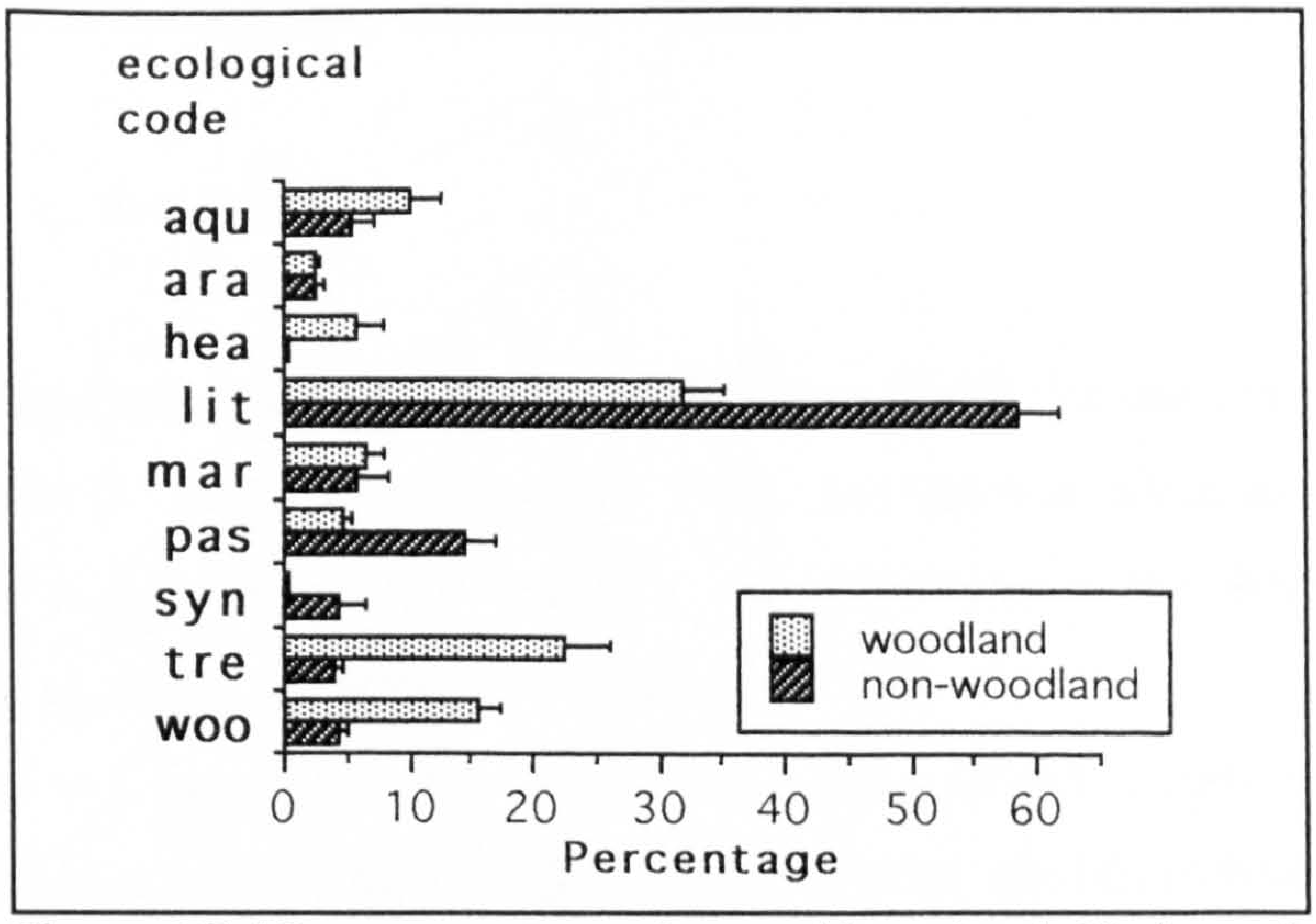


Figure 3.7 Mean percentage of assemblage (total N) in each ecological group ± S.E., for woodlands (26 samples) and non-woodland sites (18 samples).

3.5.iv Ecological diversity and dominance of modern death assemblages.

(a) *Measures of diversity*

Values of Fisher's α-diversity index (Fisher *et al.* 1943) for the samples from four modern woodland locations in the Vale of York, and other modern assemblages are given in Tables 3.16, 3.17 and 3.18, together with a measure of the Standard Error of the statistic, calculated as described by Williams (1947).

Fisher's α is a measure of the species diversity within a community, or unit of habitat (Southwood, 1978), incorporating elements of both **species richness** (or number of species in the sample, S), and **abundance** (or total number of individuals in the sample, N), related by the formula;

$$S=\alpha\log_e(1+\frac{N}{\alpha})$$

(Williams, 1947)

It assumes that the species abundance data follow a log series distribution. Kempton (1979) found that only 25 of 100 ecological data sets examined deviated from this model with χ^2 in excess of 5%, while Bullock (1971) also favoured the use of the log series to describe data for Malayan bird communities (although a truncated log-normal distribution could also have described the data), as the log series has the advantage of being less cumbersome in use, and less prone to spurious fit (where the data appear to fit a model that does not in fact describe the community accurately) than other distributions. Even where assemblages of 'opportunistic' species are considered, abundance distributions tend to follow the log-normal, although the identity of the dominant species will tend to vary, depending on prevailing conditions (MacArthur, 1960). Taylor *et al.* (1976) suggest that, for such community data, the log series should be assumed, unless proven to the contrary, and point out further advantages of α; it is a robust statistic that can still provide useful information on assemblages in which the underlying distribution deviates from the log series model, and is relatively insensitive to large fluctuations in the frequency of common species. Although many statistics for the quantification of ecological diversity have been proposed by various authors (and tested and reviewed by Taylor, 1978, and Samways, 1984), these features, along with the relative simplicity of α, commend its use. Kenward (1978) suggests that α is particularly suited to the description of insect death assemblages, which are subject to many random variables. Magurran (1988) argues that α is useful in most cases, if used in conjunction with a measure of equitability or dominance, such as the Berger-Parker dominance index, *d* (described below). If used in isolation, α provides no description of the extent to which top-ranking species dominate any assemblage.

Table 3.16 Values of diversity and dominance indices for modern woodland samples from the Vale of York.
(S = Number of distinct taxa in sample, N = Minimum number of individuals, α = Fisher's alpha diversity index (see text), d = Berger-Parker dominance ratio, D = Simpson's index of evenness).

Sample	S	N	α	SE of α	*d*	D	1/D
ACP 1	56	138	35	5	0.355	0.138	7.23
ACP 2	44	199	18	2	0.347	0.188	5.33
ACP 3	33	120	15	2	0.400	0.185	5.33
ACP 4	44	153	21	3	0.582	0.342	2.93
ACP 5	39	121	20	3	0.421	0.189	5.28
DRW 1	87	132	111	9	0.076	0.012	92.97
DRW 2	90	182	71	9	0.088	0.020	50.22
DRW 3	66	108	72	13	0.083	0.020	49.46
DRW 4	47	74	55	12	0.122	0.028	36.01
DRW 5	87	148	88	13	0.047	0.010	97.13
SW2 1	162	720	65	4	0.109	0.030	33.37
SW2 2	117	341	63	5	0.073	0.021	48.39
SW2 3	73	228	37	4	0.215	0.064	15.69
SW2 4	67	161	43	6	0.112	0.034	29.54
SW2 5	87	182	65	8	0.060	0.016	63.35
SW3 1	46	67	64	16	0.164	0.034	29.48
SW3 2	41	52	89	29	0.115	0.017	59.91
SW3 3	36	41	138	64	0.073	0.007	136.67
SW3 4	42	51	112	39	0.118	0.015	67.11
SW3 5	48	71	65	15	0.254	0.064	15.63

Table 3.17 Values of diversity and dominance indices for modern woodland samples from Kent and the Wyre Forest, Worcestershire.
(For explanation of column headings, see previous page).

Sample	S	N	α	SE of α	*d*	D	1/D
YKU	77	351	31	3	0.216	0.076	13.07
YKM 1	59	120	46	7	0.142	0.031	32.38
YKM 2	80	156	66	9	0.071	0.016	61.06
YKM 3	67	142	50	7	0.092	0.024	41.20
YKM 4	56	93	59	11	0.108	0.026	38.20
YKM 5	105	351	51	4	0.111	0.043	23.18
YKD	111	259	74	3	0.058	0.014	69.75
WYS	126	263	95	10	0.065	0.015	66.64

Table 3.18 Values of diversity and dominance indices for modern non-woodland sites: nettlebeds, compost, roof and pasture assemblages.
(For explanation of column headings, see Table 3.16).

Sample	S	N	α	SE of α	*d*	D	1/D
NTB 1	53	73	86	21	0.120	0.031	32.05
NTB 2	79	184	52	6	0.130	0.029	33.88
NTB 3	82	145	78	12	0.200	0.046	21.80
NTB 4	41	65	48	11	0.139	0.040	24.76
NTB 5	93	191	71	9	0.115	0.033	30.30
NTB 6	85	207	54	6	0.140	0.036	28.02
NTB 7	91	390	37	3	0.315	0.125	7.97
NTB 8	60	105	58	10	0.086	0.018	54.06
COM1	60	129	44	6	0.147	0.038	26.46
COM2	75	244	37	4	0.119	0.039	25.71
COM3	128	1538	33	2	0.190	0.079	12.72
RFF1	98	259	57	6	0.116	0.030	33.33
RFF2	118	438	53	4	0.082	0.027	37.04
RFF3	69	160	46	6	0.119	0.028	36.25
RFF4	147	1121	45	2	0.152	0.058	17.11
WGF1	44	74	46	10	0.108	0.027	37.04
WGF2	35	60	35	8	0.083	0.028	35.40

(b) *Rank-abundance plots for modern woodland assemblages*

Although it is not essential for the distribution of individuals to fit the log series in order for α to be valuable, there is an underlying assumption that this is the case, and the Standard Errors calculated depend on this assumption. In order to assess whether the modern woodland assemblages studied follow this distribution, graphs of rank abundance were first plotted (Figures 3.8 a-h); none of these appear to fit the hypothetical and "real community" curves presented by Whittaker (1970) and Magurran (1988). However, a further test was carried out. For a single sample from each site (as the five curves for each site appear to follow one another closely), a χ^2 test of goodness-of-fit to the log series distribution was carried out. In each case, the parameters x and α were estimated from S and N, using the equations;

$$\frac{S}{N}=[(1-x)/x][-\ln(1-x)]$$

and

$$\alpha=\frac{N(1-x)}{x}$$

Using these parameters, expected values could be derived for the numbers of species having any number of individuals, n, as described by Magurran (1988). Frequency classes with small expected values (<2) were summed. Values of x, α, and χ^2 for the samples (selected randomly from each site) are given below (Table 3.19).

Table 3.19 χ^2 test of goodness-of-fit to log series distribution for four assemblages from modern woodland

Sample	x	α	χ^2	df	p	
ACP 4	0.881	20.67	16.91	3	$p<0.001$	
DRW 2	0.721	70.60	4.31	6	$0.50>p>0.30$	n.s.
SW2 3	0.860	37.14	15.55	5	$0.01>p>0.001$	
SW3 4	0.314	115.54	0.65	1	$0.50>p>0.30$	n.s.

It would appear that the assemblages from Allerthorpe Common sample 4 (ACP4) and Stub Wood Ditch sample 3 (SW2/3) differ significantly from the expected log series distribution. However, the other two samples, Dunnington Rabbit Warren 2 (DRW2) and Stub Wood Pond 4 (SW3/4), can be described by the log series.

Original in colour

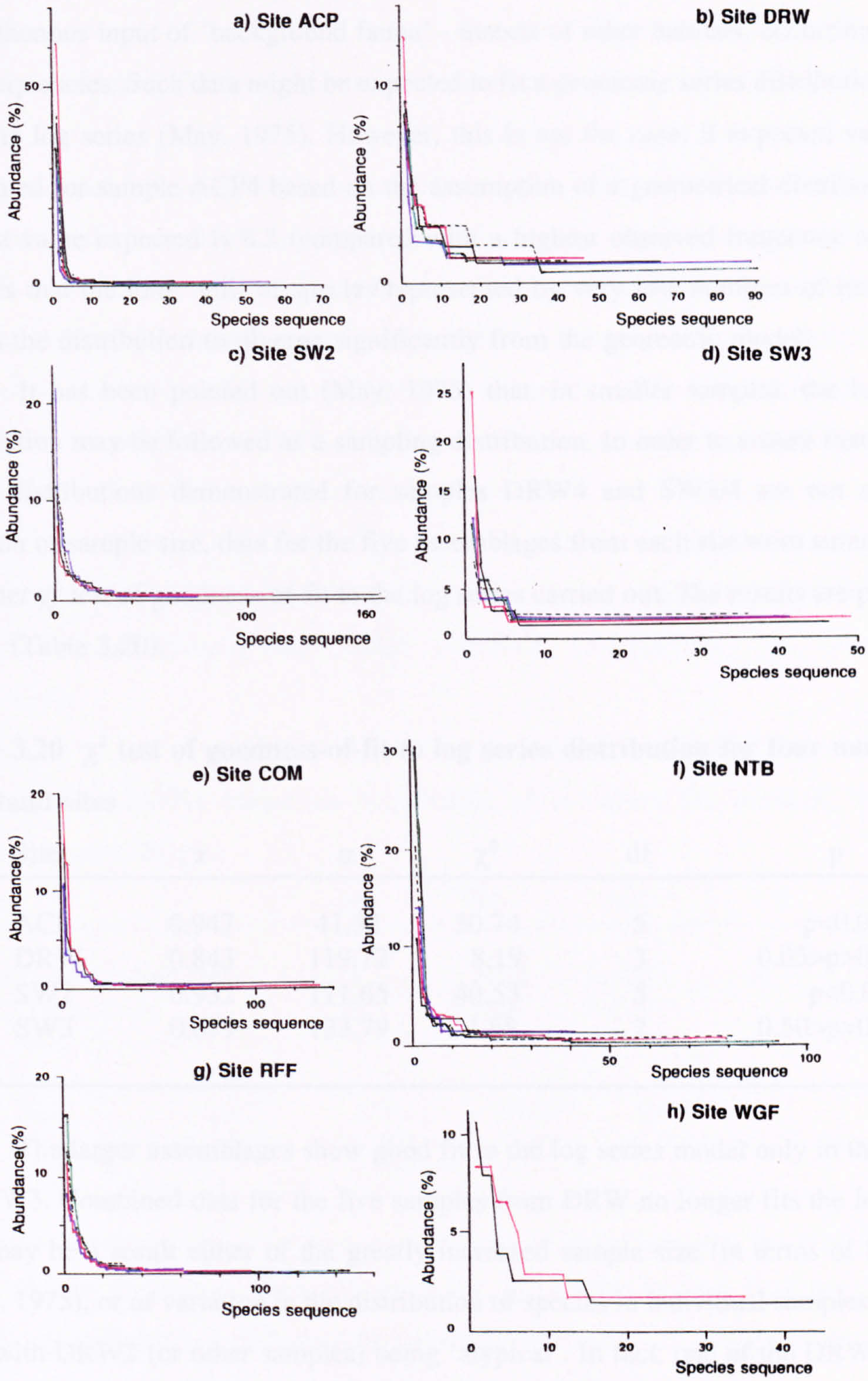


Figure 3.8 a-h Rank-abundance plots for modern Yorkshire woodlands, compost, nettlebed and roof sites.

In the case of the Allerthorpe samples, deviation from the log series may result from the high degree of dominance by the top ranking species (see below); the autochthonous fauna of this pine plantation is composed of few species, with a large allochthonous input of 'background fauna' - insects of other habitats, occurring at very low frequencies. Such data might be expected to fit a geometric series distribution rather than the log series (May, 1975). However, this is not the case; if expected values are calculated for sample ACP4 based on the assumption of a geometrical distribution, the highest value expected is 8.3 (compared with a highest observed frequency of 89). It appears that the long 'tail' of species represented by very low numbers of individuals causes the distribution to diverge significantly from the geometric model.

It has been pointed out (May, 1975) that, in smaller samples, the log series distribution may be followed as a sampling distribution. In order to ensure that the log-series distributions demonstrated for samples DRW4 and SW3/4 are not simply a function of sample size, data for the five assemblages from each site were summed, and a further χ^2 test of goodness-of-fit to the log series carried out. The results are presented below (Table 3.20).

Table 3.20 χ^2 test of goodness-of-fit to log series distribution for four modern woodland sites

Site	x	α	χ^2	df	p
ACP	0.947	41.32	30.74	5	p<0.001
DRW	0.843	119.72	8.19	3	0.05>p>0.02
SW2	0.932	111.65	40.53	5	p<0.001
SW3	0.679	133.79	1.68	2	0.50>p>0.30

The larger assemblages show good fit to the log series model only in the case of site SW3. Combined data for the five samples from DRW no longer fits the log series; this may be a result either of the greatly increased sample size (in terms of N and S) (May, 1975), or of variation in the distribution of species in individual samples from the site, with DRW2 (or other samples) being 'atypical'. In fact, one of the DRW samples (DRW1) fits the log series model well (p>0.99), while the others do not (for DRW3, 0.90<p<0.95, DRW4, 0.30<p<0.50, and DRW5, 0.50<p<0.70). There appears to be little obvious pattern in the frequency distributions of these death assemblages, although they appear to be following similar overall trends (see graphs, Figure 3.7). Both chance occurrence of single specimens imported from other environments, and post-depositional processes may be responsible for the loss of any pattern from the living community, if it exists.

(c) *Values of Fisher's α for modern samples*

As noted above, α assumes an underlying log series distribution which is not followed by all the modern woodland assemblages. Nevertheless, this statistic can still provide useful information on the diversity of communities. Its advantages include a greater degree of independence of an underlying model than other indices which incorporate S and N, and lower variability as a function of N than would be shown if S alone were used (Taylor, 1978). Of eight diversity measures tested by Taylor (1978), α proved the most able to discriminate between sites.

High values of α indicate high diversity. Results of an analysis of variance performed on the α values from the four sites are shown below (Table 3.21); the data were first logarithmically transformed (ANOVA requires that data be normally distributed).

Table 3.21 ANOVA based on logarithms of α values for modern Yorkshire woodland assemblages.

Source	df	SS	MS	VR	
Between Treatments (sites)	3	1.2096	0.4032	24.17	($p<0.01$)
Within Treatments	16	0.2669	0.0167		

Site	ACP	SW2	DRW	SW3
Mean (log α)	1.320	1.725	1.887	1.951

Where the mean values of log α for sites differ by less than the 5% Least Significant Difference (LSD), they are underlined in Table 3.21. It appears that site ACP can be distinguished from all the other modern woodland sites by its particularly low values of α. However, it appears to be impossible to distinguish the other sites on the basis of α alone.

In a second analysis of variance of logarithmically transformed α values from modern death assemblages (Table 3.22), samples with a high degree of error associated with α (SE of α > 25% of value of α) were excluded (all samples from SW3 were excluded), and samples from the non-woodland sites NTB, COM, and RFF, and from Yorkletts, Kent (midstream; YKM) included. In this case, there were also significant differences between sites. However, non-woodland samples (NTB, COM and RFF) showed no clear separation from the woodland sites on the basis of α. Values of α for NTB and RFF did not differ from those from the woodland sites SW2 and YKM by more than the 5% LSD. The mean value for site COM was significantly lower than for most of the sites, although not significantly different from RFF. Mean α for the ACP site was again significantly lower than for all other sites, and that for the DRW site higher than those for most other sites.

Table 3.22 ANOVA based on values of α for modern woods and nettlebeds

Source	df	SS	MS	VR	
Between Treatments (sites)	6	98.718	16.453	1468.08	($p<0.01$)
Within Treatments	28	0.314	0.011		

Site	ACP	COM	RFF	SW2	YKM	NTB	DRW
Mean (Log α)	1.132	1.577	1.699	1.725	1.731	1.767	1.888

Of the modern woodland sites, values of α were highest in samples from site SW3, where the maximum value (sample SW3/3) was 138. This compares with values for archaeological assemblages ranging from around 2, in granary beetle assemblages composed of a few, highly specialised synanthropic species, to 60-70 for 'outdoor' deposits with a large allochthonous component (Kenward, 1978). The particularly high values in sample SW3 may reflect the influence of increased **habitat diversity** around SW3 compared with the other sites; in particular, the close proximity of aquatic and marshland habitats, extremely poorly represented in the assemblages from the other sites. However, the error associated with values of α in SW3 samples are great, with SE of α > 45% in the case of sample SW3/3.

(d) *Dominance measures*

Two measures of the degree of dominance of samples by abundant species have been calculated and are shown in Tables 3.16-3.18. The **Berger-Parker** index, ***d***, is simply defined as the proportion of the assemblage made up of the most abundant species:

$$d = N_{max}/N$$

where N_{max} is the number of individuals of the most abundant species (Berger and Parker, 1970). Like α, this measure is free of sample bias. It shows differences in the 'evenness' or equitability of numbers of individuals between species in a sample (Southwood, 1978). *d* can vary from 0 (where there are an infinite number of equally represented species) to 1 (only one species present in the assemblage). As *d* increases, the single top ranking species accounts for a larger proportion of the total assemblage, so diversity usually decreases with increasing *d*.

Simpson's (or Yule's) index, **D**, is more complex, taking into account the abundances of each species in the assemblage, not only the single most abundant. Therefore, if an assemblage is heavily dominated by a small group of taxa, the Simpson index should give a more accurate indication of this dominance than the Berger-Parker index. Simpson's index is given by the equation

$$D=\sum\left(\frac{n_i(n_i-1)}{N(N-1)}\right)$$

Where n_i= number of individuals of the ith species (Simpson, 1949).

D may range from 0 to 1, where 0 describes an assemblage where all species are represented by single individuals, and 1 an assemblage where there is only one species present (n_i=N). D increases as the proportion of the assemblage made up of top ranking species increases. Highest values of D will be obtained where a single species is dominant, but D may be high where there is a small group of dominant taxa, whereas *d* would be low in this case. Values of D decrease as the diversity of an assemblage increases, and the reciprocal 1/D (which increases with increased diversity) is therefore the form in which the index is more often expressed (Magurran, 1988). Tables 3.16, 3.17 and 3.18 give both D and 1/D.

In practice, Simpson's index and the Berger-Parker measure will often give similar results. Magurran (1988), for example, found a significant correlation ($p<0.01$)

between the values for the two measures for moth abundance data from Banagher, Northern Ireland. Figure 3.9 shows a plot of the values of the two indices for the modern insect death assemblages from Yorkshire woodlands. The values of *d* and D are highly correlated, with a correlation coefficient (Pearson product moment) of 0.966.

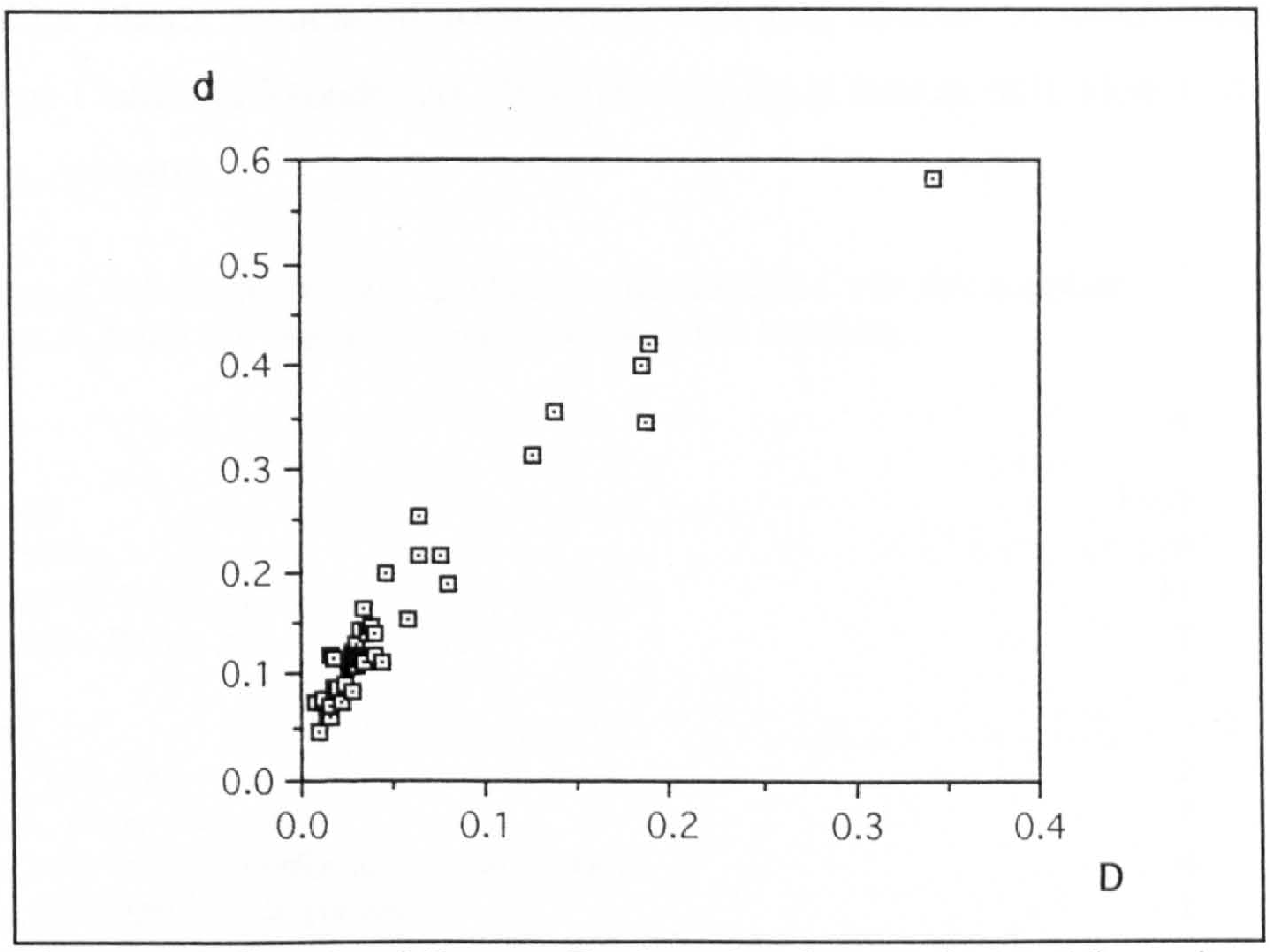


Figure 3.9 Graph of Berger-Parker dominance index (*d*) against Simpsons index (D), for death assemblages from modern sites.

The highest values of *d* from nettlebed samples (0.315, 0.200, and 0.14 in samples NTB7, NTB3 and NTB6 respectively) are artefacts caused by the 'lumping' of all Aleocharine taxa into the single RTU 'Aleocharinae spp.'(Aleocharinae in other samples were split into many RTUs). Since the original material was not accessible, the Aleocharinae could not be reclassified into the equivalent RTUs used in the other samples, so, in the three samples in which this group is dominant, *d* is greatly increased. If the Aleocharinae are excluded, the revised values of *d* for these sites are 0.213, 0.060, and 0.107, respectively.

3.5.v Hostplants of phytophagous insects in modern death assemblages.

Tables 3.23.a-j list the plants associated with beetle species recovered in the modern insect assemblages, as recorded in the entomological literature (Philp, 1991; Bullock, 1992). In Table 3.24, the hostplants are assigned to 'woodland' and 'non-woodland' groups, the former including all trees and shrubs (except hawthorn

(*Crataegus* spp.), broom (*Cytisus scoparius* (L.) Link), *Rosa* spp., and willow (*Salix* spp.)), and bracken (*Pteridium aquilinum*). The percentage of the hostplant-specific fauna with hosts in the 'woodland' group is also shown.

Table 3.23.a Plants associated with beetle and bug species in assemblages from Allerthorpe Common Woods (ACP) (excluding those insects only identified to 'cert' '3'; that is, 'possible')

n = Number of individuals of beetle and bug species associated with this hostplant
s = Number of beetle and bug species associated with this hostplant.

Hostplant	**n**	**s**
Crataegus spp.	307	2
Calluna vulgaris	128	1
Calluna vulgaris, Erica spp.	11	4
Polygonum spp., *Rumex* spp.	7	1
Pinus spp.	4	1
Quercus spp.	4	1
Pinus spp., *Picea* spp.	2	2
Quercus spp., *Alnus glutinosa*	2	1
Betula spp. (also *Corylus avellana, Populus tremula*)	2	1
Betula spp., *Salix* spp., *Alnus glutinosa*	1	1

Plants represented by a single insect: *Brassica* (or *Sinapis, Sisymbrium* spp., other Brassicaceae), Poaceae, *Salix* spp., *Betula* spp., *Urtica* spp.

Table 3.23.b Plants associated with beetle and bug species in assemblages from Dunnington Rabbit Warren Wood (DRW).

	n	**s**
Salix spp., *Betula* spp.	15	1
Quercus spp., *Alnus glutinosa*	12	1
Betula spp., *Salix* spp., *Alnus glutinosa*	10	1
Betula spp.	8	6
Crataegus spp.	8	1
Betula spp., *Alnus glutinosa, Corylus avellana*	5	1
Quercus spp.	4	1
Betula spp. (also *Corylus avellana, Populus tremula*)	3	1
Brassica spp.	3	1
Salix spp. (particularly *S. caprea*)	3	1
Sisymbrium spp., other Brassicaceae	3	2
Calluna vulgaris, Erica spp.	2	2
Poaceae	2	1
Polygonum spp., *Rumex* spp.	2	1
Quercus spp., *Betula* spp., *Corylus avellana*	2	1
Quercus spp., *Fagus sylvatica*	2	1

Plants represented by a single insect: *Lathyrus pratensis* (or *Vicia* spp.), *Lycopus europeus* (or *Mentha aquatica*), *Pinus* spp., *Quercus* (or *Betula*) spp., *Rosa* (or *Rubus* or *Fragaria*) spp., *Trifolium repens*, *Trifolium* (or *Lotus* or *Vicia*) spp., *Urtica dioica, Vicia* spp.

Table 3.23.c Plants associated with beetle and bug assemblages from Stub Wood, samples SW2.

	n	s
Quercus spp.	8	4
Sisymbrium spp., other Brassicaceae	6	2
Brassica spp.	5	2
Polygonum spp, *Rumex* spp.	5	1
Betula spp.	4	2
Poaceae	4	1
Urtica spp.	4	2
Brassica, Sinapis, Sisymbrium spp., and other Brassicaceae	2	1
Hedera helix	2	1
Polygonum spp.	2	1
Trifolium spp.	2	2

Plants represented by a single insect: Brassicaceae, *Carex* spp. (or cereals), *Cirsium arvense*, *Cirsium vulgare* (or *C. palustre*, *Carduus nutans*), *Crataegus* spp., *Polygonum amphibium*, *Pteridium aquilinum*, *Pyrus communis* (or *Mespilus* sp.), *Quercus* spp. (or *Fagus sylvatica* or *Castanea sativa*), *Ranunculus repens* (or *Anemone nemorosa* or *Caltha palustris*), *Rosa* (or *Rubus* or *Fragaria*) spp., *Salix* (or *Betula*) spp., *Salix* spp., *Solanum dulcamara*, 'Waterside plants'.

Table 3.23.d Plants associated with beetle and bug species in assemblages from Stub Wood, samples SW3.

	n	s
Salix spp.	4	2
Betula spp.	3	1
Sisymbrium spp, other Brassicaceae	3	2
Betula spp. (also *Corylus avellana*, *Populus tremula*)	2	1
Betula spp, *Alnus glutinosa*, *Corylus avellana*	1	1

Plants represented by a single insect: *Cirsium* (or *Centaurea* or *Carduus*) spp., *Equisetum* spp (particularly *E. palustre*), *Fagus sylvatica*, *Lathyrus pratensis* (or occasionally *Vicia* spp.), *Malus sylvestris*, Most Fabaceae, *Pteridium aquilinum*, *Quercus* spp. (or *Alnus glutinosa*), *Salix* (or *Betula*) spp., *Urtica* spp.

Table 3.23.e Plants associated with beetle and bug species in assemblages from Yorkletts, sample YKU.

	n	s
Ulex spp., *Cytisus scoparius*	3	2
Polygonum spp, *Rumex* spp.	3	1

Plants represented by a single insect: *Cirsium* (or *Carduus*) spp., *Cytisus scoparius*, *Fraxinus excelsior*, *Rosa* spp., *Rubus* spp., *Solanum dulcamara*, *Trifolium* spp., *Urtica dioica*.

Table 3.23.f Plants associated with beetle and bug species in assemblages from Yorkletts, samples YKM.

	n	s
Quercus spp.	12	6
Betula spp., *Alnus glutinosa*, *Corylus avellana*	10	1
Trifolium spp.	4	3
Polygonum spp., *Rumex* spp.	4	2
Quercus spp., *Fagus sylvatica*, *Castanea sativa*	4	2
Betula spp.	4	1
Ononis repens, *O. spinosa*	2	1

Plants represented by a single insect: *Cytisus scoparius* (or *Ulex* spp.), 'deciduous trees, esp. *Fagus sylvatica*', *Lathyrus* (or *Vicia*) spp., *Mentha aquatica*, 'most Fabaceae', *Ranunculus repens* (or *Anemone nemorosa* or *Caltha palustris*), *Ulmus* spp., *Vicia* spp.

Table 3.23.g Plants associated with beetle and bug species in assemblages from Yorkletts, samples YKD.

	n	s
Urtica dioica	4	3
Ulmus spp.	3	2
most Fabaceae	3	1
Polygonum spp., *Rumex* spp.	2	1
Ranunculus repens, *Anemone nemorosa*, *Caltha palustris*	2	1
Trifolium spp.	2	1

Plants represented by a single insect: *Azolla filiculoides*, *Heracleum sphondylium*, *Lotus corniculatus*, *Prunus* (or *Malus* or *Pyrus*) spp., *Rubus* spp., *Rumex* subgenus *Rumex*.

Table 3.23.h Plants associated with beetle and bug species in assemblages from Wyre Forest (WYS).

	n	s
most Fabaceae	2	1
Quercus spp.	2	1
Sisymbrium spp., other Brassicaceae	2	1

Plants represented by a single insect: *Betula* spp.(or *Corylus avellana*, *Populus tremula*), *Carex* spp., *Chamomilla recutita* (or other mayweeds), *Corylus avellana*, *Pinus* (or *Picea* or *Abies* or *Betula*) spp., Poaceae, *Salix* (or *Betula*) spp., *Tilia* spp., *Urtica dioica*, *Viburnum lantana* (or *V. opulus*).

Table 3.23.i Plants associated with beetle and bug species in assemblages from Nettlebeds (NTB).

	n	s
Urtica spp.	54	4
Trifolium spp.	6	2
Ranunculus repens, *Anemone nemorosa*, *Caltha palustris*	2	1

Plants represented by a single insect: *Cirsium arvense*, *Lycopus europeus* (or *Mentha aquatica*), *Tanacetum vulgare*, *Matricaria* spp., *Artemisia* spp., 'Waterside plants'.

Table 3.23.j Plants associated with beetles in roof assemblages (RFF)

	n	s
Trifolium spp.	26	3
Most Fabaceae (including *Trifolium*)	7	1
Urtica spp.	5	1
Brassica spp.	4	1
Rubus spp.	2	1

Plants represented by a single insect: *Capsella bursa-pastoris*, *Oenanthe aquatica* (or *O. crocata*), *Polygonum* (or *Rumex*) spp., *Ranunculus repens* (or *Anemone nemorosa* or *Caltha palustris*), *Rumex* spp., *Ulmus* spp.

Table 3.24 Insect-plant associations in modern assemblages.

Site	with specific hosts		without specific hosts		no. woodland plants		%age woodland plants	
	n	s	n	s	n	s	n	s
ACP	472	19	259	102	16	8	3.4	42.0
DRW	93	32	552	190	63	16	67.7	50.0
SW2	59	34	1578	266	18	11	30.5	32.4
SW3	23	17	260	135	11	8	47.8	47.1
YKU	14	11	337	66	1	1	7.1	9.1
YKM	49	25	813	153	33	13	67.4	52.0
YKD	22	15	237	96	4	3	18.2	20.0
WYS	16	13	247	113	7	6	43.8	46.2
NTB	66	11	1294	269	0	0	0.0	0.0
RFF	50	13	1930	206	3	2	6.0	15.4

The percentage of each assemblage with specific hostplant preferences varied greatly, from 2.5% of the individuals (in site RFF) to over 64% of individuals (in site ACP). The mean percentage of the individuals in the assemblage is 17.1% for samples from woodland sites, 3.8% for non-woodland sites (YKU, NTB and WYS). A mean of 10.4% of species in an assemblage have specific hosts; this proportion appears higher in woodland than non-woodland sites (12.8%, as opposed to 8.0% in non-woodland sites); however, the wide variation between samples means this difference between the means of woodland and non-woodland sites is not significant (t=1.45, p=0.28). Over 89% of the species have no specific hostplant, being more generalist herbivores, carnivores or detritivores.

3.6 Discussion

3.6.i Species composition of assemblages

The larger assemblages (those of around 700 individuals or more) seem to contain a high proportion of the total taxa represented in the entire deposit (Figure 3.2). However, the limits to the number of taxa recovered in any one assemblage are not purely biotic, but also involve human and taphonomic factors. Where fossils are being picked out of a large quantity of plant remains (as was the case for the modern woodland deposits), larger, more obvious remains (such as the patterned elytra of the ladybird *Propylea quattuordecimpunctata* (L.)) are more likely to be selected than the remains of smaller, cryptic species. The human is acting here as a 'predator', and may form a 'search image' (Tinbergen, 1960) for the more common remains, becoming more efficient at recovering these. With care, these effects can be minimised, although species having a soft exoskeleton, or one prone to fragmentation into many small pieces (as in some of the Cantharidae) are less likely to be recovered or identified.

Like many living communities, the death assemblages tended to contain few abundant species, and many less common taxa (Hanski and Koskela, 1977). When the number of species is plotted against the logarithm of the number of samples (Figure 3.3), the resultant graph is approximately linear. Pearson (1962), found a similar pattern in assemblages of fossil Coleoptera from post-glacial deposits at St Bees, Cumbria, and concluded that they therefore appeared to represent a natural population. However, such a pattern might be produced by sampling effects alone. Larger samples (with higher N) will contain representatives of a larger number of taxa. It is not possible to say, from the numbers of individuals of species alone, whether the death assemblage represents a living community.

The results of multidimensional scaling using dissimilarity measurements based on species lists for modern assemblages (Figure 3.4) suggest that the species composition of insect assemblages from each of the different woodland types is fairly distinct, at least for some of the woodlands investigated, such as the conifer plantation ACP. Here, assemblages show a high degree of dominance by a handful of species able to exploit the fairly specialised niches available in the conifer woodland or the heathy vegetation that preceded it on the site (Table 3.13).

However, the results of discriminant analysis suggest that the differences in the composition of assemblages between woodland and non-woodland sites (or between woodland sites of differing nature) are insufficiently predictable to be of use in reconstructing environments from the assemblages present. This may be a function of the nature of insect death assemblages, with many species occurring at low frequencies. This renders them liable to change significantly with chance events, or under the influence of post-depositional processes. Alternatively, the aggregation or dispersal of populations, resulting from habitat effects at a variety of scales (see Cromartie, 1975), or over time (Southwood, 1978), may act differentially at the different sites, diluting the larger-scale habitat distinctions being sought by discriminant analysis. The choice of taxa on which the discriminant functions were based will also have influenced the outcome of the analysis; rather than being 'woodland' taxa, these were largely general litter dwellers or eurytopic species.

Similarly, the most abundant species in modern assemblages were, in general, litter dwellers and uncoded taxa (see Tables 3.13-3.15). True 'woodland species', such as those proposed as indicators of ancient woodland by Garland (1983), were rarely present, and, where they did occur, it was often at very low population densities. Of the 57 beetle species listed as old woodland indicators for the Yorkshire area by Garland, only four were present in the assemblages from modern Yorkshire woodlands (*Anisotoma humeralis* (Fabricius), *Glischrochilus hortensis*, and *Trypodendron domesticum* (L.) from DRW, and *Dryocoetes villosus* (Fabricius) in SW2). A larger range of these taxa occurred in samples from woods at Yorkletts (*Anisotoma humeralis*, *Melasis buprestoides* (L.), *Cylindronotus laevioctostriatus* (Goeze), *Orchesia undulata* Kraatz, *Leiopus nebulosus* (L.), and *Dryocoetes villosus*). However, in none of these species did the total number of individuals over all samples exceed 5, so all were excluded from discriminant analyses.

It appears that the extent to which woodland structure can be inferred from from the species structure of beetle death assemblages is limited. Assemblages of species were distinctive at different sites, but these differences do not seem to be sufficiently predictable to identify the nature of the site in which an assemblage formed. This echoes work on modern snail communities: Paul (1975) suggested there are limits to the levels of resolution which can be obtained in the reconstruction of woodlands from their faunas; snail faunas were not significantly altered in coppiced areas. Likewise, changes in the composition of modern carabid beetle communities were found by Fishpool (1992) to be fairly poor indicators of a clearing within woodland.

The attempt to use quantitative approaches (such as discriminant analysis) to identify the origin of assemblages using the numbers individuals of insect species may be less appropriate than techniques incorporating a more qualitative element, for example, where taxa are assigned to ecological groups.

3.6.ii Ecological groupings

There is clear variation in the ecological composition of assemblages at the different sites (Figures 3.5 a-h), and these variations generally reflect the local habitats well (Figures 3.6 a-g, and Figure 3.7). Thus site SW3 shows heavy representation of 'aquatic' taxa. Site ACP has a large proportion of species associated with heathland habitats, although this may represent a lag between the death assemblage and the living insect community at the site, since afforestation of this former heathland has occurred recently.

The largest ecological grouping in most assemblages was the 'decomposer' component, 'lit'. This is generally found to be the case in archaeological deposits, and has been explained by the accumulation of organic litter in towns (Kenward, 1982). As peats and most waterlogged deposits in urban situations are largely composed of plant litter in which decomposition has been arrested, the similarity between archaeological assemblages, and modern woodland samples from leaf litter is unsurprising. However, in the urban situation, where the greater part of any assemblage is likely to be made up of autochthonous decomposer species, this component of the fauna can be further subdivided into species of foul matter and those of drier 'compost', to provide further details of the conditions under which the deposit formed. In modern woodland assemblages, most of the decomposer species were those of dry litter, eg. the staphylinid *Othius myrmecophilus* Kiesenwetter.

The number of individuals in each of the ecological groups can be used as a tool through discriminant analysis for identifying assemblages laid down in woodland, and unwooded conditions, and this would be preferable to reliance on the frequency of 'indicator species' (either singly, or as groups). Techniques such as Two-Way INdicator SPecies ANalysis (TWINSPAN), used in insect community classification, for example, by Rushton and Luff (1988), Day *et al.* (1993), and Fishpool (1992), often seem to give appropriate results which can be supported by the known ecology of the taxa involved, but the use of previously determined indicator species would appear less useful in the interpretation of death assemblages.

The attempt to classify samples as originating in woodland of a particular type, using nonparametric discriminant analysis of numbers in each ecological group appeared less successful; most of the samples were classified as belonging to group 4 (Site SW3), probably as a result of the more aquatic nature of the unclassified samples (all from woodland streams and streamsides), and SW3 (from beside a woodland pond).

3.6.iii Diversity and Dominance

Many of the studies of assemblages of living communities that have been carried out in the past have concentrated on only part of the fauna of any one site, rather than whole communities, which might be comparable with the death assemblages studied here.

Thus Day, Marshall and Heany (1993) and Day (1987) found that living carabid beetle communities in coniferous woodland were more diverse than those of nearby deciduous woods. However, had phytophagous beetles (such as the weevils) also been considered, the result is likely to have been very different; few phytophagous species in Britain can utilise alien conifers (Southwood *et al.* 1982), and Kennedy and Southwood (1984) record only 11 species of beetle found in association with the Norway Spruce *Picea abies* in Britain (compared with 67 on *Quercus robur* L. and *Q. petraea* (Mattuschka) Liebl. Sitka spruce (*Picea sitchensis* (Bong.) Carr) was the dominant species in the plantation Day *et al* studied. It is also possible that the pitfall trapping technique employed could have led to bias of results, with larger catches under conifers, where ground flora is sparse (Greenslade, 1964).

Fishpool (1992) found that carabid diversity changed less than that of plant communities along transects between open habitats and woodland, and was therefore capable of a lower resolution of habitat description. Values of α from living arthropod communities on British trees, sampled by insecticidal fogging, range from 56 (on *Salix alba* L.), and 57 (*Betula* spp.), to 106 on *Quercus* spp. (Southwood *et al.* 1982). From archaeological sites, assemblages with a high 'background' input from Saxo-Norman deposits at Saddler Street, Durham show values of α up to 60-70 (Kenward, 1978). Higher values occurred in assemblages from the early occupation phases at the 24-30 Tanner Row (General Accident) and 5 Rougier Street sites, York (mid-late 2nd century AD), where mean values of 80-90 were recorded. The highest diversity value from a single sample at these sites was 363 (SE of α=323), for a very small insect assemblage (N=29, S=28, sample number 367). Two values of 319 (SE of α=216) were found, for small assemblages (N=38, S=36). One of these (sample number 374) showed signs of being deposited by flowing water, the other (sample number 177) had built up on a hard-packed gravel surface, and contained a mixture of aquatic and other 'outdoor' species, and synanthropes (Hall and Kenward, 1990).

Values of α from most modern assemblages were therefore relatively high, particularly in woodland sites (the maximum value of α was 138, from site SW3). However, the values of α were not sufficient to determine the origin of a sample; while woodland samples were diverse (mean α for sites DRW and SW2 were 79.4 and 54.6, repectively), so were some non-woodland sites (mean α for nettlebeds, NTB, was 60.5). This concurs with Fishpool's (1992) finding, that diversity indices of carabid communities were of little value in defining habitat boundaries between woodland and grassland environments.

Day (1987) found that carabid communities from old woodland and sand dunes showed a high degree of dominance by the highest ranking species (with values of *d* up to 0.75). None of the modern death assemblages showed dominance values approaching this, and the highest values were shown in the conifer plantation (ACP) and nettlebed (NTB) sites, rather than the older woodlands. In a study of whole communities in the canopy of trees of various species, Southwood *et al.* (1982) found wide variation in the dominance index *d* from 0.07 for the introduced *Robinia pseudacacia* L., and 0.08 for the native *Salix cinerea* L., to 0.78 for *Betula* spp. They suggest that the last value may represent a species 'outbreak', from one stable population state to a second epidemic equilibrium state. Such an outbreak could be responsible for the high dominance values recorded for the ACP site.

3.6.iv Plant hosts

Since only a small part of each assemblage was made up of host-specific phytophages, attempts to reconstruct the species composition of woods from small insect assemblages may involve very small numbers of insects. Other factors, such as the variation in the number of herbivore species associated with different plants (see Chapter 2), further complicate the picture obtained of vegetation structure.

Notwithstanding the above cautions, hostplant preferences have been used to reconstruct forest structure in the vicinity of archaeological deposits at the time of accumulation. Buckland (1979) used beetle hostplant associations to provide detail on the woodland compostion at Thorne Moor. These results substantiated data from pollen analysis that suggested birch-alder fen was present in the area. The presence of oak-feeding beetles such as *Rhynchaenus avellanae* (Donovan) and *R. quercus* (L.) was used to suggest that *Quercus* spp. may have been under-represented in pollen diagrams from the site (perhaps resulting from the poor flowering of oak in unfavourable, waterlogged conditions). In deposits from the Hoxnian interglacial at Nechells, Birmingham, the occurrence of *Rhynchaenus avellanae* and *R. quercus* closely mirrored a peak in *Quercus* pollen, with the phytophagous beetles disappearing when oak declined dramatically in the locality, being replaced by *Alnus* as the dominant tree (Shotton and Osborne, 1965).

Hostplant preferences were also used by Girling (1982 and 1985) to infer woodland composition at the Stileway site (Somerset). Here, she developed a 'points' system, taking into account the degree of host specificity shown by the insect species recovered. Both Girling and Buckland used the number of insect species (rather than individuals) as an indication of the relative importance of plant species in the community. However, sampling effects alone will cause a variation in the number of species with size of the assemblage studied (see Figure 3.2). Thus the number of hostplant-specific invertebrate species in the large assemblages from abiotic city roofs (RFF) equals that in the small assemblage from Wyre (WYS), a plant-species-rich ancient woodland (Table 3.24). Therefore, the number of insect species alone cannot be used in a comparison of plant species structure for different sites, although it may be valuable at an individual site. However, large numbers of individuals (especially when of several species) associated with a plant clearly indicate local importance of that plant; thus, for example, *Quercus* spp. emerge as the top-ranking plant hosts in sites SW2 and

YKM (Tables 3.23.c, 3.23.e). For the nettlebed sites (NTB), *Urtica* feeders make up over 80% of the total number of individuals of host-specific phytophages, and there are no insects associated with woodland plants. The proportion of the assemblage, both in terms of number of individuals and species associated with 'woodland' plants is higher from woodland sites (ACP, DRW, SW2&3, WYS and YKM) than non-wooded ones (NTB, RFF, YKU) (see Figure 3.24). In all assemblages, a large number of plant species are represented by single insects, which are of little interpretative value. Among the plants most commonly represented by single insects are the vetches *Lathyrus* and *Vicia* spp., generally herbs of open, early successional habitats, whose associated insects include the weevils *Apion* and *Sitona* spp. (present as singletons in six of the ten sites listed). Suitable habitats for vetches would be patchy and ephemeral in Britain's native 'wildwood'; thus insects dependent on these plants might be expected to be highly mobile. Many *Sitona* species, in particular, are regularly found long distances from the nearest hostplants (M. G. Morris, pers. comm.). The only other plants to be represented in six of the ten sites are *Salix* or *Betula* spp. However, in this case, all records are for a single insect species, the tiny weevil *Ramphus pulicarius* (Herbst).

Although local trees are well represented in the hostplant lists of woodland assemblages, few of the woodland herbs noted (even in the immediate proximity of the deposits) are represented. Those that are include *Pteridium aquilinum* (L.) Kuhn, and (possibly) *Anemone nemorosa* L. at Stub Wood; *Leiosoma deflexum* Panzer feeds on *Anemone* as well as *Ranunculus* spp. and *Caltha palustris* L. (Bullock, 1992), but is also found in the tussocks of *Deschampsia* spp. (Luff, 1965). The minor representation of woodland herbs in the insect assemblage, even for the woods where the herb layer was relatively species-rich (such as Stub Wood), is disappointing. Woodland herbs tend to be poorly represented in pollen assemblages; few of the herbaceous 'ancient woodland indicators' have characteristic pollen, save for *Mercurialis* (though the two native species, *M. perennis* and *M. annua* L., are not separable on pollen morphological characteristics), and *Anemone nemorosa* (Day, 1993). Insect assemblages would appear to have the potential to offer complementary data indicating the presence or absence of this group of plants, but this does not seem to be feasible in practice. One reason for this may be simply that too few insects are closely associated with woodland herbs to allow them to be used as reliable indicators; Bullock (1992) records only three beetle species closely associated with *Mercurialis perennis*, none on *Paris quadrifolia* or *Hyacinthoides* *non-scripta.*

Certain obvious anomalies occur in the species lists; at site ACP, insects associated with hawthorn (*Crataegus* spp.), which was absent from the area in which sampling occurred, greatly outnumbered those reliant on pines, the dominant canopy trees here. This dominance was caused by the abundance of the psyllid bug *Psylla melanoneura*, which feeds on *Crataegus* spp., but migrates to evergreen trees as winter 'shelter plants' (Hodkinson and White, 1979). High winter mortality could lead to their dominance in these assemblages.

3.7 Conclusions

While the analysis of insect assemblages in modern woodland and non-woodland sites can provide ecological information which reflects the known ecology of these sites well, this work points out several potential pitfalls of using assemblages 'blind', e.g. without knowing detailed ecological information, as is the case when past ecological conditions are inferred from fossil insect assemblages.

Discriminant analysis of species lists seems to suggest that, while the assemblages from different sites appear to differ (see Figure 3.4), species composition at any one site is insufficiently predictable to be of use in determining the nature of the site at the time of deposition. However, the use of 'ecological groups' appears more satisfactory, and the woodland and non-woodland samples could be reliably distinguished by discriminant analysis based on the numbers of individuals in each ecological group at each site. This technique could be used to determine the origin ('woodland' or 'non-woodland') of samples of unknown provenance. More detailed ecological variation, however, could not be distinguished by discriminant analysis, even using ecological groups, and there appear to be limits to the resolution of ecological information which can be obtained from insect death assemblages.

Attempts to reconstruct the tree species structure of woodlands from the hostplant preferences of phytophagous insects present are relatively successful. However, this technique appears unable to give more detailed information about woodland vegetation, for example, the herbaceous plants present, as woodland herbs tend to have few specific phytophagous insects. It may be possible to infer futher details of woodland structure (for example, whether trees are generally senescent, or healthy), from insect assemblages (as suggested by Buckland, 1979), but the modern assemblages studied did not cover a sufficiently wide variety of woodland types to reveal this (indeed, there are probably few, if any woodlands in Britain where the tree age-structure is similar to that of the primary forest; see Chapter 6).

Chapter 4 The palaeoecology of a site at Thornton, Humberside

4.1 Introduction

Chapters 4 and 5 deal with ancient insect assemblages from two sites in the Vale of York, in order to relate the work on modern woodland insect assemblages (Chapter 3), to fossil assemblages where the ecology is unknown. Field surveys were carried out in an attempt to locate potential sites having preservation of insect remains, particularly peat strata in which waterlogging was likely to have led to good preservation of biological material. However, in order to obtain samples of sufficient bulk to yield useful beetle assemblages, it is usually necessary to process samples of several kilograms (litres) of the deposit (Buckland and Coope, 1991). This is usually only possible where the fossiliferous deposits are exposed, and the potential sites were therefore limited. The first suitable deposit, at Thornton, was a thin band of peat of comparatively recent date, sealed by alluvial deposits. The second, at St George's Field, was laid down in the Bronze Age.

4.2 The Site

Excavations in a field at Thornton, within the 200.3 ha. (494.9 acre) Melbourne and Thornton Ings Site of Special Scientific Interest (SSSI), part of the Lower Derwent National Nature Reserve (NNR), were carried out by English Nature Staff in early 1992. The site (OS map reference SE 734 456) is approximately 12 km south-east of York, 300 m from the Pocklington Canal (Figure 4.1). The soils of the area are recorded as belonging to the Crimple complex by the soil survey of England and Wales (Bullock, 1974), consisting at the surface largely of undifferentiated alluvial deposits (Figure 4.2). Furness and King (1978), however, restrict the description 'Crimple Series' to clayey alluvial soils. Those with a peaty surface layer and, occasionally, beds of peat at depth, are grouped by Furness and King in the Sulham series, which are characteristically poorly drained loamy riverine alluvium, sometimes having peaty, or, on ground near blown sand features, sandy horizons. In reality, the two soil types are often found in close association (Furness and King use a Sulham-Crimple mapping unit where the soils occur together, as local patterns of each type are too complex to map effectively).

The site itself is flat and low-lying (< 8m above OD), supporting semi-improved neutral grassland. The surrounding, better drained soils are largely composed of aeolian sands of postglacial origin, and are generally under intensive arable management (see maps, Figures 4.1 and 4.2).

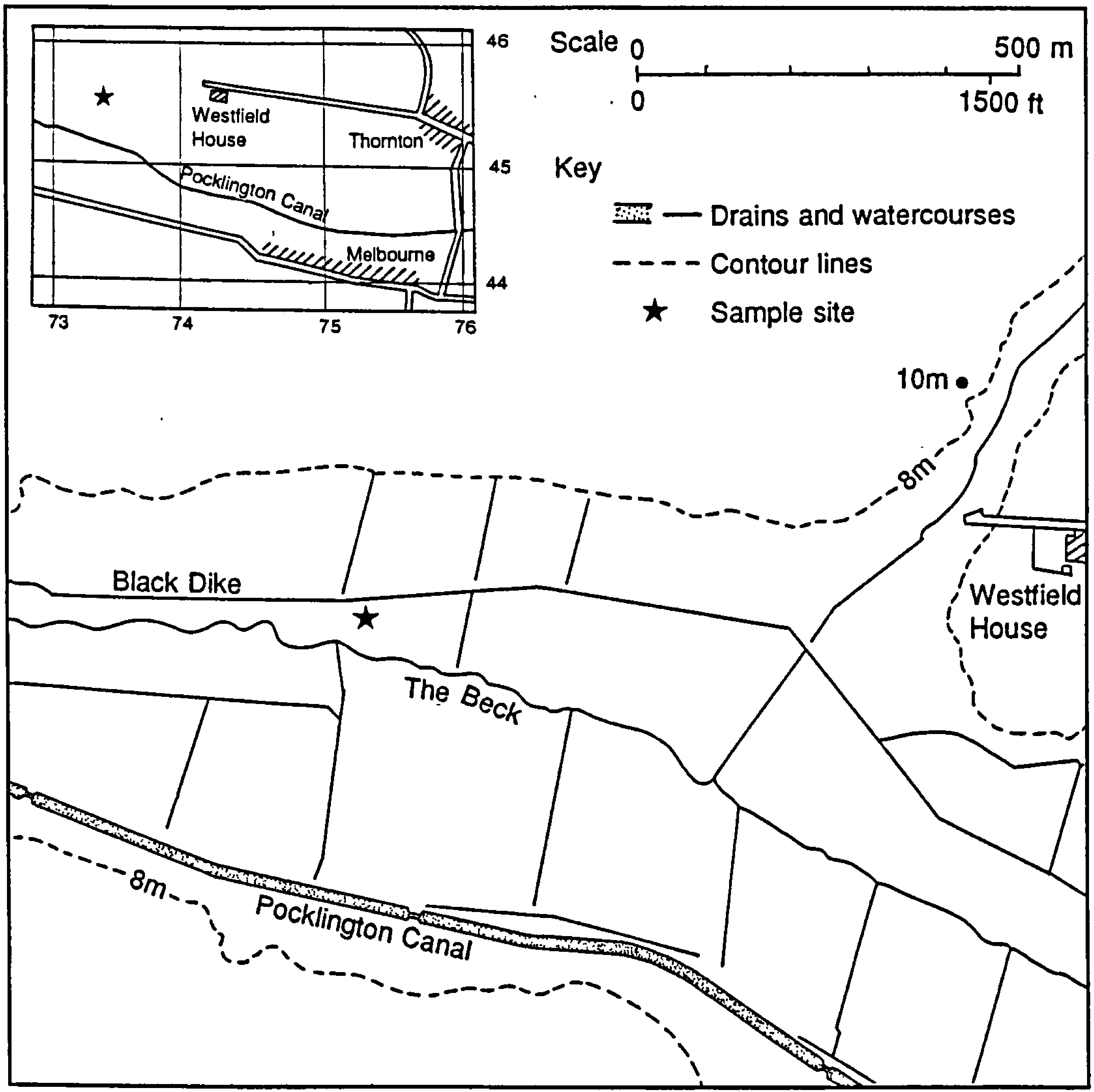


Figure 4.1 Map of area around Thornton site, showing drainage and relief. Inset; Position of site relative to villages of Thornton and Melbourne.

Buried layers of peat and grey lake clay were revealed beneath the surface loams and sands when digging occurred at the site (the stratigraphy is shown in Figure 4.3).

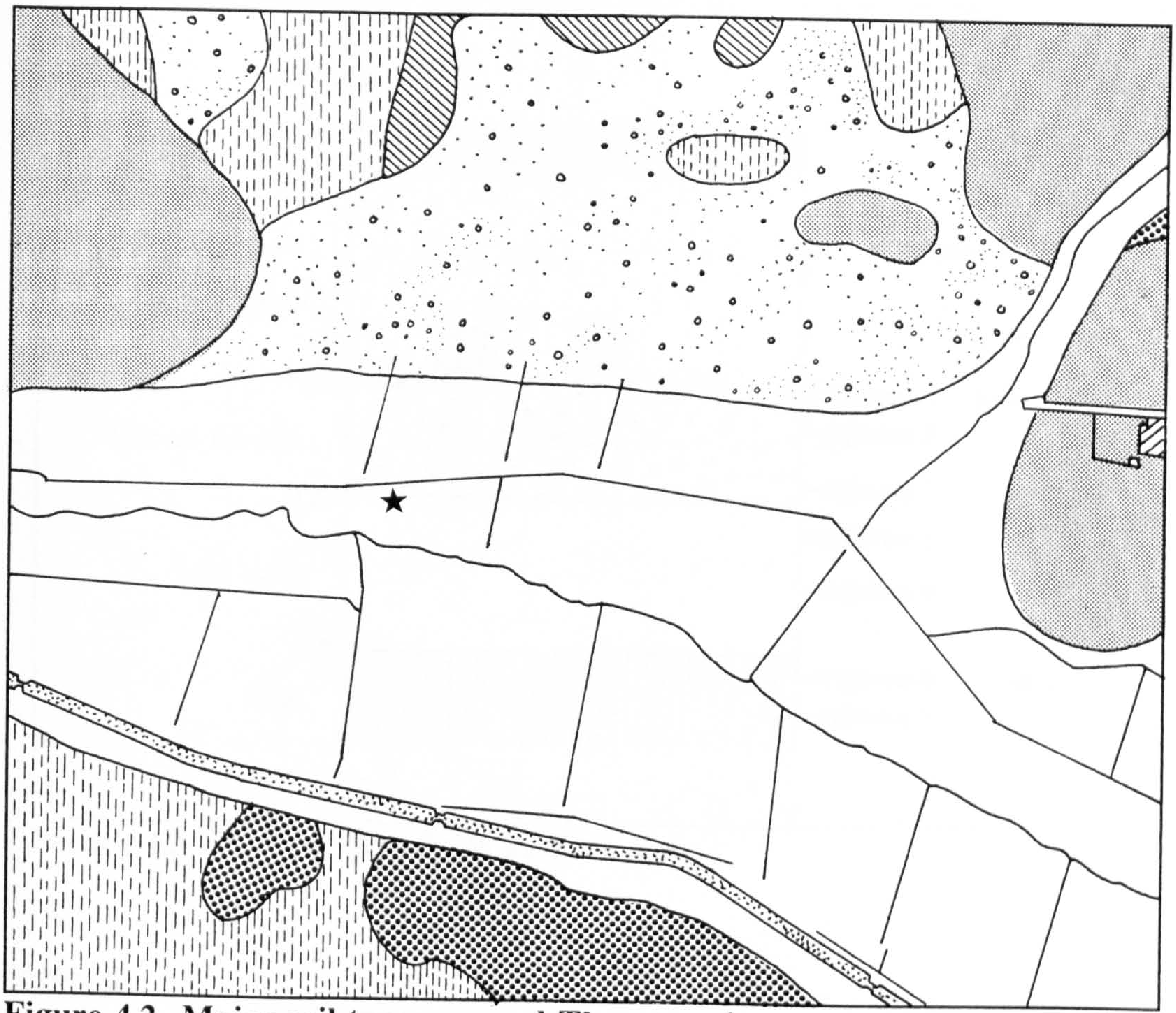


Figure 4.2 Major soil types around Thornton site (Adapted from Bullock, 1974).

Key	Soil Mapping Unit	Soil Group	Sub-Surface Geology
□	Crimple Complex	undifferentiated non-calcareous gley	alluvium, local peat layers
▥	Everingham Series	undifferentiated non-calcareous gley	postglacial aeolian sand
⁘	Holme Moor Series	podzol	postglacial aeolian sand
▩	Kexby Series	gleyed brown earth	postglacial aeolian sand
░	Naburn Series	brown earth	postglacial aeolian sand
▧	Portington Series	undifferentiated non-calcareous gley	fluvio-glacial or aeolian sand over lacustrine clay or Keuper Marl

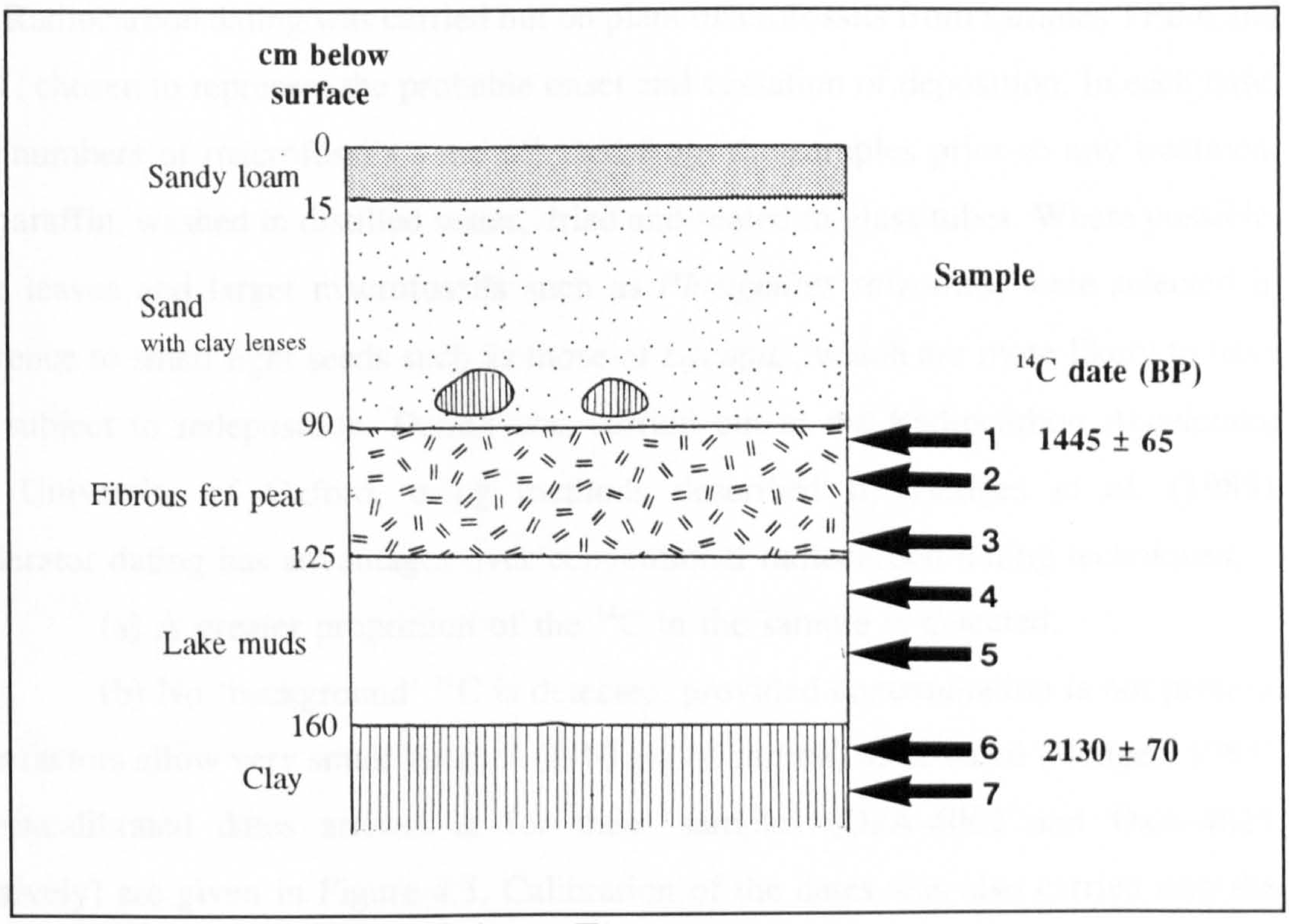


Figure 4.3 Stratigraphy of site at Thornton

4.3 Methods

Samples of the peat and underlying mud and clay were taken at intervals through the profile, each sample weighing approximately 3-4 kg. In the laboratory, these were split into subsamples of 1.5 or 2 kg for ease of processing, and paraffin flotation carried out as described by Kenward *et al.* (1980), in order to extract plant and insect fossils.

For one subsample from each sample (both subsamples for sample 7, where assemblages were small), fossils were then sorted and identified (where possible, to species level). Insect identification was carried out using the reference collections of the EAU, York, and collections of the Hope Department of Entomology, Oxford University, and the Yorkshire Museum, York. Plant macrofossils were identified using the reference collections of the EAU. The minimum numbers of individuals (MNI) represented by the insect macrofossils were counted, whereas plants were scored on a four-point scale of abundance.

The beetles and bugs identified in samples from this site were classified according to their ecological preferences, as recorded in the entomological literature (see Chapter 2).

Radiocarbon dating was carried out on plant macrofossils from samples TFB 6 and TFB 1, chosen to represent the probable onset and cessation of deposition. In each case, small numbers of macrofossils were selected from the samples prior to any treatment with paraffin, washed in distilled water, dried and sealed in glass tubes. Where possible, whole leaves and larger macrofossils such as *Phragmites* rhizomes, were selected in preference to small light seeds such as those of *Lycopus*, which are more likely to have been subject to redeposition. Dating was carried out at the Radiocarbon Accelerator Unit, University of Oxford, using methods described by Hedges *et al.* (1989). Accelerator dating has advantages over conventional radiocarbon dating techniques;

(a) A greater proportion of the ^{14}C in the sample is detected.

(b) No 'background' ^{14}C is detected, provided contamination is not present.

These factors allow very small samples (1-10 mg of carbon) to be dated (Hedges, 1983). The uncalibrated dates arrived at for these samples (OxA-4062 and OxA-4025, repectively) are given in Figure 4.3. Calibration of the dates was also carried out; this corrects for variation in the atmospheric ratio ^{12}C/^{14}C over time, using a calibration curve developed from dendrochronologically dated wood samples (Gillespie, 1984). However, the technique increases the degree of error associated with the ^{14}C date. The calibration curve developed by Stuiver and Pearson (1993) was used in this case. Calibrated ages are given below (section 4.4.i).

4.4 Results

4.4.i Calibrated radiocarbon dates from Thornton

		minimum of cal age ranges	(cal ages)	maximum of cal age ranges
Sample TFB 1	$1\sigma^*$	AD 561	**(630)**	660
	$2\sigma^*$	AD 464	**(630)**	684
Sample TFB 6	1σ	BC 337	**(170)**	45
	2σ	BC 373	**(170)**	AD 20

*1σ and 2σ ranges represent 68% and 95% confidence intervals of the calibrated ^{14}C dates.

The radiocarbon dates therefore suggest that deposition at the site spanned a period from the late Iron Age, throughout the Roman Period, and ended in the early medieval period.

4.4.ii Assemblage sizes

The size of the assemblages from Thornton, in terms of number of individuals (N) and number of taxa (S) are given in Table 4.1, along with Fisher's α index of diversity (Fisher *et al.* 1943) and associated Standard Error (estimated as described by Williams, 1947), and the Berger-Parker dominance index, *d* (Berger and Parker, 1970). The insect assemblages recovered tend to decline in size down the profile, the smallest assemblages, in terms of both the number of individuals and the number of taxa, being those from 1693 mm and 1781 mm, where the organic deposits had graded into inorganic clay. Here, the condition of those fossils that did occur was also poor, being more fragmented and eroded than the fossils found in upper layers. These assemblages therefore display relatively low values of α, and high values of *d*, as it appears that differential preservation favours a few dominant taxa, and species that occur in low numbers in the larger assemblages are absent in these smaller ones.

Table 4.1 Size of assemblages from Thornton site

Sample	Depth (mm)	N	S	α	SE of α	*d*
1	929	117	70	73	12	0.14
2	1071	164	66	41	5	0.25
3	1213	163	63	38	5	0.23
4	1355	117	64	58	9	0.15
5	1497	120	56	41	6	0.16
6	1693	83	44	38	7	0.27
7	1781	37	24	30	10	0.27

Key; N Number of individuals

S Number of taxa

α Fisher's α diversity index

d Berger-Parker dominance index (n_{max}/N where n_{max}= number of individuals of dominant species)

4.4.iii Dominant species

The dominance index *d* is high throughout the sequence. Only in samples 1, 4 and 5 does the dominant make up less than 20% of the entire assemblage. However, the dominant species differs in the upper and lower samples. The dominant species in the upper three samples (1, 2, and 3) is a delphacid bug, probably the brachypterous form of *Megamelus notula* (Germar) (Fulgoromorpha). This common species is associated with marshland vegetation (Le Quesne, 1960), often on sedges (*Carex* spp.).

The lower four samples (4, 5, 6 and 7) are each dominated by the beetle *Ochthebius minimus* (Fabricius) (Hydraenidae). This species is predominantly found in bodies of shallow water or mud (Friday, 1988), especially among vegetation in more nutrient-rich waters (Hansen, 1987).

4.4.iv Ecological groups and hostplants.

The ecological groups of the twenty most abundant species overall from the site are shown in Table 4.2, and the proportions of the beetle/bug assemblages falling into these groups shown in Figures 4.4 and 4.5. Figure 4.6 shows the variation in the proportion of the assemblage falling into each of the two major ecological groups, 'aquatic' and 'marshland' species.

Plant macrofossils identified from the flots are listed in Table 4.3, along with an ecological code for each species based on those given by Beckett (1979), who classified water plants from a Somerset site into true aquatics, species dependent on base-rich fen conditions, and generalist mire/marshland plants.

Several of the beetle and bug species identified display strong hostplant preferences. These have been used by other workers (for example, Girling, 1985) to provide further information on the plant species in the vicinity at the time the assemblages formed. Where hostplant preferences are known, they are shown in Table 4.4.

Remains of other invertebrates (Mollusca, Annelida, Crustacea) were also identified from the samples. Data for the molluscs recovered, along with an indication of their ecological preferences for those species mentioned by Sparks (1961), are shown in Table 4.5. Among the other invertebrates, earthworm egg capsules were recovered from samples 1, 2 and 3. These were identified as belonging to *Eiseniella tetraedra* (Savigny), a species found among the roots of water plants or in soils (ranging from peats to sand) near water (Sims and Gerard, 1985). The darkened colour and position over a metre beneath an alluvial soil suggested that these egg capsules were not recent contaminants. Certain invertebrate groups, such as the aquatic caddis (Trichoptera) were found throughout the sequence. The Trichoptera were represented both by larval cases, and small fragments of the wings of adult insects, but the species recovered were not identified.

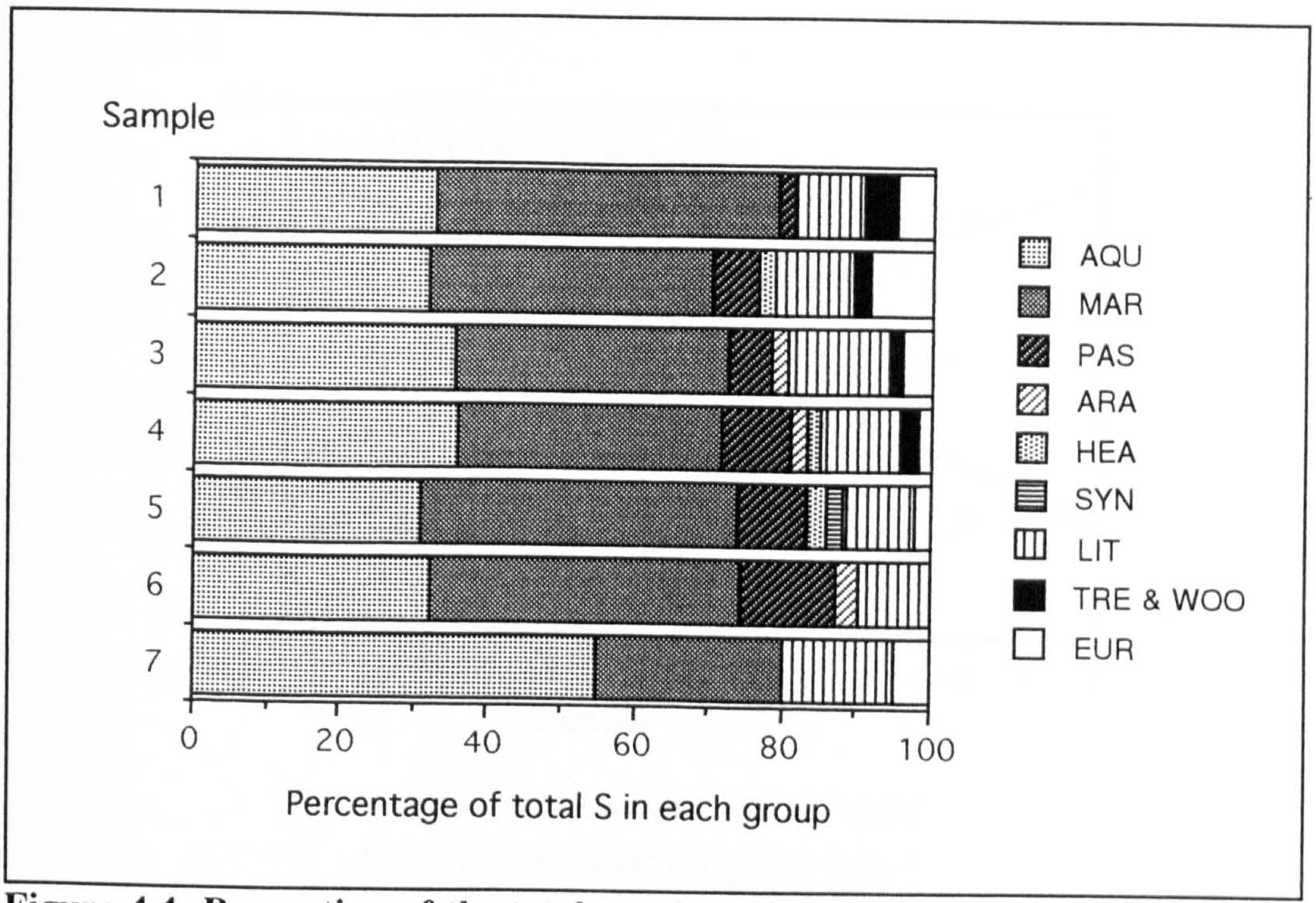


Figure 4.4 **Proportion of the total number of species (S)** in each of the major ecological groups identified (excluding uncoded taxa).

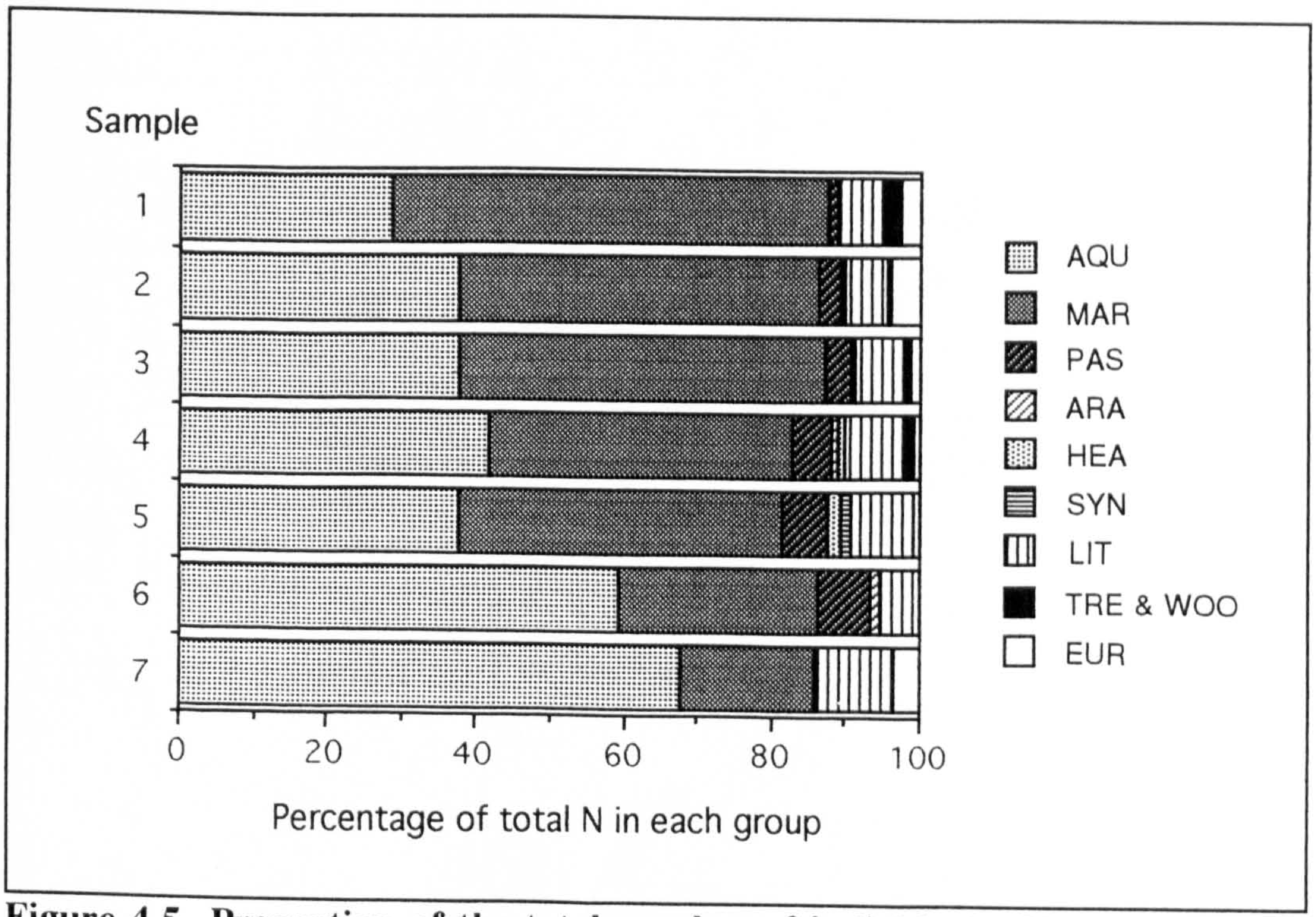


Figure 4.5 **Proportion of the total number of individuals (N)** in each of the major ecological groups identified (excluding uncoded taxa).

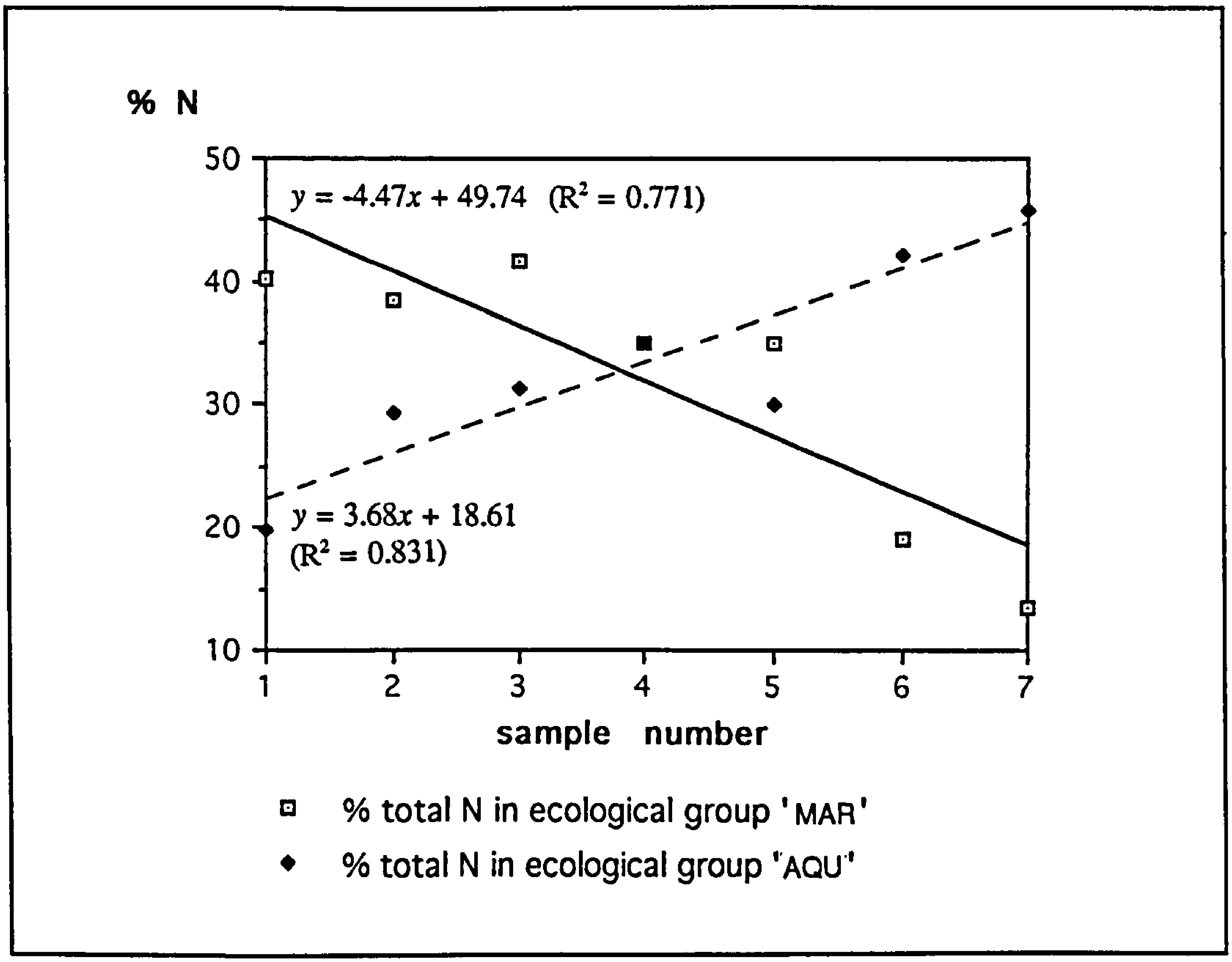


Figure 4.6 The percentage of N in each assemblage falling into the ecological groups 'aquatics' and 'marshland taxa'.

Table 4.2 The twenty most abundant beetle and bug species from Thornton

n = total number of individuals in all samples.

Species	Order (Family)	n	Ecological code assigned[1]
Megamelus notula	Hemiptera (Delphacidae)	144	MAR
Ochthebius minimus	Coleoptera (Hydraenidae)	131	AQU
Helophorus sp.	Coleoptera (Hydrophilidae)	39	UNC[2]
Noterus clavicornis	Coleoptera (Noteridae)	20	AQU
Kateretes rufilabris	Coleoptera (Nitidulidae)	14	MAR
Macrosteles sp.	Hemiptera (Cicadellidae)	14	UNC
Aleocharinae sp.2	Coleoptera (Staphylinidae)	14	UNC
Platystethus nodifrons	Coleoptera (Staphylinidae)	13	MAR
Stenus sp.1	Coleoptera (Staphylinidae)	13	UNC
Helophorus aequalis or *grandis*	Coleoptera (Hydrophilidae)	12	AQU
Plateumaris discolor or *sericea*	Coleoptera (Chrysomelidae)	12	MAR
Aleocharinae sp.1	Coleoptera (Staphylinidae)	12	UNC
Enochrus sp.1	Coleoptera (Hydrophilidae)	10	AQU
Carpelimus corticinus	Coleoptera (Staphylinidae)	10	LIT
Cyphon sp.	Coleoptera (Scirtidae)	9	UNC
Coelostoma orbiculare	Coleoptera (Hydrophilidae)	9	MAR
Limnebius truncatellus	Coleoptera (Hydraenidae)	7	AQU
Laccobius sp.	Coleoptera (Hydrophilidae)	7	AQU
Hydroporus sp.	Coleoptera (Dytiscidae)	7	AQU
Dryops sp.	Coleoptera (Dryopidae)	7	MAR

[1] See Chapter 2 for explanation of the ecological codes assigned to species.
[2] See discussion, section 4.6.

Table 4.3 The plant macrofossils found in samples from Thornton

Sample no.	1	2	3	4	5	6	7
Depth(mm)	929	1071	1213	1355	1497	1693	1781
Characeae (A)	O	F	O	O	F	-	F
Moss (U)	-	R	-	-	-	R	R
Ranunculus Subgenus *Batrachium* (A)	R	-	O	O	O	O	O
Ranunculus flammula (M)	-	-	R	-	-	R	R
Samolus valerandi (M)	-	-	-	R	-	-	-
Menyanthes trifoliata (M)	-	R	R	-	R	-	-
Eupatorium cannabinum (M)	R	-	-	-	-	-	-
Baldellia ranunculoides (M)	-	-	R	-	-	-	-
Alisma sp. (U)	R	O	-	-	-	-	R
Potamogeton coloratus (A)	-	R	-	-	-	-	-
Potamogeton sp. (A)	-	-	-	-	-	-	R
Juncus sp. (U)	-	R	-	-	-	-	R
Eleocharis palustris or *uniglumis* (U)	R	-	O	R	O	R	-
Schoenoplectus lacustris (A)	R	R	R	R	-	-	-
Cladium mariscus (F)	O	R	R	-	-	-	R
Carex sp. (U)	O	O	R	R	-	R	-
Glyceria sp. (U)	-	-	-	R	-	-	-
Phragmites australis (M)	A	A	A	F	O	F	R
Poaceae (U)	-	-	-	-	-	-	F

Key; **Ecological Codes** (modified from Beckett, 1979)

(A) = Aquatics
(F) = Base-rich Fen
(M) = Mire plants-general
(U) = Unclassified

Abundance

A = Abundant (More than approx.30 fossils per kg. sediment)
F = Frequent (Approx.15 - 30 fossils per kg. sediment)
O = Occasional (Approx.3 - 15 fossils per kg. sediment)
R = Rare (1 or 2 fossils per kg. of sediment)
\- = Absent.

Table 4.4 Plants associated with host-specific phytophagous insects from Thornton.

Plant Species	Number of individuals in Sample							Insect species
	1	2	3	4	5	6	7	
Brassicaceae						1		*Ceutorhynchus contractus*
Calluna vulgaris				1				*Strophingia ericae*
					2			*Lochmea suturalis*
Carex spp.	1	2	2	4	2			*Plateumaris discolor* or *P.sericea*
			2	1	2			*P. affinis*
Fabaceae	1							*Sitona lineatus*
Juncus spp.						1		*Euconomelus lepidus*
Juncus, Carex spp.		3	8		2	1		*Kateretes rufilabris*
Myriophyllum spp.				2				*Eubrychius velutus*
Oenanthe aquatica, O. crocata		1	1	1	1			*Prasocuris phellandri*
Phragmites australis		1	1	1	1			*Plateumaris braccata*
Poaceae		1						*Oulema melanopa*
Polygonum spp.						2		*Phytobius quadrituberculatus*
Polygonum spp., *Rumex* spp.				1				*Chaetocnema concinna*
Sparganium erectum			1		2			*Donacia marginata*
Veronica beccabunga				1				*Gymnetron beccabungae*

Table 4.5 Molluscs from Thornton (nomenclature from Kerney, 1976)

Species (ecological group)	Number of individuals in Sample						
	1	2	3	4	5	6	7
Bithynia tentaculata (C)			11	7	6		
Lymnaea palustris (A)			4	2		1	
Lymnaea peregra (A)						1	
Planorbis planorbis (B)			1	1		1	
Planorbis laevis				1			
Segmentina nitida (B)			1				

Ecological groups (from Sparks, 1961); A = "Catholic" B = "Ditch" C = "Moving water"

4.5 Rare and notable insect species

4.5.i Aquatic beetles

Many of the aquatic taxa recorded in the assemblages from Thornton are now restricted in distribution or uncommon. Four species (the dytiscids *Agabus chalconatus* (Panzer) and *Ilybius guttiger* (Gyllenhal), *Gyrinus minutus* F. (Gyrindae), and *Peltodytes caesus* (Duftschmid)(Haliplidae)) are recorded as belonging to the group 'Notable B' (occurring in only 31-100 10 km squares of the National Grid, or 8-20 vice-counties) by Foster (1992). *Haliplus variegatus* Sturm (Haliplidae) is described as 'Rare' (not endangered or vulnerable, but considered at risk, occurring in 15 or fewer 10 km. squares since 1970). The uncommon status of many of the aquatic species recorded in these samples (at least 6 of the 44, or 14% of, aquatic beetle species recovered are taxa today regarded as notable, or rarer (Foster, 1992)), is presumably a reflection of the loss of aquatic habitats through human intervention such as drainage, agricultural and industrial pollution in recent times. Climatic change may also have played a part in species loss; many of those aquatic Coleoptera presently rare in Britain are at the northern limits of their range (Anon, 1986).

4.5.ii Marsh and fenland beetles

Similarly, many of the noteworthy species in the Thornton assemblages are typically associated with marshland habitats which have become rarer as a result of man's activities. The carabids *Bembidion semipunctatum* Donovan ('Notable A' in Hyman, 1992; uncommon in Great Britain, and thought to occur in 30 or fewer squares of the National Grid, or 7 or fewer vice-counties) and *B. gilvipes* Sturm ('Notable B'), are both found in open waterside habitats, the latter also occurring on lowland peats, fens and marshes. *B. semipunctatum* is now restricted to to E. Suffolk, Gloucestershire and Worcestershire, although *B. gilvipes* is widespread but local in England and Wales. *Cercyon convexiusculus* Stephens and *C. sternalis* Sharp (Hydrophilidae) are listed in the group 'Notable B' by Foster (1992) (see above). Other species of marshland habitats regarded as noteworthy are described in more detail below.

Odacantha melanura (L.) (Carabidae)

This carabid was found in samples 3, 4, and 5. Today, it is regarded as a local species confined to the south of England (status 'Notable B' in Hyman, 1992), occurring among vegetation of wet places (Wilson, 1958), particularly beds of common reed (*Phragmites australis*). The species overwinters in the stems of *Typha latifolia* and other emergent plants (Girling, 1979). It is found no further north than Norfolk, although it has been recovered as fossil material from undated peats at Shirley Pool, and from mid-Holocene deposits from the River Calder, South Yorkshire (Dinnin, 1991).

Hydrochus ignicollis Motsch (Hydrophilidae)

Regarded as a fenland species, presently very rare in the British Isles with a decidedly southern distribution and previously unknown as fossil material (Angus, 1977). This species was present in samples 1, 2 and 6. Both *H. ignicollis* and *H. brevis* are recorded by Shirt (1987) and Foster (1992) as 'Rare'; that is, occurring (usually in small populations) in fifteen or fewer 10 km squares in Britain.

Hydrochus brevis (Herbst)

Found in samples 1 and 2. This species is known from fossil material at several sites including Thorne Moors, South Yorkshire (Buckland, 1979). It is uncommon today, and found in acidic, mesotrophic waters. However, it appears to be difficult to distinguish from the recently described *H. megaphallus*, which prefers eutrophic pools and ditches on clay (Berge Henegouwen, 1988). *H. megaphallus* is regarded as 'Vulnerable' by Foster (1992), although this recorded status may in part be a result of the relatively recent separation of the species from *H. brevis*.

Hydraena palustris Erichson (Hydraenidae)

A 'Vulnerable', relict species (Shirt, 1987, and Foster, 1992) (declining, or likely to move into the 'Endangered' category, which contains those species in imminent danger of extinction in Britain). It is associated with fenland in eastern England (Friday, 1988). *H. palustris* has also occurred in the York area in historical times, at Askham Bog (Bayford and Lawson Thompson, 1907), although the last record for the latter site appears to be in 1894 (Balfour-Browne, 1940). At Askham Bog its loss probably results from the drainage and succession to drier woodland habitats that have occurred since the late nineteenth century (Fitter and Smith, 1979). Its occurrence in the Thornton deposits (one individual, in sample 1) is a further indication that fenland conditions, with areas of shallow water, existed locally, as *Hydraena* species are relatively poorly dispersed, and tend to have local, restricted distributions (Hansen, 1987). However, in August 1987 a single specimen of *Hydraena palustris* was taken on a pond close to the Thornton site, within the Melbourne and Thornton Ings SSSI (M.

Denton, pers. comm.).

Plateumaris braccata (Scopoli) (Chrysomelidae)

A chrysomelid beetle now restricted to southern and eastern England, and Wales (status 'Notable A' in Hyman, 1992), occurred in samples 2, 3, 4, and 5. Like *O. melanura*, this species is particularly associated with *Phragmites*, and the presence of these two species suggests that reed was the dominant vegetation in at least the mid-uppermost samples. ***P. affinis*** (Kunze) ('Notable B' in Hyman, 1992) is widespread but local in England and Wales, occurring in well-vegetated marshland habitats, particularly on sedges and cotton-grass (*Carex* and *Eriophorum* spp.).

Curculionidae

Three rare marshland weevils were recorded from the Thornton assemblages: *Bagous czwalinai* Seidlitz, (a single specimen from sample 3), now an Endangered species restricted to a few *Sphagnum* bogs in the south of England.

Eubrychius velutus (Beck) (Notable B). At least two individuals were recovered in sample 4. This widespread but local phytophagous weevil is associated with water milfoil (*Myriophyllum*) species in slow-moving or stagnant-water habitats.

Gymnetron beccabungae (L.) (Notable A). A single specimen of this weevil was found in sample 4. Today, it is predominantly southern in distribution, and is associated with brooklime (*Veronica beccabunga*) (also possibly *V. scutellata* and *V. anagallis-aquatica*).

4.5.iii Others

Of the non-aquatic/marshland species, only one, *Aphodius paykulli* Bedel. (Scarabaeidae) is uncommon today ('Notable B' in Hyman, 1992). It is widespread but localised in distribution, largely restricted to downland and heathland habitats, but displays a high degree of mobility, exploiting an ephemeral and patchy food resource (dung), suggesting that its presence at the Thornton site (as a single individual, in sample 1) does not necessarily reflect local ecological conditions.

4.6 Discussion

4.6.i Marshland and aquatic taxa

Most of the Coleoptera and Hemiptera classified according to their ecology belonged to the groups 'aquatic' or 'marshland'; indeed, of the twenty most abundant taxa, thirteen belonged to one of these groups (see Table 4.2). Six of the remaining abundant species were unclassified, and only one, *Carpelimus corticinus* (Gravenhorst) (Staphylinidae), had not been placed in the aquatic or marshland groups. *C. corticinus* is found among moist litter, but also on mud in damp places (Hansen, 1951), and so its presence in the assemblages is consistent with a fauna of marshland or damp ground.

The unidentified *Helophorus* species from Thornton was assigned to the ecological group 'uncoded'. This genus contains both aquatic and terrestrial species. The truly terrestrial taxa *H. porculus* Bedel and *H. rufipes* (Bosc d'Antic) ('turnip mud beetles'), *H. nubilus* Fabricius, and *H. tuberculatus* Gyllenhal, are all recognisable on the basis of elytral characteristics (Angus, 1978). As most of the remains at the Thornton site were elytra, it seems likely that these species, if present, would have been detected. However, other members of the genus inhabit a wide range of aquatic and semi-aquatic habitats, from the edges of shallow, weedy pools to fast-flowing rivers (Friday, 1988), and are widely dispersed in flight. It was therefore felt that accurately assigning this taxon to either the 'aquatic' or 'marshland' ecological groups would be impossible without more accurate identification to a single species, or a smaller group of possible taxa.

If the total number of taxa in each assemblage is divided by ecological code (Figure 4.4), the proportions of marshland and aquatic taxa change little through the sequence of samples. However, if the total number of individuals is considered (Figure 4.5), there is a marked variation through the profile, especially in the relative size of the 'aquatic' and 'marshland' groups (see Figure 4.6). This suggests that the pool of different species may be relatively constant, and well represented through all the samples, and that the number of *individuals* in each ecological grouping may give a better indication of habitat type and any ecological changes.

In the uppermost sample, 40% of the total number of individuals belong to taxa of marshland conditions (see Figure 4.5). If aquatics and uncoded taxa are excluded, 84% of the remaining terrestrial group are marshland dwellers. At Flag Fen, Cambridgeshire, in a fossil Coleopteran assemblage laid down under well-vegetated stagnant water in marshland only 40% of the total individuals belonged to 'marshland' taxa (species associated with marsh or aquatic plants) (Robinson, 1992). Thus the upper deposits at Thornton appear strongly indicative of boggy or fenland conditions.

In the lower samples, however, the relative importance of truly aquatic species would appear to increase. Figure 4.6 shows the change in the percentages of each assemblage made up of 'aquatic' and 'marshland' taxa. Regression lines have been fitted and the equations of these lines, along with values for the coefficient of determination, R^2 (a measure of the goodness-of-fit of the data to the lines calculated) are given. In each case, the values of R^2 are high, suggesting that the data are well described by the lines fitted, which indicate a clear increase in the proportion of the fauna made up of marshland taxa, with a corresponding decrease in the proportion of aquatics, over time. The ratio marsh:aquatics in sample 1 (top of profile) is 2.04:1, whereas in the lowest sample (7), this ratio falls to 0.29:1. Although the smaller size of these lower assemblages (see Table 4.1) may make the ecological ratios more susceptible to error, and the inability to assign ecological codes to certain abundant taxa such as Helophorus sp. may influence the ratios calculated, the trend through the sequence of samples is for an increase in the marsh:aquatic ratio up the profile. This trend is reflected in the evidence of plant macrofossils (see Table 4.3); the truly aquatic water crowfoots (*Ranunculus* Subgenus *Batrachium*) are rare or absent in the uppermost samples, whereas *Phragmites australis* rhizome fragments increase in abundance in these. If an ecological index is calculated based on the weighted abundances of the aquatic and marshland taxa (with 'Abundant' = 4 and 'Rare' = 1), the values change as shown below; the score for aquatic species is similar throughout, although highest in the deepest sample (7), that for the marshland species is low at the bottom of the profile, and highest in sample 3.

Ecological index based on abundance of plant macrofossils in flots

Sample no.	1	2	3	4	5	6	7
Aquatics (A)	4	5	5	5	5	2	6
Fenland & Mire (F+M)	7	6	8	4	3	4	3

The plant species indicated by the host-specific insect phytophages (see Table 4.4) also suggest aquatic or marshy conditions; all could have originated around the margins of a body of water, or on or near fen, except possibly *Calluna vulgaris*. This may have been present on the aeolian sands close to the site.

The notable uncommon beetles are generally specialised fenland species. Most now show a more southerly distribution, suggesting that climate change may play a part in their current rarity; however, the influence of drainage and habitat destruction by human intervention would seem more likely to be a large factor. Apart from *Hydrochus brevis* (which may have been confused with *H. megaphallus*, see above), and *Bagous czwalinai*, all indicate fairly base-rich eutrophic fenland conditions at the site.

Thus the evidence from the beetle and bug, and plant assemblages through the sequence of samples appear to represent a succession from open water to marsh- or fenlike conditions, probably dominated by common reed *Phragmites australis* (Cav.)Trin ex Steudel.

All the molluscs identified from the site (see Table 4.5) are aquatic species. Molluscs are absent from the lowest sample (perhaps due to the small sample size, or poorer conditions for preservation in the clay deposit), and the two uppermost samples, suggesting that the site may have become too 'terrestrial' in nature to support these aquatic species towards the later part of the succession. By far the most abundant species was *Bithynia tentaculata* (L.), classified by Sparks (1961) as one of a group of species associated with moving water habitats. However, the presence of 'ditch' species such as *Planorbis planorbis* (L.) and *Segmentina nitida* (Müll.), typical of well-vegetated bodies of water implies that rates of water flow were probably low in the period covered by samples 3 and 4 at least, and *Bithynia* can be found in water bodies with minimal throughflow, such as canals. The smooth ramshorn, *Planorbis* (*Gyraulus*) *laevis* Alder, is listed by Macan (1977) as part of a group of molluscs found particularly in soft water. Its present centre of distribution in Britain is the North, where it is uncommon, and is found in ponds and lakes. Its presence in the snail assemblage of sample 4 again suggests slow-flowing, or even still water.

The area to the south-east of York, (and much of the rest of the Vale) has yielded very few archaeological finds dating from the Roman period, although settlement appears to have occurred in the Skipwith area from the late Iron Age. The distribution of such Roman finds as have been made, on the York and Escrick moraines (particularly, west from York towards Newton Kyme on the York moraine) suggests that these were important crossing routes of the Vale, which would, in general, have been prone to flooding, and only poorly developed, until modern agricultural improvement (Faull, 1983). Marshland and carr probably dominated the landscape in the area at this time. The site at Thornton, although low-lying itself, is close to higher, better-drained ground that might be expected to have supported terrestrial vegetation. However, there is little evidence for this from the insect assemblages.

4.6.ii Terrestrial Habitats

Evidence of other, surrounding habitats from the insect species lists is sparse; the bulk of the assemblages appear to be made up of species autochthonous to the deposit, or originating in the immediate surroundings. Species of open, managed habitats, such as grassland, are a larger proportion of most samples than are those of woodland (see Figures 4.4 and 4.5). The proportion of the terrestrial part of the assemblage made up of the dung beetles *Aphodius* and *Geotrupes* spp. varies from zero, in the deepest sample (in which the assemblage was small - only 16 terrestrial individuals), to 11.5% in sample 5. In sample 3, 8.5% of the terrestrial assemblage is made up of dung beetles, but in all other samples they account for less than 6% of insects. Robinson (1991) suggests that assemblages building up in open, mainly arable landscapes are likely to contain around 6% dung beetles, rising to 10% or more of the terrestrial assemblage in a largely pastoral landscape. Since dung beetles are generally highly mobile (as they exploit an ephemeral and patchy food resource; Koskela and Hanski, 1977), they are liable to be found as contaminants in death assemblages well away from suitable habitats (Robinson, 1983). This suggests that pastoral habitats probably existed around the area throughout the period of accumulation, but may not have been a significant part of the surrounding area at this time. However, the terrestrial assemblages are all relatively small (between 30 and 60 individuals), and therefore may not accurately reflect the immediate environment.

Very few species of woodland, or associated with trees, were recovered in these samples, and, none of these are of the group thought of as typical 'old woodland' beetles, which have been recovered from Bronze Age deposits (Buckland, 1979; Robinson, 1991). The weevil *Phyllobius argentatus* (L.) is abundant in woodlands, the adults feeding on the foliage of various tree species, and the larvae on roots (Phillips, 1992), but may also be found at woodland edges, or in more open localities. The elaterid *Athous haemorrhoidalis* (Fabricius), although common in woods, where the larvae are found among soil and litter, feeding on roots and insect larvae (Evans, 1969), is often found in scrub, overgrown gardens and associated with hedgerow trees. It appears that woodland was poorly represented in the immediate area at the time the deposits were laid down, or completely absent. Moreover, it seems unlikely that there was any significant change in woodland cover over the period of accumulation. It is possible that clearance of most of the original woodlands of the Vale could have been complete by the time of the earliest deposition at this site, although the apparently limited catchment for insect and other biological remains at the site is bound to reduce the extent to which the nature of surrounding terrestrial landscapes can be inferred.

4.7 Conclusions

Invertebrate and plant fossil assemblages from the site at Thornton suggest that the mud and peat deposit represents a successional sequence from open water to fen or marshland conditions, probably dominated by the common reed, *Phragmites australis*.

This succession took place over a period of *c.* 800 years, around 2120-1320 BP (170 BC-AD 630).

Most of each assemblage appears to be autochthonous in nature, giving very little indication of the nature of surrounding habitats. The catchment area for the site must have been small and the site isolated from allochthonous influences, with little or no throughflow of water or even aerial input of insect remains.

Chapter 5 The palaeoecology of a site at St George's Field, York

5.1 Introduction

The assemblages from Thornton gave little indication of surrounding terrestrial habitats, and there was no evidence for woodland in the area at the time of deposition. It was therefore felt necessary to study a second site in detail. Ideally, such a site would have deposits built up under a different depositional regime (and perhaps at an earlier period, if woodland clearance was already advanced by the time the Thornton peats were laid down). Fortunately, potentially interesting deposits meeting these criteria were exposed within the City of York.

5.2 The Site

Construction work was carried out in the St George's Field car park, York (SE 604 513), in 1992-1993, to provide footings for a new pumping station (see map, Figure 5.1). In previous excavations in the area, mollusc assemblages from a depth of around 3 m beneath the present ground surface had been studied, and suggested a riverside floodplain, with both autochthonous species and others originating in flood-debris (O'Connor, 1986a). In the present excavations, a depth of around 10 m below the present land surface (-1m AOD) was reached, making this one of the deepest recent excavations in the city. Because of its known archaeological interest, which includes the presence of the medieval St George's Chapel at the edge of the area to be disturbed, the site was the subject of a watching brief by the York Archaeological Trust (YAT) (Yorkshire Museum site code 92.14). At 0-1 m AOD, layers rich in organic remains were discovered. These apparently natural deposits, largely silts with good preservation of plant macrofossils, were unlike any examined in the York area before (O'Connor *et al.*, 1984). At the eastern end of the excavation, large pieces of the wood of ash (*Fraxinus excelsior*), up to around 600mm long and 300 mm in diameter, were revealed at around the level of sample 202 (+ 400mm AOD). Samples were taken for analysis from the deposits at around OD. The stratigraphy of the deposits at -1 to +1 m AOD is shown in Figure 5.2.

Unfortunately, conditions at the site meant that it was impossible to obtain an uninterrupted sequence of samples, since retaining walls were put into place as the pit was being dug, allowing only limited access to the deposits. Samples were taken at two points in the pit sides, at the eastern and western ends of the pit, on two visits to the site. On each occasion, the exposed face of the deposit was cut back to reduce possible contamination, and samples of several kilograms each taken at various vertical levels in the exposure. Samples were stored in plastic tubs before later processing.

The matrix of sample 306 (the lowest taken) was a sandy clay. Samples 305-302 contained some sand, the sand content tending to decrease in the later deposits.

However, through most of the sequence sampled, the deposit appeared relatively consistent, largely made up of grey, layered silts and clay-silts with a large proportion of organic matter including twigs and herbaceous detritus.

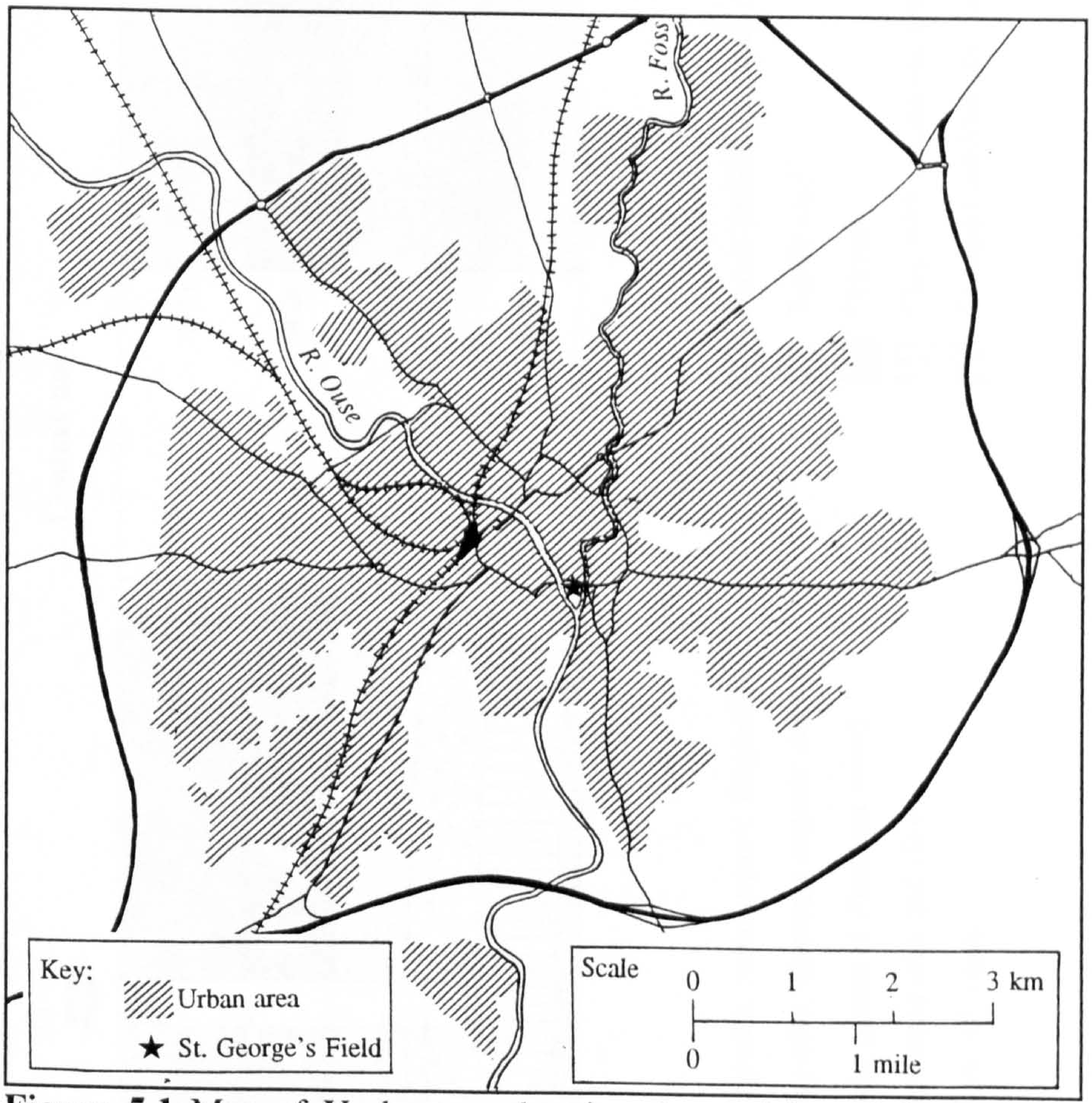


Figure 5.1 Map of York area, showing the position of St George's Field.

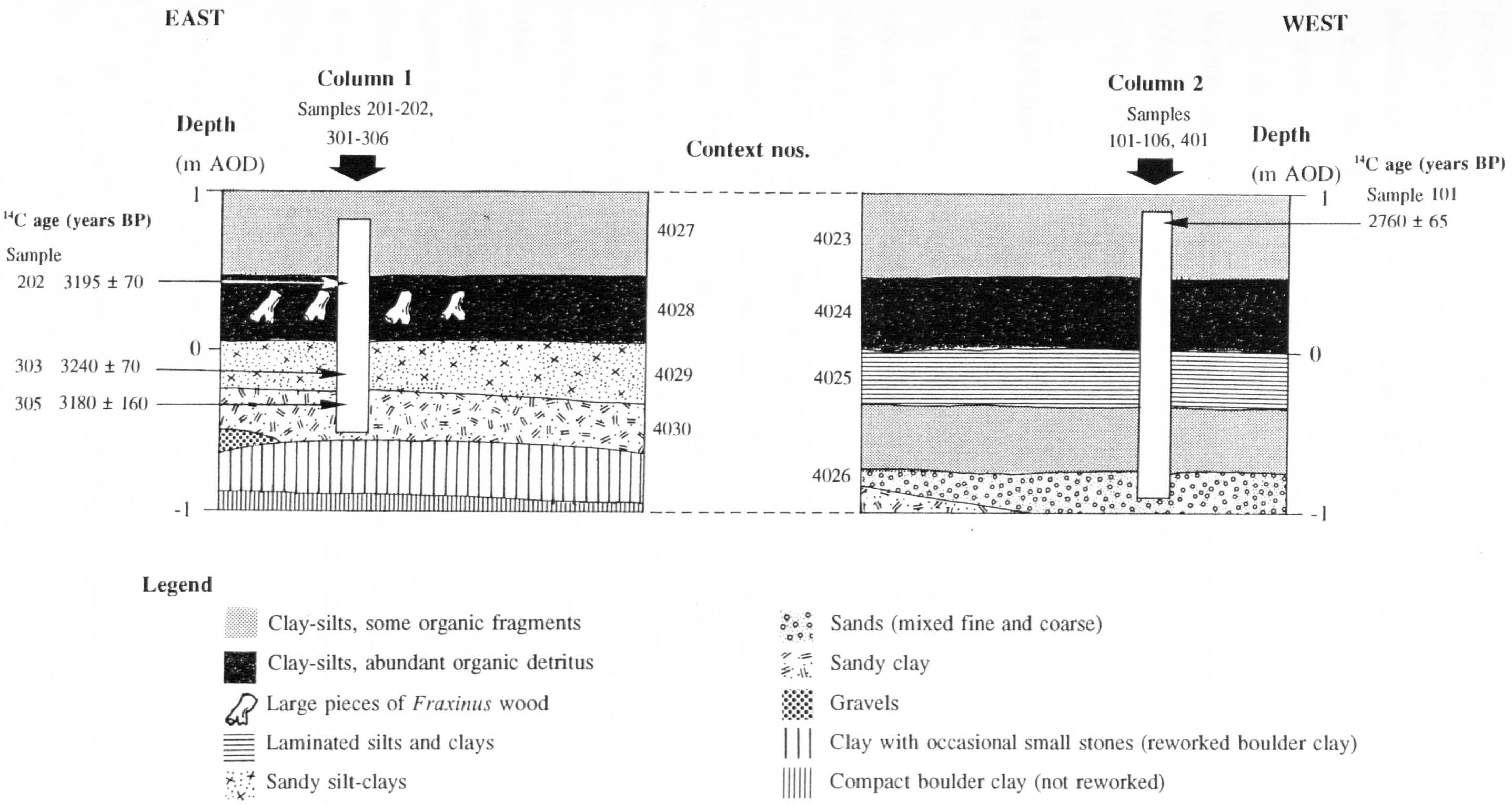


Figure 5.2 Stratigraphy of the St. George's Field Site (modified from field sketches by K. Hunter-Mann, YAT).

It appeared likely that most of the organic-rich deposits originated over a single, probably relatively short-lived period of deposition over glacial till. Comparison of levels in the pits being excavated suggested that they cut through a north-west/south-east channel in glacial deposits, with samples 303-306 representing the infilling of this channel, and those above 303 representing deposition above and beyond the original channel.

At approximately -1m AOD, the nature of the deposit changed dramatically. Beneath this level, stiff boulder clay that appeared not to have been reworked was exposed. It proved impractical to take sufficiently large samples beneath this level, as building operations did not proceed beyond this point.

5.3 Methods

Fifteen samples were taken from the exposed walls of the pit. These samples were assigned to contexts by K. Hunter-Mann, in order to identify the relative stratigraphic positions of samples.

In the laboratory, two subsamples (a and b), each of 2kg material, were processed by paraffin flotation (as described in Chapter 4) for samples 101, 104, 106, 401, 201, 202, and 303. The samples from the lowest points in the profile, 305 and 306, were smaller, and only one 2kg subsample could be taken for each.

The flot produced by each subsample was sorted, and beetles, bugs and plant macrofossils identified. In addition, 20g subsamples of the residues after flotation were taken for samples 101b, 104b, 202b and 401a. The 20g subsamples were washed through sieves of mesh 2mm, 1mm, and 300µm, and the fraction retained by each sieve hand-sorted for plant macrofossils. The residue from sample 104 contained, in addition to plant macrofossils, two bones of small mammals: an unidentified metacarpal and a terminal phalange of bank vole (*Clethrionomys glareolus* (Schreber)), identified by Dr. Keith Dobney of the EAU.

Insect taxa identified in the flots from each sample were assigned to ecological groups, and the database described in Chapter 3 was used to derive information from species lists.

Plant macrofossils from samples 101, 202, 303 and 305 were subject to ^{14}C dating at the Radiocarbon Accelerator Unit, University of Oxford (ORAU). Selection of plant macrofossils was carried out as described in section 4.3. 305 and 101 were chosen to represent the approximate probable onset and cessation of deposition of the highly organic deposits, 202 to date the deposition of the large *Fraxinus* fragments, and 303 to date the end of deposition within the confines of the possible channel, and provide a date for the fossil-bearing silts between the onset and endpoint of their deposition.

5.4 Results

5.4.i Dates of samples from St George's Field

Uncalibrated dates are shown in Figure 5.2. Dates after calibration are shown in Figure 5.3, below. The large error associated with sample 305 is a result of the highly mineral nature of this sample, which meant that little carbon could be recovered from the sample after pretreatment (R. Housley, pers. comm.). After calibration, the result for this sample appears to be indistinguishable from that for sample 303. Otherwise, the samples follow the stratigraphic order expected, with the dates for samples 202, 303, and 305 (OxA-4027, OxA-4028, and OxA-4029 respectively) being close or indistiguishable, and that for sample 101 (OxA-4026) significantly later. All four of the dated samples fall within the mid to late Bronze Age.

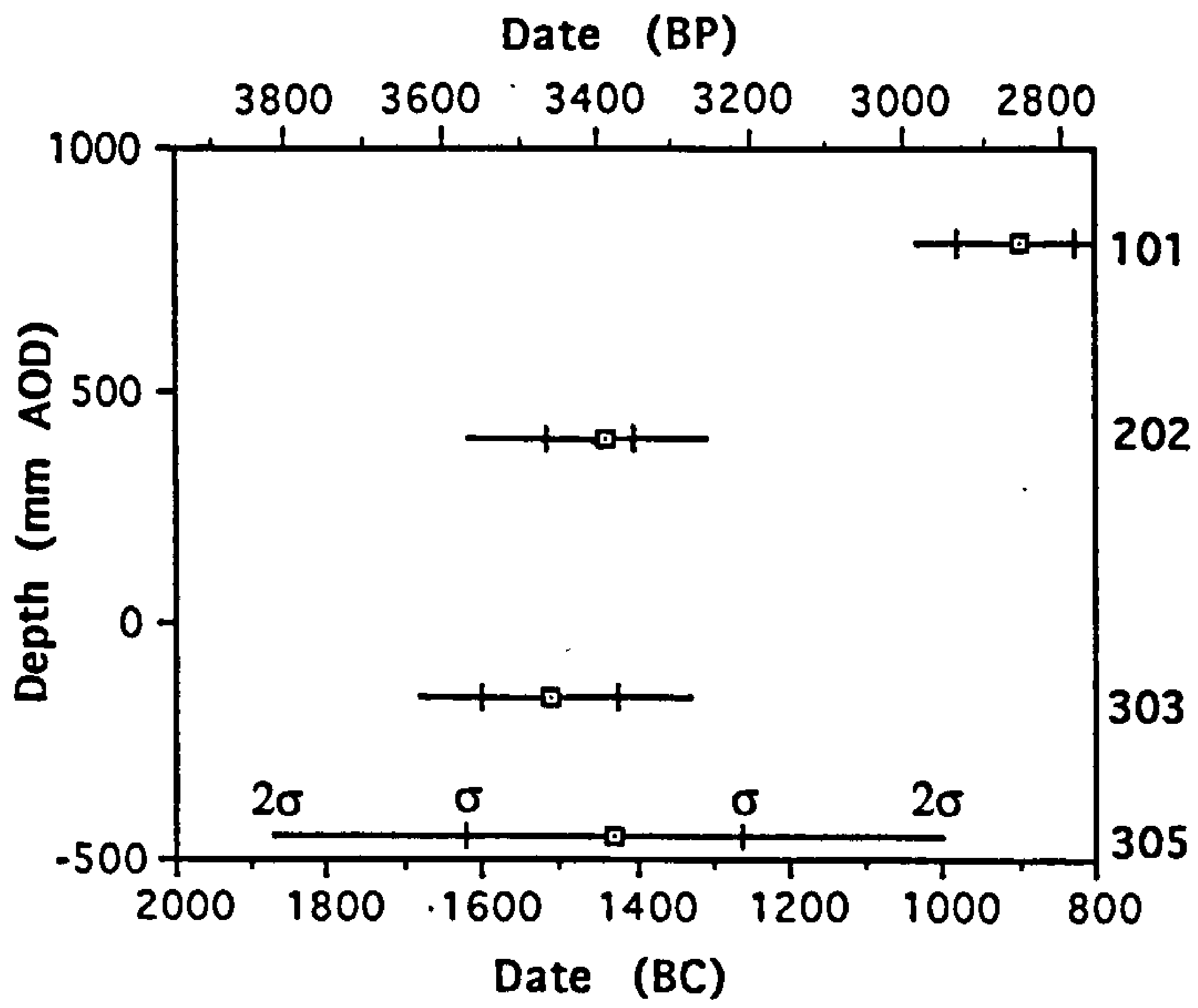


Figure 5.3 Calibrated radiocarbon dates for samples from St George's Field, with associated errors (σ and 2σ).

In order to gain more information from the St George's Field site, in particular regarding the relative ages of the deposits in the various points sampled, it would have been preferable to obtain a larger number of radiocarbon dates, such that at least the uppermost and lowest samples in each column were dated. However, in this case, a limited number of SERC-funded dates were allocated by the Advisory Committee of the ORAU and it is therefore impossible to relate precisely the samples taken at each end of the pit. Although it is therefore possible that all the samples in the sequence 101-106 were laid down after 201-202 and 301-306, the stratigraphy of the site makes this unlikely.

5.4.ii Invertebrate assemblages from St George's Field

Some statistics describing the beetle and bug assemblages from St George's Field are shown in Table 5.1. There is a marked trend in size of these assemblages, with those from lower in the profile, where the matrix of the deposit became more sandy, being smaller in terms of the absolute numbers of individuals and species recovered, and in the concentration of fossils in the deposit. Figure 5.4 shows the close correlation between position in the profile, and assemblage size. Erosion of the fossils present in the lower samples was marked, and it seems likely that conditions of preservation in the lowest deposits were poor, whereas in the more organic middle layers, a greater proportion of the initial death assemblages were preserved. However, the smaller assemblages in the lower samples may also reflect a period of more rapid water flow and hence less concentrated deposition of insect remains.

The most abundant taxon was an aquatic *Hydraena* species (*H. britteni* Joy or *H. rufipes* Curtis), with an MNI of 58, more than double that of the second-ranking species, 'Aleocharinae sp.2' (MNI = 26). Other abundant aquatic species include the *Ochthebius* species *O. minimus* (MNI = 19), *O. dilatatus* (MNI = 14), and '*Ochthebius* sp.' (MNI = 19). Marshland taxa were also well represented, the most abundant being *Prasocuris phellandrii* (MNI = 20). Few of the beetles and bugs recovered fell into the 'arable' or 'heathland' ecological groups and, although the 'pasture' species *Phyllopertha horticola* was relatively abundant (MNI = 11), other pasture species were not (the second most abundant pasture taxon, *Geotrupes* sp., was only represented by 6 individuals).

Among the most abundant taxa, woodland and tree-dependent species were well represented, including the bugs *Pentatoma rufipes* (MNI = 19), *Drymus brunneus* (MNI

= 8), and several *Psylla* species (including *P. melanoneura*, *P. brunneipennis* or *melanoneura*, and *P. ulmi* or *foersteri*, each represented by at least 7 individuals). However, most taxa recovered were represented by single, or few, individuals. Of 426 different taxa recorded from the St George's Field deposit, 220 were only present as singletons, and a further 67 were represented by only two individuals. A full list of taxa identified, and minimum numbers of individuals recovered, is given in Appendix 2.

Other insects recovered included the larval cases of a trichopteran (cf. *Limnephilus* sp.), found in all samples except 202, 303, 305 and 306, and one larval case of *Molanna* sp. was recovered. Fragments of the wings of an adult caddis were found in samples 104 and 201, and wing fragments from two individuals identified as *Glyphotaelius pellucidus* (Retzius) were found in sample 106. *G. pellucidus* is a widespread species of lakes, pools and streams (Fryer, 1991). *Limnephilus* species occur in a wide variety of aquatic habitats.

Ostracod (Crustacea) remains were recovered from most of the St George's Field samples, and it is possible that these could be used in the reconstruction of the aquatic environment in the area, as many of the ostracods show distinct preferences for particular water conditions (Neale, 1983; Henderson, 1990). However, the species present in this case were not identified.

Table 5.1 Size of beetle and bug assemblages from St George's Field

Context	Sample	Approx. depth (mm from OD)	N	S	No. indivs. kg^{-1}	α	SE of α	*d*
4023	101	+ 800	236	144	59	157	19	0.0805
4027	201	+ 750	175	120	44	168	26	0.0800
4023	104	+ 500	233	141	78	151	18	0.0386
4028	202	+ 400	222	124	56	116	14	0.0450
4029	303	- 150	85	67	21	145	37	0.0706
4025	106	- 200	109	83	27	158	34	0.0459
4030	305	- 450	88	71	44	170	45	0.0341
	306	- 600	27	25	14	156	107	0.0741
4026	401	- 900	85	75	21	302	100	0.0235

Key;	N	Number of individuals
	S	Number of taxa
	α	Fisher's α diversity index
	d	Berger-Parker dominance index (n_{max}/N where n_{max}= Number of individuals of dominant species)

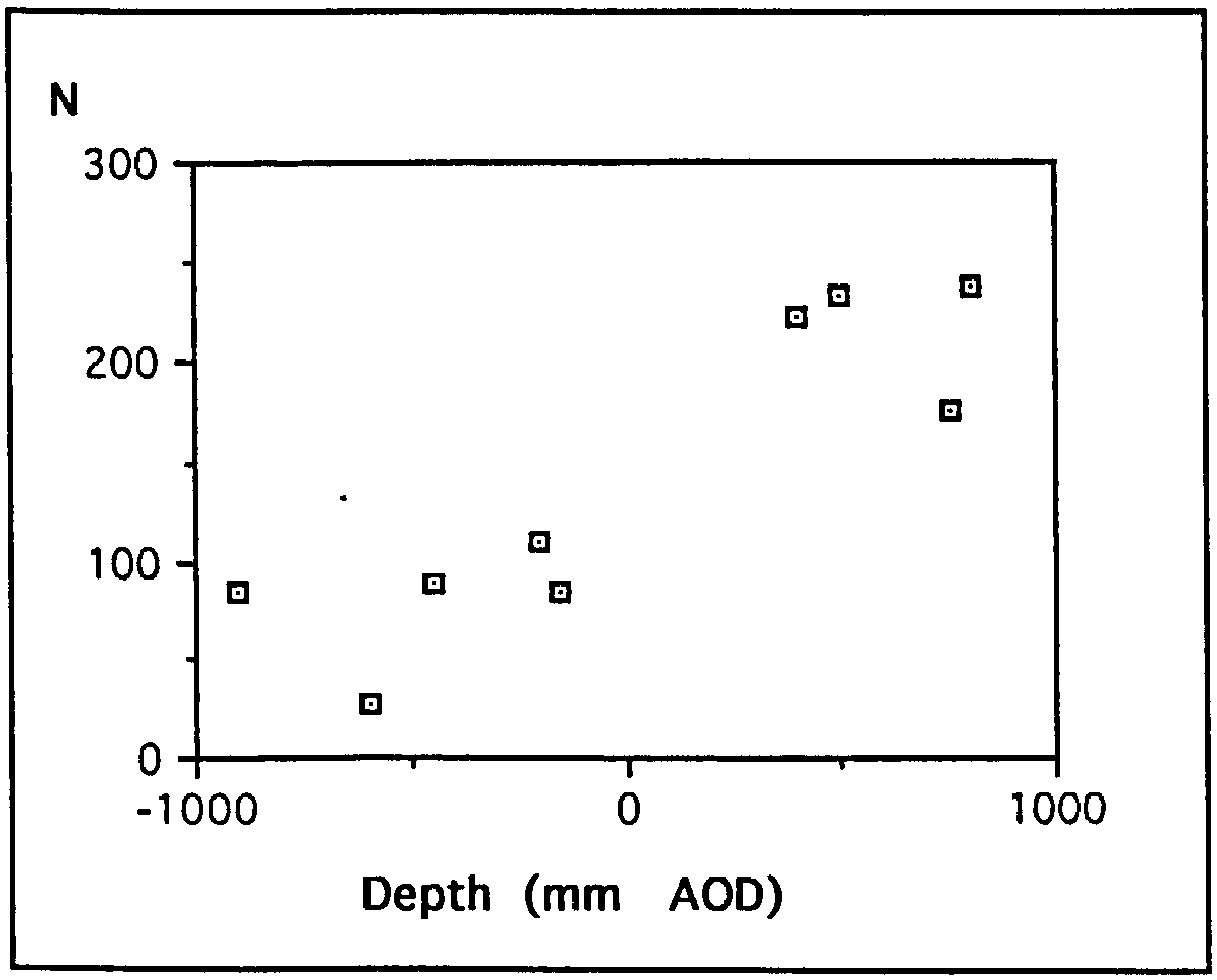


Figure 5.4 Graph showing assemblage size (N) for St George's Field samples.

The values of α in the samples are particularly high, compared with whole modern assemblages from both non-woodland and woodland sites, and with a wide range of archaeological deposits. Only the lowest α from St George's Field (116, from sample 202), is within the range of values at modern woodland sites (see Chapter 3), and all are much larger than values for death assemblages from non-woodland sites. They also far exceed values given by Kenward (1978), for archaeological assemblages with a high background input (which can reach 60-70 in the case of such assemblages from Saddler Street, Durham), and are similar to the high values obtained for the most diverse insect assemblages with a large allochthonous component, at the General Accident (24-30 Tanner Row) and Rougier Street sites, York (Hall and Kenward, 1990).

In addition to the extremely high values of α, values of the dominance index *d* are low, comparable only with the lowest values obtained for Yorkshire woodland sites (for example, site DRW, where *d* varied between 0.047 and 0.122 for the five samples) and other modern assemblages. Even assemblages from abiotic roofs in York (where the entire assemblage had been transported to the point of deposition) all show higher values of *d* than the St George's Field assemblages. Together with high α values, this indicates that the assemblages are extremely diverse, made up of small numbers of individuals from many species.

The proportion of the total number of individuals from each assemblage in each of the ecological groups recognised was as shown in Figure 5.5. The major groups throughout the profile are the aquatics ('AQU'), and taxa associated with trees and woodland ('TRE & WOO'). Species of marshland ('MAR') and litter ('LIT') environments generally make up a rather smaller proportion of the assemblage. Other environments are represented (including arable, 'ARA', pasture, 'PAS', and heathland, 'HEA'), but only by small numbers of individuals. The ecological composition of the assemblages appears to vary little through the profile, with the major groups remaining important in every sample, except in sample 303, where the tree and woodland group is relatively small, with the 'litter' taxa becoming more important than other samples. However, sample 303 is one of the smaller insect assemblages (under 100 individuals), so the degree to which it will accurately reflect local environments is bound to be less than that of larger assemblages such as 101, 104 and 202 (all over 200 individuals).

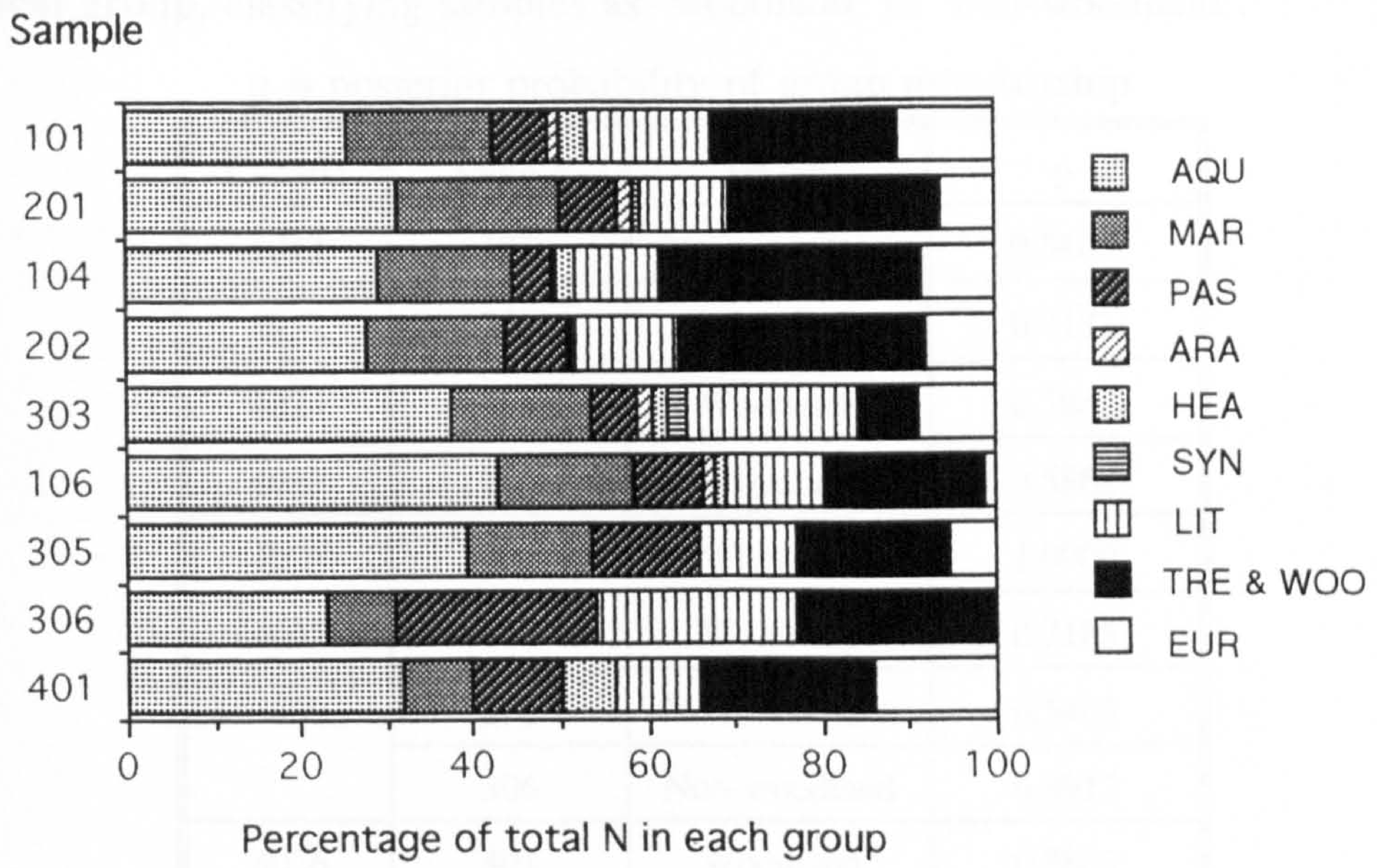


Figure 5.5 Proportion of the total N of insect assemblages falling into each of the ecological groups identified (excluding uncoded taxa), St George's Field. For explanation of abbreviated ecological codes, see text.

Since the high 'TRE & WOO' values suggested that these assemblages could have built up close to, or within, woodland, discriminant analysis was performed as described in Chapter 3. Discriminant functions were constructed using the numbers of individuals in each ecological group, for modern sites classified as 'woodland' or 'non-woodland'. These functions were then used to classify the St George's Field samples, of unknown status, as belonging to one of these classes. The results are shown below (Table 5.2).

Table 5.2 Discriminant analysis based on the numbers of individuals in each ecological group, classifying samples as 'woodland' or 'non-woodland'.

p = posterior probability of group membership

Context	Sample	Group	p
4023	101	Non-woodland	0.5405
4027	201	Woodland	0.7183
4023	104	Woodland	0.5862
4028	202	Woodland	0.5862
4029	303	Woodland	1.0000
4025	106	Woodland	0.7183
4030	305	Non-woodland	0.5405
	306	Non-woodland	0.8917
4026	401	Woodland	0.5862

Most of the samples were classified as part of the woodland group, although the probability with which they were placed was in some cases, low (e. g. for samples 104, 202 and 401). Three samples were not placed in the woodland group. Samples 305 and 306 were small assemblages, (see Table 5.1), so their classification as 'non-woodland' is likely to be an artefact. However, sample 101, the uppermost of the samples taken, was large. It is possible that, at the top of the sequence studied, woodland clearance was occurring and this sample represents the end of a period in which woodland habitats dominated the surrounding area. However, the probability attached to the placing of sample 101 in the 'non-woodland' group was low (0.5405). The possibility of misclassification cannot be ruled out (a misclassification rate of 1 in 20 samples can be expected), and it is impossible to say whether this has occurred without a fuller sequence of samples above the level of those described here.

A number of the beetle and bug taxa identified in deposits from St George's Field are associated with specific hostplants, and the plants inferred from the insect assemblages are shown in Table 5.3.

Table 5.3 Plants associated with the host-specific phytophagous insects found at the St George's Field site. (Excludes plant taxa represented by only a single insect individual.)

For description of the contexts identified, see Figure 5.2.

Plant species inferred	**Number of insect individuals in context**							**Insect species found**
	4023	**4025**	**4026**	**4027**	**4028**	**4029**	**4030**	
Quercus spp. *	1							*Ledra aurita*
Quercus spp., *Alnus glutinosa* *	9			2	12			*Pentatoma rufipes*
Quercus, Fagus and *Castanea* spp. *				1				*Dryocoetes villosus*
Oenanthe aquatica, O. crocata	15		3	2				*Prasocuris phellandrii*
Fraxinus excelsior *	4		1	4	6			*Hylesinus crenatus, H. oleiperda, H. orni, Psyllopsis fraxinicola*
Crataegus spp.	7							*Psylla melanoneura*
Betula spp. *	1							*Elasmucha grisea*
Betula spp., *Corylus avellana*, other trees. *	2				1			*Deporaus betulae, Elasmostethus interstinctus*
Betula spp., *Fagus sylvatica, Quercus* and *Ulmus* spp. *				1				*Melandrya caraboides*
Salix spp.	2			3				*Psylla brunneipennis, P. moscovita*
Urtica dioica *	2		1	1	1			*Brachypterus* sp., *Phyllobius pomaceus, Cidnorhinus quadrimaculatus*
Alnus glutinosa ***	3			1	1			*Chrysomela aenea, Oncopsis alni*
Rubus spp. *	3		1					*Batophila* spp.
Ulmus spp. *	2		1	1	1			*Psylla ulmi, Scolytus scolytus*
Calluna vulgaris, Erica cinerea	2				1			*Strophingia ericae*
Brassicaceae spp.	1				1			*Ceutorhynchus floralis*
Phragmites australis	1			1				*Paralimnius phragmitis*

Plants represented by single insects: Apiaceae spp.(or *Hedera helix*)., *Cardamine* or *Nasturtium* spp., *Carex* spp., *Hedera helix, Hypericum* spp., *Iris foetidissima* or *I. pseudacorus, Juncus* spp., *Picea* or *Pinus* spp., Poaceae, *Polygonum* or *Rumex* spp., *Sorbus aria* or *S. aucuparia, Stachys sylvatica.*

Plants represented as macrofossils: *** Abundant ** Occasional-Frequent * Rare (see Table 5.6).

Table 5.4 Summary of plants represented by beetle and bug species

Ecological group of plant	Number of plant species inferred	Number of insect individuals	Number of insect taxa
Trees and Woodland	12	37	19
Marshland	2	22	2
Other habitats	3	10	5

Again, most of the plant species inferred were trees and other woodland species. Many of these were also represented in the assemblages of plant macrofossils recovered (see Table 5.6). However, some plant species, such as *Oenanthe* spp., were inferred from the insect assemblages although absent from the macrofossil assemblages. As many *Oenanthe* species are marginal aquatic or marshland plants, it is possible that they were present in the area. However, *Oenanthe* fruits have been recorded from waterlogged deposits, including some of a preglacial date (Reid and Reid, 1907), and their absence here is puzzling. It may that the chrysomelid beetle *Prasocuris phellandrii* (L.) was exploiting another, unknown food source in this case. Alternatively, the beetle may have been part of a transported part of the assemblage, perhaps being incorporated into the deposit after arriving through flight. However, the relative abundance of this species in the deposit suggests that a breeding population was present locally. Where plants were both inferred from the insect assemblages and directly represented in the macrofossils, the importance attached to each plant species differed in the two forms of evidence. Thus the largest number of host-specific insects found are associated with oaks, and alder was only represented by small numbers of individuals of two (or possibly three) insect species. However, the plant assemblages contained abundant alder macrofossils, and only small numbers of those of oak.

5.4.iii Plant assemblages from St George's Field

The assemblages of plant macrofossils recovered from the St George's field samples included both mosses (present in the insect flots as single leaves, and in the sieved residues as leafy stems), and higher plants (seeds, leaves and other parts, mainly recovered from the sieved residues). The species recovered are listed in Tables 5.5 and 5.6 below.

Table 5.5 Mosses from St George's Field samples.

Results for two subsamples from each sample combined. * = present in flots † = present in sieved residues (samples 101B, 104B, 202B and 401A only).

Habitat preferences: E = Eurytopic, O = Open habitats (grassland, rocks) S = Damp places W = Woodland, U = Unclassified

Species (Habitat)	Sample								
	101	104	106	201	202	303	305	306	401
Antitrichia curtipendula (W)		*†	*						*†
Barbula sp. (U)	†			*					
Dicranum sp. (U)		†		*					*†
Eurhynchium striatum (E)	†								*
Eurhynchium sp. (U)	*†		*		*				*
Fissidens sp. (U)		†					*		†
Homalia trichomanoides (W)	*†	†							†
Homalothecium sp. (U)	†							*	
Hypnum sp. (U)	†			*					
Leucodon sciuroides (W)		†							†
Mnium or *Plagiomnium* sp. (U)				*					*
Neckera complanata (W)	†	*	*						*
Neckera crispa (O)	†	†							
Neckera sp. (U)		*						*	
Plagiomnium undulatum (W,S)	†	†		*					
Thamnobryum alopecurum (W)	*†	*							
Thuidium tamariscinum (W)	*								

Table 5.6 Higher plants from St George's Field samples, in ecological groups.

Fossil parts recovered:
B = Buds, bud-scales C = Cone L = Leaves S = Seeds, fruits St = Stems T = Twigs, wood.

Abundances in flots and sieved residues (samples 101B, 104B, 202B and 401A only):
A = Abundant (>30 fossils) F = Frequent (15-30 fossils) O = Occasional (3-15 fossils) R = Rare (1-2 fossils).

F = flot 2 = fraction retained by 2mm sieve 1 = fraction retained by 1mm sieve 0.3 = fraction retained by 300µm sieve.

	Fossil parts	Sample															
		101b				104b				202b				401a			
		F	2	1	0.3	F	2	1	0.3	F	2	1	0.3	F	2	1	0.3
Aquatic plants (A)																	
Potamogeton sp.	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R
Mire and marshland plants (M)																	
Alisma sp.	S	-	-	-	-	-	-	-	-	-	-	R	O	-	-	-	-
Caltha palustris	S	-	-	-	-	R	-	O	O	-	-	-	R	-	-	-	-
Eupatorium cannabinum	S	-	-	-	-	-	-	-	R	-	-	-	R	-	-	-	R
Filipendula ulmaria	S	-	-	-	-	-	-	-	R	-	-	-	R	-	-	-	-
Lycopus europaeus	S	R	-	-	R	R	-	-	-	O	-	-	O	-	-	-	R
Myosoton aquaticum	S	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
Oenanthe cf. *aquatica*	S	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-
Scirpus lacustris	S	-	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-
Schoenus nigricans	S	-	-	-	-	O	-	-	-	-	R	-	-	-	-	-	-
Thalictrum flavum	S	-	-	-	-	-	-	-	-	-	-	R	R	-	-	-	-
Trees and woodland plants (W)																	
Alnus glutinosa	C,L,S,T	F	A	A	A	R	F	A	A	R	-	-	A	O	F	F	O
cf. *Betula* sp.	B	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
Corylus avellana	S,B	-	-	-	R	-	-	-	-	-	R	R	-	-	O	-	-
Fraxinus excelsior	S,T	-	-	-	-	-	-	R	R	-	R	-	-	-	-	-	-
Ilex aquifolium	L	-	-	-	-	-	-	R	-	-	R	-	-	-	-	-	-
Mercurialis perennis	S	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-
Moehringia trinervia	S	-	-	-	-	-	R	-	-	-	-	-	R	R	-	-	-
Prunus spinosa	S	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-
Quercus sp.	L,T	R	-	R	-	-	O	R	-	-	-	-	-	-	-	-	-
Ulmus sp.	S,B	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-
Disturbed ground (D)																	
Arenaria serpyllifolia	S	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-
Chenopodium ficifolium	S	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
Chenopodium cf. *album*	S	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
Polygonum aviculare agg.	S	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-
Sambucus nigra	S	-	-	-	-	-	-	R	-	O	-	-	O	-	-	O	-
Stellaria media	S	-	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-
Valerianella sp. (*carinata* or *locusta*)	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-
Other habitats (O)																	
Ranunculus Section *Ranunculus*	S	-	-	O	R	-	-	-	R	-	R	-	-	R	-	-	-
Stellaria cf. *neglecta*	S	-	-	-	-	-	-	-	R	-	-	R	-	-	-	-	-
Uncoded (U)																	
Carex sp. (2-sided fruits)	S	-	-	R	-	-	-	-	-	-	-	R	-	-	-	-	-
Carex sp. (3-sided fruits)	S	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-
Cirsium or *Carduus* sp.	S	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
Cyperaceae sp.	S	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
Juncus sp.	S	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-
Poaceae sp.	S,St	-	-	-	R	-	O	-	-	-	-	-	-	-	-	R	-
Ranunculus sp	S	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
Rumex sp.	S	-	-	-	-	-	R	-	-	O	-	O	-	-	-	-	-
Salix sp.	L	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-
Stachys sp.	S	-	-	R	-	-	-	-	-	-	-	R	-	-	-	-	-
Stellaria sp.	S	-	-	-	-	-	-	-	-	-	-	-	R	-	-	-	-
Viola sp.	S	-	-	-	R	-	-	-	-	-	-	R	-	R	-	-	-

Other species recovered from flots; *Alopecurus* sp. (U)(seed, from 202C), *Elatine hydropiper* (A)(seed, 305), *Galeopsis* sp. (U)(nutlet, 201B), *Hypericum hirsutum* (U)(seed, 202C), *Prunella vulgaris* (O)(seed, 106A), *Ranunculus* Subgenus *Batrachium* (A)(seed, 104A), *Rubus idaeus* (W)(seed, 202C), *Silene dioica* (D)(seeds, 202C), *Urtica dioica* (M)(achene, from 202C).

In both mosses and higher plants, different suites of species were recovered in the flots and residues. In the case of the mosses, the differences in the species recovered by each method seemed to be random. Wherever both the sieved residues and flots were examined, the sieved residues contained a larger number of moss taxa, except in the case of sample 202, where only one species was recovered (in the flot).

Four of the seventeen moss taxa recovered were 'woodland' species (Smith, 1978), making this the coded group represented by the largest number of taxa (seven taxa could not be assigned an ecological code, as their identification could not be carried to specific level).

In the higher plants, certain taxa, including those with tiny or floating seeds, were best recovered by the flotation method. Thus certain species, such as *Elatine hydropiper* L., with small seeds, only appeared in the insect flot. Others, such as *Lycopus europaeus* L., the seed of which bears a corky flotation device and is adapted to water-dispersal, were well represented in the flots. However, consideration of the flot alone would have overlooked, or underestimated the importance of other taxa such as *Corylus avellana* L., represented by fragments of nutshell and bud-scales in the sieved residues alone. Kenward *et al.* (1980), and Robinson (1981) warn against reliance on flotation methods alone for plant macrofossil recovery, because of this inherent bias. Ideally, both the plant remains recovered in insect flots, and those obtained by sieving the residues remaining after flotation, should be studied to give as full a picture as possible of the environment of a site.

If the plants in each ecological group are assigned points reflecting their relative abundance, with the points given generally representing the mid-point of the potential range, such that Abundant (>30 fossils) = 50 points, Frequent (15-30 fossils) = 22 points, Occasional (3-15 fossils) = 9 points and Rare (1-2 fossils) = 1 point, Table 5.6 can be summarised as shown in Table 5.7, below.

Table 5.7 Size of ecological groups represented in the plant assemblages, weighted by abundance of taxa recovered. For explanation of weighting, see text.

Plant ecological group	Sample			
	101	104	202	401
Aquatic	-	-	-	1
Mire and Marshland	2	31	36	3
Trees and woodland	176	137	58	71
Disturbed ground	-	2	22	10
Other	10	2	2	1
Uncoded	5	11	26	2

In every sample, the 'trees and woodland' ecological group was dominant. The 'mire and marshland' group was also important, and many of the uncoded taxa probably belonged to one of these groups (for example, the plants recorded as *Carex*, *Juncus* and Cyperaceae sp. were probably all marsh plants, *Salix* sp. a tree or marshland shrub, and *Viola* sp. probably a woodland herb). This adds further evidence to the suggestion that the samples represent a period when woodland habitats dominated the catchment. The scarcity of remains of truly aquatic plants is surprising, and suggests that the deposit may have been laid down under still or slow-flowing water in marshland close to the main course of one of the rivers, rather than in the river itself.

5.4.iv Insect species of note from St George's Field

Woodland species

Woodland species uncommon or rare in the Britain today include *Melandrya caraboides* (L.) (Melandryidae) (1 specimen, found in 1 sample) and *Melasis buprestoides* (Eucnemidae) (4 specimens, in 4 samples). Both are saproxylic species, the larvae feeding on dead wood. *Melandrya caraboides* is strongly associated with old woodland in the Sheffield area, although less so in Yorkshire generally, and in Derbyshire (Garland, 1983). It is widespread but locally distributed in Britain today, and Hyman (1992) recorded its status as 'Notable B' (not falling into any of the Red Data Book categories of rarity, but only occurring in 31-100 10km squares of the British

National Grid). *Melasis buprestoides* larvae feed on dead wood in standing trees and fallen woods, mainly in southern England, but extending north to Yorkshire (Mendel, 1988). In the Sheffield area, Garland (1983) regards it as uncommon, and mainly restricted to ancient woods or parklands. However, it is more common in the Yorkshire/Derbyshire region, where it appears to be only a weak indicator of ancient woodland status. Nationally, the species is graded as '3', that is, one of a group of species occurring widely in woods, which may collectively indicate ancient woods (Harding, 1978; Harding and Rose, 1986).

Ledra aurita (L.) (Hemiptera, Cicadellidae) is a large woodland bug, especially associated with oak, and with a distribution today reaching no further north than Herefordshire and Norfolk (Le Quesne, 1965). A single specimen (forewing fragment) was found in the St George's Field samples.

Rabocerus foveolatus (Ljungh) (Salpingidae). A single specimen of this species (associated with dead wood, and under bark in woodland habitats), was recovered. Hyman (1992) records its present status in Britain as 'Notable A' (occurring in 30 or fewer 10km squares of the National Grid). However, it is widespread in Britain, occurring as far north as the Clyde region.

Trichonyx sulcicollis (Reichenbach) (Pselaphidae), is the largest (and possibly rarest) pselaphid beetle in Britain, now confined to the south, although old records exist for York and Carlisle, and it is frequently found in urban archaeological assemblages (H. K. Kenward, pers. comm.). In Britain, it has been recorded from tree stumps, particularly elm (Pearce, 1957), and in association with ants. However, in Sweden, it is found on *Quercus* spp. (Palm, 1959).

Many of the rare and notable species identified could be classified as 'woodland' taxa, suggesting that the assemblages represent old-forest conditions, with a range of species that are today regarded as indicative of undisturbed, ancient woodlands.

Marshland species

Badister dilatatus Chaudoir (Carabidae). One individual of this widespread but local species was found. Its present centres of distribution in Britain are southern England and Wales, where it is found in fens and beside standing water, amongst vegetation (Hyman, 1992).

Cercyon sternalis Sharp and *Hydrochus carinatus* Germar (Hydrophilidae) were both present, the first species as a single individual, the second in two samples (one individual in each). *H. carinatus* is now rare (status = 'RDB 2' in Foster, 1992), with a limited range in East Anglia, which led Balfour-Browne (1958) to suggest that it was a recent arrival from continental Europe. Both are species found amongst vegetation and litter in fens (Friday, 1988).

A single individual of the hydraenid *Hydraena palustris* was recorded. For a discussion of the present distribution and ecology of *H. palustris*, see section 4.5.ii.

Mononychus punctumalbum (Herbst) (Curculionidae). A single individual was recovered. *M. punctumalbum* is found in only 4 British vice-counties, all in southern England (no further north than Wiltshire; Jones, 1977), amongst vegetation on cliff-tops and beside dykes. *M. punctumalbum* feeds on *Iris foetidissima* L. and *I. pseudacorus* L.

Aquatic species

A number of the water beetle species recorded from St George's Field are listed as uncommon by Foster (1992). The elmids *Normandia nitens* (Müller) (4 individuals, found in 3 samples) and *Stenelmis canaliculata* (Gyllenhal) (1 individual) are recorded as having status 'Notable B'. *N. nitens* is associated with clean running water (Friday, 1988), *S. canaliculata* with rivers and large lakes (Robinson, 1991). The latter species was first discovered in Britain in the shallows of Lake Windermere, where the lake floor was shaded by alder (Robinson, 1981). *Oulimnius rivularis* (Rosenhauer) (Elmidae), is rarer ('Notable A'). One individual of this species, now found in fen drains in eastern England, was identified.

The dytiscid beetle *Agabus melanarius* Aubé ('Notable B') was recorded as a single individual. In Britain, this species is only known from woodlands and their immediate vicinity, where it inhabits shallow bodies of water containing leaf litter (Balfour-Browne, 1958). Its present, scattered, distribution includes North Yorkshire.

5.4.v Plant species of note from St George's Field

Elatine hydropiper L.

A single seed of *Elatine hydropiper* was recorded in sample 305. Fossil remains of this species have been recorded at several sites of Ipswichian (around 130000-119000 yrs BP) and earlier date (Reid and Reid, 1907). However, this annual plant of small lakes and ponds is now rare and locally distributed in Britain (Stace, 1991). The occurrence of a single small seed may be an instance of long-distance dispersal, from the headwaters of the River Ouse or Foss, but it is possible that open banks of riverside mud could have been maintained to support local populations of this plant.

Ulmus sp.

Elm bud-scales and a single fruit were recovered in sample 101B. The latter appears to be an unusual record, as elm fruits are rarely preserved as fossil material. Godwin (1975) records the recovery of *Ulmus* fruits from deposits of the Ipswichian interglacial period at Trafalgar Square (Franks, 1960). However, these are not noted in the original paper by Franks. The presence of elm in the area at the time of deposition is supported by the occurrence of elm-feeding insects such as *Scolytus scolytus* (Fabr.) (see Table 5.3).

Since the wych elm, *Ulmus glabra* Hudson, is the only species known to reproduce freely by seed today, it seems most likely that the fruit record refers to this species. However, the possibility that this may belong to another of the native elms, *Ulmus minor* Miller, *U. plotii* Druce or *U. procera* Salisb., cannot be excluded (especially if summer temperatures at this period were higher than those today; see section 5.5.iii).

Valerianella sp.

A single seed of *Valerianella carinata* Lois, or *V. locusta* (L.) Laterr. was recovered from sample 401A. Both of these species are uncommon weeds of arable land, and *V. carinata* is only found today in England south of Yorkshire (Godwin, 1975).

5.5 Discussion

5.5.i Hydrological regime and taphonomy at St George's Field

The position of the St George's Field site, near the confluence of the Rivers Foss and Ouse, suggests that deposition occurred in moving water. However, the aquatic beetles and bugs recovered include species representative of a number of different habitats, including fens and standing water, as well as rivers.

When the taxa in the 'aquatic' ecological group are divided further on the basis of their preferred habitat (using Friday, 1988, for Coleoptera, and Southwood and Leston, 1959, for Hemiptera), those of still water bodies greatly outnumber those of flowing waters (see below). In addition, the 'marshland' component of the St George's field insect assemblages was also large (overall, 128 individuals of 54 taxa). This suggests that over the period of deposition, the area was probably predominantly marshy, with pools providing microhabitats suitable for species preferring still water with submerged litter. Deposition of the assemblage appears to have taken place in shallow, still or slow-flowing water, perhaps at the margin of one of the faster-flowing rivers.

Table 5.8 Division of the 'aquatic' ecological group by preferred habitat.

	No. of taxa	No. of individuals
Rivers and running water	8	37
Ponds, ditches and standing water	13	65
Fen and fen carr	2	6
Eurytopic aquatics	23	147

The superabundance of macrofossils of *Alnus glutinosa* in most samples studied (see Table 5.6), and the presence of insects associated with alder (Table 5.3), lends further support to this inference, and suggests that local vegetation was dominated by alder carr, or at least that a few mature alder trees were present in the immediate vicinity. The occurrence of *Stenelmis canaliculata* also favours an interpretation of still or slow-flowing water, overhung by alder trees.

The presence of other elmid species (such as *Esolus parallelopipedus),* a group now generally restricted to clear running waters, and largely absent from lowland British rivers today (Robinson, 1991), suggests that some of the waterways in the area were fast flowing, with gravel substrate. However, as Elliott (1967) points out, aquatic insects make up a large proportion of the 'drift' of invertebrate remains carried downstream, and these remains are more likely to represent a transported component of the fauna than are the terrestrial or marshland taxa.

The high diversity and associated low values of the dominance index *d*, of the insect assemblages strongly suggest that the assemblages do not accurately represent whole communities of insects dying and being deposited *in situ*. Instead, it seems likely that small numbers of most species reached the point of deposition after being transported from surrounding habitats and communities.

At times, this area will have been subject to inundation from the Rivers Foss and Ouse, particularly at times of rapid runoff and snowmelt in the Pennines and Howardian Hills, where forest clearance may have been significantly more advanced compared with that in the Vale of York. Aquatic and riverside insects would have been carried downstream by such floods, possibly from headwater streams. Aquatics may also have arrived through their own powers of dispersal. Although certain aquatic and fenland beetles (such as members of the genus *Hydraena*) have poor dispersal abilities, often being brachypterous or even apterous (Balfour-Browne, 1958), many others (including most of the Dytiscidae) fly readily (Grensted, 1939).

Insects of terrestrial habitats represented in the samples may also have been carried from upstream, as well as entering the deposit after aerial transport. Robinson (1991) suggests that around 50% of the Coleoptera of lowland riverine assemblages at Runnymede Bridge, Berkshire, and similar sites, will have originated in a strip extending 50 metres on either side of the river extending 0.5 km upstream.

There was no evidence at the St George's Field site for any direct human influence in the transportation of insect remains, and the only possible synanthrope in the deposits was the furniture beetle, *Anobium punctatum* (Degeer). This species is now a major pest (Hickin, 1975), but is regarded as previously being a native member of the British woodland fauna (Robinson, 1991). The site therefore differs from many of the Bronze Age deposits studied, such as those at Thorne Moors (Buckland, 1979), and on the Somerset Levels (Girling, 1980, 1984), where the human influence on the local landscape is manifest in the construction of wooden trackways and other structures.

The uniformity of the deposits and associated insect assemblages at St George's

Field suggest that deposition occurred under a single hydrological regime, and there is little evidence, from the insect assemblages at least, for a change in the representation of terrestrial habitats in the catchment area over the majority of this period. The relatively consistent nature of deposits and assemblages also argues against their deposition by flash floods.

5.5.ii Terrestrial habitats represented in the St George's Field assemblages

The human landscape: arable, heathland and pasture habitats

Few of the taxa recovered at St George's Field give any indication of arable conditions (5 species, 7 individuals). Even these may have been able to find a sufficiently open habitat in the disturbed ground of local riverbanks and cliffs. The carabids *Acupalpus meridianus* (L.), *Pterostichus melanarius* (Illiger) and *Trechus quadristriatus* (Schrank) are all relatively eurytopic in open habitats, *P. melanarius* in particular being found in a variety of situations ranging from arable land to meadows and even forest edges (Lindroth, 1986). The other insects in the 'arable' group are *Apion (Protapion)* sp. (Apionidae), and *Ceutorhynchus floralis* (Paykull) (Curculionidae). Weevils of the subgenus *Protapion* are common pests of crops such as the clovers (*Trifolium* spp.), but may also be found on restharrow (*Ononis* spp.) and other wild Fabaceae. Some, such as *Apion difforme* Ahrens, are primarily found in damp grasslands and marshes. *C. floralis* is today commonly encountered as a pest of *Brassica* crops (Morris, 1991). However, it feeds on many species of native Brassicaceae, including *Rorippa sylvestris* (L.) Besser, often found alongside streams, lakes and on riverside shingle (Clapham *et al.*, 1987) and the coastal herb *Cakile maritima* Scop. (Scherf, 1964). Thus, although these weevils display a measure of host-specificity on crop plants today, their presence in these deposits does not reflect their cultivation at the time of deposition. The occurrence of these taxa as pests of arable crops appears to be an opportunistic development from their original feeding habits on wild relatives of crop plants, to exploit large potential food sources in the 'culture-steppe' landscape created by man (Hammond, 1974).

The plant species associated with cultivation recovered as macrofossils at the site are also relatively broad in their ecological requirements, and many of the smaller weeds of disturbed ground, such as *Polygonum aviculare* agg., *Arenaria serpyllifolia* L., *Valerianella* sp. and *Chenopodium* spp. could have grown on bare banks maintained by river flow. The shrub *Sambucus nigra* L. is more strongly associated with nitrogen-rich, disturbed ground around human settlements. However, it is found in some natural woodland situations (Godwin, 1975), and the seeds are dispersed by birds, so may be found beneath roosting sites some distance from the fruiting plants. Elder is virtually ubiquitous in more recent archaeological assemblages, and it is probably of little use in the reconstruction of past environments (A. R. Hall, pers. comm.).

In contrast to the 'arable' component of the assemblage, species of meadow and pasture-lands were relatively well represented. Fifty-eight individuals of 31 taxa were present in the deposit as a whole, and 4.1-10% of the total individuals in each assemblage were in the 'pasture' ecological group (excluding the small samples 305 and 306, where the percentage was greater). Among these insects were the dung beetles *Aphodius contaminatus* (Herbst), *A. prodromus* (Brahm) and *A. sphacelatus* (Panzer), and *Geotrupes spiniger* (Marsham) and *G. stercorosus* (Scriba). Other species associated with dung included the staphylinids *Gyrohypnus angustatus* Stephens, *Platystethus arenarius* (Fourcroy), *Tachinus marginellus* (Fabr.) and *T. signatus* Grav., and *Cercyon pygmaeus* (Illiger) (Hydrophilidae) and *Onthophilus striatus* (Forster) (Histeridae) (Skidmore, 1991).

However, the dung beetle component was small in comparison with that from other archaeological faunas. Only 1.9% of the total terrestrial individuals, and 1.8% of terrestrial taxa from the site, were scarabaeid and geotrupid dung beetles (*Aphodius* and *Geotrupes* spp.). In contrast, Robinson (1983) reports figures of 10-30% terrestrial Coleoptera in this group from various Iron Age and Roman sites. At Wilsford, Wiltshire, over 30% of the entire beetle assemblage (32% of the terrestrial beetle assemblage), was composed of these dung beetles (Osborne, 1969). If other dung-feeding Coleoptera were also taken into account, 50% of the beetles at Wilsford can be placed in this ecological group (Osborne, 1989). It has been suggested that values of around 10% can be expected in largely open, pastoral landscapes away from concentrations of domesticated animals (Robinson, 1991). This figure will rise where stock are kept closely confined, but lower figures (of around 6%) can be expected where the landscape, although open, is largely devoted to arable land-use. Robinson's (1991) prediction that a insect assemblages from closed forest will contain less than 1% dung beetles seems to suggest that some pastoral farming occurred in the catchment of the St George's Field site, although massive woodland clearance is ruled out by the importance of the woodland component of the fauna. Dung beetles tend to be widely-dispersed (Hanski and Cambefort, 1991), and their presence in the deposits may reflect distant pasture land-use. Of the plant fossils, few are of species associated with grassland. *Ranunculus* Section *Ranunculus* (*R. acris* L., *R.bulbosus* L. or *R. repens* L.) seeds were present in several samples, and *Prunella vulgaris* L. and *Urtica dioica* L. were represented by single fossils. *U. dioica* is regularly found in nutrient-rich fenland habitats in addition to pastures (Stace, 1991), and other species identified here as grassland plants (for example, *R. repens*) may also be found in open marshland or beside water. Overall, the environmental evidence indicates that open grassland was not an important part of the landscape in the catchment over the period, if any was present.

A small but definite heathland (or moorland) component occurred in the fauna (6 species, 13 individuals), including the psyllid *Strophingia ericae* (Curtis), associated with heather, *Calluna vulgaris* L. (Hodkinson and White, 1979). Other heathland species included the cicadellid bug *Aphrodes trifasciatus* (Geoffroy in Fourcroy), the carabid *Bradycellus ruficollis* (Stephens) and the leaf beetle *Galeruca tanaceti* (L.). *B. ruficollis* is found in under *Calluna* bushes in open, heathy places (Lindroth,1986). *G. tanaceti* feeds on low herbaceous plants, including *Thymus* spp., in dry, sandy and grassy places in Britain (Fowler, 1890), but is recorded as a pest of vegetable and cutflower crops in Holland (Mohr, 1966). Dry heathland habitats dominated by *Calluna* are still found in the Vale of York today, on marginal lands such as Skipwith Common south of York, the largest lowland heath in northern England (Webb, 1986). The aeolian sands in the area to the north-east of York (Matthews, 1970) often support dry heath. On the poorly-drained Strensall Common, 9.5 km north of York, wet heath vegetation, largely dominated by *Erica tetralix* L. and *Molinia caerulea* (L.), is predominant (Adams, 1971). In many areas, cessation of management or change of management regime in the present century has led to the loss of these communities. Allerthorpe Common was largely planted with conifers by the Forestry Commission (see section 3.2.i), whereas many smaller areas were subject to natural succession processes, becoming invaded with birch and pine when former grazing pressures were reduced (as at Rabbit Warren Wood, Dunnington). Some of the heathland areas persist, through active management for nature conservation purposes (on Skipwith Common and part of Allerthorpe Common). Many heathlands in the area are probably ancient in origin; on the gravels of Holderness, heath vegetation appears to have developed in the Neolithic period, after a phase of woodland clearance associated with the elm decline (Clark and Godwin, 1956). However, in this case, the small size of the heathland component of the St George's Field assemblages makes it impossible to ascribe these insects to an origin on heathland developing on cleared land in the area. In an area of nutrient-poor, acid sandy glacial deposits or moraine, the disturbance created by rivers would have been sufficient to provide the open, light and warm conditions required for the establishment and growth of heather (Beijerinck, 1940), without the need to invoke large scale human clearance to explain their presence.

The insects and plants of disturbed-land habitats, today ocurring in association with ecosystems created and managed by man, generally make up only a small part of the assemblages from St George's Field. The size of this component of the flora and fauna would appear to be consistent with entirely natural maintenance of early successional habitats. The localised disturbance caused by unmanaged lowland rivers flowing through forested landscape can be considerable, and acts as a major influence the composition of vegetation. In a study of the lowlands of the Peruvian Amazon, Salo *et al.* (1986) found that a 'climax' forest was in fact a mosaic of communities, with 12% of the floodplain in earlier successional stages. The migration of river channels is further modified by seasonal flooding, which would have been an important feature of the Ouse and Foss before the effective canalisation of these rivers, and construction of floodbanks.

Woodland and trees

Woodland taxa make up an important part of the St George's Field assemblages; overall, 17% of the beetle and bug taxa (19% of terrestrial taxa) and 14% of the individuals (18% of the terrestrial individuals) fall into the 'woodland' and 'tree-dependent' ecological groups. Robinson (1991) suggests that these groups will form around 20% of the terrestrial insect assemblage in a deposit laid down in closed woodland conditions. In Neolithic woodland assemblages from Hampstead Heath, around 40% of the insect taxa recovered required the presence of trees (Girling, 1991). In the 'old forest' fauna of Bronze Age date at Stileway, Somerset, identified by Girling (1985), thirty of the eighty species recorded (37.5%) could be assigned to a 'woodland' ecological group. However, in terms of the numbers of individuals of all taxa recovered, the 'woodland' group became less significant; only about 13% of the total number of individuals in the assemblage were in this group.

The results of discriminant analysis (using functions derived from the study of modern woodland assemblages), further support the hypothesis that all the assemblages were formed in an environment in which woodland habitats were prevalent in the catchment (although there may have been some indication, in the uppermost sample, of woodland clearance; see Table 5.2). This technique relies on the numbers of individuals in an ecological group, rather than the number of taxa recorded, and its apparent efficiency, together with the wide discrepancies between the numbers of taxa at woodland sites (see above) suggests that the numbers of individuals may be a more reliable ecological measure than the number of taxa. The latter technique weights both abundant and rare species equally and, as any assemblage contains a large number of species represented by a single individual (see Chapter 3), the species composition of an assemblage may therefore be determined to a large extent by chance.

Among the woodland insects recovered, some of the species are shared with assemblages from deposits (dated about 3000 BP) at Thorne Moors (Buckland, 1979). *Melasis buprestoides*, *Grynobius planus* and *Anobium punctatum* feed on dead and decaying wood, and *Aspidiphorus orbiculatus* (Gyllenhal) (Sphindidae) on fungal hyphae on decaying wood. Other species, such as *Othius punctulatus* (Goeze) (Staphylinidae), are litter dwellers (Evans, 1969), and a third group, including the weevils *Deporaus betulae* (L.) and *Strophosomus melanogrammus* (Forster), are herbivorous. However, the assemblages from St George's Field appear to be a more balanced woodland fauna, including a greater diversity of herbivores in addition to deadwood species that dominated the assemblages at Thorne Moors. In addition, the hostplants of the beetles and bugs suggest that the composition of the woodlands at each site were very different (see below).

Composition of the woodland

The plants which can be inferred from insect assemblages are largely woody species. These tend to carry a larger number of associated insect taxa than do herbs, providing a habitat with a greater degree of architectural complexity (and therefore more potential niches for plant-feeding invertebrates), as well as simply a larger surface area for colonisation. Both these factors should tend to increase the number of phytophagous taxa associated with a plant species (Southwood, Moran and Kennedy, 1982). The plants most heavily represented in the insect assemblages are the oaks, *Quercus* spp., represented by only rare-occasional leaf fragments and twigs in the plant macrofossil assemblages studied. In contrast, alder, although heavily represented in the plant fossil assemblages, and obviously abundant in the area at the time of deposition, was represented by few phytophagous insects: the chrysomelid beetle *Chrysomela aenea* L., the homopteran bug *Oncopsis alni* (Schrank), and (possibly) the heteropteran bug *Pentatoma rufipes* (L.) (the latter species is less host-specific than *C. aenea* or *O. alni*). Alder has a smaller phytophagous fauna than does oak (e.g. 16 host-specific beetle species, compared with 67 on oak; Kennedy and Southwood, 1984), so will tend to be under-represented in the insect fauna, while its presence in the immediate vicinity of waterlogged deposits (e.g. overhanging river margins and marshes) may cause it to be over-represented in the plant fossil assemblages.

In the inferred importance of oak, the assemblages at St George's Field are similar to the old forest faunas at Stileway, Somerset (Girling, 1985), rather than Bronze Age deposits from Runnymede Bridge, Berkshire (Robinson, 1991), where insect species associated with rosaceous trees (and other light-demanding plants including ash, *Fraxinus excelsior* and willows, *Salix* spp.) were dominant in a fauna strongly suggesting an open, largely deforested landscape. However, the presence of ash in the vicinity of St George's Field is indicated in both the plant and insect fossil assemblages. This species is light-demanding and fast-growing, and is undoubtedly favoured by human intervention, particularly forest clearance on base-rich soils: the extensive ash-dominated woods of limestone soils in Britain appear to be of anthropogenic origin (Godwin, 1975). However, ash was present in the forests of the early postglacial period, although it may have been restricted to natural clearings and areas of disturbance caused by, for example, the death of trees (Pennington, 1970). Its presence at this site may reflect the disturbance associated with the natural movement of the river channel (see above), as may the presence of insects associated with the shrubby species *Corylus avellana*, and *Crataegus* spp.

Birches (*Betula* spp.) were represented by several insect species and possible bud-scales. In the Atlantic 'wildwood', these trees were probably restricted to fen woodland habitats, and were inferred as a major component of the Middle Bronze Age fen woodland vegetation at Thorne Moors from pollen and fossil insect assemblages

(Buckland, 1979). It seems possible that these trees could have been growing alongside alder in the vicinity of the St George's Field deposit, forming birch-alder carr similar to that found today at Askham Bog near York (Fitter and Smith, 1979).

Notably absent from the plant and insect assemblages are indications of the presence of lime (*Tilia*), which was probably a major component of the British 'wildwood' (Rackham, 1980). Lime fruits have been recovered from deposits at Shustoke, Warwickshire (Kelly and Osborne, 1964), and sites in Nottinghamshire and South Yorkshire (see Buckland, 1979), and insects associated with *Tilia* spp. were found at Shustoke, Thorne Moors and other sites of Neolithic and Bronze age dates. In the Humberhead Levels, lime declines drastically at around 2500 BP, possibly resulting from a raised water-table (Buckland, 1979), or human intervention. It may be that the low-lying, wet soils of the Vale of York did not provide ideal conditions for the growth of lime, although Godwin (1975) suggests that fen-edge woodlands provided suitable habitats for *T. cordata* Mill.

5.5.iii Evidence for climate change from St George's Field

Many of the unusual insect species recorded at St George's Field (see 5.4.iii, above), now show markedly southern distributions (e.g. *Ledra aurita*, *Badister dilatatus*, *Mononychus punctumalbum*), although none are extinct in Britain.

In the case of some other insect faunas of Bronze Age date, the presence of species outside their current ranges has been used as evidence of a warmer, or at least, more continental climate than at present.

Deposits at Pilgrim Lock, Warwickshire (dated 2770-3006 BP), and Wilsford, Wiltshire (*c.* 3330 BP), contained abundant Scarabaeid beetles of the genus *Onthophagus*, including *O. fracticornis* (Preyss.) and *O. nutans* (F.). The former species is now extremely rare, the latter now apparently extinct in Britain (Jessop, 1986). Osborne (1969; 1988; and 1989) interpreted these insects as evidence that the Bronze Age climate of the south of England may have been similar to that of mid-France today, where *Onthophagus* species are common.

At Runnymede Bridge, Berkshire, deposits dating 2800-2950 BP contained woodland taxa now extinct in Britain, and insects with a distinct southerly range today (e.g. the weevil *Liparus coronatus*), but none of these require a climate substantially different from today's (Robinson, 1991). Similarly, at Stileway, Somerset (where deposits accumulated over a period of 1500 years from around 4470 BP), habitat loss outweighed climatic change as a cause of range contraction in the beetle species identified (Girling, 1985). Bronze Age assemblages from Thorne Moors, Yorkshire (*c.* 3000 BP) contained some taxa no longer extant in Britain but still present in Scandinavia, implying that the climate may have been more continental in nature, with higher summer temperatures than at present (Buckland, 1979).

Overall, insect evidence suggests that, in the period 4000-3000 BP, Britain experienced summer temperatures slightly higher than those of today (Osborne, 1982), and this is supported by other forms of evidence (Lamb, 1982). While there is no strong evidence from the fauna at St George's Field for mean temperatures significantly higher than those of the present day (once habitat loss is also taken into account as a factor), the species lists would fit into the general pattern of slightly higher temperatures inferred from other Bronze Age insect assemblages. In the later Bronze Age, climatic deterioration seems to have occurred (beginning between 3050 and 2950 BP), bringing to an end this warmer, drier period (Burgess, 1974).

5.6 Conclusions: human influence on the Vale of York in the Bronze Age period.

Elgee (1930) adopts a threefold division of the Bronze Age for north-east Yorkshire:

Early Bronze Age	3950 - 3450 BP
Mid Bronze Age	3450 - 2750 BP
Late Bronze Age	2750 - 2350 BP,

Whilst Spratt (1982) uses the following division:

Late Neolithic/earliest Bronze Age	4450 - 3650 BP
Early Bronze Age	3650 - 3250 BP
Late Bronze Age	3250 - 2550 BP

The St George's Field deposits therefore appear to have formed in the later part of the Bronze Age.

Although settlement on the North York Moors appears to have been advanced by the early-mid Bronze Age and, on the Yorkshire Wolds, human influence on the landscape was great at a much earlier date (Bush, 1988), little evidence remains for permanent settlement in the Vale at this period. The discovery of middle-late Bronze Age axes and other implements at several sites has been used as evidence of a shift in population from the surrounding upland areas to the Vale (Longworth, 1965), but these finds are grouped in the Topcliffe-Baldersby area, and on the York moraine, pointing to the use of these raised features as trackways for crossing the Vale (Willmot, 1959). There appears to be no evidence of Bronze or Iron-Age earthworks in the Vale west of the Ouse, and very little in the eastern part of the Vale. However, Iron Age barrows extend along the York and Escrick moraines (Ramm, 1978), and there are records of a concentration of these features at Skipwith Common (SE 645 377), and at Thorganby Common, near Skipwith (SE 666 400) (Stead, 1961 and 1979) suggesting that permanent settlement of the central Vale of York was under way by the early Iron Age. Recent excavations south-west of Easingwold have given further evidence for Iron Age settlement, and iron smelting, on a low-lying part of the Vale (Whyman, in press).

At around 3775 ± 100 BP, a period of marine transgression began that brought tidal waters into the Vale of York. Sea level change would have aggravated the flooding of the River Ouse, which must have been a major deterrent to early settlement in the Vale (Kirk, 1959).

Permanent clearance of the forests of the English lowlands began around 4000 BP (Turner, 1970), and was probably well under way by the time deposition at St George's Field began (*c.* 3240 BP), but there is little evidence for major alteration of woodland habitats in the catchment area of these deposits, now occupied by the City of York.

Chapter 6 Modern and fossil insect assemblages: an overview

6.1 Communities and Death assemblages

As discussed by Evans (1972), a death assemblage of any group of animal remains does not necessarily represent a living community. A series of taphonomic processes occurs during and after the period of accumulation, which may hinder the interpretation of local environments from an assemblage.

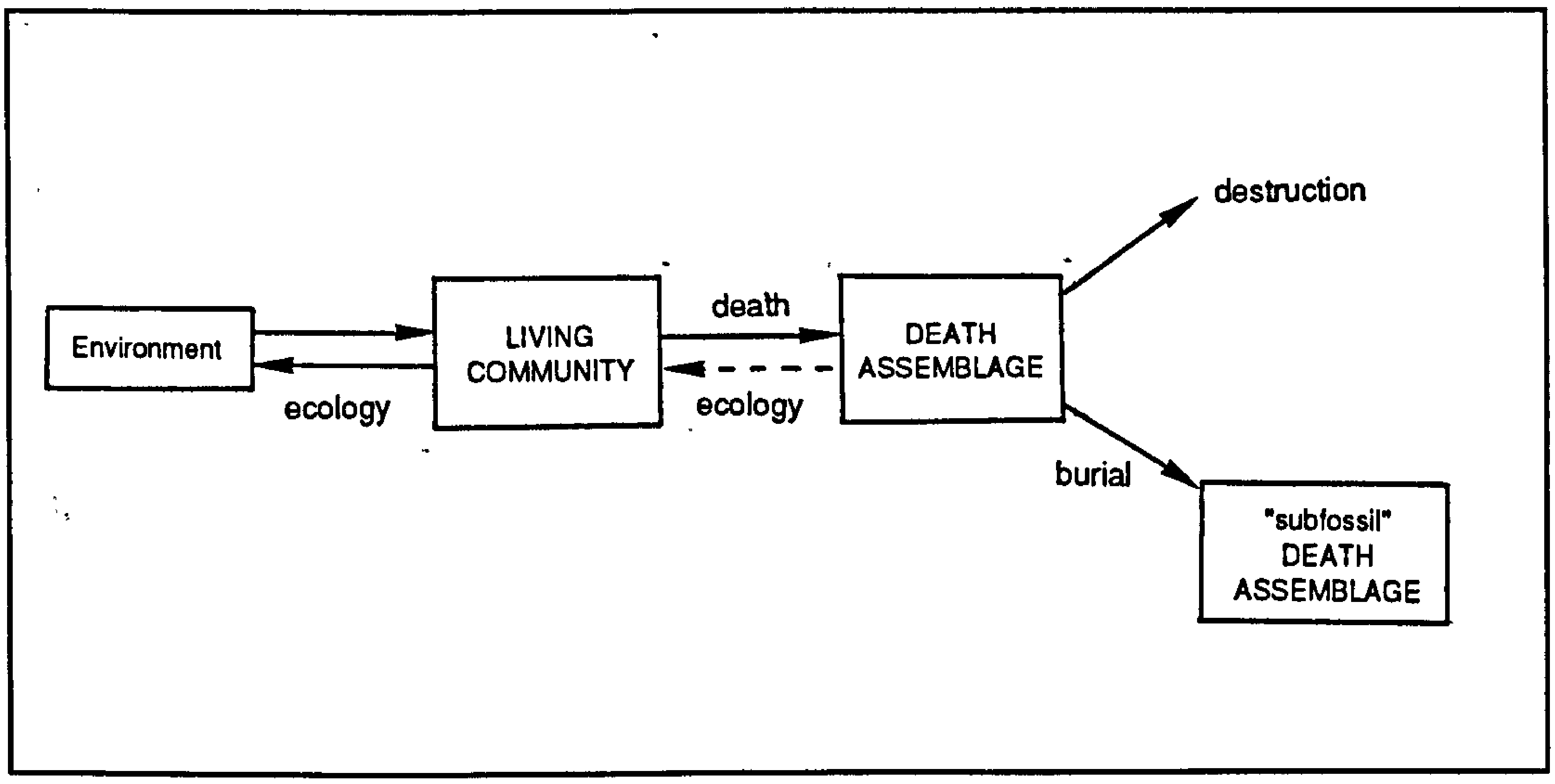


Figure 6.1 The origins of a fossil death assemblage (modified, after Evans, 1972).

Death assemblages lose the three-dimensional structure and temporal variation of living communities (Fishpool, 1992), and these must therefore be inferred by interpretation of aspects of the assemblage and surrounding sediments. It is in this area that there would appear to be most scope for finding modern correlates of ancient communities in order to interpret the implications of the ancient fauna recovered.

The study of modern death assemblages in order to understand and interpret fossil assemblages would appear to be a valuable technique with the potential for much further work, to answer specific questions. For example, the use of discriminant analysis as a tool to recognise woodland communities from the numbers of individuals in an assemblage belonging to each of the ecological groups recognised seems to be useful, as the process can take into account the numbers in several ecological groups, rather than simply, say, the 'woodland' group.

Studies of living communities of insects have tended to concentrate on single groups or guilds (see, for example, Day, 1987; Day *et al.*, 1993; Fishpool, 1992, all working on carabids, and Claridge and Wilson, 1982), because of the problems of defining the limits of an ecosystem, and of sampling 'whole communities'. Recently, techniques such as insecticidal fogging of tree canopies have allowed efficient sampling across a wide range of arthropod groups in a single locality (Southwood *et al.*, 1982; Stork, 1987), and certain specialised communities (such as phytotelmata in tropical forests) have been comprehensively studied (for example, Cotgreave *et al.*, in press). This has led to advances in the study of the composition of communities, and there is considerable scope for the further use of such techniques to elucidate community structure in modern woodlands, although the very diversity of the insect communities examined has caused problems of interpretation.

Processes of decay and sorting act on insect remains as soon as death assemblages begin to form (see Figure 6.1), and these may act differentially on the various taxa, altering the relative representation of species in the death assemblage. For these reasons, and the problems involved in sampling whole faunas satisfactorily, the study of modern assemblages probably remains the most efficient method of gathering information on ancient assemblages.

However, there are limits to the extent to which the results of such studies can be applied to archaeological assemblages, as a result of a combination of several factors. The insect communities of Britain have changed greatly in the postglacial period (Hammond, 1974), as habitats have waxed and waned in response to changing climate and, perhaps more importantly, human intervention. In the case of woodland habitats, in particular, this means that there are probably no undisturbed areas of 'primary' woodland left in Britain (Marren, 1990), and, therefore, no direct comparanda for the faunas rich in 'Urwaldtiere' reported from some ancient sites (see, for example, Buckland, 1979; Kelly and Osborne, 1964; Girling, 1985; 1991). The fate of the old forest insects of Britain has been mixed; several, such as *Cerambyx cerdo*, have become extinct, whilst others survive in small, isolated pockets of land such as Windsor Great Park, Moccas Park and Sherwood Forest, where sufficient dead wood habitats remain to sustain relict populations (Harding and Rose, 1986). These areas are often landscaped parks, grazed by deer and stock, and probably have little structural resemblance to the primary forests of Europe, other than in the relative abundance of dead wood. Generally, woodlands in Britain possess few 'old forest' insects. The arrival of species from geographically remote areas, usually as a result of introduction (deliberate or accidental) by man, has also influenced the composition of insect communities. Although it has been postulated (Crawley, 1987) that longer-established ecosystems, such as ancient forests, should be more resistant to invasion by new species than early successional ones, this is not invariably the case (demonstrated, among plants, by the success of *Rhododendron ponticum*, introduced to Britain in 1763, as an invader in woodland habitats; Elton, 1958). Among the insects, some of the most abundant species in woodlands are those that have been introduced in the present century (e.g. the lathridiid *Aridius bifasciatus* (Reitter), introduced from Australia in 1949, and now widespread in litter habitats). Of 26 'particularly successful' beetle colonists of Britain introduced since AD 1800, listed by Hammond (1974), four are noted as having particular affinity for woodland habitats. Three of these (*Corticeus fraxini* (Kugelann), *Harmonia quadripunctata* (Pontoppidan), and *Plegaderus vulneratus* Panzer) are associated with coniferous trees, the diversity and extent of which have also been increased by human intervention; the only species found on deciduous trees to have established itself in recent times appears to be *Aulonium trisulcum* (Fourcroy). Even so, the composition of insect faunas, including those of deciduous woodland, has changed significantly in the period of man's influence on the British landscape.

6.2 Catchment areas and the depositional environment

The relative size of catchments, and depositional regime under which each assemblages has accumulated will vary between sites, and the catchments of different forms of environmental evidence also differ. At the moated site at Cowick, South Humberside, pollen evidence provided greater support for the importance of woods in the vicinity than the insect assemblages, perhaps as a result of the difference in the size of catchment areas for light, well-dispersed pollen from trees at the edge of woods, and woodland beetles, which are often poorly dispersed (Hayfield and Greig, 1989). Such disparities in the evidence provided by different forms of environmental data argues for the study of as many forms of fossil biological remains as possible from each site studied.

Even within a single form of environmental evidence, the representation of different species in the assemblage will vary; insect-pollinated plants produce far less pollen than do wind-pollinated ones, where the pollen is widely dispersed by air movement. For this reason, certain trees such as the insect-pollinated limes tend to be under-represented in pollen diagrams from lake sediments and peats (Godwin, 1975), and others such as *Pinus* and *Betula* are consistently over-represented in pollen diagrams, relative to the importance of the trees in woodland composition (Faegri and Iversen, 1964). The representation of different species in the pollen record is also influenced by local factors such as the stresses imposed by soil chemistry, drainage and illumination (Andersen, 1973). In the area of palynology, much work on recent assemblages has been carried out to calculate practical 'correction factors' to allow for such inherent bias in the pollen record (see, for example, Andersen, 1973; 1984). However, in contrast, equivalent work in entomology is less developed. The flight component of communities has been studied by intercept trapping (see Cooter, 1991; Owen, 1992), and has revealed that certain beetle families (such as the Carabidae and Curculionidae) appear to be under-represented, and others (including the Leiodidae) over-represented in the airborne assemblage, relative to the importance of each family in the British beetle fauna as a whole (Owen, 1993). In addition to the apparent difference in readiness of beetles of various groups to take to the wing, the depositional regime at each site will play a part in the ultimate structure of the assemblage. Air movements around the point of deposition would appear likely to play a part in the composition and nature of assemblages (see Kenward, 1985). However, in the case of both modern woodland sites, and the site at Thornton, which seems to have been marsh/reedswamp surrounded by generally open land, the insect assemblages appear to have originateded largely from very local sources, despite the fact that local air movements differed greatly between the sites. At Thornton, the open nature of the vegetation may have meant that there was little variation in wind speed or air pressure over the site, and deposition was therefore limited. This would not appear to be the case for modern woodlands, where the presence of trees should influence air movements and, therefore, the depositional regime. At St George's Field, this situation is complicated by the probable additional input of water-transported material. As shown by the data for assemblages upstream and downstream of a wood at Yorkletts, Kent, water transport of insects from environments upstream can influence the ecological composition of assemblages further downstream (to the extent that assemblages downstream of woodland may be misclassified as woodland assemblages by discriminant analysis on the species composition of the assemblage), but the effect on the whole assemblage of such transport may not be long-lasting; at Yorkletts, assemblages from deposits less than a kilometre from woods were already recognisably different from those within the wood, with a smaller 'woodland' component, and discriminant analysis of the numbers in ecological groups suggests that this site could be recognised as being outside woodland. Elliot (1967) noted that it was the aquatic, rather than the terrestrial, invertebrate assemblage which made up the most important component of the transported fauna of a Dartmoor stream. In slower-moving, lowland rivers (such as those on most of the Vale of York), the effects of transport are also likely to be less important in determining composition of insect assemblages, than for faster-moving upland streams. Robinson (1991) suggests that, for such lowland rivers, 50% of the insect assemblage will probably have originated over as short a distance as 0.5 km upstream. However, the exact effects of water-mediated transport and deposition depend on a myriad of hydrological factors, and are difficult to predict. This is an area in which further research on accumulating modern insect assemblages is necessary, although it seems likely that depositional conditions in individual watercourses will vary greatly. Thus, for any assemblage which may have been laid down in, or close to, running water, interpretation is bound to be complicated.

The period over which deposition has occurred will also vary between fossil sites, as it appeared to do in the modern assemblages. A seasonal peak in insect mortality may well be represented by the abundance of remains of the psyllid *Psylla melanoneura* in the Allerthorpe Common site (ACP), while the importance of heather-feeders at this site, which outweighed that of the surviving heather plants (see below), indicates that temporal integration of assemblages can act on those that have gathered over only a short period. The effects of such time-compression must be aggravated in those archaeological deposits that have accumulated slowly, offering more suitable conditions for incorporation and integration of abundant insect remains, over a long period (although slow accumulation of a deposit may equally allow a greater degree of decay of insect remains, leading to a smaller preserved assemblage per unit volume).

6.3 Post-depositional processes

The effects of post-depositional taphonomic processes vary greatly, depending on the individual conditions at each site, and often appear to have unpredictable consequences.

However, some patterns do emerge. Differential preservation of the remains of different species, or different body parts within a single taxon, may be obvious at certain sites. The thin exoskeletons of aphids (Hemiptera, Homoptera) disappear rapidly following deposition in aerobic sediments (Hill, 1989). In the litter of a compost heap, a seasonal peak in the concentration of aphid remains in the late summer and autumn was followed by a rapid decline in the concentration of recognisable fragments over the winter months. In contrast, fragments of certain beetle elytra, and parts of the exokeletons of some bugs, are generally resistant to destruction even in very poor preservational conditions. Thus remains of the heather feeding species *Lochmaea suturalis* and *Strophingia ericae* were found in abundance at the ACP site, although heather itself was no longer abundant there.

Post-depositional corrosion acts differentially on taxa for all forms of environmental evidence; for pollen, for example, Andersen (1984) suggests that the pollen of *Calluna* and the Poaceae, and the spores of pteridophytes may be particularly resistant to decay, and therefore over-represented in deposits where erosional activity has taken place. In the case of insect remains, it seems likely that even a short period of decomposer activity following deposition of assemblages can lead to bias in the species structure of the assemblage relative to the living community.

In addition to the differential preservation of species, different body parts of the same taxon may be more or less resistant to post-depositional erosion. This also tends to alter the nature of the death assemblage, and can aggravate problems associated with the identification of species (for example, where different body parts from the same insect occur in such different numbers that they are not associated by the investigator as originating on the same insect). At Thornton, several hundred forewings of *Megamelodes notula* were isolated, but few heads, or other body parts of any Homopterans were noted. Had these been available, the identification of *Megamelodes* and other species could have been confirmed or strengthened. The effects of differential preservation may be aggravated by further bias introduced by water-sorting of deposits, or associated with extraction methods used to recover assemblages.

In contrast to the initial accumulation of assemblages, in which stochastic processes, and the patchy distribution of biological populations, may play a significant part, it seems likely that the post-depositional fate of insect remains may be more predictable. Although elements of chance are likely to have a role in determining whether conditions are suitable for preservation of any biological materials, where they are, the relative rates of decay of different types of fossil may be predictable, and this would be a suitable subject for further study.

6.4 Insect-plant relationships

The use of insect hostplant specificity to reconstruct tree species structure in woodlands appears to be successful, although, for the sites examined, the presence or absence of herbs could not be determined from the insect assemblages alone.

The number of insect species associated with particular plants varies. For any plant species, the size of the associated insect herbivore fauna depends on a number of factors, including the size and architectural complexity of the individual plant, and 'historical' factors, including the former extent of the plant species in native vegetation (thus the oaks, major component species of the postglacial primary forests over a large part of the British Isles, have many associated insects), and whether the plant is native, or has been introduced from elsewhere (Southwood, 1961).

Woodland herbs, historically covering a smaller total area than native trees, and offering a much smaller biomass and surface area to colonising insects today, will support fewer species, and fewer individuals of those species, than will trees. Lawton (1983) finds that the species richness of insect herbivores associated with a plant species declines in the series: trees > shrubs > perennial herbs > weeds and other annuals > monocotyledons (excluding grasses, due to unreliability of data). Trees support between 1.5 and 3 times the number of associated insect herbivore species than do woody shrubs, and these in turn carry 1.5-3 times the insect herbivores of perennial herbs (Lawton, 1986). It therefore appears unlikely that species feeding on woodland herbs will be reliably represented in insect death assemblages.

6.5 Future work

From this study it appears that significant evidence for the broad ecological conditions and even, to some extent, the tree species structure of woodlands, can be gained from the insect assemblages accumulating within modern woodlands. However, there appear to be limits to the resolution achievable in such studies, and there is great scope for further investigation of modern assemblages building up under woodland conditions (perhaps, for example, in coppice stands at different stages of regeneration), to define the degree of ecological information that can be obtained. Studies of assemblages in true primary forest might yield better comparanda for the assemblages formed in prehistory, but such forests are rare in Europe, and probably non-existent in Britain. Even where fragments of the European virgin forest remain, in Poland and other eastern European countries, ecological conditions may not directly reflect those of Britain's early forests (Marren, 1990).

Other areas of interest where research needs to be carried out are the influence of depositional regime on the accumulating assemblage (see above), which could have played a large part in determining differences in the representation of species in the Thornton and St George's Field assemblages, and the effects of post-depositional erosion and taphonomic processes on insect remains.

The two fossil sites studied in the Vale of York yielded interesting insect and plant assemblages, and the implication that woodland clearance does not appear to have occurred in the York area by the late Bronze Age contrasts strongly with the findings of other workers on the surrounding highlands (see, for example, Bush, 1988; Tinsley, 1975; Jones *et al.*, 1979). However, the wide temporal spacing of the two sites, and the relatively short period of deposition at each one, make it impossible to draw any general conclusions about the change in the nature and extent of woodland in the Vale of York from this work alone. It is hoped that future studies of many more sites, covering a wide range of periods will be possible. If possible, a single part of the Vale should be studied, for example, the environs of York, which is centrally placed and as far as possible from the surrounding uplands. York's surrounding countryside is atypical of the Vale as a whole in the historical period, as a result of the influence of the major urban centre on its hinterland, and this must be taken into account in such studies. Provided sites with preservation of biological remains are available, as many forms of environmental evidence as possible, including insect and plant macrofossils, pollen, and, where they are preserved, ostracods and mollusc remains, should be studied. There are indications that sites with the potential to yield interesting assemblages (including strong woodland components in both animal and plant remains) exist in the Vale of York, and recent excavations at Selby, and beside the River Derwent at North Duffield, have revealed promising deposits.

Definitions and abbreviations

EAU	Environmental Archaeology Unit, University of York
HKK	Mr. H. K. Kenward
MJH	The Author
MNI	Minimum Number of Individuals
N	Total number of individuals in an assemblage
RTU	Recognisable Taxonomic Unit
S	Total number of taxa in an assemblage
SQL	Structured Query Language
YAT	York Archaeological Trust

Ecological Codes (see also Chapter 2):

AQU	aquatic taxa
ARA	arable
EUR	eurytopic (inhabiting several or many habitat types)
HEA	heathland
LIT	litter-dwelling
MAR	marshland
PAS	pasture
SYN	synanthropic (in habitats created by man)
TRE	associated with trees
UNC	uncoded: species which could not be assigned to any of the other ecological groups
WOO	woodland

Woodland terms:

Primary woodland Woodland on a site that has never been entirely cleared of tree cover by man (see Peterken, 1977).

'Wildwood' or **'Urwald'** Britain's primary woodland as it existed before human influence became a significant factor in the landscape (before the elm decline of *c.* 5500-5000 BP), or woods that resemble this original woodland.

Ancient woodland Woodlands with a history of at least 400 (or, sometimes, 300; Rackham, 1980) years.

Secondary woodland Woodland on a site that, at some stage in its post-glacial history, been cleared of tree cover by humans. Secondary woodlands may, however, still be regarded as 'ancient'.

BIBLIOGRAPHY

Adams, D. H. (1971). Vegetation. pp.13-14 in Matthews, B. Soils in Yorkshire I. Sheet SE 65 (York East). *Soil Survey Record* **6**. Rothamsted Experimental Station, Harpenden.

Addyman, P. V. (1991). Lloyds Bank, Pavement. *The Archaeology of York* **8**(3), 180-237. Council for British Archaeology, London.

Allen, A. A. (1956). Maple confirmed as the host-tree of *Gastrallus immarginatus* Müll. (Col., Anobiidae) at Windsor. *Entomologist's Monthly Magazine* **92**, 42.

Allen, A. A. (1969). *Ernoporus caucasicus* Lind. and *Leperisinus orni* Fuchs (Col., Scolytidae) in Britain. *Entomologist's Monthly Magazine* **105**, 245-249.

Allen, S. E. (1974). *Chemical analysis of ecological materials.* Blackwell, Oxford.

Andersen, S. T. (1973). The differential pollen productivity of trees and its significance for the interpretation of a pollen diagram from a forested region. pp 109-116 in Birks, H. J. B., and West, R. G. (eds). Quaternary plant ecology. The 14th symposium of the British Ecological Society, March 1972. Blackwell, Oxford.

Andersen, S. T. (1984). Forests at Løvenholm, Djursland, Denmark, at present and in the past. *Det Kongelige Dansk Videnskabennes Selskab Biologiske Skrifter* **24**:1, 5-180, plates I-XXVI.

Angus, R. B. (1976). A re-evaluation of the taxonomy and distribution of some European species of *Hydrochus* Leach (Col.,Hydrophilidae). *Entomologist's Monthly Magazine* **112**, 177-201.

Angus, R. B. (1978). The British species of *Helophorus*. *Balfour-Browne Club Newsletter* **11**, 2-15.

Anon (1986). Rare and endangered water beetles in Europe. *Balfour-Browne Club Newsletter* **37**, 1-12.

Balfour-Browne, F. (1940-60). *British Water Beetles.* Vols I-III. Ray Society, London.

Bartley, D. D. (1962). The stratigraphy and pollen analysis of lake deposits near Tadcaster. *New Phytologist* **61**, 277-287.

Bayford, E. G. and Lawson Thompson, M. (1907). Coleoptera (Beetles). pp.219-244 in Page, W. (ed) *The Victoria County History; York.* Vol. **1**. Archibald Constable and Co., London.

Beckett, S. C. (1979). The palaeobotanical background to the Meare Lake Village sites. *Somerset Levels Papers* **5**, 18-25.

Beijerinck, W. (1940). *Calluna*: a monograph on scotch heather. *Verh. Akad. Wet. Amst.* (3rd Sect.) **38**, 1-180.

Benham, R. (1975). Swarming of *Helophorus brevipalpis* Bedel. (Coleoptera, Hydrophilidae) in N. Devon. *Entomologist's Monthly Magazine* **111**, 127-128.

Berge Henegouwen, A. L. van. (1988). *Hydrochus megaphallus*, a new and widespread water beetle described from the Netherlands (Coleoptera, Hydrophilidae). *Balfour-Browne Club Newsletter* **42**, 18-21.

Berger, W. H. and Parker, F.L. (1970) Diversity of planktonic foraminifera in deep sea sediments. *Science* **168**, 1345-7.

Best, H. (1641, reprinted 1857). Rural economy in Yorkshire in 1641. *Publications of the Surtees Society* **33**. Durham.

Birks, H. J. B., and Birks, H. H. (1980). Quaternary palaeoecology. Edward Arnold, London.

Boycott, A. E. (1934). The habitats of land Mollusca in Britain. *Journal of Ecology* **22**, 1-38.

Bradshaw, R. H. W., Coxon, P., Greig, J. R. A., and Hall, A. R. (1981). New fossil evidence for the past cultivation and processing of hemp *(Cannabis sativa* L.) in Eastern England. *New Phytologist* **89**, 503-510.

Buckland, P. C. (1975). Synanthropy and the death-watch: a discussion. *The Naturalist* **100**, 37-41.

Buckland, P. C. (1976). The environmental evidence from the Church Street Roman sewer system. *The Archaeology of York* **14**(1), 1-44. Council for British Archaeology, London.

Buckland, P. C. (1979). Thorne Moors: a palaeoecological study of a Bronze Age site. *University of Birmingham Department of Geography Occasional Publication* **8**.

Buckland, P. C., and Coope, G. R. (1991). *A bibliography and literature review of Quaternary entomology*. J. R. Collis, Sheffield.

Buckland, P. C. and Kenward, H. K. (1973). Thorne Moor: a palaeoecological study of a Bronze Age site. *Nature* **241**, 405-406.

Bullock, J. A. (1971a). The investigation of samples containing many species I. Sample description. *Biological Journal of the Linnaean Society* **3**, 1-21.

Bullock, J. A. (1971b). The investigation of samples containing many species II. Sample comparison. *Biological Journal of the Linnaean Society* **3**, 23-56.

Bullock, J. A. (1992). Host plants of British beetles: a list of recorded associations. *The Amateur Entomologist* **11a**. Amateur Entomologists' Society, Feltham, Middx.

Bullock, P. (1974). Soils in Yorkshire III; Sheets SE 64/74 (Escrick/Barmby Moor). *Soil Survey Record* **16**. Rothamsted Experimental Station, Harpenden.

Burgess, C. (1974). The Bronze Age. pp. 165-232 in Renfrew, C. (ed.) *British prehistory: a new outline*. Duckworth, London.

Bush, M. B. (1988). Early Mesolithic disturbance: a force on the landscape. *Journal of Archaeological Science* **15**, 453-462.

Carter, A. (1989). *Inventory of ancient woodland (provisional): Harrogate, Hambleton, Selby and York districts.* Nature Conservancy Council, Peterborough.

Chrystal, R. N. (1948). *Insects of the British woodlands.* Warne, London.

Clapham, A. R., Tutin, T. G., and Moore, D, M. (1987) *Flora of the British Isles* (Third Edn.). Cambridge University Press, Cambridge.

Claridge, M. F., and Wilson, M. R. (1982). Insect herbivore guilds and species-area relationships: leafminers on British trees. *Ecological Entomology* **7**, 19-30.

Clark, J. G. D. (1971). *Excavations at Starr Carr.* Cambridge University Press, Cambridge.

Clark, J. G. D., and Godwin, H. (1956). A Maglemosian site at Brandesburton, Holderness. *Proceedings of the Prehistoric Society* **22**, 6-22.

Coope, R. (1991). The study of the 'nearly-fossil'. *Antenna* **15**(4), 158-163.

Cooter, J. (1980). A note on *Ernoporus caucasicus* Lind. (Col., Scolytidae) in Britain. *Entomologist's Monthly Magazine* **116**, 112.

Cooter, J. (1991). Collecting equipment. pp 1-11 in Cooter, J. *et alii* (1991) *A Coleopterist's Handbook* (Third Edn.). Amateur Entomologists' Society, Feltham.

Cooter, J. *et alii* (1991). *A Coleopterist's Handbook* (Third Edn.). Amateur Entomologists' Society, Feltham.

Cotgreave, P., Hill, M. J., and Middleton, D. A. J. (in press). Patterns in body size and population abundance of bromeliad tank faunas. *Biological Journal of the Linnaean Society.*

Cowling, G. C. (1967). *The history of Easingwold and the Forest of Galtres.* Advertiser Press Ltd., Huddersfield.

Cowper Reed, F. R. (1901). *The geological history of the rivers of East Yorkshire.* C. J. Clay & Sons, London.

Crawley, M. J. (1987). What makes a community invasible? pp. 429-454 in Gray, A. J., Crawley, M. J., and Edwards, P. J. (eds) *Colonisation, succession and stability.* The 26th symposium of the British Ecological Society. Blackwell, Oxford.

Cromartie, W. J. (1975). The effect of stand size and vegetational background on the colonisation of cruciferous plants by herbivorous insects. *Journal of applied ecology* **12**, 517-533.

Crowson, R. A. (1981). *The biology of the Coleoptera.* Academic Press, London.

Darby, H. C., and Maxwell, I. S. (1962). *The Domesday geography of Northern England.* Cambridge University Press, Cambridge.

Date, C. J. (1986). *An introduction to database systems,* Volume **1** (Fourth Edn.). Addison Wesley, Reading, MA.

Day, K. R., Marshall, S., and Heaney, C. (1993). Associations between forest type and invertebrates: ground beetle community patterns in a natural oakwood and juxtaposed conifer plantations. *Forestry* **66**, 37-146.

Day, K. R., (1987). The species and community characteristics of ground beetles (Coleoptera: Carabidae) in some Northern Ireland nature reserves. *Proceedings of the Royal Irish Academy* **B 87**(4), 65-82.

Day, S. P. (1993). Woodland origin and 'ancient woodland indicators': a case-study from Sidlings Copse, Oxfordshire, UK. *The Holocene* **3**(1), 45-53.

Dempster, J. P. (1968). Intraspecific competition and dispersal as exemplified by a psyllid and its anthocorid predator. pp 8-17 in Southwood, T. R. E. (ed.) 'Insect abundance'. *Symposia of the Royal Entomological Society of London* **4**. Blackwell, Oxford.

Dinnin, M. H. (1991). The sub-fossil occurrence of the Great Silver Water Beetle *Hydrophilus piceus* (L.)(Col. Hydrophilidae) at Shirley Pool, S. Yorks. *The Naturalist* **116**, 55-59.

Dixon, A. F. G. (1973). Biology of Aphids. *Studies in Biology* **44**. Edward Arnold, London.

Dreisig, H. (1980). Daily activity, thermoregulation and water loss in the tiger beetle *Cicindela hybrida. Oecologia* (Berlin) **44**, 376-389.

Drift, J. van der. (1959). Field studies on the surface fauna of forests. *Bijdragen tot de dierkunde* **29**, 79-103.

Duffey, E. A. J. (1952). Coleoptera Cerambycidae. *Handbooks for the identification of British Insects* vol. V, part 12. Royal Entomological Society, London.

Duffey, E. A. J. (1968). The status of *Cerambyx* L. (Col., Cerambycidae) in Britain. *Entomologist's Gazette* **19**, 164-166.

Elgee, F. (1930). *Early man in North-East Yorkshire.* Private publication.

Elliot, J. M. (1967). Invertebrate drift in a Dartmoor stream. *Archiv für Hydrobiologie* **63**, 202-237 + Plate 1.

Ellis, S. (1990). Soils. pp 29-42 in Ellis. S., and Crowther, D. R. (eds.) *Humber perspectives: a region through the ages.* Hull University Press, Hull.

Elton, C. S. (1958). *The ecology of invasions by animals and plants.* Chapman and Hall, London.

Elton, C. S. (1966). *The pattern of animal communities.* Methuen, London.

Ely, W. A. (1986). Yorkshire Naturalist's Union excursions in 1985. Acaster Malbis, 1 June: Entomology. *The Naturalist* **111**, 101.

Evans, G. (1975). *The life of beetles.* George Allen & Unwin, London.

Evans, J. G. (1972). *Land snails in archaeology.* Seminar Press, London.

Evans, M. E. G. (1969). The surface activity of beetles in a Northern English wood. *Transactions of the Society for British Entomology* **18**, 247-262.

Evans. M. E. G. (1990). Habits or habitats: do carabid locomotor adaptations reflect habitats or lifestyles? pp.295-306 in Stork, N. E. (ed.) *The role of ground beetles in ecological and environmental studies.* Intercept, Andover.

Faegri, K., and Iversen, J. (1964). *Textbook of pollen analysis* (Second Edn.). Blackwell, Oxford.

Faull, M. L. (1983). Roman and Anglo-Saxon settlement patterns in Yorkshire: a computer-generated analysis. *Landscape History* **5**, 21-40.

Fife, M., and Walls, P. J. (1973). *The River Foss from Yearsley village to York: its history and natural history.* William Sessions, York.

Finney, D. J. (1974). Problems, data and inference. *Journal of the Royal Statistical Society. Series A.* **137**, 1-24.

Fisher, R. A., Corbet, A. S., and Williams, C. B. (1943). The relationship between the number of species and the number of individuals in a random sample of an animal population. *Journal of animal ecology* **12**, 42-58.

Fishpool, M. (1992). *Investigation of the responses of land snails and carabid beetles to vegetation boundaries, with reference to the interpretation of subfossil assemblages.* Unpublished PhD. thesis, University of Wales (College of Cardiff).

Fitter, A. H. and Smith, C. J. (eds.)(1979). *A wood in Ascam: a study in wetland conservation.* Sessions/Yorkshire Naturalists' Trust, York.

Fix, F., and Hodges, J. L. (1951). *Discriminatory analysis; non-parametric discrimination; small sample performance.* US School of Aviation Medicine, Project no. 21-49-004, Report no. **11**. Randolf Field, Texas.

Forsythe, T. G. (1987). Common ground beetles. *Naturalists' Handbook* **8**, Richmond Publishing, Slough.

Foster, G. N. (1986). Nationally notable species in Britain. *Balfour-Browne Club Newsletter* **37**, 19.

Foster, G. N. (1992). Water beetle statuses. Appendix 1 (pp. 17-18) in Hyman, P. S. A review of the scarce and threatened Coleoptera of Great Britain, Part 1. *U.K. Nature Conservation* **3**. J.N.C.C., Peterborough.

Fowler, Rev. W. W. (1887-91). *The Coleoptera of the British Islands.* Vols. **I-VI**. L. Reeve and Co., London.

Franks, J. W. (1960). Interglacial deposits at Trafalgar Square, London. *New Phytologist* **59**, 145-152 + plate 6.

Freude, H., Harde, K. W., and Lohse, G. A. (1965-1983). *Die Käfer Mitteleuropas* **1-11**. Goecke and Evers, Krefeld.

Friday, L. E. (1988). A key to the adults of British Water Beetles. *Field Studies* **7**, 1-51/*Field Studies Council AIDGAP publication* **189**, Field Studies Council, Preston Montford.

Fryer, G. (1991). *A natural history of the lakes, tarns and streams of the English Lake District.* Freshwater Biological Association, Ambleside.

Furness, R. R., and King, S. J. (1978). Soils in North Yorkshire IV, Sheet SE 63/73 (Selby). *Soil Survey Record* **56**. Rothamsted Experimental Station, Harpenden.

Garland, S. P. (1983). Beetles as primary woodland indicators. *Sorby Record* **21**, 3-38.

Gaunt, G. D., Jarvis, R. A., and Matthews, B. (1971). The Late Weichselian sequence in the Vale of York. *Proceedings of the Yorkshire Geological Society* **38**, 281-284.

Gaunt, G. D, and Tooley, M. J. (1974). Evidence for Flandrian sea-level changes in the Humber estuary and adjacent areas. *Bulletin of the Geological Survey of Great Britain* **48**, 25-41.

Gibbons, B. (1993). The Wyre Forest NNR, Hereford and Worcester. *British Wildlife* 4(4), 246-248.

Gilbertson, D. D. (1984). Early Neolithic utilisation and management of alder carr at Skipsea Whithow Mere, Holderness. *Yorkshire Archaeological Journal* **56**, 17-22.

Gillespie, R. (1984). *Radiocarbon User's Handbook.* Oxford University Committee for Archaeology Monograph **3**.

Girling, M. A. (1980). The fossil insect assemblage from the Baker site. *Somerset Levels Papers* **6**, 36-42.

Girling, M. A. (1982). Fossil insect faunas from forest sites. pp 129-146 in Bell, M. and Limbrey, S. (eds.) 'Archaeological aspects of woodland ecology'. *British Archaeological Reports International Series* **146**.

Girling, M. A. (1984). Investigations of a second insect assemblage from the Sweet Track. *Somerset Levels Papers* **10**, 79-91.

Girling, M. A. (1985). An old forest beetle fauna from a Neolithic and Bronze Age peat deposit at Stileway. *Somerset Levels Papers* **11**, 80-83.

Girling, M. A. (1991). Mesolithic and later assemblages interpreted from the insect assemblages of West Heath Spa, Hampstead. pp 80-89 in Collins, D., and Lorimer, D. (eds.) 'Excavations at the Mesolithic site on West Heath, Hampstead, 1976-1981'. *British Archaeological Reports British Series* **217** (1991 for 1989).

Girling, M. A., and Greig, J. R. A. (1977). Paleoecological investigations of a site at Hampstead Heath, London. *Nature* **268**, 45-47.

Godwin, Sir H. (1975). *History of the British Flora: a factual basis for phytogeography* (Second Edn.). Cambridge University Press, Cambridge.

Greenslade, P. J. M. (1964). Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of animal ecology* **33**, 301-310.

Greenslade, P. J. M. (1968). Habitat and altitude distribution of Carabidae (Coleoptera) in Argyll, Scotland. *Transactions of the Royal Entomological Society of London* **120**, 39-54.

Greenslade, P. J. M., and Southwood, T. R. E. (1962). The relationship of flight and habitat in some Carabidae (Coleoptera). *The Entomologist* **95**, 86-88.

Grensted, L. W. (1939). Colonization of new areas by water beetles. *Entomologist's Monthly Magazine* **75**, 174-175.

Hall, A. R. (1982). Seeing the wood for the trees. *Interim* **8**(3), 21-25.

Hall, A. R., Gosden, S. M., Greig, J. R. A., and Fitter, A. H. (1979). The history of Askham Bog. pp. 8-21 in Fitter, A. H. and Smith, C. J. (eds) *A wood in Ascam: a study in wetland conservation.* Sessions/Yorkshire Naturalist's Trust, York.

Hall, A. R. and Kenward, H. K. (1980). An interpretation of biological remains from Highgate, Beverley. *Journal of archaeological science* **7**, 33-51.

Hall, A. R. and Kenward, H. K. (1990). Environmental evidence from the Colonia: General Accident and Rougier Street. *The Archaeology of York* **14**(6), pp.289-434, plates II-IX, fiche 3-11. Council for British Archaeology, London.

Hall, A. R., Kenward, H. K., and Robertson, A. (1993a). Medieval and post-medieval plant and invertebrate remains from Area X, The Bedern (south-west), York. *Ancient Monuments Laboratory Report* 56/93.

Hall, A. R., Kenward, H. K., and Robertson, A. (1993b). Medieval and post-medieval plant and invertebrate remains from Area IV, The Bedern (north-east), York. *Ancient Monuments Laboratory Report* 57/93.

Hall, A. R., Kenward, H. K., and Robertson, A. (1993c). Medieval and post-medieval plant and invertebrate remains from Area II, The Bedern (north-east), York. *Ancient Monuments Laboratory Report* 58/93.

Hall, A. R., Kenward, H. K., and Williams, D. (1980). Environmental evidence from Roman deposits in Skeldergate. *The Archaeology of York* **14**(3), pp.101-156. Council for British Archaeology, London.

Hall, A. R., Kenward, H. K., Williams, D, and Greig, J. R. A. (1983). Environment and living conditions at two Anglo-Scandinavian sites. *The Archaeology of York* **14**(4), pp.157-240, plate I, fiche 1. Council for British Archaeology, London.

Hall, R. (1984). *The Viking dig*. Bodley Head, London.

Hammond, P. M. (1974). Changes in the British coleopterous fauna. pp 323-369 in Hawksworth, D. L.(ed). 'The changing flora and fauna of Britain'. Proceedings of a symposium held at the University of Leicester, April 1973. *Systematics Association Special Volume* **6**. Academic Press, London.

Hansen, V. (1951). Biller XV; Rovbiller 1. *Danmarks fauna* **57**, Dansk Naturhistorisk Forening.

Hansen, M. (1987). The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* **18**. E. J. Brill/Scandinavian Science Press, Leiden.

Hanski, I. (1980). The community of coprophagous beetles (Coleoptera, Scarabaeidae and Hydrophilidae) in northern Europe. *Annales Entomologica Fennica* **46**(3), 57-73.

Hanski, I, and Cambefort, Y. (1991). Spatial Processes. pp 283-304 in Hanski, I.,and Cambefort, Y. (eds.) *Dung beetle ecology*. Princeton University Press, Princeton.

Hanski, I., and Koskela, H. (1977). A re-examination of a debate on methods of ecological classification in Finland in the 1940s. *Annales Entomologica Fennici* **43**, 7-20.

Harding, P. T. (1978). *A bibliography of the occurrence of certain woodland Coleoptera in Britain, with special reference to timber-utilising species associated with old trees in pasture.* (CST Report no. 161). Nature Conservancy Council, Banbury.

Harding, P. T., and Plant, R. A. (1978). A second record of *Cerambyx cerdo* L. (Coleoptera: Cerambycidae) from sub-fossil remains in Britain. *Entomologist's Gazette* **29**, 150-152.

Harding, P. T., and Rose, F. (1986). Pasture-woodlands in lowland Britain: a review of their importance for wildlife conservation. Institute of Terrestrial Ecology, Abbots Ripton.

Harris, A. (1961). *The rural landscape of the East Riding of Yorkshire 1700-1850. A study in historical geography.* Oxford University Press, Oxford.

Harrison, B. (1984). The Vale of York: assarting and the open fields in the 12th and 13th centuries. pp. 10-12 in *The Archaeology and landscape history of the Vale of York.* Preliminary summaries of papers to be delivered at a conference at the University of York, February 1984.

Hayfield, C., and Greig, J. (eds.)(1989). Excavation and salvage work on a moated site at Cowick, South Humberside, 1976. *Yorkshire Archaeological Journal* **61**, 41-70.

Hedges, R. E. M. (1983). The accelerator technique for C14 measurement: its implications for radiocarbon dating. pp. 42-50 in Ottaway, B. S. (ed.) 'Archaelogy, Dendrochronology and the Radiocarbon Calibration Curve'. *University of Edinburgh Department of Archaeology Occasional Paper* **9.**

Hedges, R. E. M., Law, I. A., Bronk, C. R., and Housley, R. A. (1989). The Oxford accelerator mass spectrometry facility: technical developments in routine dating. *Archaeometry* **31**(2), 99-114.

Henderson, P. A. (1990). Freshwater Ostracods. Synopses of the British fauna (new series) **42.** Published for the Linnaean Society of London, & Estuarine and Coastal Sciences Association by Universal Book Services/W. Backhuys, Oegstgeest.

Hickin, N. E. (1971). *The natural history of an English forest.* Hutchinson, London.

Hickin, N. E. (1975). *The insect factor in wood decay* (Third Edn.). Associated Business Programmes, London.

Hill, M. J. (1989). *A study of the death assemblage of a decomposer ecosystem.* Unpublished B.Sc. project, Department of Biology, University of York.

Hodkinson, I. D., and White, I. M. (1979). Homoptera Psylloidea. *Handbooks for the identification of British Insects* vol. **II**, part 5(a). Royal Entomological Society, London.

Hoffman, A. (1958). Coléoptères Curculionides **3.** *Faune de France* **62.** Librairie de la Faculté des Sciences, Paris.

Hyman, P. S. (1992). A review of the scarce and threatened Coleoptera of Great Britain, Part 1. *U.K. Nature Conservation* **3.** J.N.C.C., Peterborough.

Jessop, L. (1986). Dung beetles and chafers (Coleoptera: Scarabaeoidea). *Handbooks for the identification of British Insects* **5**(11). Royal Entomological Society, London.

Jones, R. A. (1977). *Mononychus punctumalbum* (Herbst) (Col., Curculionidae) in Wiltshire. *Entomologist's Monthly Magazine* **113**, 246.

Jones, R. L., Cundill, P. R., and Simmons, I. G. (1979). Archaeology and palaeobotany on the North York Moors and their environs. *Yorkshire Archaeological Journal* **51**, 15-22.

Jones, R. L., and Gaunt, G. D. (1976). A dated late Devensian organic deposit at Cawood, near Selby. *The Naturalist* **101**, 121-123.

Joy, N. H. (1932, Reprinted 1976). *A Practical Handbook of British Beetles.* Vols **I** & **II.** E. W. Classey, Faringdon.

Kelly, M and Osborne, P. J. (1964). Two faunas and floras from the alluvium at Shustoke, Warwickshire. *Proceedings of the Linnaean Society of London* **176**, 37-65.

Kempton, R. A. (1979). Structure of species abundance and measurement of diversity. *Biometrics* **35**, 307-322.

Kennedy, C. E. J., and Southwood, T. R. E. (1984). The number of species of insects associated with British trees: a reanalysis. *Journal of Animal Ecology* **53**, 455-478.

Kent, D. H. (1992). *List of the vascular plants of the British Isles.* Botanical Society of the British Isles, London.

Kent, Sir P. (1980). *British Regional Geology: Eastern England, from the Tees to the Wash* (Second Edn.). Institute of Geological Sciences/NERC. HMSO, London.

Kenward, H. K. (1976). Reconstructing ancient ecological conditions from insect remains: some problems and an experimental approach. *Ecological Entomology* **1**, 7-17.

Kenward, H. K. (1978). The analysis of archaeological insect assemblages: a new approach. *The Archaeology of York* **19**(1), pp. 1-68, plates I-IV. Council for British Archaeology, London.

Kenward, H. K. (1982). Insect communities and death assemblages, past and present. pp.71-78 in Hall, A. R., and Kenward, H. K. (eds), 'Environmental Archaeology in the urban context'. *Council for British Archaeology Research Report* **43.**

Kenward, H. K. (1985). Outdoors - Indoors? The outdoor component of archaeological insect assemblages. pp. 97-104, + 2 figures, in Fieller, N. R. J., Gilbertson, D. D., and Ralph, N. G. A. (eds) 'Paleobiological investigations: research design, methods and data analysis'. Symposia of the Association for Environmental Archaeology **5B.** *British Archaeological Reports International Series* **266.**

Kenward, H. K., and Allison, E. P. (in press). Rural origins of the urban insect fauna. in Hall, A. R., and Kenward, H. K. (eds). 'Urban-rural connections: perspectives from environmental archaeology'. *Symposia of the Association for Environmental Archaeology.*

Kenward, H. K., and Hall, A. R. (in prep.). Biological evidence from Anglo-Scandinavian deposits at 16-22 Coppergate. *The Archaeology of York* **14**(7).

Kenward, H. K., Hall, A. R., and Jones, A. K. G. (1980). A tested set of techniques for the extraction of plant and animal macrofossils from waterlogged archaeological deposits. *Science and Archaeology* **22**, 3-15.

Kenward, H. K., Hall, A. R., and Jones, A. K. G. (1986). Environmental evidence from a Roman well and Anglian pits in the legionary fortress. *The Archaeology of York* **14**(5), pp.241-288, fiche 2. Council for British Archaeology, London.

Kenward, H. K. and Williams, D. (1979). Biological evidence from the Roman warehouses at Coney Street. *The Archaeology of York* **14**(2), pp. 45-100. Council for British Archaeology, London.

Kenward, H. K., Williams, D., Spencer, P. J., Greig, J. R. A., Rackham, D. J., and Brinklow, D. A. (1978). The environment of Anglo-Scandinavian York. pp 58-73 in Hall, R. A. (ed.) 'Viking age York and the North'. *Council for British Archaeology Research Report* **27**.

Kerney, M. P. (1976). *Atlas of the non-marine mollusca of the British Isles.* Conchological Society of Great Britain and Ireland/Natural Environment Research Council, Abbots Ripton.

Key, R. S. (1986). Review of invertebrate sites in England: Humberside. Invertebrate site Register. *CSD Report* **634**, parts **1** & **2**. Nature Conservancy Council, Peterborough.

Kirk, M. (1959) Physiogeography. pp. 13-32 in Willmot, G. F., Biggins, J. M., and Tillott, P. M. (eds.) *York: a survey, 1959.* British Association for the Advancement of Science, York.

Kloet, G. S., and Hincks, W. D. (1964). A check list of British insects (Second Edn., revised). Part 1: small orders and Hemiptera. *Handbooks for the identification of British Insects* vol. **XI**(1). Royal Entomological Society, London.

Kloet, G. S., and Hincks, W. D. (1972). A check list of British insects (Second Edn., revised). Part 2: Lepidoptera. *Handbooks for the identification of British Insects* vol. **XI**(2). Royal Entomological Society, London.

Kloet, G. S., and Hincks, W. D. (1977). A check list of British insects (Second Edn., revised). Part 3: Coleoptera and Strepsiptera. *Handbooks for the identification of British Insects* vol. **XI**(3). Royal Entomological Society, London.

Knowles, G. C. (1990). The Humber and its people during the medieval period. pp 357-372 in Ellis. S., and Crowther, D. R. (eds.) *Humber perspectives: a region through the ages.* Hull University Press, Hull.

Koskela, H and Hanski, I. (1977). Structure and succession in a beetle community inhabiting cow dung. *Annales Zoologici Fennici* **14**, 204-223.

Lachenbruch, P. A. (1975). *Discriminant analysis.* Hafner, New York.

Lachenbruch, P. A., and Goldstein, M. (1979). Discriminant analysis. *Biometrics* **35**, 69-86.

Lamb, H. H. (1982). Reconstruction of the course of postglacial climate over the world. pp. 11-32 in Harding, A. F. (ed.) *Climatic change in later prehistory.* Edinburgh University Press, Edinburgh.

Lans, R. F. van der. (1988). *Introduction to SQL.* Addison Wesley, Reading, MA.

Lawton, J. H. (1983). Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* **28**, 23-39.

Lawton, J. H. (1986). Surface availability and insect community structure - the effects of architecture and fractal dimension of plants. pp. 317-331 in Juniper, B., and Southwood, Sir T. R. E. (eds.) *Insects and the plant surface.* Edward Arnold, London.

Lekander, B., Bejer-Petersen, B., Kangas, E., and Bakke, A. (1977). The distribution of bark beetles in the Nordic countries. *Acta Entomologica Fennica* **32**, 1-37 + 78 maps.

Le Quesne, W. J. (1960). Hemiptera (Fulgomorpha). *Handbooks for the identification of British Insects* vol. **II**, part 3. Royal Entomological Society, London.

Le Quesne, W. J. (1965). Hemiptera (Cicadomorpha). *Handbooks for the identification of British Insects* vol. **II**, part 2(a). Royal Entomological Society, London.

Le Quesne, W. J. and Payne, K. R. (1981). Cicadellidae (Typhlocybinae) with a checklist of the British Auchenorhyncha (Hemiptera, Homoptera). *Handbooks for the identification of British Insects* vol. **II**, part 2(c). Royal Entomological Society, London.

Lindroth, C. H. (1949). Die Fennoskandischen Carabidae. *Göteborgs Kungliga Vetenskaps och Vitterhets Samhälle Handl.* (Ser. B) **3**, Allgemeiner Teil.

Lindroth, C. H. (1976). Coleoptera, Carabidae. *Handbooks for the identification of British insects* 5(2). Royal Entomological Society, London.

Lindroth, C. H. (1986). The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* **15**, Parts 1 & 2. E. J. Brill/Scandinavian Science Press. Leiden.

Lindroth, C. H. (ed.)(1992). Ground beetles (Carabidae) of Fennoscandia: A zoogeographic study. Vols I-III. Intercept, Andover.

Longworth, I. H. (1965). *Regional archaeologies; Yorkshire.* Cory, Adams and Mackay, London.

Luff, M. L. (1965). A list of Coleoptera occurring in grass tussocks. *Entomologist's Monthly Magazine* **101**, 240-245.

Macan, T. T. (1977). A key to the British fresh- and brackish-water gastropods. *Freshwater Biological Association Scientific Publication* **13**. (Fourth Edn.). Freshwater Biological Association, Ambleside.

MacArthur, R. H. (1960). On the relative abundance of species. *American Naturalist* **94**, 25-36.

Maelfait, J-P., and Desender, K. (1990). Possibilities of short-term carabid sampling for site assessment studies pp. 217-226 in Stork, N. E. (ed.) *The role of ground beetles in ecological and environmental studies.* Intercept, Andover.

Magurran, A. E. (1988). *Ecological diversity and its measurement.* Chapman and Hall, London.

Majerus, M. and Kearns, P. (1989). Ladybirds. *Naturalists' Handbook* **10**, Richmond Publishing, Slough.

Manby, T. (1984). Hunting, gathering and farming in the Vale of York: changing exploitation of resources. pp. 5-6 in *The archaeology and landscape history of the Vale of York.* Preliminary summaries of papers to be delivered at a conference at the University of York, February 1984.

Marren, P. (1990). Woodland heritage. *Britain's ancient woodland.* David & Charles, Newton Abbot.

Matthews, B. (1970). Age and origin of aeolian sand in the Vale of York. *Nature* **227**, 1234-1236.

Matthews, B. (1971). Soils in Yorkshire I. Sheet SE 65 (York East). *Soil Survey Record* **6**. Rothamsted Experimental Station, Harpenden.

May, R. M. (1975). Patterns of species abundance and diversity. pp. 81-120 in Cody, M. L., and Diamond, J. M. (eds.) *Ecology and evolution of communities.* Harvard University Press, Cambridge, MA.

McKenna, W. J. B. (1991). The plant, molluscan, insect and parasite remains. pp 209-215 in Armstrong, P., Tomlinson, D., and Evans, D. H. (eds.) *Excavations at Lurk Lane, Beverley, 1979-82.* Sheffield Excavation Reports **1**.

Mendel, H. (1988). *Provisional atlas of the click beetles* (Coleoptera: Elateroidea) *of the British Isles.* Biological Records Centre, Institute of Terrestrial Ecology, Monks Wood.

Millett, M., and McGrail, S. (1987). The archaeology of the Hasholme logboat. *Archaeological Journal* **144**, 69-155.

Mohr, K. H. (1966). Chrysomelidae. pp. 95-280 in Freude, H., Harde, K. W., and Lohse, G. A. *Die Käfer Mitteleuropas* **9**. Goecke and Evers, Krefeld.

Morris, M. G. (1991). Weevils. *Naturalists' Handbook* **16**. Richmond Publishing, Slough.

Morris, M. G. (1990). Orthocerous weevils. Coleoptera: Curculionoidea (Nemonychidae, Anthribidae, Urodontidae, Attelabidae, and Apionidae). *Handbooks for the identification of British Insects* vol. **5**(16). Royal Entomological Society, London.

Neale, J. W. (1983). The ostracods and uniformitarianism I. The later record: recent, Pleistocene and Tertiary (Presidential Address 1981). *Proceedings of the Yorkshire Geological Society* **44**, 305-326 + figures 1-7.

Norris, A., Bartley, D. D., and Gaunt, G. D. (1971). An account of the deposit of shell marl at Burton Salmon, West Yorkshire. *The Naturalist* **96**, 57-63.

Norušis, M. J./SPSS Inc. (1990). *SPSS advanced statistics user's guide.* SPSS Inc., Chicago.

O'Connor, T. P. (1986a). Preliminary report on a mollusc assemblage from St George's Field, York. *Ancient Monuments Laboratory Report* **1/86.**

O'Connor, T. P. (1986b). Bones from archaeological deposits in York: an overview of results to 1986. *Ancient Monuments Laboratory Report* **47/86.**

O'Connor, T. P., Hall, A. R., Jones, A. K. G., and Kenward, H. K. (1984). Ten years of environmental archaeology at York. pp. 166-172 *in* Addyman, P. V., and Black, V. E. (eds.) *Archaeological papers from York presented to M. W. Barley.* York Archaeological Trust, York.

Osborne, P. J. (1969). An insect fauna of late Bronze Age date from Wilsford, Wiltshire. *Journal of Animal Ecology* **38**, 555-566.

Osborne, P. J. (1971). An insect fauna from the Roman site at Alcester, Warwickshire. *Britannia* **2**, 156-165.

Osborne, P. J. (1972). Insect faunas of Late Devensian and Flandrian age from Church Stretton, Shropshire. *Philosophical Transactions of the Royal Society* **B 263**, 327-367.

Osborne, P. J. (1974). An insect assemblage of Early Flandrian age from Lea Marston, Warwickshire, and its bearing on the contemporary climate and ecology. *Quaternary Research* **4**, 471-486.

Osborne, P. J. (1982). Some British later prehistoric insect faunas and their climatic implications. pp. 68-74 in Harding, A. F. (ed.) *Climatic change in later prehistory.* Edinburgh University Press, Edinburgh.

Osborne, P. J. (1988). A late Bronze Age date insect fauna from the River Avon, Warwickshire, England: Its implications for the terrestrial and fluvial environment and for climate. *Journal of Archaeological Science* **15**, 715-727.

Osborne, P. J. (1989). Insects. pp. 96-99 in Ashbee, P., Bell, M., and Proudfoot, E. (eds.) 'Wilsford Shaft: excavations 1960-2'. *English Heritage Archaeological Report* **11.** Historic Buildings and Monuments Commission for England, London.

Owen, J. A. (1992). Catching beetles with a simple flight-interception trap. *Coleopterist* **1**, 22-26.

Owen, J. A. (1993). Use of a flight-interception trap in studying the beetle fauna of a Surrey wood over a three year period. *The Entomologist* **112**, 141-160.

Palm, T. (1959). Die Holz- und Rinden-Käfer der Süd- und Mittelschwedischen Laubbäume. *Opuscula Entomologica Supplementum* **XVI.**

Paul, C. R. C. (1975). The ecology of mollusca in ancient woodland. 1: The fauna of Hayley Wood, Cambridgeshire. *Journal of Conchology* **28**, 301-327.

Paul, C. R. C. (1978). The ecology of mollusca in ancient woodland. 3: Frequency of occurrence in West Cambridgeshire woods. *Journal of Conchology* **29**, 295-300.

Pearce, E. J. (1957). Coleoptera (Pselaphidae). *Handbooks for the identification of British insects* Vol **IV** (9). Royal Entomological Society, London.

Pearson, G. W., and Stuiver, M. (1993). High-precision bidecadal calibration of the radiocarbon time scale 500-2500 BC. *Radiocarbon* **35**, 25-33.

Pearson, R. G. (1962). The Coleoptera from a late-glacial deposit at St Bees, West Cumberland. *Journal of Animal Ecology* **31**, 129-150.

Peel, R. F., and Palmer, J. (1955). The physiography of the Vale of York. *Geography* **40**, 215-227.

Penney, M. M. (1966). Studies on certain aspects of the ecology of *Nebria brevicollis* (F.)(Coleoptera, Carabidae). *Journal of animal ecology* **35**, 505-512.

Pennington, W. (1970). Vegetation history in the north-west of England: a regional synthesis. pp. 41-80 in Walker, D., and West, R. G. (eds.). *Studies in the vegetational history of the British Isles*. Cambridge University Press, Cambridge.

Peterken, G. F. (1974). A method for assessing woodland flora for conservation using indicator species. *Biological Conservation* **6**, 239-245.

Peterken, G. F. (1981). *Woodland conservation and management*. Chapman & Hall, London.

Phillips, W. M. (1992). Assemblages of weevils (Curculionoidea) in the lower tree canopy of a mixed temperate woodland. *The Entomologist*, **111**, 61-78.

Philp, E. G. (1991). Vascular plants and the beetles associated with them. pp.183-194 in Cooter, J. *et alii* (1991) *A Coleopterist's Handbook* (Third Edn.). Amateur Entomologists' Society, Feltham.

Pope, R. D. (1953). Coccinellidae and Sphindidae. *Handbooks for the identification of British insects* **5**(7). Royal Entomological Society, London.

Purdy, J. D. (1976). pp. 5-11 in Allison, K. J. (ed.) *Victoria History of the Counties of England. Yorkshire, East Riding*, Vol **III**. Institute of Historical Research, University of London. Oxford University Press, Oxford.

Rackham, O. (1972). Grundle House: on the quantities of timber in certain East Anglian buildings in relation to local supplies. *Vernacular Architecture* **3**, 3-8.

Rackham, O. (1980). *Ancient woodland*. Edward Arnold, London.

Radley, J., and Simms, C. (1967). Wind erosion in East Yorkshire. *Nature* **216**, 20-22.

Ramm, H. (1978). *The Parisi.* Duckworth, London.

Reid, C., and Reid, E. M. (1907) On the pre-glacial flora of Britain. *Journal of the Linnaean Society (London)* **38**, 206-227, + 5 plates.

Robinson, M. (1981). The Iron Age to Early Saxon environment of the Upper Thames terraces. pp.251-286 in Jones, M. and Dimbleby, G. (eds.) 'The environment of man: the Iron Age to the Anglo-Saxon period'. *British Archaeological Reports British Series* **87.**

Robinson, M. (1983). Arable/Pastoral ratios from insects? pp.19-55 in Jones, M. (ed.) 'Integrating the subsistence economy'. *British Archaeological Reports International Series* **181.**

Robinson, M. (1991). The Neolithic and Late Bronze Age insect assemblages. Chapter 17 (pp. 277-327) in Needham, S. (ed.) *Excavation and salvage at Runnymede Bridge, 1978: The Late Bronze Age waterfront site.* British Museum Press, London.

Robinson, M. (1992). The Coleoptera from Flag Fen. *Antiquity* **66**, 467-469.

Rodwell, J. S.(ed.)(1991). *British plant communities* **I**: Woodlands and scrub. Cambridge University Press, Cambridge.

Rushton, S. P., and Luff, M. L. (1988). The use of multivariate ordination techniques to assess the effects of chlorpyrifos on ground beetle and spider communities in grassland. *British Crop Protection Council Monograph* **40**, pp. 175-181. BCPC, Farnham.

Salo, J., Kalliola, R., Häkkinen, I., Mäkkinen, Y., Niemalä, P., Puhakka, M., and Coley, P. D. (1986). River dynamics and the diversity of Amazon lowland forest. *Nature* **322**, 254-258.

Samways, M. J. (1984). A practical comparison of diversity indices based on a series of small agricultural ant communities. *Phytophylactica* **16**, 275-278.

SAS (1989). SAS/STAT User's Guide, Version 6 (Fourth Edn.). Volumes **1** and **2.** SAS Institute Inc., Cary, N. C.

Scherf, H. (1964). Die Entwicklungstadien der mitteleuropäischen Curculioniden (Morphologie, Bionomie, Ökologie). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **506**, Frankfurt.

Shirt, D. B. (ed.) (1987). *British Red Data Books*: **2** Insects. Nature Conservancy Council, Peterborough.

Shirt, D. B. (1991). Scarabaeoidea. pp. 97-102 in Cooter, J. *et alii* (1991). *A Coleopterist's Handbook* (Third Edn.). Amateur Entomologists' Society, Feltham.

Shotton, F. W., and Osborne, P. J. (1965). The fauna of the Hoxnian interglacial deposits at Nechells, Birmingham. *Philosophical Transactions of the Royal Society* B, **248**, 353-378.

Simmons, I. G., Atherden, M., Cundill, J. B., Innes, J. B., and Jones, R. L. (1982). Prehistoric Environments. pp. 33-99 in Spratt, D. A. (ed.) 'Prehistoric and Roman Archaeology of North-East Yorkshire'. *British Archaeological Reports British Series* **104**.

Simpson, E. H. (1949). Measurement of diversity. *Nature*, **163**, 688.

Sims, R. W. and Gerard, B. M. (1985). Earthworms. *Synopses of the British Fauna (New Series)* **31**. Linnaean Society of London/Estuarine and Brackish-Water Sciences Association.

Skidmore, P. (1991). Insects of the British cow-dung community. *AIDGAP Occasional publication* **21**, Field Studies Council, Preston Montford.

Skinner, B. (1984). *Colour identification guide to the moths of the British Isles (Macrolepidoptera).* Penguin, Harmondsworth.

Smith, A. H. (1956). English place-name elements II. *English Place-Name Society* Vol. **XXVI**. Cambridge University Press, Cambridge.

Smith, A. J. E. (1978). *The moss flora of Britain and Ireland.* Cambridge University Press, Cambridge.

South, R. (1961). *The moths of the British Isles*, series **1** & **2**. New Edition, 1961. Wayside and Woodland Series, F. Warne, London.

Southwood, T. R. E. (1961). The number of species of insect associated with various trees. *Journal of Animal Ecology* **30**, 1-8.

Southwood, T. R. E. (1962). Migration of terrestrial arthropods in relation to habitat. *Biological reviews of the Cambridge Philosophical Society* **37**, 171-214.

Southwood, T. R. E. (1978). *Ecological methods* (Second Edn.). Chapman and Hall, London.

Southwood, T. R. E., and Leston, D. (1959). *Land and water bugs of the British Isles.* F. Warne, London.

Southwood, T. R. E., Moran, V. C., Kennedy, C. E. J. (1982). The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology* **51**, 635-649.

Sparks, B. W. (1961). The ecological interpretation of Quaternary non-marine mollusca. *Proceedings of the Linnaean Society of London* **172**, 71-80.

Spratt, D. A. (ed) (1982). Prehistoric and Roman archaeology of North-East Yorkshire.

British Archaeological Reports British Series **104.**

SPSS (1990). *SPSS reference guide.* SPSS Inc., Chicago.

Stace, C. (1991). *New flora of the British Isles.* Cambridge University Press, Cambridge.

Stead, I. M. (1961). A distinctive form of La Tène barrow in Eastern Yorkshire and on the continent. *Antiquaries Journal* **41,** 44-62.

Stead, I. M. (1979). *The Arras Culture.* Yorkshire Philosophical Society, York.

Stork, N. E. (1987). The guild structure of arthropods from Bornean rainforest trees. *Ecological Entomology* **12,** 69-80.

Stork, N. E. (ed.)(1990). *The role of ground beetles in ecological and environmental studies.* Intercept, Andover.

Stuiver, M., and Pearson, G. W. (1993). High-precision bidecadal calibration of the radiocarbon time scale AD 1950-500 BC and 2500-6000 BC. *Radiocarbon* **35,** 1-23.

Sutton, S. L., and Beaumont, H. E. (eds.) (1989). *Butterflies and moths of Yorkshire: distribution and conservation.* Yorkshire Naturalist's Union, Doncaster.

Taylor, L. R. (1963). Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology* **32,** 99-117.

Taylor, L. R. (1978). Bates, Williams, Hutchinson - a variety of diversities. pp. 1-18 in Mound, L. A., and Waloff, N. (eds.) 'Diversity of insect faunas'. *Symposia of the Royal Entomological Society of London* **9.** Blackwell, Oxford.

Taylor, L. R., Kempton, R. A., and Woiwod, I. P. (1976). Diversity statistics and the log series model. *Journal of Animal Ecology* **45,** 255-271.

Tinbergen, L. (1960). The natural control of insects in pinewoods. 1: Factors influencing the intensity of predation by songbirds. *Archives Néerlandaises de Zoologie* **13,** 266-336.

Tinsley, H. (1975). Cultural influences on Pennine vegetation with particular reference to North Yorkshire. *Transactions of the Institute of British Geographers* (New Series) **1,** 310-322.

Thiele, H-U. (1977). Carabid beetles in their environments. Zoophysiology and Ecology vol. **10.** Springer-Verlag, Berlin.

Tomlinson, P. (1993 for 1992). Design and implementation of a relational database for archaeobotanical records from Great Britain and Ireland. *Circaea* **10**(1), 1-30.

Turner, J. (1965). A contribution to the history of forest clearance. *Proceedings of the Royal Society, London* B **161,** 343-353.

Turner, J. (1970). Post-neolithic disturbance of British vegetation. pp. 97-116 in Walker, D., and West, R. G. *Studies in the vegetational history of the British Isles.* Cambridge University Press, Cambridge.

Verdcourt, B.(1983). A hazard for water beetles. *Entomologist's Monthly Magazine* **119,** 110.

Watkins, C. (1990). *Woodland management and conservation.* David & Charles, Newton Abbot.

Webb, N. (1986). *Heathlands.* New Naturalist, Collins, London.

Whittaker, R. H. (1970). *Communities and ecosystems.* Macmillan, New York.

Whyman, M. (in press). By-pass operation. *Interim* **18**(3).

Wightman, W. R. (1964). *Some aspects of the historical geography of the Vale of Pickering area 1086-1350 AD.* Unpublished Ph.D Thesis, University of Durham.

Wightman, W. R. (1968). The pattern of vegetation in the Vale of Pickering area c. 1300 AD. *Transactions of the Institute of British Geographers* **45,** 125-142.

Williams, C. B. (1947) The logarithmic series and its application to biological problems. *Journal of Ecology* **34,** 253-271.

Willmot, G. F. (1959). Prehistory. pp. 85-94 in Willmot, G. F., Biggins, J. M., and Tillott, P. M. (eds.) *York: a survey, 1959.* British Association for the Advancement of Science, York.

Wilson, W. A. (1958). Coleoptera of Somerset. *Somersetshire Archaeology and Natural History Society. Supplement to Proceedings* Vols. **101** and **102.**

Appendices

Appendix 1: Species lists of beetles and bugs from modern Yorkshire woodland sites

	Ecological code			ACP					DRW					SW2					SW3		
Hemiptera		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Heteroptera																					
Acanthosoma haemorrhoidale	tre	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elasmostethus interstinctus	woo	1	-	1	-	-	1	-	-	1	1	-	-	-	-	-	-	1	-	-	1
Elasmucha grisea	woo	-	-	-	-	-	-	1	1	-	-	-	1	-	-	1	-	-	-	-	-
Pentatoma rufipes	tre	-	-	1	-	1	1	2	1	2	2	-	-	-	-	-	-	-	-	-	1
Pentatoma rufipes (nymph)	tre	-	-	-	-	-	-	2	-	1	1	-	-	-	-	-	-	-	-	-	-
Pachybrachius fracticollis	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Stygnocoris pedestris	hea	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Stygnocoris sp.	unc	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-
Drymus brunneus	woo	2	1	-	1	2	3	5	5	-	3	4	4	1	3	6	1	1	-	-	-
Scolopostethus decoratus	hea	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scolopostethus sp.	unc	1	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Lygaeidae sp.	unc	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lygaeidae sp. (nymph)	unc	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acalypta parvula	eur	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-
Derephysia foliacea	tre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Tingis cardui	mar, pas	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Empicoris vagabundus	tre	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nabis or *Dolichonabis* sp.	unc	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dolichonabis limbatus	mar, pas	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Temnostethus sp.	unc	-	3	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Temnostethus or *Anthocoris* sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Anthocoris nemoralis	tre	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Anthocoris nemoralis or *nemorum*	unc	-	-	-	-	-	-	-	-	-	-	10	3	1	1	-	-	-	-	-	-
Anthocoris sp.	unc	1	-	-	1	-	1	1	-	1	-	-	1	-	-	-	-	-	1	-	-
Acompocoris pygmaeus	woo	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-

Acompocoris sp.	unc	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cimicidae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Loricula elegantula	tre	-	-	-	-	-	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-
Loricula pselaphiformis	tre	2	-	-	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myrmedobia tenella	woo	-	-	-	-	-	1	-	-	-	3	-	1	-	1	2	-	-	-	-	-
Myrmedobia sp.	woo	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Deraeocoris lutescens	tre	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Deraeocoris ruber	mar, pas, tre	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
Harpocera thoracica	woo	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Psallus sp.	tre	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-
Psallus sp.1	tre	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psallus sp.2	tre	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyllecoris histrionicus	woo	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Mecomma ambulans	mar, woo	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Mecomma sp.	mar, woo	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
Lygus sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Miridae sp.	unc	1	1	1	1	-	-	-	1	-	-	-	1	1	1	-	-	-	-	1	-
Miridae sp.2	unc	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Miridae (nymph)	unc	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-
Corixa sp.	aqu	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Hesperocorixa sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	1	1
Sigara sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Corixidae sp.	aqu	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Heteroptera sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Homoptera																					
Cercopis vulnerata	woo	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Aphrophora alni	tre	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	1
Neophilaenus sp.	unc	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Neophilaenus or *Philaenus* sp.	unc	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
Oncopsis flavicollis	woo	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Oncopsis tristis	woo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	1
Oncopsis sp.	tre	-	-	-	-	-	3	4	2	1	-	-	1	-	2	-	-	-	-	-	-

Macropsis or *Oncopsis* sp.	unc	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Ulopa reticulata	hea	1	2	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Idiocerus sp.	tre	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Aphrodes trifasciatus	hea	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aphrodes sp.	unc	-	-	-	-	-	1	-	1	-	2	-	-	-	-	1	1	-	-	-	1
Aphrodes sp.1	unc	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Aphrodes sp.2	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Cicadomorpha sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-
Fulgoromorpha sp.	unc	-	-	1	1	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-
Cixius sp.	unc	1	-	-	-	-	1	2	1	-	1	-	1	-	-	-	-	-	-	1	-
Conomelus anceps	mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	5	1	1	-	1
Ditropis pteridis	woo	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
Delphacodes venosus	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Delphacodes sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	1	-	3	-	-	-	-	-
Megamelodes sp.	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Strophingia ericae (adult)	hea	-	48	6	-	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Strophingia ericae (nymph)	hea	13	20	13	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aphalara polygoni	mar, pas	-	1	1	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psylla ambigua	mar, tre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
Psylla brunneipennis or *pulchra*	mar, tre	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Psylla hartigi	woo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Psylla mali	tre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Psylla melanoneura	tre	49	69	48	89	51	2	-	-	1	5	-	-	1	-	-	-	-	-	-	-
Psylla pyricola	tre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Psylla sp.	unc	-	-	-	-	-	-	-	1	-	-	2	1	-	1	1	-	-	-	1	-
Trioza abdominalis or *munda*	pas, woo	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trioza remota	woo	1	-	1	1	1	1	-	1	-	2	-	-	-	-	-	-	-	-	-	-
Trioza urticae	pas, woo	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Aphidoidea sp.	unc	9	-	15	9	1	6	9	9	1	-	8	6	-	1	2	1	-	-	1	-
Homoptera sp.1	unc	-	-	-	-	-	1	-	-	-	-	1	1	-	-	-	-	1	-	-	-
Homoptera sp.2	unc	-	-	-	-	-	1	-	-	-	-	2	-	1	-	-	-	-	-	-	-
Homoptera sp.3	unc	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-

Homoptera sp.	unc	-	-	-	1	-	-	-	1	1	-	-	-	-	1	-	-	-	-	-	-
Hemiptera sp.	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Hemiptera sp. (nymph)	unc	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coleoptera																					
Leistus rufescens	mar, woo	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Notiophilus biguttatus	lit, woo	-	1	-	-	-	-	1	1	-	1	-	-	-	-	-	1	-	-	-	-
Loricera pilicornis	mar, woo	1	-	-	-	-	-	-	-	-	1	3	1	-	-	1	-	-	-	-	-
Clivina fossor	eur	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Trechus obtusus	eur	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Trechus obtusus or *quadristriatus*	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Bembidion properans	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Bembidion quadrimaculatum	ara, mar	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-
Bembidion articulatum	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Bembidion biguttatum	mar, woo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Bembidion guttula	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Bembidion guttula or *unicolor*	mar	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-
Bembidion unicolor	woo	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-
Bembidion sp.	unc	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-
Pterostichus diligens	mar, woo	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-
Pterostichus melanarius	ara, pas	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Pterostichus nigrita	mar	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Pterostichus strenuus	woo	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-
Pterostichus sp.	unc	-	-	-	1	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-
Calathus melanocephalus	ara, hea, pas	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Agonum fulignosum	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Amara sp.	unc	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-
Bradycellus harpalinus	hea	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Bradycellus ruficollis	hea	3	5	1	2	2	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Bradycellus verbasci	hea, woo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Demetrias atricapillus	mar, pas	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-
Dromius melanocephalus	pas	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-

Dromius quadrimaculatus	woo	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-
Dromius quadrinotatus	woo	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Carabidae sp.	unc	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-
Hydroporus sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1
Hydroporus sp.1	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Hydroporus sp.2	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Hydroporinae sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Agabus bipustulatus	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-
Agabus sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Ilybius sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Dytiscidae sp.	aqu	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Dytiscidae sp.1	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Dytiscidae sp.2	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Helophorus brevipalpis	aqu	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	6	-
Helophorus aequalis or *grandis*	aqu	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-
Helophorus longitarsis,griseus or *minutus*	aqu	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-
Helophorus sp.	unc	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	11	6	1	-	19
Sphaeridium lunatum/scarabaeoides	pas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Cercyon convexiusculus	lit, mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Cercyon melanocephalus	lit, pas	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Cercyon quisquilius	lit, pas	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Cercyon sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Cercyon sp. (terrestrial)	unc	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
Megasternum obscurum	lit	-	-	-	-	-	-	-	-	-	-	2	-	1	1	-	-	-	-	-	-
Sphaeridiinae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Anacaena globulus	aqu	-	-	-	-	-	1	-	1	1	4	-	-	-	-	-	1	-	-	1	1
Anacaena sp.	aqu	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-
Laccobius sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1
Enochrus sp.	aqu	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Chaetarthria seminulum	mar	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Hydrophilinae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Ochthebius minimus	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1
Ochthebius sp.	aqu	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-
Ochthebius or *Hydraena* sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
Hydraena nigrita	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Hydraena testacea	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	2
Hydraena sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
Limnebius sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-
Ptenidium sp.	eur	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Acrotrichis sp.	eur	2	1	2	2	-	3	-	2	9	3	5	6	11	-	-	1	-	-	1	-
Acrotrichis sp.1	eur	-	-	-	-	-	-	-	-	-	-	-	-	-	18	7	-	-	-	-	-
Acrotrichis sp.2	eur	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
Anisotoma humeralis	lit	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Ptomaphagus medius or *subvillosus*	lit	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Nargus velox	lit	-	2	-	1	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-
Nargus wilkini	lit	-	-	-	-	-	-	-	-	-	-	-	1	-	2	2	-	-	-	-	-
Nargus sp.	lit	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-
Choleva spadicea	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Choleva sp.	lit	1	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-
Catops or *Sciodrepoides* sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Catops nigricans	lit	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Catops nigricans or *fulignosus*	lit	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Catops nigrita	lit	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Catops tristis	lit	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Catops sp.	unc	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Colon sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Aclypea opaca	lit	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Silpha atrata	woo	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-

Neuraphes sp.	lit	-	-	-	-	-	1	1	-	2	-	-	-	2	1	-	-	-	-	-	-
Stenichnus sp.	lit	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
Staphylinidae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	1	-	9	-	-	-	-	-
Micropeplus fulvus	lit	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Micropeplus porcatus	lit	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Metopsia retusa	lit	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Megarthrus affinis	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Megarthrus depressus	lit	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-
Megarthrus sinuaticollis	lit	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Megarthrus sp.	lit	-	-	-	1	-	-	1	1	-	-	-	4	-	1	2	-	-	-	1	-
Megarthrus sp.1	lit	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Megarthrus sp.2	lit	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Proteinus atomarius or *macropterus*	lit	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Proteinus brachypterus	lit	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	1	-
Proteinus macropterus	lit	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Proteinus ovalis	lit	-	-	-	-	-	-	-	-	-	-	2	2	-	-	1	1	-	-	-	-
Proteinus sp.	lit	1	-	-	-	-	-	-	1	-	1	-	-	2	-	-	-	-	-	-	-
Proteinus sp.2	lit	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Megarthrus or *Proteinus* sp.	unc	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Anthobium atrocephalum	lit	1	-	-	-	-	2	1	-	-	-	1	1	-	1	-	-	-	-	-	-
Anthobium unicolor	lit	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Anthobium sp.	unc	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Olophrum piceum	hea	2	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Olophrum piceum or *fuscum*	hea, mar, pas	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Acidota cruentata	lit	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Lesteva heeri	lit, mar	1	2	1	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lesteva longoelytrata	lit, mar	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	1	1
Acrolocha sulcula	pas	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Omalium caesum	lit	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Omalium italicum	lit	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Omalium rivulare	lit	-	-	-	-	-	-	-	-	-	1	-	-	1	-	1	-	-	-	-	-

Omalium sp.	lit	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-
Xylodromus concinnus	lit	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Omaliinae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Coprophilus striatulus	lit	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Syntomium aeneum	woo	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-
Carpelimus bilineatus	eur	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Carpelimus corticinus	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Aploderus caelatus	lit	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Platystethus arenarius	pas, lit	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-	-
Platystethus cornutus gp. (*P. cornutus* or *degener*)	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
Platystethus nitens	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Anotylus complanatus	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Anotylus inustus	pas, lit	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Anotylus nitidulus	lit	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-
Anotylus rugosus	lit	-	-	-	1	-	2	3	1	-	-	4	3	1	-	-	-	-	-	1	1
Anotylus sculpturatus gp. (*A. mutator* or *sculpturatus*)	lit	-	-	-	-	-	-	1	1	1	1	3	1	-	-	2	-	1	1	-	-
Anotylus tetracarinatus	lit	1	-	-	1	2	2	16	-	2	1	56	12	1	1	3	-	1	1	1	2
Oxytelus laqueatus	lit	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Oxytelus sculptus	lit	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-
Stenus impressus	woo	1	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-
Stenus juno	mar	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Stenus sp.	unc	-	1	-	1	-	-	-	-	-	-	-	1	-	-	1	-	-	-	1	-
Stenus sp.1	unc	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Stenus sp.2	unc	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Stenus sp.3	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Stenus sp.4	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Euaesthetus sp.	mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Lathrobium brunnipes	lit, mar	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Lathrobium brunnipes, *fulvipenne*, or *geminum*	lit, mar	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Lathrobium fovulum or *brunnipes*	lit, mar	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-

Lathrobium geminum	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Lathrobium sp.	unc	1	1	-	-	1	1	2	1	-	1	-	-	-	-	1	-	-	-	-	1
Lathrobium sp.2	unc	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Rugilus sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Othius myrmecophilus	lit	4	2	3	5	1	10	14	8	7	6	30	23	7	4	11	-	-	-	1	-
Othius punctulatus	woo	-	-	2	-	-	1	1	-	-	-	-	2	1	-	1	-	-	-	-	-
Atrechus affinis	lit	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xantholinus linearis or *gallicus*	lit	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Xantholinus linearis	lit	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xantholinus linearis gp. (*X. gallicus, linearis* or *longiventris*)	lit	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-
Xantholinus or *Gyrohypnus* sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Philonthus cognatus	eur	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Philonthus decorus	woo	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-	-
Philonthus jurgans or *micans*	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Philonthus politus	lit	-	-	-	-	-	1	1	1	-	-	-	1	-	-	-	-	-	-	-	-
Philonthus rotundicollis	eur	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
Philonthus splendens	lit	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Philonthus varius	woo	-	-	-	-	-	-	3	-	-	1	-	-	-	-	-	-	-	-	-	-
Philonthus sp.	unc	-	-	-	-	-	1	-	1	-	-	-	-	-	-	1	-	1	1	-	1
Philonthus sp.1	unc	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-
Philonthus sp.2	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Philonthus sp.3	unc	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Philonthus sp.4	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Philonthus sp.5	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Philonthus or *Quedius* sp.	unc	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quedius lateralis	lit	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quedius sp.	lit	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Staphylininae sp.	unc	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Staphylinidae sp.1	unc	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Staphylinidae sp.2	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Habrocerus capillaricornis	lit	-	-	-	-	-	-	-	-	-	-	1	1	2	3	3	-	-	-	-	-

Mycetoporus sp.	lit	1	2	1	1	-	1	-	1	-	-	4	-	1	-	-	-	-	-	1	-
Lordithon thoracicus	woo	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Bobitobius or *Lordithon* sp.	woo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Sepedophilus littoreus	woo	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Sepedophilus sp.	unc	1	-	-	-	-	-	1	-	1	1	-	-	1	-	-	-	-	-	-	-
Tachyporus chrysomelinus	eur	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
Tachyporus hypnorum	eur	-	1	-	1	-	2	2	3	2	3	15	9	1	4	7	2	2	-	-	2
Tachyporus nitidulus	eur	-	-	-	-	-	-	-	-	-	-	-	1	-	3	-	-	-	-	-	-
Tachyporus obtusus	eur	-	-	-	1	1	1	-	-	-	3	13	2	-	-	3	-	-	-	-	-
Tachyporus solutus	eur	1	-	-	-	-	-	2	-	2	-	-	-	4	1	-	-	-	-	-	-
Tachinus bipustulatus	tre	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Tachinus humeralis	lit	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tachinus laticollis or *marginellus*	lit	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tachinus marginellus	lit	-	-	-	-	-	-	-	-	-	-	5	1	1	-	-	1	-	-	-	-
Tachinus signatus	lit	-	-	-	-	-	1	-	-	1	-	-	-	2	1	-	-	-	-	-	-
Tachinus subterraneus	lit	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tachinus sp.	unc	-	-	-	-	-	-	1	-	-	-	2	-	-	1	-	-	-	-	-	-
Myllaena sp.	mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Leptusa ruficollis	woo	1	-	1	-	2	-	4	2	-	1	-	-	-	1	-	-	-	-	-	-
Autalia impressa	lit	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Falagria or *Cordalia* sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Calodera sp.	mar	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Calodera or *Chiloporata* sp.	mar	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Deubelia picina	mar	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Oxypoda sp.	lit	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Oxypoda sp.1	lit	-	-	-	-	-	-	-	1	-	-	6	-	-	-	-	-	-	-	-	-
Oxypoda sp.2	lit	-	-	-	-	-	-	-	-	-	-	16	-	-	-	-	-	-	-	-	-
Oxypoda sp.3	lit	-	-	-	-	1	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-
Oxypoda sp.4	lit	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Aleochara sp.1	lit	-	-	1	1	-	2	7	1	3	1	18	7	3	3	4	-	-	1	-	-
Aleochara sp.2	lit	-	-	-	-	-	-	-	-	-	-	1	-	-	1	2	-	-	-	-	-
Aleocharinae sp.1	unc	-	-	-	-	-	1	-	-	1	1	25	13	12	17	3	1	-	2	-	-

Aleocharinae sp.2	unc	-	-	-	-	-	-	-	-	-	-	22	1	-	1	-	1	-	-	2	-
Aleocharinae sp.3	unc	-	-	-	-	-	-	-	-	-	1	-	9	-	-	1	-	-	-	1	1
Aleocharinae sp.4	unc	1	-	-	-	-	3	-	-	-	-	-	4	-	-	6	-	-	-	2	1
Aleocharinae sp.5	unc	-	-	-	-	-	1	1	2	-	2	3	3	2	-	7	-	-	-	-	1
Aleocharinae sp.6	unc	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	1	-
Aleocharinae sp.7	unc	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-
Aleocharinae sp.8	unc	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-
Aleocharinae sp.9	unc	-	-	-	-	-	1	1	-	-	3	3	4	4	1	1	-	-	-	1	-
Aleocharinae sp.10	unc	-	-	-	-	-	-	-	-	-	-	-	6	2	-	-	-	-	-	-	-
Aleocharinae sp.11	unc	-	-	-	-	-	-	1	-	-	-	-	2	-	-	1	-	-	-	-	-
Aleocharinae sp.12	unc	1	-	-	-	-	-	-	-	1	-	-	1	3	1	2	-	-	-	-	-
Aleocharinae sp.13	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-
Aleocharinae sp.14	unc	1	-	-	-	-	-	1	-	-	-	-	-	6	2	1	-	-	-	-	-
Aleocharinae sp.15	unc	-	1	-	-	-	2	-	2	-	-	-	5	-	1	1	-	-	-	-	-
Aleocharinae sp.16	unc	-	-	1	1	-	-	-	1	-	-	5	3	2	2	1	-	-	-	-	-
Aleocharinae sp.17	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-
Aleocharinae sp.19	unc	-	-	-	-	-	-	-	-	-	-	16	4	19	13	-	-	-	-	-	-
Aleocharinae sp.20	unc	-	-	1	-	-	1	-	1	-	-	19	-	2	-	-	-	-	-	-	-
Aleocharinae sp.21	unc	-	-	-	-	-	-	-	-	-	-	5	-	1	-	-	-	-	-	-	-
Aleocharinae sp.22	unc	-	-	-	-	-	-	1	1	-	-	10	1	-	-	-	-	-	-	-	-
Aleocharinae sp.23	unc	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
Aleocharinae sp.24	unc	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	-
Aleocharinae sp.25	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-
Aleocharinae sp.26	unc	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Aleocharinae sp.27	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Aleocharinae sp.28	unc	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Aleocharinae sp.29	unc	-	-	-	-	-	-	-	1	-	-	-	-	2	-	-	-	-	-	-	-
Aleocharinae sp.30	unc	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-
Aleocharinae sp.31	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-
Aleocharinae sp.32	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Aleocharinae sp.34	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Aleocharinae sp.35	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-

Bryaxis puncticollis	lit	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-
Bryaxis sp.	lit	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1	-	-	-	-	-
Pselaphidae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Geotrupes sp.	pas	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Aphodius contaminatus	pas	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Aphodius equestris	woo	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Aphodius sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-
Serica brunnea	pas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Microcara testacea	mar, woo	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Cyphon padi	mar	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Cyphon sp.	unc	-	-	-	-	-	-	-	-	-	1	2	3	-	-	1	1	1	-	1	-
Simplocaria semistriata	eur	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Cytilus sericeus	hea	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oulimnius sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Athous haemorrhoidalis	tre	-	-	-	-	-	1	1	-	-	-	5	3	1	-	-	-	-	-	-	1
Athous sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
Agriotes acuminatus	pas	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-	-	-	-	-
Agriotes obscurus	pas	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Agriotes pallidulus	pas	-	-	-	-	-	-	-	-	-	-	5	-	-	1	2	-	1	-	-	-
Agriotes sp.	pas	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Dalopius marginatus	woo	-	-	-	1	3	1	2	3	1	3	4	4	-	1	1	1	-	1	-	-
Denticollis linearis	woo	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Elateridae sp.	unc	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Trixagus dermestoides	woo	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	-
Cantharis cryptica	tre	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-

Rhagonycha femoralis or *testacea*	eur	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Rhagonycha fulva	eur	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Rhagonycha lignosa	tre	-	1	-	-	-	2	-	1	-	-	-	-	-	-	-	1	-	-	-	-
Rhagonycha lutea	eur	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Malthinus balteatus or *serripunctatus*	tre	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Malthinus sp.	tre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Malthinus or *Malthodes* sp.	tre	-	2	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Malthodes marginatus or *minimus*	tre	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
Malthodes sp.	tre	1	-	-	1	4	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cantharidae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Grynobius planus	woo	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Anobium punctatum	syn, woo	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Anobiidae sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Brachypterus glaber	eur	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-
Brachypterus urticae	eur	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Meligethes aeneus	ara, pas	2	-	-	-	1	1	5	1	-	3	-	4	1	2	-	-	-	-	-	-
Meligethes sp.	unc	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1	1	-	-	-	-
Meligethes sp.1	unc	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-
Meligethes sp.2	unc	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-	-	-	-	-	-
Epuraea melanocephala	eur	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Epuraea sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Glischrochilus hortensis	woo, lit	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Monotoma sp.	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Rhizophagus bipustulatus	woo	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhizophagus dispar	woo	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cryptophagus sp.	unc	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Atomaria impressa	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Atomaria nitidula	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-

Atomaria sp.	unc	1	1	2	2	1	2	-	3	-	-	-	-	49	-	-	2	-	1	-	-
Atomaria sp.1	unc	-	-	-	-	-	-	2	-	1	1	79	25	-	15	7	-	-	-	1	-
Atomaria sp.2	unc	-	-	-	-	-	-	3	-	-	-	5	1	-	1	-	-	-	-	1	-
Atomaria sp.3	unc	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-
Phalacrus caricis or *corruscus*	ara, mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Stilbus testaceus	pas	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Stilbus sp.	unc	-	-	-	-	-	-	-	-	-	-	3	-	1	-	-	-	-	-	-	-
Phalacridae sp.	unc	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Adalia bipunctata	eur	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Adalia decempunctata	tre	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Aphidecta obliterata	woo	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coccinella septempunctata	eur	-	-	-	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-
Coccinella undecimpunctata	eur	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Propylea quattuordecimpunctata	eur	-	1	-	-	-	-	-	-	-	2	1	-	1	-	-	-	-	-	-	-
Halyzia sedecimguttata	woo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Stephostethus lardarius	lit	1	-	-	1	1	2	1	1	1	1	34	13	11	2	3	1	-	1	-	-
Aridius bifasciatus	lit	1	3	2	2	1	1	-	-	-	-	5	1	1	-	2	-	-	-	-	-
Aridius nodifer	lit	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	1	-	-	-	1
Lathridius pseudominutus	lit, syn	-	-	-	-	-	-	-	-	-	1	-	-	-	2	2	-	-	-	-	-
Enicmus transversus or histrio	lit	-	1	1	-	-	3	2	3	1	2	18	5	18	1	2	-	-	-	2	1
Enicmus sp.	lit	2	-	-	1	-	-	-	-	-	-	15	-	3	-	1	-	-	-	-	-
Enicmus sp.1	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
Enicmus sp.2	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
Corticaria elongata	eur	-	-	-	-	-	-	-	-	-	-	2	9	-	2	-	-	-	-	-	-
Corticaria sp.	unc	-	-	-	-	-	-	-	-	-	-	-	4	1	1	1	-	-	1	1	-
Corticarina fuscula	lit	-	-	-	-	2	-	4	-	4	4	-	-	-	-	-	-	-	-	1	-
Corticarina sp.	lit	-	-	-	3	-	-	-	-	-	-	2	-	5	1	2	-	-	-	-	1
Cortinicara gibbosa	lit	-	2	-	-	-	1	-	4	-	3	5	7	1	1	1	-	-	-	-	1
Corticarina or *Cortinicara* sp.	lit	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Octotemnus glabriculus	tre	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Cis sp.	tre	-	-	-	-	-	1	1	-	-	-	1	1	-	-	-	-	-	-	-	-
Cisidae sp.	tre	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mycetophagidae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Salpingus castaneus	tre	1	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhinosimus planirostris	tre	-	-	-	-	-	1	1	-	-	2	-	-	-	-	-	1	-	-	-	-
Anaspis maculata	tre	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Anaspis rufilabris	tre	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Anaspis sp.	tre	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-
Lema cyanella	pas, woo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Oulema melanopa	eur	-	1	-	-	-	-	-	-	1	1	1	2	1	-	-	-	-	-	-	-
Oulema sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Cryptocephalus labiatus	eur	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Cryptocephalus pusillus	eur	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-
Gastrophysa sp.	mar, pas	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Galerucella sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
Lochmaea caprea	mar, tre	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Lochmaea suturalis	hea	2	5	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Luperus longicornis	woo	1	-	-	-	-	3	3	1	1	2	-	-	-	-	-	-	-	-	-	-
Phyllotreta nemorum	ara	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-
Phyllotreta undulata	ara	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-
Phyllotreta undulata or nemorum	ara	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Longitarsus sp.	unc	-	5	-	-	-	1	-	1	-	-	1	-	-	-	-	-	-	-	1	-
Chaetocnema arida, confusa or *hortensis*	unc	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chaetocnema concinna	ara, pas	-	-	-	-	-	-	1	1	-	-	1	3	-	-	1	-	-	-	-	-
Chaetocnema sp.	unc	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Psylliodes affinis	ara	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Chaetocnema or *Psylliodes* sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-

Halticinae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Cassida vibex	mar, pas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Deporaus betulae	woo	-	-	-	-	-	-	2	-	1	2	-	-	-	-	-	-	1	-	-	-
Rhynchites nanus	tre	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Apion sp.	unc	-	-	-	-	-	-	3	1	-	3	-	2	-	-	1	-	1	-	-	-
Apion sp.1	unc	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Apion sp.2	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Apion sp.3	unc	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-
Apion sp.4	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Apion sp.5	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Apion (Thymapion) sp.	mar,pas	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Apion (Eutrichapion) ervi	pas	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Apion (Eutrichapion) viciae	pas	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Apion (Eutrichapion) virens	ara, pas	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apion (Eutrichapion) sp.	unc	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Apion subulatum	pas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Apion (Protapion) sp.	ara, pas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Otiorhynchus singularis	woo	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-
Phyllobius argentatus	woo	-	-	-	1	1	2	4	3	1	2	19	6	2	1	1	-	2	3	1	3
Phyllobius calcaratus	tre, woo	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-
Phyllobius calcaratus or *pomaceus*	woo	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-
Phyllobius pyri	woo	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	1	-	-	-	-
Phyllobius viridiaeris	mar, pas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Phyllobius sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
Polydrusus cervinus	woo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Polydrusus sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	1
Phyllobius or *Polydrusus* sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	1
Barypeithes araneiformis	tre	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Barypeithes pellucidus	tre	-	-	-	-	-	-	-	-	-	-	7	12	3	2	3	1	-	1	-	-
Strophosomus melanogrammus	woo	-	-	-	1	1	-	1	-	-	-	6	4	2	1	2	-	-	-	-	-

Strophosomus sus	hea	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Barynotus obscurus	eur	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Sitona hispidulus	pas	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Sitona lepidus	ara, pas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sitona lineatus	eur	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Sitona puncticollis	ara	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Sitona striatellus or *lineellus*	ara, pas	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Sitona sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Leiosoma deflexum	mar, pas, woo	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Anoplus plantaris	tre	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Cossoninae sp.	tre	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Acalles ptinoides	hea	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acalles sp.	woo	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-
Dorytomus sp.	mar, woo	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Notaris acridulus	mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Notaris sp.	mar	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Grypus equiseti	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Coeliodes dryados	woo	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-
Coeliodes rubicundis	woo	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coeliodes sp.	woo	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Coeliodes or *Cidnorhinus* sp.	unc	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Zacladus sp.	mar, pas	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Micrelus ericae	hea	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cidnorhinus quadrimaculatus	pas	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Ceuthorhynchidius sp.	mar, pas	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-
Ceutorhynchus assimilis	ara	-	-	-	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Ceutorhynchus contractus	ara	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	1	1	-	-	-
Ceutorhynchus floralis	ara	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Ceutorhynchus melanostictus	mar	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Ceutorhynchus quadridens	ara	-	-	-	-	-	1	-	-	-	-	5	-	-	-	-	-	1	-	-	-
Ceutorhynchus quadridens/picitarsis	ara	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Ceutorhynchus sp.	unc	-	-	-	-	-	-	-	1	-	-	1	1	1	-	1	-	-	-	-	-

Rhinoncus sp.	unc	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Phytobius quadrinodosus	mar, pas	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Phytobius quadrituberculatus or *waltoni*	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Phytobius sp.	unc	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-
Anthonomus rubi	eur	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-
Curculio pyrrhoceras	woo	-	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	-
Rhynchaenus fagi	woo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Rhynchaenus sp.	woo	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Ramphus pulicarius	woo	1	-	-	-	-	3	2	5	3	2	-	-	-	-	1	-	-	1	-	-
Curculionidae sp.	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-
Pityopthorus pubescens	woo	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dryocoetes villosus	woo	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Trypodendron domesticum	woo	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Scolytidae sp.	tre	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-

Appendix 2: Species lists of beetles and bugs from Thornton and St. George's Field

		Thornton							St. George's Field								
		1	2	3	4	5	6	7	101	104	106	201	202	303	305	306	401
Hemiptera																	
Heteroptera																	
Elasmostethus interstinctus	woo	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-
Elasmucha grisea	woo	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Eysarcoris fabricii	woo	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Pentatoma rufipes	tre	-	-	-	-	-	-	-	2	2	2	2	9	1	1	-	-
Pentatoma rufipes (nymph)	tre	-	-	-	-	-	-	-	-	2	1	-	-	-	-	1	-
Pentatomidae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Drymus brunneus	woo	-	-	-	-	-	-	-	2	2	-	1	-	-	1	1	1
Drymus sp.	unc	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-
Scolopostethus sp.	unc	-	-	-	1	-	-	-	-	-	1	1	1	1	-	-	1
Acalypta parvula	eur	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Dictynota sp.	pas, hea	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Derephysia foliacea	tre	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Nabidae sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Temnostethus sp.	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Anthocoris nemoralis or *nemorum*	unc	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-
Anthocoris nemorum	eur	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
Anthocoris sp.	unc	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-
Acompocoris sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Loricula pselaphiformis	tre	-	-	-	-	-	-	-	-	1	-	1	2	-	-	-	-
Psallus sp.	tre	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Miridae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Saldula saltatoria	mar	1	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-
Saldula sp.	unc	-	-	-	-	-	-	-	1	1	1	-	2	1	-	-	-
Saldula sp. (nymph)	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
Chartoscirta cincta	aqu	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-

Hebrus or *Microvelia* sp.	unc	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Hesperocorixa sp.	aqu	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-
Sigara sp.	aqu	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Corixidae sp.	aqu	1	1	-	-	-	1	2	-	-	1	-	-	-	-	-	1
Heteroptera sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Homoptera																	
Aphrophora alni	tre	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Philaenus spumaris	eur	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Neophilaenus or *Philaenus* sp.	unc	-	-	-	-	-	-	-	3	3	-	1	1	2	1	-	-
Megopthalmus sp.	unc	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Ledra aurita	woo	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Oncopsis alni	mar, tre	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Oncopsis sp.	tre	-	-	-	-	-	-	-	1	2	-	-	1	-	-	-	-
Macropsis sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-
Macropsis or *Oncopsis* sp.	unc	-	-	-	-	-	-	-	-	1	1	1	1	-	2	-	-
Agallia sp.	unc	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-
Aphrodes bifasciatus	pas, mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Aphrodes trifasciatus	hea	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	2
Aphrodes sp.	unc	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Jassargus pseudocellaris	pas, mar	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Paralimnius phragmitis	mar	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-
Macrosteles sp.	unc	-	1	3	2	1	4	3	-	-	-	-	-	-	-	-	-
Cicadomorpha sp.	unc	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Fulgoromorpha sp.	unc	1	-	1	-	1	-	-	-	1	-	-	-	-	-	-	-
Cixius sp.	unc	-	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-
Kelisia vitipennis	pas, mar	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kelisia sp.	unc	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Euconomelus lepidus	mar	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-
Conomelus anceps	mar	-	-	-	1	-	-	-	1	-	-	-	-	1	-	-	-
Megamelus notula	mar	16	41	3	16	18	1	-	-	-	-	-	-	-	-	-	-
Megamelodes quadrimaculatus	mar	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Megamelodes sp.	mar	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-

Megamelodes sp.2	mar	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Delphacodes sp.	unc	-	-	-	-	-	-	-	-	4	-	-	1	-	2	1	-
Strophingia ericae	hea	-	-	-	1	-	-	-	1	1	-	-	-	1	-	-	-
Aphalara polygoni	mar, pas	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Psyllopsis fraxinicola nymph	tre	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-
Psylla albipes	tre	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Psylla brunneipennis	mar, tre	-	-	-	-	-	-	-	1	-	-	-	3	-	-	-	-
Psylla brunneipennis or *melanoneura*	mar, tre	-	-	-	-	-	-	-	4	-	3	-	-	-	-	-	-
Psylla mali or ulmi	tre	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Psylla melanoneura	tre	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-
Psylla moscovita	mar, tre	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Psylla ulmi	tre	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Psylla ulmi or *foersteri*	tre	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-
Psylla sp.	unc	-	-	-	-	-	-	-	2	-	1	3	1	2	1	-	1
Psylla or *Psyllopsis* sp. (nymph)	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Psyllidae sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Trioza sp.	unc	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Aphidoidea sp.	unc	1	-	-	-	-	1	-	2	4	1	-	7	-	2	-	-
Homoptera sp.	unc	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-
Coleoptera																	
Cychrus caraboides	woo	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Carabus arvensis, monilis or *nemoralis*	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Carabus nemoralis	eur	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-	1
Carabus sp.	unc	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	1
Leistus sp.	unc	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Notiophilus biguttatus or *rufipes*	woo	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Elaphrus cupreus	mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Dyschirius globosus	eur	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dyschirius sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Clivina collaris	eur	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Clivina sp.	eur	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-

Patrobus assimilis	eur	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Patrobus atrorufus	eur	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
Patrobus sp.	unc	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Trechus obtusus or *quadristriatus*	unc	-	-	-	-	-	-	-	3	2	-	-	2	-	1	-	2
Trechus quadristriatus	ara, pas	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-
Trechus rivularis	mar, woo	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Trechus sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Bembidion semipunctatum	mar	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bembidion gilvipes	mar	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Bembidion assimile	mar	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Bembidion articulatum	mar	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Bembidion obtusum	ara, mar	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Bembidion biguttatum	mar, woo	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Bembidion guttula	mar	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-
Bembidion guttula or *unicolor*	mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Bembidion unicolor	woo	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Bembidion sp.	unc	-	-	1	-	-	-	-	-	-	-	1	2	-	1	-	-
Bembidion (Bembidion) sp.	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Bembidion (Peryphus) sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Tachys bistriatus	mar	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Pterostichus angustatus or *oblongopunctatus*		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Pterostichus madidus	eur	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterostichus melanarius	ara, pas	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Pterostichus minor	mar	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterostichus nigrita	mar	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterostichus oblongopunctatus	woo	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1
Pterostichus diligens or *strenuus*	mar	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-
Pterostichus vernalis	mar	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Pterostichus sp.	unc	-	-	-	1	-	-	-	1	-	-	-	2	-	1	-	-
Abax parallelopipedus	woo	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-
Calathus sp.	unc	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-

Agonum albipes	lit, mar	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-
Agonum assimile	woo	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Agonum marginatum	mar	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Agonum micans	mar	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Agonum moestum	mar	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Agonum piceum	mar	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Agonum sp.	unc	-	-	1	1	1	-	-	1	-	1	1	1	-	-	1	2
Agonum (Europhilus) sp.	mar	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amara sp.	unc	-	-	-	-	1	-	-	-	-	1	1	-	-	-	-	1
Bradycellus ruficollis	hea	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Acupalpus meridianus	ara, pas	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Acupalpus sp.	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Badister dilatatus	mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Badister sp.	mar	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Chlaenius sp.	mar	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Odacantha melanura	mar	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-
Dromius quadrimaculatus	woo	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Carabidae sp.	unc	1	-	-	-	-	-	1	-	-	-	-	1	1	-	-	1
Peltodytes caesus	aqu	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-
Haliplus variegatus	aqu	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Noterus clavicornis	aqu	1	2	4	2	4	4	2	-	-	-	-	-	-	-	-	-
Noterus sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Hygrotus inequalis	aqu	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Hygrotus sp.	aqu	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coelambus sp.	aqu	-	1	-	1	-	-	1	-	-	-	-	-	-	-	-	-
Hydroporus palustris	aqu	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-
Hydroporus incognitus or *palustris*	aqu	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Hydroporus sp.	aqu	2	2	2	1	-	-	-	2	3	-	-	1	1	-	-	1
Hydroporus sp.1	aqu	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-
Hydroporus sp.2	aqu	-	-	2	1	-	1	-	-	-	-	1	-	-	-	-	-
Graptodytes pictus	aqu	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-

Deronectes latus	aqu	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Potamonectes depressus elegans	aqu	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-
Hydroporinae sp.	aqu	-	-	-	-	1	-	1	1	1	1	1	-	-	1	-	-
Hydroporinae sp.1	aqu	1	2	-	1	1	-	-	-	-	-	-	-	-	-	-	-
Hydroporinae sp.2	aqu	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Hydroporinae sp.3	aqu	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Hydroporinae sp.4	aqu	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Hydroporinae sp.5	aqu	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Hydroporinae sp.6	aqu	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Hydroporinae sp.7	aqu	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Agabus bipustulatus	aqu	-	-	1	-	1	-	-	-	-	1	-	-	-	1	-	-
Agabus bipustulatus or *striolatus*	aqu	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Agabus chalconatus	aqu	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Agabus melanarius	aqu	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Agabus striolatus	aqu	-	-	-	-	-	-	-	1	-	1	-	-	1	1	-	1
Agabus sp.	aqu	-	-	-	-	-	-	-	2	1	-	1	-	-	1	-	-
Agabus or *Ilybius* sp.	aqu	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1	1
Ilybius guttiger	aqu	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhantus exsoletus	aqu	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Rhantus sp.	aqu	1	-	-	-	-	1	1	-	-	1	-	-	-	1	-	-
Colymbetes fuscus	aqu	-	-	-	-	-	1	-	-	-	1	-	-	-	1	-	2
Dytiscus sp.	aqu	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dytiscidae sp.	aqu	-	-	-	-	-	-	-	1	1	2	-	1	-	1	1	-
Gyrinus minutus	aqu	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Gyrinus sp.	aqu	1	1	1	-	-	-	-	-	1	-	-	-	-	1	-	-
Hydrophilidae sp.	unc	-	-	-	-	-	-	-	1	-	-	-	-	1	-	2	-
Hydrophilidae sp.2	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Hydrochus brevis or *megaphallus*	mar	2	2	-	-	-	-	-	-	1	-	-	-	1	-	-	1
Hydrochus carinatus	mar	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-
Hydrochus ignicollis	mar	1	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Helophorus brevipalpis	aqu	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	1

Helophorus grandis	aqu	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Helophorus aequalis or *grandis*	aqu	4	2	2	3	1	-	-	-	1	-	-	-	-	-	-	-
Helophorus sp.	unc	1	8	7	3	7	8	3	4	-	2	2	1	3	2	-	-
Coelostoma orbiculare	mar	1	1	-	2	3	1	1	-	-	-	-	-	-	-	-	-
Cercyon analis	eur	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Cercyon convexiusculus	lit, mar	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Cercyon melanocephalus	lit, pas	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-
Cercyon pygmaeus	lit	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-
Cercyon sternalis	mar	-	-	-	-	1	1	-	-	-	-	-	-	-	1	-	-
Cercyon sp.	unc	-	-	1	-	-	1	-	-	1	1	2	-	-	-	-	-
Megasternum obscurum	lit	-	-	-	-	-	-	-	3	-	1	1	4	-	-	2	-
Hydrobius fuscipes	aqu	-	-	1	1	-	1	-	1	1	-	1	1	-	-	-	-
Anacaena sp.	aqu	-	-	-	-	-	-	-	-	2	1	1	-	-	-	-	-
Laccobius bipunctatus	aqu, mar	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Laccobius sp.	aqu	-	-	2	1	2	-	1	1	-	1	2	3	-	1	-	-
Enochrus coarctatus	aqu	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-
Enochrus sp.	aqu	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Enochrus sp.1	aqu	-	3	-	1	2	2	-	-	1	-	-	-	-	-	-	-
Enochrus sp.2	aqu	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Cymbiodyta marginella	mar	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
Hydrophilinae sp.	unc	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Histeridae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Onthophilus striatus	lit,pas	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Ochthebius auriculatus	aqu	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-
Ochthebius dilatatus	aqu	-	-	-	-	-	-	-	-	4	-	4	5	-	-	-	1
Ochthebius minimus	aqu	5	27	20	18	19	22	10	3	3	-	5	8	-	-	-	-
Ochthebius sp.	aqu	-	-	1	-	-	-	-	-	-	4	-	-	1	2	-	1
Hydraena britteni or *rufipes*	aqu	2	2	-	-	-	-	-	19	8	3	14	10	3	1	-	-
Hydraena palustris	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Hydraena testacea	aqu	-	-	-	-	-	-	-	1	1	-	1	5	-	-	-	1

Hydraena sp.	unc	1	-	-	-	-	-	-	-	-	1	-	-	1	-	1	1
Limnebius truncatellus	aqu	1	-	6	-	-	-	-	-	2	5	-	1	-	3	-	2
Limnebius truncatellus or *papposus*	aqu	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Limnebius sp.	aqu	-	-	1	-	-	-	1	-	1	1	-	1	-	-	-	1
Ptenidium sp.	eur	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Acrotrichis sp.	eur	1	-	-	-	-	-	-	3	4	1	-	1	1	-	-	2
Ptiliidae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Colon brunneum	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Oiceoptoma thoracicum	lit	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Silpha atrata	woo	-	-	-	-	-	-	-	-	1	-	2	-	-	1	-	-
Silpha sp.	unc	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Silphidae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Neuraphes sp.	lit	-	-	-	-	-	-	-	2	-	-	-	-	1	2	-	-
Staphylinidae sp.	unc	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-
Micropeplus staphylinoides	lit	-	-	-	-	-	-	-	2	-	-	-	1	1	1	-	-
Proteinus ovalis	lit	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
Proteinus sp.	lit	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-
Anthobium atrocephalum	lit	-	-	-	-	-	-	-	1	2	-	-	1	1	-	-	-
Anthobium unicolor	lit	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-
Anthobium sp.	unc	-	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-
Olophrum piceum	hea	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Olophrum sp.	unc	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Lesteva heeri	lit, mar	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-
Lesteva longoelytrata	lit, mar	-	1	-	1	-	-	-	2	1	1	2	4	-	-	-	-
Lesteva pubescens	lit	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Lesteva sp.	unc	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-
Anthophagus caraboides	lit	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Eusphalerum minutum	eur	-	-	-	-	-	-	-	-	-	1	2	-	1	-	-	-

Eusphalerum primulae	eur	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Eusphalerum sorbi or *sorbicola*	eur	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Eusphalerum sp.	unc	-	-	-	-	-	-	-	-	1	-	1	1	1	1	-	-
Dropephylla ioptera	eur	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Omalium rivulare	lit	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Thinodromius arcuatus	lit, mar	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Carpelimus bilineatus	eur	-	-	-	-	-	-	-	4	1	-	-	4	1	-	-	-
Carpelimus corticinus	lit	2	2	2	1	3	-	-	1	-	-	-	-	-	1	-	-
Carpelimus elongatulus	mar, woo	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carpelimus rivularis	eur	-	1	1	-	1	-	-	1	1	-	1	2	-	-	-	-
Carpelimus subtilicornis	lit	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Carpelimus sp.	unc	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-
Platystethus arenarius	pas, lit	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-
Platystethus nodifrons	mar	-	1	3	3	2	3	1	1	-	-	-	-	-	-	-	-
Anotylus nitidulus	lit	-	-	1	-	-	-	1	2	-	1	-	1	-	-	-	-
Anotylus rugosus	lit	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Anotylus sculpturatus gp. (*A. mutator* or *sculpturatus*)	lit	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
Anotylus or *Oxytelus* sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Stenus bimaculatus	mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Stenus juno	mar	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-
Stenus similis	eur	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Stenus sp.	unc	-	-	-	-	-	-	-	2	1	-	1	-	-	1	-	-
Stenus sp.1	unc	5	2	1	1	1	1	-	-	-	-	-	-	-	-	-	-
Stenus sp.2	unc	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-
Stenus sp.3	unc	2	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Stenus sp.4	unc	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euaesthetus laeviusculus	mar	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paederus riparius	mar	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lathrobium longulum	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Lathrobium sp.	unc	1	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Lithocharis sp.	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-

Astenus sp.	unc	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Rugilus rufipes or *subtilis*	lit	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Rugilus sp.	unc	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Othius myrmecophilus	lit	-	-	-	1	3	1	-	2	-	-	-	1	-	-	-	-
Othius punctulatus	woo	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Leptacinus sp.	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Gyrohypnus angustatus	lit	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Gyrohypnus sp.	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Xantholinus linearis gp. (*X. gallicus*, *linearis*, or *longiventris*)	lit	-	-	-	-	1	-	-	-	1	1	1	-	-	-	-	-
Xantholinus longiventris	lit	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Xantholinus sp.	lit	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Erichsonius cinerascens	mar	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Erichsonius sp.	lit	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Philonthus decorus	woo	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	1
Philonthus jurgans	lit	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Philonthus sp.	unc	-	-	1	-	-	-	1	1	1	1	1	1	-	-	-	1
Philonthus sp.1	unc	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Philonthus sp.2	unc	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Philonthus sp.3	unc	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Philonthus sp.4	unc	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Philonthus or *Quedius* sp.	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
Gabrius splendidulus	lit	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Gabrius sp.	unc	-	2	1	2	-	-	-	-	-	-	-	2	1	-	-	-
Staphylinus erythropus	lit	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Quedius sp.	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Staphylininae sp.	unc	-	-	-	2	-	-	-	-	1	-	-	-	1	1	1	-
Tachyporus hypnorum	eur	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Tachyporus sp.	eur	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-
Tachinus corticinus	lit	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-
Tachinus marginellus	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Tachinus signatus	lit	-	-	-	-	-	-	-	-	3	-	1	1	1	-	-	1

Tachinus sp.	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-
Cilea silphoides	lit	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Tachyporinae sp.	unc	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
Leptusa ruficollis	woo	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxypoda sp.2	lit	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Oxypoda sp.3	lit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Oxypoda sp.4	lit	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Aleochara sp.	lit	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Aleochara sp.1	lit	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Aleochara sp.2	lit	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Aleocharinae sp.1	unc	-	6	3	1	1	1	-	5	5	3	4	2	1	-	-	-
Aleocharinae sp.2	unc	-	2	3	3	2	1	1	5	6	4	2	5	1	3	-	-
Aleocharinae sp.3	unc	-	-	-	-	1	-	-	-	-	-	2	-	-	-	-	-
Aleocharinae sp.4	unc	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aleocharinae sp.5	unc	-	-	-	-	-	-	-	2	2	1	-	-	-	-	-	-
Aleocharinae sp.6	unc	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-
Aleocharinae sp.7	unc	4	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-
Aleocharinae sp.8	unc	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-
Aleocharinae sp.9	unc	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	1
Aleocharinae sp.12	unc	-	-	-	-	-	-	1	1	-	-	1	-	1	-	-	1
Aleocharinae sp.13	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Aleocharinae sp.14	unc	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-
Aleocharinae sp.15	unc	-	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Aleocharinae sp.16	unc	-	-	1	1	-	2	-	1	-	-	1	1	-	-	-	-
Aleocharinae sp.17	unc	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Aleocharinae sp.18	unc	-	-	1	-	-	-	-	2	-	-	1	1	-	-	-	-
Aleocharinae sp.19	unc	2	1	-	-	-	-	-	1	-	1	2	-	-	-	-	1
Aleocharinae sp.20	unc	-	-	-	-	-	-	-	3	-	-	1	-	-	-	-	-
Aleocharinae sp.21	unc	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Aleocharinae sp.22	unc	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-
Aleocharinae sp.23	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Aleocharinae sp.26	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Aleocharinae sp.28	unc	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	1

Aleocharinae sp.29	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
Aleocharinae sp.30	unc	1	-	-	-	-	-	-	-	1	-	2	2	1	-	-	-
Aleocharinae sp.31	unc	1	-	1	-	2	1	-	4	6	1	6	3	1	1	-	1
Aleocharinae sp.34	unc	1	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-
Aleocharinae sp.35	unc	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Aleocharinae sp.36	unc	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-
Aleocharinae sp.37	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Aleocharinae sp.38	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Aleocharinae sp.39	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Aleocharinae sp.40	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Aleocharinae sp.41	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Aleocharinae sp.42	unc	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Aleocharinae sp.43	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Aleocharinae sp.44	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Aleocharinae spp.	unc	-	1	-	2	-	-	-	2	2	1	2	1	1	1	-	1
Trichonyx sulcicollis	tre	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Bryaxis bulbifer or *curtisii*	eur	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Bryaxis sp.	lit	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-
Bryaxis or *Bythinus* sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Brachygluta sp.	unc	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Brachygluta or *Reichenbachia* sp.	unc	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Pselaphidae sp.	unc	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Geotrupes spiniger	pas	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Geotrupes stercorosus	pas	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-
Geotrupes sp.	pas	-	-	-	-	1	1	-	-	1	1	1	1	-	-	1	1
Aphodius ater	pas	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Aphodius contaminatus	pas	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Aphodius depressus	pas	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
Aphodius paykulli	pas	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aphodius prodromus	pas	-	2	-	-	3	-	-	-	-	-	-	2	-	-	-	-

Aphodius prodromus or *sphacelatus*	pas	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Aphodius sphacelatus	pas	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	1
Aphodius sp.	unc	-	-	-	-	-	-	-	2	2	1	-	-	1	-	-	1
Serica brunnea	pas	-	-	-	-	-	-	-	-	-	-	2	2	-	1	-	-
Melolontha sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Phyllopertha horticola	pas	-	1	1	1	-	1	-	2	1	2	-	2	1	1	-	2
Scarabidae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Dascillus cervinus	eur	-	-	-	-	-	-	-	2	-	-	1	1	-	-	-	-
Dascillidae or Scirtidae sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Elodes marginata	mar	-	-	-	-	-	-	-	2	3	-	-	-	-	-	-	-
Elodes sp.	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Microcara testacea	mar, woo	-	-	-	-	-	-	-	4	1	-	-	-	-	-	-	-
Cyphon coarctatus	mar	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Cyphon padi	mar	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-
Cyphon punctipennis	mar	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyphon sp.	unc	1	-	1	-	1	2	1	2	-	1	1	6	2	-	-	2
Cyphon sp.1	unc	-	1	-	-	-	-	-	-	2	-	-	1	-	-	-	-
Cyphon sp.2	unc	-	1	-	-	-	-	-	-	1	-	-	3	-	-	-	-
Cytilus sericeus	hea	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dryops sp.	mar	1	1	3	-	1	1	-	1	-	-	2	3	-	-	-	1
Dryops sp.1	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Dryops sp.2	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
Esolus parallelopipedus	aqu, mar	-	-	1	-	1	-	-	1	1	3	-	3	4	1	-	1
Limnius volckmari	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Normandia nitens	aqu	-	-	-	-	-	-	-	-	-	1	1	-	2	-	-	-
Oulimnius rivularis	aqu	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Oulimnius major or *tuberculatus*	aqu	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Oulimnius sp.	aqu	-	-	-	-	-	-	-	-	-	2	1	3	6	3	-	2

Stenelmis canaliculata	aqu	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Hypnoidus riparius	mar	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-
Zorochros minimus	mar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Cidnopus minutus	pas	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Athous haemorrhoidalis	tre	-	-	1	-	-	-	-	-	-	-	1	1	-	-	-	-
Athous sp.	unc	-	-	-	-	-	-	-	1	1	1	2	-	-	-	-	1
Ctenicera cuprea	pas	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Selatosomus incanus	eur	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
Selatosomus sp.	unc	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1
Agriotes acuminatus	pas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Agriotes acuminatus or *pallidulus*	pas	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
Agriotes sp.	pas	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Dalopius marginatus	woo	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	1
Elateridae sp.	unc	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	1
Trixagus dermestoides	woo	-	-	-	-	-	-	-	-	1	-	1	1	-	1	-	-
Trixagus sp.	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Melasis buprestoides	woo	-	-	-	-	-	-	-	1	-	-	1	2	-	-	-	-
Cantharis sp.	unc	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Malthinus or *Malthodes* sp.	tre	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Malthodes sp.	tre	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Cantharidae sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Grynobius planus	woo	-	-	-	-	-	-	-	-	-	1	-	3	-	-	-	-
Anobium punctatum	syn, woo	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-
Kateretes rufilabris	mar	-	3	8	-	2	1	-	-	-	-	-	-	-	-	-	-
Brachypterus sp.	eur	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Meligethes sp.	unc	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-
Epuraea sp.	unc	-	1	-	-	-	-	-	-	1	-	-	-	-	1	-	-

Epuraea or *Meligethes* sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Aspidiphorus orbiculatus	tre	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Cryptophagidae sp.	unc	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Cryptophagus sp.	unc	-	-	-	-	-	-	-	1	-	1	-	1	-	-	-	1
Atomaria sp.	unc	-	-	-	-	-	-	-	1	2	-	1	-	-	-	-	-
Atomaria sp.2	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Cerylon ferrugineum	tre	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Cerylon sp.	tre	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Corylophus cassidoides	lit, tre	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Stephostethus lardarius	lit	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Stephostethus sp.	lit	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Lathridius minutus gp.	lit	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Lathridius pseudominutus	lit, syn	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Enicmus sp.	lit	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Corticarina fuscula	lit	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Corticarina sp.	lit	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Cortinicara gibbosa	lit	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Lathridiidae sp.	unc	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Cisidae sp.	tre	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Rabocerus foveolatus	tre	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Salpingus sp.	tre	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-
Melandrya caraboides	woo	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Anaspis maculata	tre	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-
Anaspis sp.	tre	-	-	-	-	-	-	-	1	1	-	-	1	-	1	1	1

Cerambycidae sp.	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Donacia marginata	mar	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-
Donacia sp.	mar	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
Plateumaris affinis	mar	-	-	2	1	2	-	-	-	-	-	-	-	-	-	-	-
Plateumaris braccata	mar	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-
Plateumaris discolor	mar	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plateumaris discolor or *sericea*	mar	1	1	2	4	2	-	-	-	-	-	1	-	-	-	-	-
Plateumaris sp.	mar	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Donacia or *Plateumaris* sp.	mar	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Donaciinae sp.	unc	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-
Lema or *Oulema* sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Oulema melanopa	eur	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Chrysolina hyperici	eur	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Chrysolina sp.	unc	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-
Gastrophysa sp.	mar, pas	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Hydrothassa sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Hydrothassa or *Prasocuris* sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Prasocuris phellandrii	mar	-	1	1	1	1	-	-	4	9	2	3	2	-	-	-	-
Chrysomela aenea	tre	-	-	-	-	-	-	-	2	-	-	1	1	-	-	-	-
Chrysomela sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Galerucella sp.	unc	-	-	-	-	-	-	-	-	-	2	-	-	-	1	1	-
Galeruca tanaceti	hea, pas	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-
Lochmaea suturalis	hea	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
Phyllotreta tetrastigma	mar, pas	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Phyllotreta sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Phyllotreta or *Psylliodes* sp.	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Longitarsus sp.	unc	-	-	-	-	-	-	-	2	-	-	-	-	1	-	-	-
Batophila aerata	eur	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
Batophila sp.	pas, woo	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-
Chaetocnema concinna	ara, pas	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Chaetocnema sp.	unc	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-

Psylliodes sp.	unc	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Halticinae sp.	unc	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
Chrysomelidae sp.	unc	-	-	-	-	-	-	-	3	2	2	1	2	-	1	1	-
Chrysomelidae or Leiodidae sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Deporaus betulae	woo	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Apion sp.	unc	-	1	-	-	-	-	-	1	-	-	-	-	1	-	-	1
Apion (Protapion) sp.	ara, pas	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Phyllobius argentatus	woo	-	1	-	-	-	-	-	-	1	1	1	1	-	-	-	-
Phyllobius calcaratus	tre, woo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Phyllobius pomaceus	pas	-	-	-	-	-	-	-	-	2	-	-	-	-	-	1	-
Phyllobius sp.	unc	-	-	-	-	-	-	-	3	2	1	1	-	-	-	1	-
Polydrusus sp.	unc	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Barypeithes sulcifrons	eur	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Brachysomus echinatus	eur	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Strophosomus capitatus	tre	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Strophosomus melanogrammus	woo	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-
Strophosomus capitatus or *melanogrammus*	woo	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Sitona lineatus	eur	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhinocyllus conicus	pas	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Leiosoma sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Magdalis armigera or *carbonaria*	tre	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Magdalis sp.	tre	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Anoplus or *Rhynchaenus* sp.	unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Rhyncolus lignarius	tre	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Bagous czwalinai	mar	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Bagous sp.	mar	-	1	-	1	-	1	1	-	-	-	-	-	-	-	-	-
Bagous sp.2	mar	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Dorytomus sp.	mar, woo	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Thryogenes sp.	mar	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Mononychus punctumalbum	mar	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-

Cidnorhinus quadrimaculatus	pas	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Ceuthorhynchidius sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Ceutorhynchus contractus	ara	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Ceutorhynchus floralis	ara	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-
Ceutorhynchus sp.	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-
Eubrychius velutus	aqu, mar	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Phytobius quadrituberculatus	mar	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
Phytobius sp.	unc	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Ceuthorhynchinae sp.	unc	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Anthonomus rubi	eur	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Anthonomus sp.	unc	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Gymnetron beccabungae	mar	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Curculionidae sp.	unc	-	1	-	-	-	-	-	1	1	-	2	1	2	1	-	-
Scolytus scolytus	tre	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Hylesinus crenatus	tre	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Hylesinus oleiperda	tre	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-	-
Hylesinus orni or *varius*	tre	-	-	-	-	-	-	-	-	1	-	3	-	-	-	-	1
Hylesinus varius	tre	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-
Polygraphus poligraphus	tre	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Dryocoetes villosus	woo, tre	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Scolytidae sp.	tre	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-

Appendix 3: Notes on the occurrence of beetle species in woodland habitats

* = Species of doubtful status, including immigrant and adventitious species of fairly regular occurrence.
fp. = foodplant

All species which have been associated with woodland communities in any of the published works examined are listed, together with numerical code (based on position in Kloet and Hincks, 1977), a measure of their apparent overall dependence on woodland habitats, and notes. Extinct species have been excluded.

Codes for strength of association with woodland;

1	Strongly associated with woodland; only, or very largely found in established woods
2	Usually found in woodland, but able to survive and breed in other habitats
3	Sometimes in woods, but also regularly in other habitats
4	Occasionally found in woods, but generally eurytopic
5	Rarely in woods(in Britain).

Abbreviations;

E = Eurytopic; In many different habitats.
S = Stenotopic; only in few, similar habitat types.
H = Habitat.

CARABIDAE

(Nomenclature follows Kloet and Hincks, 1977)

001A/001-/001-
Cicindela campestris Linnaeus, 1758 4

1) 'Especially prominent on peaty soil, but also in clayey, sandy and gravelly areas, such as bare ground in *Calluna* vegetation and sunny woodland paths.'
3) E. Xerophile. H dry woods. fields, sandy shores, etc.
6) 'In woods, in sandy places.'
10) 'Common and generally distributed in sandy places.'

001A/001-/005-
Cicindela sylvatica Linnaeus, 1758 4

1) 'On dry, sandy and sun-exposed ground, mainly in open pine forest...also on heaths'.
3) E. Psammophile. H sandy *Calluna*-heath, light pinewoods, dunes (In East, moors).
10) 'Local; sandy heaths'

001C/003-/001-
Cynchrus caraboides Linnaeus, 1758 ssp.*rostratus* Linnaeus, 1761 2

1) 'Predominantly a woodland species, preferring deciduous forest on shady, rather moist soil rich in humus. Often in tree stumps and fallen trunks.'
2) 'In damp deciduous and coniferous woods, from the lowlands to the dwarf scrub zone.'
3) E. Hygrophile, silvicole. H damp woods, woodland edges.
4) A nocturnal woodland species (at Silwood).
7) 'May be found in woodland.'
14) Upland bogs and woods (Northern Ireland).
15) Associated with closed canopy woodland at Silwood Park, but with grassland in Argyll.

001D/004-/005-
Carabus glabratus Paykull, 1790 ssp. *lapponicus* Born, 1908 5

1) 'In the lowland exclusively in forests, notably dark moist spruce-mixed forests rich in mosses, but also in beech forests. In mountainous regions..it is also an inhabitant of open country.'
2) (of typical form)'in large and old woods' (lapponicus replaces typical form in highlands of Alps).
8) listed in Ecological group 'woodland species; occurring predominantly in woodland'.
10) 'A mountain species. Snowdon, Cader Idris, hills above Langdale.'
14) Upland bogs and woods (Northern Ireland).

001D/004-/006-
Carabus granulatus Linnaeus, 1758 4

1) 'Hygrophilous...wet meadows and open, deciduous forests on moist,clayish soil; often in stands of alder...spends the daytime and winter in tree stumps and felled timber.'
3) E. Hygrophile, silvicole. H damp woods, meadows, fields.
10) 'Marshy places, in rotten willows, or under pond refuse.'

001D/004-/008-
Carabus intricatus Linnaeus, 1761 3

1) In Scandinavia, 'confined to deciduous ravine forests, usually beech'
In Central Europe, 'often in mountain forests'.
2) 'In mid-altitude woods, seldom above 1500m.'
3) E. Thermophile. H light woods, woodland edges, sunny banks.
10) 'In woods under moss and lichens on trunks of old oaks and other trees, or under bark.'

001D/004-/012-
Carabus problematicus Herbst, 1786 ssp.*gallicus* Gehin, 1885 3

1) In Denmark 'a rather common inhabitant of light deciduous forests, notably of oak'
'Considered a true forest species in C.Europe.'
3) E. Silvicole. H woods.
4) Greenslade regards this as a forest species, but one of bracken/scrub at the edge of woodlands, rather than intensely shaded dense woodland.
10) 'Common and widely distributed in England and Scotland, both in lowland and mountainous districts.'
13) in Netherlands, highest densities recorded at the edges of beech wood (perhaps averse to the deep shade and lack of undergrowth within the wood).
15) At Silwood Park, associated with open-canopy woodland, but in Argyll, in grassland.

1/004-/013-
1/004-/014-
Carabus violaceus Linnaeus, 1758 3

1) 'A eurytopic forest species preferring light deciduous or coniferous forest'.
2) From the lowlands to the high mountains, in woods and tundra.
3) E. H light woods, meadows, open land.
4) Widely distributed at Silwood, in woods, arable land and grass heath.
6) Associated with woodland
8) In ecological grouping 'WOODLAND SPECIES; occurring predominantly in woodland'.
13) Caught in all forests investigated in trapping study, even coniferous with little undergrowth. Predator of caterpillars.

001D/005-/001-
Calosoma inquisitor (Linnaeus, 1758) 1

1) 'Open deciduous forests, notably of oak...the prey consisting of larvae and pupae, mostly of Geometridae and Tortricidae.'
2) 'Generally in oakwoods, common near outbreaks of lepidoptera larvae, especially *Tortrix viridana* L.'
3) E. Silvicole, arboricole. H deciduous woods.
6) 'especially associated with woods, being fairly common in oakwoods of S E England.'
10) 'On oaks in woods'
11) Hunts lepidoptera larvae in the canopy of oak and other trees round about.
13) Occasionally trapped on the forest floor in Spring (Netherlands), but generally inhabits treetops.
16) Listed (Appendix 2) with 'species which occur widely on wooded land, but which are collectively characteristic of ancient woodland with dead-wood habitats'(Group 3 of 3, where 1 is 'only occurs in ancient woodland').

001D/005-/002-
Calosoma sycophanta (Linnaeus, 1758) *1

1) In Central Europe, inhabits both coniferous and deciduous forests. Prefers oak, but less strictly associated with it than *C.inquisitor.*
3) E. Silvicole, arboricole. H woods, woodland edge, gardens.
10) Not really a native, but only an occasional visitant (to Britain).
13) 'hunts lepidoptera larvae in oak and other trees'.

001E/006/001-
Leistus ferrugineus (Linnaeus, 1758) **3**

1) 'More xerophilous than *L. rufescens* or *L. rufomarginatus*, occurring in open country...in hedges, and in open woodland.'.
2) 'On warm, particularly sandy ground, sometimes far from water'.
3) E. H loamy and loam/sand arable fields, woodland edges, light woods.
4) A woodland edge species, or in open woodland.

001E/006-/004-
Leistus rufescens (Fabricius, 1775) **4**

1) 'Among wet leaves in moist, shady sites in hardwood forest, for instance along brooks in ravines and in alder-swamps'.
2) In reedswamps, in the North in woods.
3) E. Hygrophile, ripicole. H stony and gravelly stream- and river-banks, meadows.
7) 'Leistus spp.' may be found in woodland.
8) Listed under ecological grouping 'WOODLAND SPECIES; occurring predominantly in woodland' (also 'very wet areas').
10) 'Damp places at the roots of grass'.

001E/006-/005-
Leistus rufomarginatus (Duftschmid, 1812) **4**

1) 'Mainly in deciduous forest, notably light stands of beech'
2) 'Predominantly in deciduous forests'
3) E. Hygrophile, silvicole. H damp decid. woods, swampy heath.
8) Listed under ecological grouping 'WOODLAND SPECIES; occurring predominantly in woodland'.
11) Often/regularly found under bark, deadwood, etc.

001E/008-/001-
Nebria brevicollis (Fabricius, 1792) **3**

1) 'A eurytopic woodland species, predominantly in deciduous forests, in Scandinavia mainly of beech...also on shady ground in open country.'
2) In Central Europe, common, and most frequent habitat woodland(particularly deciduous woods) with marked humus layers.
3) E. Hygrophile, silvicole. H humus-rich decid. woods, woodland edges, damp copses and hedges, floodmeadows, gardens.
4) Essentially an inhabitant of woodland litter, although populations extend into other habitats.
10) 'Very abundant and widely distributed; one of our commonest British insects'
11) Often/regularly found under bark, deadwood, etc.
14) Upland bogs, woodland.
15) Associated with closed canopy woodland at Silwood Park, but a wide range of habitats, including grassland, in Argyll.

001F/009-/003-
Notiophilus biguttatus (Fabricius, 1779) **4**

1) 'A eurytopic woodland species, inhabiting clearings in both deciduous and coniferous forests'
3) E. Xerophile, silvicole, phytodetriticole. H light woods, woodland edges, gardens, heath, dunes.
10) 'Abundant everywhere throughout the kingdom'
12) Frequent in wet and dry Oak/Birchwoods in N W Germany, but fairly eurytopic.
13) A diurnal inhabitant of woodland litter.

001F/009-/005-
Notiophilus palustris (Duftschmid, 1812) **5**

1) 'Hygrophilous...occurring in rather shady localities on humus-rich soil. Found in deciduous woodland among litter and mosses, eg, in the drier places of *Alnus glutinosa* swamps, as well as in open country.'
2) In Central Europe, from lowlands to high alpine. Frequent throughout. Hygrophilous, shade-loving.
3) E. Hygrophile, praticole, phytodetriticole. H damp woods, gardens, watermeadows, wet heath, banks, etc.
9) 'Hygrophilous; in leafy woods' but recorded (once only) from wrack fauna.

001F/009-/007-
Notiophilus rufipes Curtis, 1829 **3**

1) 'A woodland species, living among litter and moss in deciduous forest on somewhat moist and shady ground'
2) Thermophilous. Particularly in beechwoods and on marshy soils
3) E. Thermophile. H Heaths, dunes, marshy soils, warm banks, dry woods, sandy floodmeadows.
4) A diurnal woodland species...narrowly restricted to litter
12) More stenotopic-in damp oak-birchwoods (in N W Germany).

001G/011-/001-
Elaphrus cupreus Duftschmid, 1812 **5**

1) 'At the margins of standing or slow-flowing waters...especially typical of eutrophic fens in open country as well as in deciduous woodland.'
2) On muddy banks in valley deposits.
3) E. Hygrophile, ripicole, limicole. H muddy and reedy banks, shady beaches in woods, marshy woods.
9) Hygrophilous-on beaches with some vegetation.
10) Damp places; on the mud at the margins of streams and rivers.

001H/012/001-
Loricera pilicornis (Fabricius, 1775) **4**

1) 'Predominantly a eurytopic forest species, not preferring any particular forest community; also in the open countryside'
2) In C Europe, most frequent. Likes damp, soft soils; also moorland/swamp.
3) E. Hygrophile, phytodetriticole. H damp decid. woods, wood-pasture, forest edges, hedges and copses, gardens, banks, swamp, damp fields.
9) 'Hygrophilous. Beaches, and forests in damp situations'
10) 'On the borders of rivers and streams, at the roots of trees, and in various other situations'
12) Caught in both dry and damp oak-birchwood in N W Germany.
13) In a wide range of habitats (including arable land)

001I/014-/002-
Clivina fossor (Linnaeus, 1758) **5**

1) Eurytopic, usually occurring in open countryside.
2) Most common on damp ground, not restricted to banks/beaches.
3) E. Hygrophile, terricole. H damp heavy soils, fields, damp meadows.
4) Pasture/woodland edge species
9) 'Mesophilous. Eurytopic'
10) 'Damp places, on the banks of streams etc.'

001K/017-/001-
Patrobus assimilis Chaudoir, 1844 **5**

1) In N Fennoscandia, rather eurytopic.
In S Scandinavia, exclusively found in damp localities, predominantly peaty woods with birch and alder, and a rich vegetation dominated by *Sphagnum*, *Carex*, etc.
2) Apparently boreomontane, but also in N German moorland/bog.
3) S. Tyrphophile. H moors, marsh woodland.
10) 'Rather widely distributed, but always on moors or in hilly and mountainous districts'

001K/017-/002-
Patrobus atrorufus (Ström, 1768) **3**

1) 'A hygrophilous species, predominantly occurring in humid deciduous forests on clayish mull soil'
2) 'Frequent on the N German plain, rarer on mountains. Particularly in wood-pasture'
3) E. Hygrophile, silvicole. H damp wood pasture, parks, fields.
8) Listed in the group 'WOODLAND SPECIES; occurring predominantly in woodland'
9) 'Mesophilous, eurytopic'
10) Common and widely distributed; Mountains, moors and woods.

001L/021A/002-
Trechus obtusus Erichson, 1837 **5**

1) Occurring in moderately humid and usually shaded sites, eg. hedges, thin deciduous forest.
3) E. Hygrophile, silvicole. H damp deci. woods and river meadows, marshes, damp shaded fields.
10) Sandy places on the coast and inland.

001L/021A/004-
Trechus rivularis (Gyllenhal, 1810) **5**

1) In peaty woods with a growth of birch, alder or willow and with a vegetation domuinated by *Sphagnum*, *Carex*, ferns etc.
3) S. Tyrphophile, sphagnicole. H moors, marshy riverbanks, alder swamp.
10) 'Very Rare'. Two localities mentioned; Whittlesea Mere, Holme Fen.

14) Upland bogs and woodland (Northern Ireland).

001L/021A/006-
Trechus secalis (Paykull, 1790) **5**

1) In woodland (mainly water-meadow forests) as well as in open country; rich meadows and arable land.
3) E. Hygrophile. H river and streambanks, floodmeadows, wet fields and woods.
10) 'Damp sandy banks of ponds and rivers, often common in flood refuse'.

001M/023N/028-
Bembidion monticola Sturm, 1825 **5**

1) 'Along small rivers and brooks...on sparsely vegetated or barren banks in somewhat shaded situations, eg. in deciduous forest. In C Europe and Britain predominantly in mountains.'
2) On banks of small rivers/streams.
3) S. Hygrophile, ripicole. H fine sand and gravel banks of streams. Sand-mud banks of small rivers, beneath steep loamy banks.
10) Deep in the crevices of sandy banks, also stumps of old willows etc. near streams and rivers. Appears to be found more abundantly in hilly and mountainous districts, yet is by no means a mountain species.

001M/023Q/038-
Bembidion gilvipes Sturm, 1825 **4**

1) '..predominantly in marshes and on the shores of fresh waters, usually occurring in somewhat shady sites among litter, eg under *Salix* and *Alnus*...Also in deciduous forest swamps with vigorous forest swamps with vigorous growth of *Solanum*, *Lysimachia*, etc.'
2) Common in N, less so in S. In wet meadows, on banks, also in fen woodland.
3) S. Hygrophile, phytodetriticole. H damp fields, floodmeadows, swampy woods and banks.
10) Sandy and gravelly places on banks of rivers, often found in numbers in flood refuse'.

001M/023Q/039-
Bembidion schuppelii Dejean, 1831 **4**

1) 'Predominantly on river banks, in rather dense vegetation of, eg. grasses and *Carex*...in C Europe often in marshy woodland.'
2) In C Europe, more montane; Not throughout in N Germany but most frequent in marshy woodland and muddy, shaded banks.
3) S. Hygrophile, ripicole, silvicole. H muddy shaded banks of woodland pools, marshy woodland.
10) 'A Northern species, amongst grass on the margin of streams'.

001M/023R/041-
Bembidion clarki Dawson, 1849 **4**

1) 'On moist and semi-shaded ground in wooded areas, eg under *Alnus* and *Salix*, usually occurring at the border of ponds and temporary pools.'
3) S. Hygrophile, ripicole, paludicole. H by swampy woodland pools.
10) 'Marshy places, at the roots of grass and in moss. Local and not common.'

001M/023X/051-
Bembidion harpaloides (Serville, 1821) **4**

2) In floodmeadows under rotten bark and at the base of willows and poplars.
3) S. Hygrophile, ripicole, often corticole or subterranean. Stream and riverbanks, floodmeadows.
6) A predator which often inhabits tree crowns.
22) 'Marshy places, at roots of grass etc. Also hibernating under bark'.

001M/023Y/054-
Bembidion biguttatum (Fabricius, 1779) **5**

1) 'On moist mull soil in somewhat shady sites, eg eutrophic fens, usually among tall vegetation. Also in open woodland at the margins of ponds and pools'.
3) E. Hygrophile, paludicole, phytodetriticole. Marshy and muddy banks, marsh, damp fields, wet arable land.

001M/023Y/055-
Bembidion guttula (Fabricius, 1792) 4

1) On moist clay or clay-mixed soil near freshwater, usually in open land in rich vegetation of *Carices*, grasses, etc., but also in light deciduous forest'.
2) In C Europe, most common in the foothills of mountains beside all kinds of waterbody, also in wet meadows.
3) E. Hygrophile. H mud and gravel banks, marshy banks, damp floodmeadows and fields.
10) One of the commonest and most abundant of British beetles; generally distributed over almost the whole of Europe.

001M/023Y/058-
Bembidion unicolor Chaudoir, 1850 3

1) In moderately moist shady habitats. Found among litter and moss on sparsely vegetated spots, notably in deciduous woodland on mull soil, eg drier parts of alder swamps, margins of brooks and ponds.
2) In C Europe in wet woods, very common.
3) E. Hygrophile, paludicole, phytodetriticole. H marsh, moors, marshy open woods, damp floodmeadows, wet decid. woods.
8) Listed in group 'WOODLAND SPECIES; occurring predominantly in woodland'.
10) 'Marshy places, especially on heaths, at roots of grass etc. Local, but often common where it occurs'.

001M/024-/002-
Tachys bisulcatus (Nicolai, 1822) *5

1) 'Originally associated with coniferous forest, now usually found at sawmills in heaps of damp, fermenting spruce bark'.
2) On lowland and mountains by water under stones, etc. Also in damp sawdust.
3) E, mostly xylo- and phytodetriticole. H Banks, woods, gardens, waste places.
10) 'Taken first..benath stones on the seashore near South Shields (1863). Has not occurred, apparently, for many years; it is a rare species on the continent.'

001M/024-/004-
Tachys micros (Fischer von Waldheim, 1828) 5

2) S and C Europe. In C Europe, rarer.
Sand and gravel banks under damp stones but also in brick quarries, fens and woodlands.
3) E. Hygrophile, ripicole. H sand and gravel banks of streams and rivers, brick pits, gravel pits, swamps, damp woods.

001O/026-/001-
Stomis pumicatus (Panzer, 1795) 4

1) 'Notably on clayey..mull-rich, moderately humid soil in meadows and fields; also in gardens, parks and open deciduous forest.'
2) In C Europe, hygrophilous.
3) E. Hygrophile, phytodetriticole. H damp loamy woodland edges, hedges and gardens, loamy banks, floodmeadows and fields.
4) A woodland species, especially bracken and open woodland.
10) Under stones, flood refuse etc.

001O/027-/002-
Pterostichus aethiops (Panzer, 1796) 3

1) 'A woodland species, living among moss and leaves or under bark of tree stumps in deciduous as well as coniferous forests. In C Europe predominantly in mountain forests.'
2) Montane and subalpine in E and C Europe, W to England.
3) E. Hygrophile, silvicole. H damp decid. and mixed woods, banks of woodland streams.
5) 'On mountains'.
10) A mountain species, plentiful on Snowdon, Cheviots, Scottish Highlands.

001O/027-/008-
Pterostichus diligens (Sturm, 1824) 5

1) Confined to wet habitats...shore zone of lakes and rivers, meadows and swamps, both in forest and in open country...especially typical of oligotrophic and dystrophic lakes and *Sphagnum* bogs.
2) Hygrophilous, particularly in swampy places.
3) S. Hygrophile, paludicole, phytodetriticole. H marshes, boggy banks, moor, marshy heath, marsh woodland, strandlines.
9) Euryhygric, Eurytopic. Prefers medium moisture both in forests, swamps and on shores.
10) 'Common and widely distributed.'
30) upland bogs and woodlands.

0010/027-/014-

Pterostichus madidus (Fabricius, 1775) 3

1) Eurytopic; in C Europe, mainly in woodland.
In Britain, notably in open country, often on cultivated soil.
3) E. H decid. woods (mostly Fagetalia and Querco-Carpinetum), wood edges, floodmeadows, dry fields and waqste places, dry slopes, quarries.
6) Associated with woodland
10) 'Common throughout the kingdom'

0010/27-/015-

Pterostichus melanarius (Illiger,1798) 5

1) Very eurytopic. Clearly favoured by human activity-common inhabitant of arable land, parks, gardens, but also forest edges and light woods.
2) Eurytopic. Favoured by cultivation.
3) E. Hygrophile. H; prefers densely vegetated loamy fields, floodmeadows, pasture. woodland edges, hedges and gardens, gravel- and clay-pits.
4) A nocturnal species of grassland and arable fields.
10) 'Under stones etc; common and widely distributed.'

0010/027-/016-

Pterostichus minor (Gyllenhal, 1827) 4

1) A hygrophilous species, in almost every type of wet habitat with rich vegetation, both in open country and forest (shore-zone of eutrophic lakes, *Sphagnum* bogs, alder swamps etc.).
2) Eurytopic on banks and in fens (C Europe).
3) E. Hygrophile, paludicole, freq. phytodetriticole. Swamps and boggy banks by stagnant water with tall vegetation. Moors, alder swamp.
4) An inhabitant of damp and often shady places.
10) Marshy places, at roots of grass. Locally common.

0010/027-/017-

Pterostichus niger (Schaller, 1783) 3

2) Favours fairly damp deciduous forest.
3) E. Hygrophile, silvicole. H damp woods, woodland edge, loam pits, copses, loamy gardens, shaded banks, brick pits. Littoral-strandlines.
4) A widespread species occurring in woodland and grassland but less frequently on arable land.
8) listed in group 'WOODLAND SPECIES; occurring predominantly in woodland'.
9) 'Mesophilous, Eurytopic'.
10) 'Under stones and loose bark etc. common and widely distributed.'
13) Trapped in small numbers in Dutch woods.

0010/027-/019-

Pterostichus oblongopunctatus (Fabricius, 1787) 2

1) A eurytopic woodland species-usually in light stands on moderately dry, sour humus soil. In the Atlantic climate of W. Norway, also in open country.
2) In the whole of C Europe frequent in woods; adults overwinter in moss and in rotten stumps.
3) E. Xerophile, silvicole. H dry to fairly damp decid. and mixed woods, hedges, copses, heaths.
5) Generally in old tree stumps.
8) listed in group 'WOODLAND SPECIES; occurring predominantly in woodland'.
10) 'In woods, under chips,etc'Abundant in Forest of Dean, Bagley Wood (Oxford), Langworth Wood(Lincoln), local in Scotland ('in fir woods').
12) Caught in both dry and damp Oak/Birch forest, N W Germany; eurytopic.
13) Trapped commonly in Dutch forest; most dense populations in deciduous stands.
14) Moorland and older woodland.

0010/027-/020-

Pterostichus strenuus (Panzer, 1796) 4

1) A characteristic species of the litter layer of damp deciduous forest on clayey, mull-rich soil, eg beech foest, drier parts of alder swamps. Also shaded sites in open country.
2) In litter and moss of wet woods.
3) Ubiquitous. Hygrophile, freq. phytodetriticole.

8) listed in group 'WOODLAND SPECIES; occurring predominantly in woodland'.
9) In leaf litter, mosses and on shores, but not in swamps.
10) Damp places, under stones, and at roots of grass. Common and widely distributed.

0010/027-/021-
Pterostichus vernalis (Panzer, 1795) 5

1) A hygrophilous species, preferring eutrophic fens and moist meadows...occasionally found in water-meadow forest.
2) 'Flood meadows and fens'.
3) E. Hygrophile, phytodetriticole. H loamy fields, meadows, waste places, forest edges, damp woodlands, wet peat, brick pits, coastal sand.
4) 'Found in fens, carr and badly drained grassland'.
9) 'Hygrophilous. On shores and wet meadows' Reported from wrack fauna in Baltic.
10) Very abundant in marshy places, on the banks of rivers under stones, at roots of grass, etc.'

0010/028-/001-
Abax parallelopipedus (Piller and Mitterpacher, 1783) 2

1) A eurytopic forest-dwelling species, occurring in different forest communities, in Scandinavia..notably beech; also parks etc.
2) Woodland dweller, particularly in beechwoods of Alps.
3) E. Hygrophile, silvicole. H; prefers woods (mainly Fago-Quercetum and Querco-Carpinetum) woodland edges and clearings, hedges.
4) A woodland species, most frequent in bracken and scrub rather than bare litter.
7) May be found in woodland.
8) listed in group 'WOODLAND SPECIES; occurring predominantly in woodland'.
14) Upland bogs and woodland.

0010/029-/005-
Calathus micropterus (Duftschmid, 1812) 3

1) 'Predominantly a woodland species, living among litter and moss on moderately dry ground in light deciduous or coniferous forest'.
3) E. Weakly xerophile, silvicole. H heath, dunes, pinewoods, moors, damp clearings and woodland edges.
10) Almost entirely confined to hilly or mountainous districts.
12) Caught in dry oak/birchwood in N W Germany, at quite high frequency.

0010/029-/007-
Calathus piceus (Marsham, 1802) 3

1) A forest-dwelling species, occurring in the litter layer of deciduous (rarely coniferous) forest, notably light stands of beech, also parks and gardens.
3) E. Weak hygrophile, silvicole. H heath, pinewoods, dunes, dry woodland edges and deciduous woods, alder swamps.
4) Occurs in the same woodland habitats as *Nebria brevicollis* (woodland litter).
7) May be caught in woodland.
8) listed in group 'WOODLAND SPECIES; occurring predominantly in woodland'.
10) 'Sandy places beneath moss and leaves'.

0010/033-/001-
Synuchus nivalis (Panzer, 1797) 5

1) 'Predominantly on rather dry ground in open country...with sparse vegetation of grasses, *Calluna*, etc. Often on cultivated land; also in forest edges and in light woods.'
2) Favours open, moderately shaded ground.
3) E. Xerophile. H heath, dune, sandpits, brick pits, dry woodland edges and clearings, sandy gardens, fields.
4) Occurs in edge of woodland, in bracken and scrub, and in grassland.
10) 'Damp places, under stones etc.'

0010/035-/002-
Agonum assimile (Paykull, 1790) 2

1) A stenotopic species of deciduous forests on mull-rich soil..in cool and wet, shaded habitats among litter, under bark of tree stumps, etc. often near water...particularly characteristic of stands of *Alnus* and *Fraxinus*. Also in damp and shaded sites in parks and gardens. Hibernating adults usually aggregate in fallen trees and stumps.
2) In moss and tree stumps and under loose bark.
3) E. Hygrophile, silvicole. H damp decid. woods, swamp forests, damp hedges and copses, floodmeadows, swampy and muddy

banks, wet fields.
7) In woodlands.
8) listed in group 'WOODLAND SPECIES; occurring predominantly in woodland'.
10) 'At roots of trees, under loose bark etc.'
11) 'Often/fairly regularly found under loose bark, dead wood on ground, etc.'

0010/035-/005-
Agonum fulignosum (Panzer, 1809) 5

1) A hygrophilous species, living on different kinds of moist, often shaded ground, notably marshy woodland, eg. alder swamps. Also fens/border zones of eutrophic lakes and rivers.
2) Eurytopic, wet woodlands.
3) E. Hygrophile, paludicole. H eu- and mesotrophic moors- absent from most oligotrophic bogs. Swamp, marsh woodland, banks, wet vegetation-rich pasture.
10) 'Damp and marshy places.'

0010/035-/008-
Agonum livens (Gyllenhal, 1810) 3

1) In marshy deciduous forests, notably in stands of alder and birch, living among litter and moss.
2) In marshy (particularly beech-) forest.
3) E. Hygrophile. Swampy woods and alder carr, marshy meadows, damp pasture-woodland, muddy shores.
10) Damp and marshy places, inland and on the coast; rare.

0010/035-/010-
Agonum micans Nicolai, 1822 5

1) On eutrophic lake shores and river banks, occurring on muddy clay-soil in sparse but often tall *Scirpus/Carex* etc. Often in rather shaded sites under *Salix* bushes or in sparse growth of *Alnus* or *Fraxinus*.
2) Stenotope. Shores/banks
3) E. Hygrophile. Swamps, banks and alder swamp, damp meadows.
10) Marshy places, near banks of rivers and ponds; also under bark of fallen trees; by sweeping rushes,etc.

0010/035-/011-
Agonum moestum (Duftschmid, 1812) 4

1) More or less shaded sites on clayey/muddy shores of eutrophic lakes and ponds, eg. among *Phragmites*. Also in marshy deciduous forest, notably alder swamps with rich vegetation of *Carex*, *Lysimachia*, etc.
3) E. Hygrophile, paludicole. H swampy and muddy banks, damp woods.
9) Often together with *A. viduum* in swampy places.

0010/035-/012-
Agonum muelleri (Herbst, 1784) 4

1) 'Common inhabitant of agricultural land... also in gardens and clear-felled areas in forests...strongly heliophilous.'
2) Wet places
3) E. Hygrophile (North-Xerophile), heliophile. Freq. phytodetriticole. H often tilled soils, banks, loamy floodmeadows and fields, brickpits, damp woodland edges, alder swamp.
13) Wide habitat range, occurring in damp places but also arable fields with dry, sandy soil. Overwintering adults common under bark/other refuges in woodland.
10) 'Damp and marshy places; common and widely distributed'.

0010/035-/014-
Agonum obscurum (Herbst, 1784) 3

1) Predominantly in deciduous and mixed forests, among litter and moss. Particularly numerous in stands of alder and ash in forest swamps, among wet leaves around trees and stumps
2) In C Europe, throughout, most common in meadow-and swamp-woodland.
3) E. Hygrophile, silvicole. H damp and swampy woods and woodland edges, floodmeadows, moorland drains, damp heaths, clay pits.

0010/035-/016-
Agonum quadripunctatum (Degeer, 1774) 3

1) Attracted to sites of fire. Occurs in forests (notably coniferous/mixed stands) and near human habitations, but has high powers of dispersal and has repeatedly been found in drift material on the seashore.

3) E. Xerophile, freq.corticole, also synanthropic. H burnt areas of woods, riverbanks, moor, heath.
5) Among burnt pine needles
11) Although primarily a ground dweller, this species is regularly found under the bark of burnt trees and stumps, where it appears to develop; eg, under pine bark. Found frequently early August in birch, alder and oak near assarts and areas of total deforestation.

001O/035-/021-
Agonum versutum Sturm, 1824 4

1) Very hygrophilous. Prefers open country, but also found in moderately shaded sites, eg open forest.
2) On level ground and open banks.
3) E. Hygrophile. H unshaded marshy banks, moors, damp woods and meadows, shady swampy places in woods.

001O/035-/022-
Agonum viduum (Panzer, 1797) 5

1) A eurytopic shore dweller, living at the margins of fresh and brackish waters, usually among rich vegetation. Prefers open sunny ground but also occurs in somewhat shaded sites, eg open woodland.
2) Eurytopic near water.
3) E. Hygrophile, paludicole. H marsh, moor, swampy and muddy banks, wet pasture.
9) 'Hygrophilous. Eurytopic beach species'.
12) Caught in dry and damp oak/birchwood, N W Germany; Eurytopic.

001Q/037-/003-
Amara anthioba Villa, 1833 5

1) Both in open country, usually on sandy, sparsely vegetated, often cultivated soil, and in woodland.
3) E. Thermophile, freq. synanthrope. H heath, dunes, sandbanks, sandpits, sandy gardens, warm slopes, vineyards.

001Q/037-/013-
Amara equestris Duftschmid, 1812 5

1) 'Preferably on open or faintly shaded ground, on dry sandy soil with scattered, usually grassy vegetation; for instance in gravel pits, along forest edges, in grassland and fields..recently abandoned cultivated land'
3) E. Xerophile. H warm, dry places. Heath/steppe, heath, sandy coasts and riverbanks, dry fields and waste places, dry light woods and clearings.
10) Local and rare. Chalky and sandy places, under stones and at roots of grass.

001Q/037-/021-
Amara lunicollis Schiödte, 1837 5

1) Rather eurytopic..*Calluna* heaths, not too dry grassland, meadows and arable.. in open woodland, etc.
3) E. Xerophile. H heath, moor, dunes, sandy riverbanks, waste places, dry fields and woodland edges, dry light woods and pinewoods, dry gardens, loess slopes.
4) Typical of grass heaths, absent from woodland habitats and infrequent on arable land.
10) Marshy places, at roots of grass, trees, etc.

001Q/037-/026-
Amara praetermissa (Sahlberg, C R., 1827) 5

1) Mainly in dry, open country...sometimes chalky or clayey soil with scattered vegetation...also among litter in deciduous forests.
2) In high mountains, frequent; in the lowlands, much rarer. Seems to be spreading in Boreo-montane habitat.
3) E. Xerophile. H warm slopes, chalk grassland, quarries and sandpits, sandy stream- and river-banks, dry fields and woods, sandy coasts.
10) Chalky places, at roots of grass etc.

001S/039-/001-
Harpalus rufipes (Degeer, 1774) 5

1) Eurytopic...on almost every kind of open ground...especially typical of cultivated fields, meadows and gardens...less frequent in open woodland.
2) Eurytopic, esp. cultivated land. Favours loamy soil. (Can become a pest of strawberry crops).
3) E. Xerophile, campicole. Favours cultivated soils, loamy fields, waste places and gardens, brick pits, pine forest, sandy banks,dry woodland edges, banks, also rubbish dumps.

4) 'essentially an arable land species'.

001S/039-/012-

Harpalus rufibarbis (Fabricius, 1792) **5**

1) Rather eurytopic, preferring open meadows, parks, gardens and arable fields, also in open woodland.
2) 'In light deciduous woodland and arable, also sand- and gravel-pits'.
3) E. Xerophile, phytodetriticole. H dry fields, sandy banks, sand and gravel pits, light decid. woodland.

001S/039-/023-

Harpalus latus (Linnaeus, 1758) **5**

1) Very eurytopic-both in open country...and light deciduous forest.
2) In Central Europe, frequent in light forest.
3) E. H light woods, woodland edges, copses, floodmeadows, heath, pinewoods, moors, sandpits, sandy-loamy fields, streambanks, dunes and dry banks.
9) Mesophilous, Eurytopic.

001S/039-/026-

Harpalus quadripunctatus (Dejean, 1829) **4**

1) The most prominent forest-dwelling *Harpalus*. It lives mainly in fairly shady deciduous or mixed forests, on moderately humid, notably gravelly/stoney ground with *Rubus* etc. Also in open country under bushes, in forest edges and in tall meadow vegetation.
2) Prefers mountain woodland; scarce in lowlands.
3) E. Silvicole. H light dry woods, wood edges, hedges, pine heaths, pinewood clearings and warm slopes, meadows.
10) A very local Northern species, chiefly confined to Highlands of Scotland.

001S/039-/032-

Harpalus tardus (Panzer, 1797) **5**

1) Rather xerophilous...dunes, grassland, sandy heaths...less abundant in moderately shaded habitats like forest edges, open pine forest, etc.
2) In C. Europe, eurytopic in open country. Not high mountains.
3) E. Xerophile, phytodetriticole. H heath, dunes, light pineheath, dry river meadows, sand- and gravel-pits, dry woodland edges and gardens, vineyards.
10) Sandy places under stones, etc. Common on coast and inland.

001S/042-/001-

Diachromus germanus (Linnaeus, 1758) ***5**

1) On moderately dry meadow ground, often in somewhat shaded sites...In C. Europe frequently found in cereal fields.
3) E. H pasture woodland, clearings. In West, warm banks, gravel pits, dunes.
10) Very rare..In marshy places.

001S/044-/002-

Trichocellus placidus (Gyllenhal, 1827) **3**

1) Rather eurytopic, occurring in moderately shaded and moist sites, dwelling among moss and litter under deciduous trees and bushes in thin forest, forest edges, thickets or fens. It avoids very wet and dark forest swamps.
2) On damp humus soils in meadows and deciduous woods
3) E. Hygrophile, paludicole. H swampy banks, meadows and moors, damp decid. woodland.
5) Marshy places
8) Listed in ecological group 'WOODLAND SPECIES; occurring predominantly in woodland'.

001S/045-/004-

Bradycellus harpalinus (Serville, 1821) **3**

2) Common in C. Europe; pretty eurytopic, but prefers litter of heath and moorland soils.
3) E. Xerophile. H heath, moor, dunes, sand and loam pits, dry fields, woodland edges and gardens, pasture-woodland.
8) Listed in ecological group 'WOODLAND SPECIES; occurring predominantly in woodland'.

001S/045-/006-
Bradycellus sharpi (Joy, 1912) 3

2) In damp moss in woodland edge
3) S. Hygrophile, silvicole. H in damp decid. woods, damp woodland edges.
8) Listed in ecological group 'WOODLAND SPECIES; occurring predominantly in woodland'.
10) Damp places in moss and roots of grass, also under leaves and refuse near ponds.

001S/045-/007-
Bradycellus verbasci (Duftschmid, 1812) 4

1) In open or moderately shaded ground, usually on sandy or gravelly soil. Is especially typical of woodland glades, forest edges and clear-felled areas.
3) E. Hygrophile. H damp sandy woodland edges, clearings, gardens, wet banks, brick works,swampy fields.

001S/046-/001-
Stenolophus mixtus (Herbst, 1784) 5

1) In wet habitats, eg in swamps and at the margin of standing waters. The species prefers muddy soil with rich vegetation of sedges, etc. occurring in both woods and wet meadows.
2) Most frequent in meadows and marshland.
3) E. Hygrophile, paludicole, halotolerant, phytodetriticole. H swamp, damp floodmeadows, loam pits, saline places.
10) Local; In marshy places.

001S/046-/002-
Stenolophus skrimshiranus (Stephens, 1828) 5

1) Very hygrophilous, preferring wet, clayey and mull-rich soil on more or less shaded ground near the coast. Usually occurs on the shores of pools and ponds, eg. in alder swamps, and somewhat shaded sites in open country.
2) In C. Europe most rare, sporadic by swampy pools.
3) S. Hygrophile, paludicole, phytodetriticole. H swampy banks and fields, muddy coasts.
10) Local; marshy places, in moss and flood refuse and at roots of grass.

001S/047-/002-
Acupalpus consputus (Duftschmid, 1812) 5

1) At the margin of small stagnant waters, often such which dry up in summer, usually living on mull-rich clay soil in moderately shaded sites, eg in light deciduous forest and bushy meadows.
2) Stenotope, bank/beach dweller; by water under damp leaflitter.
3) E. Hygrophile, halotolerant, paludicole. H swampy banks, swamp woodland, damp floodmeadows, saline places.
10) Marshy places, in moss, etc.

001S/047-/004-
Acupalpus dubius (Schilsky, 1888) 4

1) In moist, more or less shaded sites...usually...at the margin of ponds and pools, in open country and in forest, dwelling among moss and dead leaves.
2) 'Prefers marshy places'.
3) E. Hygrophile, paludicole, phytodetriticole. H swamps,wet banks, moors, moory heath, alder carr, loam pits.

001S/047-/007-
Acupalpus flavicollis (Sturm, 1825) 5

1) Preferred habitat riverbanks in open country, especially on fine moist sand with a thin layer of silt, and sparse vegetation...also found at the margin of lakes and ponds...in open country and in forest.
2) By water, and in bogs.
3) E. Hygrophile, paludicole. H swamp, swampy banks and woods, moors, marshy heath, loam pits.
10) Local and rare; marshy places, amongst debris of reeds, etc.

001T/049-/001-
Badister anomalus (Perris, 1866) 4

1) Habitats as *B.peltatus* (see below), the two often found together.
3) S. Hygrophile, ripicole. H swampy river and sea beaches.

001T/049-/002-
Badister bipustulatus (Fabricius, 1792) **5**

1) The most eurytopic *Badister*, occurring in dry and moist habitats...particularly prominent in open deciduous forest and forest edges, also open, sandy grassland.
2) Generally common in C.Europe, preferring swampy places. In N.,in drier, light woodland.
3) S. Heliophile, xerophile. H warm slopes, chalk grassland, dry banks, dunes, quarries, dry woodland edges.
9) Mesophilous. prefers leaf litter.
10) Damp and marshy places at the roots of willows etc. also in moss, under stones, etc.

001T/049-/003-
Badister dilatatus Chaudoir, 1837 **5**

1) Wet muddy or clayey soil at the margin of eutrophic lakes and ponds, among...tall vegetation, or in the shade of bushes and scattered trees in forest meadows.
3) S. Hygrophile, paludicole. H swampy banks by standing or slow-flowing water.

001T/049-/005-
Badister peltatus (Panzer, 1797) **4**

1) Similar habitat to *dilatatus*(see above)(often found together). *B.peltatus* is more often encountered at the margin of small temporary pools in shaded sites in deciduous forest.
3) S. Hygrophile, paludicole. H swamp, swamp woodland, marshy shaded banks.
10) Very local and rare; in marshy places.

001T/049-/006-
Badister sodalis (Duftschmid, 1812) **4**

1) Predominantly in deciduous woodland, occurring on moist, mull-rich, clayey soil in somewhat shaded sites...especially abundant in forest swamps and at the margin of temporary pools living among moss and leaves...also in forest habitats remote from water.
2) Under vegetation in swampy places.
3) E. Hygrophile. H swamp, swampy banks, wet heath, damp woodland, brickworks.
10) Not uncommon in marshy places; also, drier places (chalky districts etc.) under moss and dead leaves.

001T/049-/007-
Badister unipustulatus Bonelli, 1813 **3**

1) Stenotopic-moist and warm mull-rich clay soils in rather shaded sites, usually near stagnant water. Especially typical of forest swamps under deciduous trees and bushes, eg. alder and birch. Beetles occur among moss and leaves; in winter, under tree bark.
2) By shady woodland pools.
3) S. Hygrophile. H shaded swampy banks, riverbanks, marsh woodland, by shady woodland pools, boggy soils.
10) Marshy places, at roots of grass etc.

001Z/056-/001-
Lebia chlorocephala (Hoffmann, 1803) **4**

1) In meadows and grassland on moderately humid, usually clayey soil, in open country and woodland glades.
2) Predominantly in old forests and damp meadows with loamy soil.
3) E. Xerophile, herbicole. H heath, dry slopes, sandpits, quarries, dry woodland edges and meadows.
10) Under stones, and in moss; also found on broom and beneath junipers.

001Z/056-/002-
Lebia cruxminor (Linneus, 1758) **3**

1) In meadows with rich vegetation on more or less dry gravelly soil both in open country and forest edges and glades.
2) Adults and larvae feed on phytophagous caterpillars.
3) E. Xerophile, herbicole, arboricole. H warm, dry slopes, dry woodland edges and clearings, sandpits.
9) Mesophilous. In vegetation.
10) Very rare; damp places in woods, etc. Found in moss, beaten from broom, under faggots and stones.

001Z/058-/001-
Dromius agilis (Fabricius, 1787) **2**

1) 'An arboreal species, living on both coniferous and deciduous trees. In the mountains, reaching the birch region. From Spring to Autumn, beetle occurs on stems and branches, in winter under bark, usually at the base of trunks'.
2) Under bark of large trees.
3) E. Silvicole, corticole. H woods, heaths, floodmeadow.
5) 'Chiefly behind oak bark'.
10) 'Under bark of beech, apple, etc. and among the damp herbage of river banks'.
11) The most arboreal *Dromius* on both deciduous and coniferous trees.

001Z/058-/002-
Dromius angustus Brullé, 1834 **2**

1) Arboreal; In Scandinavia, almost confined to pine woods on sandy soil, in C. Europe also on spruce and broadleaves.
2) By preference on pine.
3) E. Silvicole, corticole. H pinewood, heath, dry spruce woods, mixed woodland.

001Z/058-/006-
Dromius meridionalis Dejean, 1825 **2**

1) Arboreal, mostly on dead branches of deciduous trees, formerly on wattles in Lolland and Folster (Denmark).
3) S. Silvicole, corticole. H woodland edges.
5) 'Under bark'.
10) 'Under bark of beech, apple etc. commoner than *D.agilis*'.

001Z/058-/008-
Dromius quadrimaculatus (Linnaeus, 1758) **1**

1) Arboreal, predominantly occurring on deciduous trees, for instance oak and beech, in southernmost Scandinavia also frequently on pine and spruce. An inhabitant of stems and branches, hunting at night for small arthropods.
2) In Central Europe, common under bark and moss on trees, particularly pines and spruce.
3) E. Silvicole, corticole. H woods, woodland edges, floodmeadows, heath.
10) Common and widely distributed under the bark of various trees.
11) Often a predominant species in deciduous old forest.

001Z/058-/009-
Dromius quadrinotatus (Zenker in Panzer, 1800) **2**

2) 'Under bark of trees, especially pine and spruce but also deciduous trees'.
3) E. Silvicole, corticole. H woods, woodland edges, floodmeadows, gardens, heath.
5) 'Under bark'.
10) Under bark, generally distributed and common.
11) 'A species of conifers, exceptionally in deciduous trees, eg. black alder'.

001Z/058-/010-
Dromius quadrisignatus Dejean, 1825 **2**

1) Arboreal, living on different kinds of deciduous trees; also on dead branches and twigs on the ground. On Folster (Denmark), found on wattles.
3) S. Corticole. H floodmeadows.
10) 'Not common, under bark of oak, apple, etc'.

CURCULIONOIDEA

(Nomenclature follows Morris, 1990) fp.=foodplant.

890-.001-.001-
Cimberis attelaboides Fabricius, 1787 **1**

17) Woodland species-*Pinus spp.* (eg, Caledonian forest relicts).
2) On *Pinus*, damaging to the top shoots.
10) On Scotch fir, N.England and Scotland; Found on male flowers of pine, on which female lays eggs.
23) fp. *Pinus sylvestris.*

891-.001-.001-
Platyrhinus resinosus (Scopoli, 1763) **2**

17) Woodland species-on the fungus *Daldinia concentrica*, usually on ash.
2) On fungi of beech (rarely alder), in summer months.
10) In fungi (*Sphaeria*) on trees, especially old beech and ash, also birch and alder.
23) fp. fungus *Daldinia concentrica* on *Fraxinus excelsior.*

891-.002-.001-
Tropideres sepicola (Fabricius, 1792) **3**

17) Woodland/hedge species-dead wood
2) On dead branches of various species-oak, beech, aspen.
10) In woods, in dead branches of oak and hornbeam.
23) fp. *Quercus* spp.

891-.002-.002-
Tropideres niveirostris (Fabricius, 1798) **3**

17) Woodland/hedge species-dead wood
2) Dead branches cut from deciduous trees, brushwood, etc.
10) In dead branches of oak, hazel, beech and lime; by beating dead hedges and faggot stacks in woods.
23) fp. *Quercus* spp.

891-.003-.001-
Platystomos albinus (Linnaeus, 1758) **3**

17) Woodland/hedge species-dead wood
2) On dead wood, particularly rotting fungus-infested beech and alder stumps.
10) In decaying trees, especially oaks, willows and birches.
23) fp. decaying *Quercus* spp., *Betula* spp., *Salix* spp.

891-.004-.001-
Anthribus fasciatus (Forster, 1771) **3**

17) Woodland/hedge species. Associated with scale insects.
7) In decaying whitethorn and elm. Larvae parasitic on scale insects.
23) Feeds as larva in coccids on *Crataegus* spp.

891-.004-.002-
Anthribus nebulosus (Forster, 1771) **3**

17) Woodland/hedge species. Associated with scale insects.
2) Polyphagous on deciduous and coniferous trees.
10) In decaying whitethorn, also firs and hazels.

891-.006-.001-
Choragus sheppardi Kirby,W., 1819 **3**

17) Woodland/hedge species-in old ivy, hawthorn etc.
2) Young larvae in fungi, development completed in fallen wood-Ivy, whitethorn, sallow etc.
10) In dead twigs and hedges, etc.

892-.001-.001-
Attelabus nitens (Scopoli, 1763) 1

17) Woodland species-*Quercus* (leaf-roller)
2) Particularly *Quercus*, also *Castanaea*, *Alnus* and *Corylus* spp.
11) On *Quercus*, *Castanaea*.
10) On young oaks, etc.
21) On oaks (in Outwoods, Leicestershire, 1981-3).
23) fp. *Quercus* spp.

892-.002-.001-
Apoderus coryli (Linnaeus, 1758) 1

17) Woodland species-*Corylus* (leaf-roller)
2) On *Corylus*, more rarely other deciduous species.
20) Leafroller in diverse species; *Corylus*, *Alnus*, *Fagus*, *Quercus*, *Salix*, and, more rarely, *Betula pendula*.
11) On *Fagus*, *Corylus*, *Quercus* spp., etc.
10) On young hazels.
23) fp. *Corylus avellana*.

892-.003-.001-
Rhynchites caeruleus (Degeer, 1775) 3

17) On *Crataegus*.
2) On woody Rosaceae, orchard pest.
20) Orchard pest.
10) On various Pomaceae; sometimes does considerable damage to pear trees; also on whitethorn flowers.
23) fp. *Crataegus* spp., *Pyrus* spp.

892-.003-.004-
Rhynchites cupreus (Linnaeus, 1758) 3

17) on *Sorbus aucuparia*
2) On woody Rosaceae, particularly *Sorbus*, *Prunus* spp. Occasionally a pest of fruit crops.
20) On diverse Rosaceous trees; *Prunus* spp., *Sorbus aucuparia*, *Malus* and *Crataegus* spp.
10) On the flowers of mountain ash, also whitethorn, apple, sloe, etc.
23) fp. *Sorbus aucuparia*.

892-.003-.005-
Rhynchites cavifrons Gyllenhal, 1833 1

17) Woodland species-on *Quercus*.
2) Larvae develop in small branches of *Quercus*, pupates in soil.
20) Common in Northern forests(of France).
10) On young hazel, birch, oak etc. in woods.
23) fp. *Quercus* spp.

892-.003-.006-
Rhynchites olivaceus Gyllenhal, 1833 1

17) Woodland species-on *Quercus*
4) Adult on various Rosaceous trees(*Prunus*, *Crataegus*)-numerous at flowering period.
10) On young birch, hazel, etc. in woods.
23) fp. *Quercus* spp.

892-.003-.007-
Rhynchites sericeus Herbst, 1797 *1

17) Woodland species-on *Quercus*

892-.003-.008-
Rhynchites aeneovirens (Marsham, 1802) 1

17) Woodland species-on *Quercus*
7) On young oaks, hazel, etc. in woods and hedges.

23) fp. *Quercus* spp.

892-.003-.009-
Rhynchites aequatus (Linnaeus, 1767) **3**

17) 'Semi-Woodland' species-on *Crataegus* and *Malus* spp.
2) On Rosaceous trees and shrubs, frequently *Crataegus*. Can become a pest on fruit trees.
20) Live on numerous Rosaceous spp. (*Crataegus, Sorbus, Prunus, Malus* spp.) Orchard pest around Paris.
10) On whitethorn flowers.
23) fp. *Crataegus* spp.

892-.003-.010-
Rhynchites germanicus Herbst, 1797 **4**

2) On herb and shrub species. Can be a pest of *Fragaria* and *Salix*.
10) On young trees in woods, especially oaks; often found by sweeping herbage.
23) fp. herbaceous Rosaceae.

892-.003-.011-
Rhynchites interpunctatus Stephens, 1831 **1**

17) Woodland species-on *Quercus*
10) On young trees in woods and hedges.
23) fp. *Quercus* spp.

892-.003-.012-
Rhynchites longiceps Thomson,C. G., 1888 **3**

17) Semi-Woodland species-on *Salix*
2) On *Salix*, rarely *Betula* spp.
20) On *Salix caprea, Betula* sp.
23) fp. *Salix* spp.

892-.003-.013-
Rhynchites nanus (Paykull, 1792) **3**

17) Semi-Woodland species-on *Betula*
2) On *Alnus, Betula, Salix* spp.
20) On *Betula* spp.
10) On young birches in woods.
21) On birch (in Outwoods, Leicestershire, 1981-3).
23) fp. *Betula* spp.

892-.003-.015-
Rhynchites tomentosus Gyllenhal, 1839 **3**

17) Semi-Woodland species-on *Salix* and *Populus* spp.
2) *Salix*, rarely *Populus* spp.
10) On aspens, willow, young oak, hazel, birch, etc.
23) fp. *Salix* spp.

892-.004-.001-
Byctiscus betulae (Linnaeus, 1758) **1**

17) Woodland species-especially on *Corylus*.
2) Adult Mid April-Sept. in mixed deciduous woodland; leaf roller.
20) On *Betula pendula, Corylus, Fagus, Populus tremula* and *P.alba, Salix caprea, Alnus, Carpinus, Acer, Crataegus*, and *Prunus* spp.
10) In woods on young birch and hazel.
23) fp. *Populus* spp., *Salix* spp., *Corylus avellana,Betula* spp.

892-.004-.002-
Byctiscus populi (Linnaeus, 1758) **2**

17) Woodland species-on *Populus*, especially *P.tremula*.

20) On *Populus*, *Betula*, and various *Salix* spp.
11) On *Populus*, *Ulmus*, *Betula* spp.
10) On young aspens.
23) fp. *Populus* spp.

892-.005-.001-
Deporaus betulae (Linnaeus, 1758) 1

17) Woodland species-on *Betula* spp.
2) Prefers *Betula* spp., also other deciduous trees, especially in dry places.
20) On numerous forest trees.
10) On birch, alder, hornbeam, hazel and beech; chiefly, however, on young birches.
22) On birch (mainly), alder, hazel, and oak (in Outwoods, Leicestershire, 1981-3).
23) fp. *Betula* spp.

892-.005-.002-
Deporaus mannerheimi (Hummel, 1823) 1

17) Woodland species-on *Betula* spp.
2) On *Betula*, more rarely *Salix* and *Corylus*.
20) Adult on *Betula*, *Corylus avellana*.
10) On young birches, in woods, etc.
23) fp. *Betula* spp.

893E.001-.001-
Apion pallipes Kirby,W., 1808 1

17) Woodland species. On *Mercurialis perennis*, especially on calcareous soils
2) Larvae mine stems of *M. perennis*
20) Adult hibernates at base of *M. perennis*.
10) On *Mercurialis perennis* and *Allium*, especially in chalky districts.
23) fp. *Mercurialis perennis*.

893Q.001-.006-
Apion minimum Herbst, 1797 3

17) Semi-Woodland species-on *Salix* spp.
4) Larvae live in the galls of certain Hymenoptera, on *Salix* spp.
10) On various species of *Salix*.
23) fp. *Salix* spp.

893Q.001-.012-
Apion simile Kirby,W., 1811 1

17) Woodland species-on *Betula* spp.
2) Larvae develop in the catkins of *Betula pendula*.
10) On birch (*B. pendula*).
22) On birch (in Outwoods, Leicestershire, 1981-3).
23) fp. *Betula* spp.

CURCULIONIDAE

(Nomenclature follows Kloet and Hincks, 1977)

894A.001-.017-
Otiorhynchus singularis (Linnaeus, 1767) **2**

17) Arboreal woodland species
2) In C.Europe, often in mountains to Subalpine; polyphage on shrubs and conifers.
19) Larvae found feeding on grasses and fine roots of both trees and herbs. Adult flightless, seldom strays to sites where a grassy vegetation is absent. Feeds on a wide range of woody plants, often found in association with *Strophosomus melanogrammus*. Pest of forest plantings on grassy sites, esp. *Molinia caerulea*.
6) Recorded on the continent as a pest of young oak. Attacks leading shoots; also feeds on silver fir and spruce.
10) By beating young trees, hedges, etc. Pest of raspberries.
21) On beech, birch, oak, rhododendron, sycamore (in Outwoods, Leicestershire 1981-3).

894A.002-.001-
Caenopsis fissirostris (Walton,J., 1847) **2**

17) Occurs in woodland, especially acid oakwoods
2) Adults under bark, foliage or dead plant remains.
10) Sandy places, in thick wet moss.

894A.002-.002-
Caenopsis waltoni (Boheman, 1843) **2**

17) Occurs in woodland, especially acid oakwoods
2) On and under *Plantago coronopus*, common by coast.
10) Sandy and chalky places, in moss, gravel pits, under stones, etc.

894A.007-.001-
Phyllobius argentatus (Linnaeus, 1758) **2**

17) Arboreal, woodland species
2) Local and rare, in broadleaf and, rarely, coniferous forests.
19) Commoner on broadleaves, but frequently damaging to conifers; larvae on the roots of a wide range of herbaceous and woody plants. Can completely defoliate broadleaves, eg. *Betula* spp.
10) On young birches, oaks, etc. in woods, also in whitethorn hedges.
21) Several tree species (beech, sycamore, oak, birch, hazel, rarely alder), in a variety of microhabitats (Outwoods, Leicestershire).

894A.007-.003-
Phyllobius calcaratus (Fabricius, 1792) **2**

17) Arboreal, woodland species
2) Polyphage on various shrubs, particularly *Alnus* and *Betula* spp.
10) On alders, also on various bushes, in hedges, etc.
21) Mainly on alder and sycamore, damp places.

894A.007-.004-
Phyllobius maculicornis Germar, 1824 **2**

17) Arboreal, woodland species
2) In deciduous woods and scrub.
10) On young oak, hazel, etc. in hedges; by sweeping herbage on the borders of woods.

894A.007-.005-
Phyllobius oblongus (Linnaeus, 1758) **2**

17) Arboreal, woodland species
2) Polyphagous on shrubs and trees, favours Rosaceous trees.
10) On elms and apple trees, etc. also on low shrubs, in hedges etc.

894A.007-.007-
Phyllobius pyri (Linnaeus, 1758) **2**

17) Arboreal, woodland species
2) Larvae probably develop in grass roots-adult on low plants, particularly grasses.
19) Commoner on broadleaves, but frequently damaging to conifers; larvae on the roots of a wide range of herbaceous and woody plants. Can completely defoliate broadleaves, eg. *Betula* spp.
10) On whitethorn, young trees in woods, nettles, etc.
21) Only on birch and oak.

894A.007-.008-
Phyllobius roboretanus Gredler, 1882 **2**

19) Can completely defoliate broadleaves, eg. *Betula* spp. Larvae feed on roots of a wide range of herbaceous and woody plants.

894A.007-.010-
Phyllobius viridicollis (Fabricius, 1792) **3**

19) Can completely defoliate broadleaves, eg. *Betula* spp. Larvae feed on roots of a wide range of herbaceous and woody plants.
10) On flowers of *Hieracium*, *Alchemilla*, *Artemesia maritima*, and by general sweeping.

894B.008-.001-
Polydrusus cervinus (Linnaeus, 1758) **2**

17) Arboreal, woodland species
2) On deciduous trees, particularly *Quercus* and *Betula* spp.
10) On young trees, in woods, hedges, etc. (especially on oak, birch, and fir).
21) Only on birch and oak.

894B.008-.004-
Polydrusus flavipes (Degeer, 1775) **2**

17) Arboreal, woodland species
2) Principally on *Quercus*.
10) On young trees in woods, etc.

894B.008-.006-
Polydrusus marginatus Stephens, 1831 **2**

17) Arboreal, woodland species
2) On conifers, *Quercus*, and Rosaceous species.

894B.008-.007-
Polydrusus mollis (Ström, 1768) **2**

17) Arboreal, woodland species
10) Woods and hedges; on young birches, oaks, hazels, sallows, etc.

894B.008-.008-
Polydrusus pilosus Gredler, 1866 **2**

17) Arboreal, woodland species (mainly on conifers)
2) On various deciduous trees.

894B.008-.010-
Polydrusus pterygomalis Boheman, 1840 **2**

17) Arboreal, woodland species
2) On various deciduous trees.
10) On young oak, hazel, beech, etc. in woods.

894B.008-.012-
Polydrusus sericeus (Schaller, 1783) 2

17) Arboreal, woodland species
2) On various deciduous trees and shrubs.
10) On shrubs and trees (oak, hazel, willow, etc.)

894B.008-.013-
Polydrusus undatus (Fabricius, 1781) 2

17) Arboreal, woodland species
2) On various deciduous trees.
10) On young oaks and other trees and bushes.
21) Clear preference for birch.

894B.009-.001-
Barypeithes araneiformis (Schrank, 1781) 4

10) In moss, in woods, occasionally damages strawberries.

894B.012-.001-
Strophosomus capitatus (Degeer, 1775) 3

17) occurs in woodland
2) Larvae on *Calluna vulgaris.*
6) Recorded on the continent as a pest of oak, beech,pine and douglas fir. Also, attacks birch in Britain.
10) On young hazel, oak, broom, etc. in woods and hedges.
21) On birch and oak (in Outwoods, Leicestershire, 1981-3).

894B.012-.004-
Strophosomus melanogrammus (Forster, 1771) 2

2) Imago on various deciduous and coniferous trees. Sometimes damaging to young conifers. Larvae live on *Rumex obtusifolius* and *Aira flexuosa.*
10) On various trees; oak, hazel, fir,etc.
11) Larvae live in soil, feeding on grass roots. Adults attack aerial parts of spruce, larch and oak.
17) Woodland species-common on various trees
18) Often, but not invariably, occurs on oak saplings.
21) Mainly on birch, beech, oak, Occasionally alder, hazel, pine, sycamore (in Outwoods, Leicestershire, 1981-10) fp. many trees, particularly *Corylus avellana.*

894B.012-.006-
Strophosomus sus Stephens, 1831 5

6) Foodplants *Erica* and *Calluna*; attack needles of young pine in plantations, especially where the heather has been cleared prior to planting.
10) On *Erica* and *Calluna*; very common...in all heathy districts.
23) fp. *Calluna vulgaris, Erica* spp.

894B.017-.001-
Barynotus moerens (Fabricius, 1792) 3

17) Woodland species-associated with *Mercurialis perennis*
10) Under stones, in moss, flood refuse, etc; also by sweeping among bracken.

894B-.018-.001-
Tropiphorus elevatus (Herbst, 1795) 2

17) Woodland species-herb layer
10) In moss, under stones, etc; rarely by sweeping herbage.

894B.018-.003-
Tropiphorus terricola (Newman, 1838) 2

10) On *Mercurialis perennis*, especially in chalky districts.

894C.020-.010-
Sitona lineatus (Linnaeus, 1758) **5**

17) Often found in woods, as it is abundant and a ready flyer
10) On various Papilionaceae, clover, vetches, peas, etc...it is hard to find a place...where this pest does not occur.
21) Taken on birch in Outwoods, Leicestershire (1981-3).
23) fp. *Trifolium* spp., *Vicia* spp., *Lathyrus* spp., *Pisum sativum* and almost all other Leguminosae.

894F.029-.001-
Cionus alauda (Herbst, 1784) **3**

17) Often occurs in woods, on *Scrophularia nodosa*
23) fp. *Scrophularia* spp., *Verbascum* spp.

894F.029-.002-
Cionus hortulanus (Fourcroy, 1785) **3**

17) Often occurs in woods, on *Scrophularia nodosa*
23) fp. *Scrophularia* spp., and occasionally *Verbascum* spp. and *Buddleia* spp.

894F.029-.005-
Cionus scrophulariae (Linnaeus, 1758) **3**

17) Often occurs in woods, on *Scrophularia nodosa*
23) fp. *Scrophularia* spp., and occasionally *Verbascum* spp. and *Buddleia* spp.

894F.029-.006-
Cionus tuberculosus (Scopoli, 1763) **3**

17) Often occurs in woods, on *Scrophularia nodosa*
10) Marshy places, on *Scrophularia nodosa* and *S.aquatica*.
23) fp. *Scrophularia* spp., particularly *S. auriculata*.

894F.030-.001-
Cleopus pulchellus (Herbst, 1795) **3**

17) Often occurs in woods, on *Scrophularia nodosa*
2) Prefers partial shade, on *Scrophularia* spp., possibly also *Verbascum thapsus* and *V. nigrum*.
23) fp. *Scrophularia* spp., *Verbascum* spp.

894G.033-.001-
Hylobius abietis (Linnaeus, 1758) **2**

17) Pinewood pest
2) On various *Pinus* and *Picea* spp.
19) As an adult, feeds on bark of all conifers, also frequently strips bramble. Breeds in conifer stumps.
6) Adults feed on bark of young stems of Scots Pine and other conifers. Larvae feed in fallen wood or stumps at least partially buried in the ground.
10) On pines and firs. Taken on thistles in Southsea, with no pines or firs within two miles.
23) fp. *Pinus* and *Picea* spp.

894G.035-.001-
Leiosoma deflexum (Panzer, 1795) **3**

17) Often in woods; *Ranunculus* feeder
2) Larvae on roots of *Ranunculus repens*, *R.montanus*, *Anemone nemorosa* and *Caltha palustris*.
10) Damp places; in moss and at roots of grass; occasionally by sweeping herbage. Appears to live on various Ranunculaceae.
23) fp. *Ranunculus repens*, *Anemone nemorosa*, *Caltha palustris*.

894G.037-.001-
Achonidium unguiculare (Aubé, 1850) **2**

17) In acid oakwoods, but also in the open. Biology unknown.

894J.040-.001-
Pissodes castaneus (Degeer, 1775) **2**

17) Pine pest
19) Breeds in *Pinus* trash, adult aggressive feeder on young growth.
6) Larvae feed in the sapwood of young *Pinus* stems.
10) On firs and pines.
23) fp. *Pinus* spp.

894J.040-.002-
Pissodes pini (Linnaeus, 1758) **2**

17) Pine pest
19) Breeds in older, thicker barked stems of *Pinus* than *P.castaneus* (above); more Northern species.
6) Larvae feed in the sapwood of pine or spruce trees 15 years or more old.
10) On fir and pine trees.
23) fp. *Pinus* spp.

894J.040-.003-
Pissodes validirostris (Sahlberg,C. R., 1834) **2**

17) Pine pest
2) Larvae in pinecones, beetle April-May in litter at the base of isolated pine trees, May-June in the branches.
19) Feeds in the cones (and leaders) of *Pinus sylvestris.*
23) fp. *Pinus* spp.

894K.041-.001-
Magdalis armigera (Fourcroy, 1785) **4**

17) In dead wood, *Ulmus* spp.
19) In dead branches >15cm. dia. Very common in Dutch elm diseased trees.
11) On elm, often in tunnels with *Scolytus laevis.*
10) By beating dead hedges, dead twigs, etc., on elm.
23) fp. *Ulmus* spp.

894K.041-.002-
Magdalis barbicornis (Latreille, 1804) **4**

17) In dead wood, woody Rosaceae spp.
10) In hedges, etc; attached to certain Rosaceae; larva has been found in the branches of *Malus communis.*
23) fp. *Malus* spp., *Crataegus* spp., *Prunus* spp.

894K.041-.003-
Magdalis carbonaria (Linnaeus, 1758) **3**

17) In dead wood, *Betula* spp.
11) Lives chiefly in *Betula* attacked by *Scolytus ratzenburgi*; but not in stems with the bark beetle, but in the dry wood. Has also been recorded from hazel.
10) On *Betula alba* (*B. pendula*).
23) fp. *Betula* spp.

894K.041-.004-
Magdalis cerasi (Linnaeus, 1758) **4**

17) In dead wood, *Prunus* and perhaps *Quercus* spp.
2) Larvae in woody Rosaceae.
10) In dead hedges, dead blackthorn twigs, etc. Appears to be attached to various species of Rosaceae; larva attacks the branches of the pear, apple, hawthorn, etc.
23) fp. *Crataegus* spp., *Malus* spp., *Pyrus* spp., *Quercus* spp.

894K.041-.005-
Magdalis duplicata Germar, 1818 **2**

17) In dead wood, *Pinus* spp.
2) Larvae in pines, also spruce and larch.

10) On Scotch fir; very local.
23) fp. *Pinus* spp.

894K.041-.006-
Magdalis memnonia (Gyllenhal in Faldermann, 1837) **2**

17) In dead wood, *Pinus* spp.
23) fp. *Pinus* spp.

894K.041-.007-
Magdalis phlegmatica (Herbst, 1797) **2**

17) In dead wood, Pinus spp.
2) Larvae in thin branches of pine, also spruce and larch.
10) On scotch fir; very local, a Northern species.
23) fp. Pinus spp.

894K.041-.008-
Magdalis ruficornis (Linnaeus, 1758) **4**

17) In dead wood, Prunus, Malus, etc.
2) Larvae in branches of Rosaceous trees.
10) In dead hedges, etc.; the species is chiefly attached to species of Prunus.
23) fp. Prunus spp.

894L.042-.001-
Anoplus plantaris (Naezen, 1794) **2**

17) Betula feeder
2) Larvae leafminers, pupate in soil, beetles on birch and alder shrubs.
10) On young birch, alder, etc. in woods.
21) On birch (in Outwoods, Leicestershire, 1981-3).
23) fp. Betula spp.

894L.042-.001-
Anoplus roboris Suffrian, 1840 **2**

10) On alders, also on oaks.
23) fp. Alnus glutinosa.

894N.044-.001-
Euophryum confine (Broun, 1881) **2**

17) All Cossonines feed in dead wood, but this species is particularly associated with woodland.

894N.045-.001-
Pentarthrum huttoni (Broun, 1881) **4**

2) In deciduous wood, also reported from *Pinus maritima.*
10) In damp and decaying wood, especially of casks, etc.
22) Graded 3; 'Species which occur widely in wooded land, both primary and secondary, but which are collectively characteristic of primary areas'.

894N.046-.001-
Mesites tardii (Curtis, 1825) **3**

17) Particularly associated with woodland; *Ilex* and other species.
2) *Ilex*, also reported from copper beech.
10) In old holly trees; also occasionally in beech.
22) Graded 3; 'Species which occur widely in wooded land, both primary and secondary, but which are collectively characteristic of primary areas'.

894N.048-.002-
Cossonus parallelopipedus (Herbst, 1795) **2**

22) Graded 3; 'Species which occur widely in wooded land, both primary and secondary, but which are collectively characteristic of primary areas'.

894N.049-.001-
Eremotes ater (Linnaeus, 1758) **2**

17) Particularly associated with woodland; *Pinus* spp.
11) Almost always in the wood of dead and decaying conifers.
10) In decaying elm, fir, etc.
23) fp. *Pinus* spp.

894N.050-.002-
Rhyncolus lignarius (Marsham, 1802) **2**

17) Particularly associated with woodland
11) Found in aspen, beech, oak and elm.
10) In decaying elms, oaks, ivy, etc.

894N.050-.003-
Rhyncolus truncorum (Germar, 1824) **1**

17) Particularly associated with woodland
2) In dead conifer wood, more rarely deciduous wood. May be a pest in buildings (in beams and floorboards).
11) Rare(Sweden), known from copper beech,beech groves and oak.
10) In decaying maple, etc; rare.
22) Graded 1; 'Species which are known to have occurred in recent times only in areas believed to be primary forest/parkland/woodland'.
23) fp. *Acer* spp.

894N.053-.001-
Dryopthorus corticalis (Paykull, 1792) **1**

17) Very rare 'ancient woodland indicator' species
2) In ancient pine stumps, also damp rotting wood of various deciduous trees.
11) In both coniferous and deciduous wood (pine and oak), alongside ants (*Lasius* spp. in particular).
22) Graded 1; 'Species which are known to have occurred in recent times only in areas believed to be primary forest/parkland/woodland'.

894P.055-.001-
Trachodes hispidus (Linnaeus, 1758) **2**

17) Woodland species;in dead faggots and *Carpinus* bark.
2) Lives in dead wood, particularly deciduous.
11) Larvae develop in dead trunks and branches of various deciduous trees (alder, aspen, mountain ash, lime, beech, oak, and elm).
10) In woods; by beating old faggots of oak and beech sticks; rare.
22) Graded 3; 'Species which occur widely in wooded land, both primary and secondary, but which are collectively characteristic of primary areas'.
23) fp; old twigs of *Fagus sylvatica* and *Quercus* spp.

894Q.056-.001-
Cryptorhynchus lapathi (Linnaeus, 1758) **4**

17) Osier pest
2) In willow and alder, rarely poplar, also birch.
19) Larva bores tunnels in stems; serious pest of Osier beds, and *Populus* spp.
20) On *Salix* and *Betula* spp.
6) Adult damages trees by feeding on bark and foliage, larva mine stems. Attack willow and poplars, also birch and alder.
23) fp. *Salix* spp.

894Q.057-.001-
Acalles ptinoides (Marsham, 1802) **4**

17) Dead wood species
2) Larvae may develop in *Calluna*.
20) On branches of *Calluna vulgaris*.
11) (Norway and Denmark) often in old branches of *Calluna vulgaris*. Also found in deciduous woods.
10) Heathy places, by beating branches of fir, etc. Occasionally found in moss and dead leaves, and in sand-pits.

894Q.057-.002-
Acalles roboris Curtis, 1835 **2**

17) Dead wood species
2) Favours dead branches (oak, beech, chestnut) also small silver fir.
11) Mostly at the trunk of oak and in dry branches, rarely of spruce brushwood and various deciduous trees.
10) By beating dead twigs of oaks, etc.; in hedges and woods.

894Q.057-.003-
Acalles turbatus Boheman, 1844 **2**

17) Dead wood species
2) Fallen leaves and rotten branches of various shrubs and trees.
10) By beating dead hedges, in poplar faggots, etc.

894R.061-.001-
Dorytomus affinis (Paykull, 1800) **3**

17) All *Dorytomus* spp. are associated with *Salix* and *Populus* spp; this species particularly in woodlands.
2) On poplars, especially aspen.
20) Larvae in female catkins of poplars(*P.tremula* and *P.nigra*).
10) On aspens; very rare.
23) fp. *Populus tremula*.

894R.061-.002-
Dorytomus dejeani Faust, 1882 **3**

17) All *Dorytomus* spp. are associated with *Salix* and *Populus* spp; this species particularly in woodlands.
2) On poplars, especially aspen.
10) On young aspens and sallows.
23) fp. *Populus tremula*.

894R.061-.007-
Dorytomus melanopthalmus (Paykull, 1792) **3**

17) All *Dorytomus* spp. are associated with *Salix* and *Populus* spp; this species particularly in woodlands.
2) On *Salix* spp.
10) On sallows (*Salix caprea*, *S. cinerea*, etc.)
23) fp. *Salix* spp.

894R.061-.008-
Dorytomus rufatus (Bedel, 1888) **3**

17) All *Dorytomus* spp. are associated with *Salix* and *Populus* spp; this species particularly in woodlands.
2) On various *Salix* spp.
10) On sallows.
21) On willow (in Outwoods, Leicestershire, 1981-3).
23) fp. *Salix* spp.

894R.061-.009-
Dorytomus salicinus (Gyllenhal, 1827) **3**

17) All *Dorytomus* spp. are associated with *Salix* and *Populus* spp; this species particularly in woodlands.
2) On *Salix cinerea*, *S. amygdalina*, *S. aurita* and *S. caprea*.
20) On *Salix aurita* and *S. caprea*.
10) On willows.

23) fp. *Salix cinerea, S. caprea, S. aurita.*

894R.061-.011-
Dorytomus taeniatus (Fabricius, 1781) 3

17) All *Dorytomus* spp. are associated with *Salix* and *Populus* spp; this species particularly in woodlands.
2) On various *Salix spp.*, also *Populus tremula.*
10) On willows and sallows.
21) On willow (in Outwoods, Leicestershire, 1981-3).
23) fp. *Salix* spp., *Populus* spp.

894R.061-.012-
Dorytomus tortrix (Linnaeus, 1761) 3

17) All *Dorytomus* spp. are associated with *Salix* and *Populus* spp; this species particularly in woodlands.
2) On poplars, especially *P.tremula.*
20) Wet places, on *Populus tremula* and *P.pyramidalis.*
10) On aspens and willows.
23) fp. *Populus tremula.*

894S.071-.001-
Rutidosoma globulus (Herbst, 1795) 3

17) Woodland species-on *Populus tremula*
10) On sallows...according to Bedel, on the shoots of *Populus tremula* and *P.alba.*
23) fp. *Populus tremula.*

894S.072-.001-
Coeliodes dryados (Gmelin in Linnaeus, 1789) 2

17) Woodland species associated with *Quercus* spp.
10) On young oaks, in woods and hedges.
23) fp. *Quercus* spp.

894S.072-.002-
Coeliodes erythroleucos (Gmelin in Linnaeus, 1789) 2

17) Woodland species associated with *Quercus* spp.
10) By beating young oaks, etc in woods and copses.
23) fp. *Quercus* spp.

894S.072-.003-
Coeliodes nigritarsis Hartmann, 1895 2

17) Woodland species associated with *Betula* spp.
23) fp. *Betula* spp.

894S.072-.004-
Coeliodes ruber (Marsham, 1802) 2

17) Woodland species associated with *Quercus* spp.
10) On young oaks in copses and hedges.
23) fp. *Quercus* spp.

894S.072-.005-
Coeliodes rubicundus (Herbst, 1795) 2

17) Woodland species associated with *Betula* spp.
2) Larvae on the female catkins of *Betula pendula*, in Alps, also *B.nana.*
10) By sweeping herbage and beating young trees, especially birch.
21) On birch (mainly), and oak (in Outwoods, Leicestershire, 1981-3).
23) fp. *Betula* spp.

894U.091-.001-
Anthonomus bituberculatus Thomson, C. G., 1868 **3**

17) Woodland species associated with *Crataegus* spp.
2) Prefers *Prunus padus* also *P.domestica* and *Crataegus.*
10) By beating hedges.
23) fp. *Crataegus* spp.

894U.091-.003-
Anthonomus chevrolati Desbrochers, 1868 **3**

1) Woodland species associated with *Crataegus* spp.
10) On whitethorn, service tree etc.
23) fp. *Crataegus* spp.

894U.091-.004-
Anthonomus conspersus Desbrochers, 1868 **3**

17) Woodland species associated with *Sorbus aucuparia*
2) In damp, cool environments on *Sorbus aucuparia.*
10) On mountain ash.
23) fp. *Sorbus aucuparia.*

894U.091-.006-
Anthonomus humeralis (Panzer, 1795) **3**

17) Woodland species associated with *Malus* spp.
2) Prunus spp. particularly *P.padi.* Prefers cool and damp places.
23) fp. *Malus* spp.

894U.091-.007-
Anthonomus pedicularius (Linnaeus, 1758) **3**

17) Woodland species associated with *Crataegus* spp.
10) On the flowers of whitethorn and also on other shrubs and trees, but mostly attached to the former.
23) fp. *Crataegus* spp.

894U.091-.008-
Anthonomus piri Kollar, 1837 **3**

17) Woodland species associated with *Malus* spp.
23) fp. *Malus* spp.

894U.091-.009-
Anthonomus pomorum (Linnaeus, 1758) **3**

17) Woodland species associated with *Malus* spp.
10) On apple trees and also (but less commonly) on pear trees.
23) fp. *Malus* spp.

894U.091-.011-
Anthonomus rufus Gyllenhal, 1836 **3**

17) Woodland species associated with *Prunus* spp.
23) fp. *Prunus spinosa.*

894U.091-.012-
Anthonomus ulmi (Degeer, 1775) **3**

17) Woodland species associated with *Ulmus* spp.
10) On elms, etc.
23) fp. *Ulmus* spp.

894U.091-.013-
Anthonomus varians (Paykull, 1792) 2

17) Woodland species associated with *Pinus* spp.
2) On pine, also rarely on silver fir.
10) On scotch fir.
23) fp. *Pinus sylvestris.*

894U.09-.001-
Brachonyx pineti (Paykull, 1792) 2

17) Woodland species associated with *Pinus* spp.
2) Larva mines in pine needles.
19) Larva feeds in needles in bud, adult on mature needles of *Pinus.*
10) On young scotch fir.
23) fp. *Pinus sylvestris.*

894V.093-.001-
Curculio betulae (Stephens, 1831) 2

17) Woodland species, associated with *Betula* spp.
10) On birch (*Betula pendula*) and sloe.
21) On birch (Outwoods, Leicestershire, 1981-3).
23) fp. *Betula* spp.

894V.093-.002-
Curculio glandium Marsham, 1802 2

17) Woodland species, associated with *Quercus* spp.
2) Larvae develop in acorns.
19) Larvae eat out contents of acorn and cause early fall.
10) Chiefly on species of oak (*Quercus robur, Q. ilex,* etc.), but occasionally hazel.
23) fp. *Quercus* spp.

894V.093-.003-
Curculio nucum Linnaeus, 1758 2

17) Woodland species, associated with *Corylus avellana*
2) Larvae develop in hazelnuts.
19) Larvae eat out contents of acorns, causing early fall. Adults feed on buds and shoots.
10) On hazel, in woods and hedges; local.
23) fp. *Corylus avellana.*

894V.093-.004-
Curculio pyrrhoceras Marsham, 1802 2

17) Woodland species, associated with *Quercus* spp.
2) On oak, larvae develop in the galls of wasp *Diplolepis folii.*
10) On oak, willows, hazels, etc.
21) On birch, oak (Outwoods, Leicestershire, 1981-3).
23) fp. *Quercus* spp.

894V.093-.005-
Curculio rubidus (Gyllenhal, 1836) 2

17) Woodland species, associated with *Betula* spp.
2) On *Salix* and *Betula* bushes.
10) On birch (*Betula pendula*); often by sweeping herbage under birch trees.
23) fp. *Betula* spp.

894V.093-.006-
Curculio salicivorus Paykull, 1792 *2*

17) Woodland species, associated with *Salix* spp.
2) Larvae develop in the galls of the wasp *Pontania* on willow, particularly *Salix viminalis.*
10) On willows; the larva has been observed in galls of *Nematus* on osier, *Salix viminalis.*
23) fp. *Salix* spp.

894V.093.007-
Curculio venosus (Gravenhorst, 1807) 2

17) Woodland species, associated with *Quercus* spp.
2) Larvae develop in oak, overwinters in soil.
10) On oaks- in woods and hedges.
21) On oak (Outwoods, Leicestershire, 1981-3).
23) fp. *Quercus* spp.

894V.093-.008-
Curculio villosus Fabricius, 1781 2

17) Woodland species, associated with *Quercus* spp.
2) Larvae develop in the galls of wasp *Biorhiza terminalis*, on oak.
10) On oaks and hazels, especially the former.
21) On oak (Outwoods, Leicestershire, 1981-3).
23) fp. *Quercus* spp.

894W.097-.001-
Ellescus bipunctatus (Linnaeus, 1758) 4

17) On *Salix* spp.
2) Larvae develop in the catkins of *S.cinerea.*
10) On sallows and poplars.
23) fp. *Salix* spp.

894W.098-.001-
Acalyptus carpini (Fabricius, 1792) 4

17) On *Salix* spp.
2) On willows, larva develops in catkins.
10) On species of *Salix*, usually found on the catkins in Spring.
23) fp. *Salix* spp.

894Y.102-.001-
Rhynchaenus alni (Linnaeus, 1758) 3

17) Arboreal, on *Ulmus* spp.
19) Pest of *Betula* and *Alnus* spp.; larvae mine leaves.
20) Larvae mine *Alnus glutinosa* leaves.
10) On elms, etc.; often by beating dead hedges and under loose bark.
23) fp. *Ulmus* spp.

894Y.102-.002-
Rhynchaenus avellanae (Donovan, 1797) 2

17) Arboreal, on *Corylus avellana* and *Quercus* spp.
2) On oak.
10) On hazels and oaks, etc.
23) fp. *Corylus avellana.*

894Y.102-.003-
Rhynchaenus decoratus (Germar, 1821) 4

17) Arboreal, on *Salix purpurea*
2) On willows, rarely poplars.
20) On *Salix triandus, fragilis*, and *purpurea.*

10) On the leaves of willows; the larva has been found on *Salix fragilis.*
23) fp. *Salix purpurea.*

894Y.102-.004-
Rhynchaenus fagi (Linnaeus, 1758) **2**

17) Arboreal, on *Fagus sylvatica*
19) Adult feeding causes 'shot holes' on *Fagus* leaves, larvae mine leaves.
10) On beech.
23) fp. *Fagus sylvatica.*

894Y.102-.005-
Rhynchaenus foliorum (Müller, O. F., 1764) **3**

17) Arboreal, on *Salix* spp.
2) On Salix spp., particularly *S.cinerea* and *S.caprea.*
10) On various willows and sallows (*Salix cinerea, S. alba, S. caprea,* etc.)
23) fp. *Salix* spp.

894Y.102-.006-
Rhynchaenus iota (Fabricius, 1787) **5**

17) On *Myrica gale*
2) On *Myrica gale,* also *Populus, Alnus, Betula* and *Salix* spp.
10) On *Myrica gale,* in boggy places; has also been observed on the leaves of birch.
23) fp. *Myrica gale.*

894Y.102-.008-
Rhynchaenus pilosus (Fabricius, 1781) **2**

17) Arboreal, on *Quercus* spp.
20) Larvae mine leaves of *Quercus* spp. Adult hibernates in mosses, etc.
10) On oak, birch, holly, etc.
23) fp. *Quercus* spp.

894Y.102-.010-
Rhynchaenus quercus (Linnaeus, 1758) **2**

17) Arboreal, on *Quercus* spp.
10) On oaks.
23) fp. *Quercus* spp.

894Y.102-.011-
Rhynchaenus rusci (Herbst, 1795) **2**

17) Arboreal, on *Betula* spp.
20) Larvae on *Betula* and *Populus nigra.*
10) On hazel, birch, oak, etc. in woods.
23) fp. *Betula* spp.

894Y.102-.012-
Rhynchaenus salicis (Linnaeus, 1758) **3**

17) Arboreal, on *Salix* spp.
2) *Salix* spp., particularly *S.cinerea.* Rarely *Populus* spp.
20) Larvae on *Salix fragilis* and *S. cinerea.*
10) On willows and sallows; the larva has been observed on *S. fragilis.*
23) fp. *Salix* spp.

894Y.102-.013-
Rhynchaenus stigma (Germar, 1821) **2**

17) Arboreal, on *Salix*, *Betula*, *Corylus*
20) Larvae on *Salix* spp., *Populus*, *Betula*, *Alnus*.
10) On sallows, willows, alders etc.
23) fp. *Salix* spp., *Alnus glutinosa* and at times other catkin-bearing trees.

894Y.102-.014-
Rhynchaenus testaceus (Müller, O. F., 1776) **2**

17) Arboreal, on *Alnus glutinosa*
10) On alder and wild cherry.
23) fp. *Alnus glutinosa*.

894Y.103-.001-
Ramphus oxyacanthae (Marsham, 1802) **2**

17) Arboreal, on woody Rosaceae
23) fp. *Crataegus* spp.

894Y.103-.002-
Ramphus pulicarius (Herbst, 1795) **2**

2) *Betula*, *Salix*, *Populus* and *Myrica* spp.
10) On willows, cherry, birch, apple, etc.
17) Arboreal, on *Salix* or *Betula* spp.
20) Larva lives and pupates in *Betula* and *Salix* leaves.
23) fp. *Salix* spp.

References

1) **Lindroth, C. H.** (1986). The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* **15**, Parts 1 & 2. E. J. Brill/Scandinavian Science Press. Leiden.

2) **Freude, H., Harde, K. W., and Lohse, G. A.** (1976, 81, 83). *Die Käfer Mitteleuropas.* Vols. **2**, **10** and **11**. Goecke and Evers, Krefeld.

3) **Koch, K.** (1989). *Die Käfer Mitteleuropas*, Ökologie **1**. Goecke and Evers, Krefeld.

4) **Greenslade, P. J. M.** (1965). On the ecology of some British carabid beetles with special reference to life histories. *Transactions of the society for British Entomology* **16**, 149-179.

5) **Joy, N. H.** (1932, reprinted 1976). *A practical Handbook of British Beetles.* E. W. Classey, Faringdon.

6) **Chrystal, R. N.** (1948). *Insects of the British Woodlands.* Warne, London.

7) **Cooter, J.** (3rd. edn. 1991). *A Coleopterist's Handbook.* Amateur Entomologists' Society, Feltham.

8) **Forsythe, T. G.** (1987). Common Ground Beetles. *Naturalist's Handbooks* **8**. Richmond Publishing, Slough.

9) **Backlund, H. O.** (1945). Wrack fauna of Sweden and Finland, Ecology and chorology. *Opuscula Entomologica* **5**. Lund.

10) **Fowler, W. W.**(1887). The Coleoptera of the British Islands **1**: Adephaga-Hydrophilidae, and **5**: Heteromera-Rhychophora-Abnormal Coleoptera. L. Reeve & Co., London.

11) **Palm, T.** (1959). Die Holz-und Rinden-käfer der süd und Mittelschweidischen laubbäume. *Opuscula Entomologica Supplementum* **15**. Entomologiska Sällskapet, Lund.

12) **Rabeler, W.** (1969). Zur Kenntnis der Nordwestdeutschen Eichen-Birchenwald fauna. *Schriftenreihe vegkunde* **4**, 131-154.

13) **Drift, J. van der.** (1951). Analysis of the community in a beech forest floor. *Tijdschrift voor entomologie* **94**, 2-168.

14) **Day, K. R.** (1987). The species and community characteristics of ground beetles(Coleoptera, Carabidae) in some Northern Ireland nature reserves. *Proceedings of the Royal Irish Academy* **B 87**,65-82.

15) **Greenslade, P. J. M.** (1968). Habitat and altitude distribution of

Carabidae(Coleoptera) in Argyll, Scotland. *Transactions of the Royal Entomological Society of London* **120**, 39-54.

16) **Harding, P. T., and Rose, F.** (1986). Pasture-woodlands in lowland Britain: a review of their importance for wildlife conservation. Institute of Terrestrial Ecology, Abbots Ripton.

17) **Morris, M. G.** pers.comm.

18) **Girling, M. A.** (1982). Fossil insect faunas from forest sites. pp 129-146 in Bell, M. and Limbrey, S. (eds.) 'Archaeological aspects of woodland ecology'. *British Archaeological Reports International Series* **146**.

19) **Bevan, D.** (1987). Forest Insects; a guide to insect feeding on trees in Britain. *Forestry Commission Handbook* **1**. HMSO, London.

20) **Hoffman, A.** (1958). Coléoptères Curculionides **3**. *Faune de France* **62**. Librairie de la Faculte des Sciences, Paris.

21) **Phillips, W. M.** (1992). Assemblages of weevils (Curculionoidea) in the lower tree canopy of a mixed temperate woodland. *The Entomologist* **111**, 61-78.

22) **Harding, P. T.** (1978). *A bibliography of the occurrence of certain woodland Coleoptera in Britain, with special reference to timber-utilising species associated with old trees in pasture.* (CST Report no. 161). Nature Conservancy Council, Banbury.

23) **Philp, E. G.** (1991). Vascular plants and the beetles associated with them. pp.183-198 in **J Cooter** *et alii*. *A Coleopterist's Handbook* (3rd edn.). Amateur Entomologists' Society, Feltham.