Natural England Commissioned Report NECR163

Palaeoecological evidence to inform identification of potential climatic change refugia and areas for ecological restoration

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Foreword

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

Background

A variety of evidence suggests that species may be able to withstand the effects of climate change in localised environments known as refugia. These are areas in which specific environmental conditions create local climates that can act as a buffer against broader scale climatic changes. Refugia are areas where species can persist, despite the surrounding areas becoming unsuitable due to climate change.

This report is part of a project to investigate the characteristics of potential refugia and identify sites with the appropriate characteristics at a range of spatial scales. This work was commissioned to:

- Investigate, using palaeoecological data, the characteristics of potential climatic change refugia.
- Understand the extent to which palaeoecological data can help inform opportunities for, and constraints on, ecological restoration.

The results of this report and the related report *Climate change refugia for the flora and fauna of England* (NECR162) will be used by Natural England and others to target conservation efforts at the areas that could improve species' abilities to cope with climatic change in situ and to inform the creation of new conservation areas and ecological networks.

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Further information

This report can be downloaded from the Natural England website: **www.gov.uk/natural-england**. For information on Natural England publications contact the Natural England Enquiry Service on 0845 600 3078 or e-mail **enquiries@naturalengland.org.uk**.

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Photograph: Coring the lake sediments for palaeoecological study at Little Langdale Tarn SSSI, Cumbria, a site notified for its aquatic habitat diversity and the diversity of surrounding terrestrial habitats. (Richard Jones/University of Exeter).

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1. Executive summary

- Sustainable stewardship of the natural environment during the 21st century will depend much on helping species cope with climatic and land-use change. Broadly, two approaches could help to achieve this: (1) improve species' abilities to cope with climatic change *in situ*; and (2) maintain viable ecological networks, involving more, better, bigger, and better-connected areas of wildlife habitat, in part to help species colonize locations that become climatically more suitable. Past changes can help us understand long term ecological processes, which in turn can help to inform how habitats and species will respond to future changes.

- The aims of this report are twofold. Firstly, to investigate, using palaeoecological data, the characteristics of potential climatic change refugia (areas that are likely to remain protected or relatively climatically stable in the future, thereby enabling species and assemblages to persist despite climatic change making surrounding areas potentially unsuitable). Targeting conservation efforts at such areas could improve species' abilities to cope with climatic change *in situ*. Secondly, to understand the extent to which palaeoecological data can help inform opportunities for and constraints on ecological restoration, to inform the creation of new conservation areas and ecological networks.

- We identified areas of England in which the palaeoecological data are of best quality and most abundant. We compiled a comprehensive database, summarising the existence of Holocene and Lateglacial palaeoecological data across England (time period covered: c. 14 ka BP (years Before Present) to date). We then mapped locations from which palaeoecological data have been collected and summarised the duration and sample frequency of these data. Pollen data provided the most information and therefore formed the basis for quality control. We developed a protocol for determining the selection of geographic regions for more detailed study based on the duration of the pollen record, the temporal resolution of the pollen record, the degree of chronological control in terms of number(s) of dates, the spatial resolution of data, and the number of pollen grains and spores counted in each sample.

- On the basis of this assessment, we identified three geographic regions for more detailed analyses. These were: (i) a region hereafter termed the East of England, containing parts of Norfolk, Suffolk and Cambridgeshire; (ii) a region hereafter termed North East England, which encompasses the North Pennines, parts of Northumberland, Tyne & Wear, Durham and North Yorkshire; and (iii) a region hereafter termed North West England, which includes Cumbria and parts of North Lancashire. For each study area, a more detailed overview of data quality is provided, along with descriptions of the vegetation character of the regions. We also provide an account of the potential for these data to inform the identification of potential climatic change refugia and areas for ecological restoration.

- We show that palaeoecological data can provide an important context for discussions relating to ecological restoration and/or the appropriate management of degraded habitats. In some cases these data may establish the long-term relict status of a community or habitat, help determine the relative importance of different drivers of habitat change (such as management activities and climatic change), or provide insight into ecosystem processes and function. The palaeoecological data presently available, however, would not provide such insights for the varied habitat types in need of restoration. Additional targeted data collection might be possible in some cases where existing data do not suffice, although this is unlikely to be a panacea for all species.

- Palaeoecological data can also provide an important context for any discussion regarding likely refugial status, helping to reveal the mechanisms that promote species' persistence. However, in order to identify fine-scale climatic change refugia using palaeoecological data, it would be necessary formally to compare changes in the palaeoecological records from localities hypothesised to have refugial properties with those that do not.

- Overall, the usefulness of palaeoecological data for conservation purposes will depend principally upon the specific questions being asked, the species/habits involved and the locality as well as the proxy being examined. We propose a key hypothesis relating to refugial potential that could potentially be answered with further data collection, and propose ways in which such data collection could usefully be targeted.

2. Rationale

Biodiversity conservation and environmental management increasingly depend on our ability to ensure that species can persist in the face of climatic change. Partly in response to the adverse effects on biodiversity of climatic change, the Making Space for Nature Report (Lawton *et al.* 2010), and Defra's response to it (Defra 2011), set out the need to deliver more, better, bigger, and better-connected areas of wildlife habitat. More specifically, there are two potential courses of action for conserving climate-sensitive species: a) improve species' abilities to cope with climatic change in habitats within their existing range that are becoming less climatically favourable; and b) shepherd species towards uncolonised habitats that are already or becoming climatically suitable. To help inform these approaches, two particular research priorities have been identified by Natural England:

(i) To investigate the characteristics and locations of potential **climatic change refugia**, which could make an important contribution to future ecological networks as core areas that support the persistence of species in the face of changing environmental conditions.

(ii) To understand the **opportunities for and constraints on ecological restoration**, to create new conservation areas and ecological networks.

Both research priorities can, in part, be informed by palaeoecological evidence. The concept of refugia has its origins in palaeoecological research, and palaeoecological data can provide a long-term perspective on the opportunities and constraints for ecological restoration. Palaeoecological studies can be used to understand long-term ecological processes (e.g. Anderson *et al.* 2006; Chambers *et al.* 2006; Willis *et al.* 2010), and have the potential to help inform conservation (Huntley, 1991a). Palaeoecological study permits understanding of the processes behind change, alternate steady states and natural variability, as well as informing habitat restoration (e.g. Chambers & Daniell 2011; Davies & Bunting 2010). While palaeoecology will not provide exact analogues for future scenarios, it may allow understanding of resilience and how habitats and species have responded to various forcing factors, including climate and human intervention (e.g. Grant & Edwards 2008), giving an indication of the types of vegetation that existed in the past. It can also inform perception of landscapes and landscape change (e.g. Shaw & Whyte 2013), and help to engage people with their cultural and natural heritage. Additionally, most species in European habitats have evolved under and adapted to past natural disturbance regimes (Bengtsson *et al.* 2000). Therefore, an understanding of former natural and human disturbance dynamics is essential to preserve and restore biodiversity, as well as ecosystem functions, in the human-dominated habitats of England.

3. Project aims and objectives

Using palaeoecological evidence, the aims of this project were to: 1) investigate the characteristics of potential climatic change refugia; and 2) to understand the opportunities for and constraints on ecological restoration, when creating new conservation areas and ecological networks. Specific objectives were as follows:

(1) To compile a comprehensive database, summarising the existence of Holocene (and Lateglacial) palaeoecological data across England.
(2) To map locations from which palaeoecological data have been collected and to summarise the duration and sample frequency of these data.
(3) To determine the type of palaeoecological data best suited to determining the characteristics of potential climatic change refugia and opportunities for and constraints on ecological restoration.
(4) To evaluate which types of palaeoecological data are most suitable for evaluating species and habitat persistence.
(5) To summarise the existing palaeoecological data from the selected geographic regions.
(6) For each geographic region, to use the available information to comment on: (a) the quality and availability of data from that region; (b) the long-term landscape history; and (c) likely species/habitat occurrence trends. We also summarise the extent to which such data could be used to inform the identification of climatic refugia and opportunities for and constraints on ecological restoration.
(7) In conjunction with a parallel project on potential climatic change refugia (Box 1), to examine the spatial overlap between refugia identified using recent ecological responses to climatic change and the existence of palaeoecological data.
(8) To summarise the potential for using palaeoecological data to investigate the characteristics and locations of potential climatic change refugia and to understand the opportunities for and constraints on ecological restoration, as a technique to create new conservation areas and ecological networks.
(9) To discuss the implications for future palaeoecological data collection, including identification of any areas where basic data collection and research is needed, to inform future research priorities in this field.

4. Background

4.1. Species responses to climatic change and the importance of refugia

Recent climatic change has resulted in numerous species shifting in latitude and elevation as new areas become climatically suitable, and areas within their current range become climatically unsuitable (Thomas *et al*. 2006; Chen *et al*. 2011). Future climatic change is predicted to have a larger effect: on the basis of mid-range climate-warming scenarios and projections of decreases in species range extents, 15–37% of species could be 'committed to extinction' by 2050 (Thomas *et al.* 2004). Given the potential threat from climatic change, the effective targeting of conservation resources to meet the objectives of the Lawton *et al.* (2010) review will depend on our ability to predict the responses of species and ecological communities to climatic change. To date, however, most predictions for the effects of climatic change on biodiversity have either: (a) been derived using coarse-resolution information on climate and species' distributions; or (b) been based predominantly on climate-induced impacts on biodiversity in the last few decades (Peterson & Townsend 2001; Pearson & Dawson 2003). This leads to several potential misrepresentations of the impacts of climatic change on biodiversity and therefore the potential for ecological restoration.

Box 1. Summary of parallel study investigating potential climate change refugia for wild species in England (see Suggitt *et al.* 2014 for further details).

It has been proposed that species may be able to withstand the effects of climatic change in localised environments, known as microrefugia (Box 2), where specific environmental conditions act as a buffer against the detrimental effects of coarser scale changes to the climate. This report addresses published evidence for the nature of such refugia, and empirical evidence for their existence in England, based on recent changes to the distributions of a wide range of taxa. A review of the literature on the properties of refugia emphasises the importance of three characteristics of microclimate in increasing refugium potential: i) extreme conditions relative to surroundings; ii) stable conditions relative to trends or variability in the wider landscape; iii) spatially isolated conditions relative to surroundings (Ashcroft *et al.* 2012). These properties of the landscape were modelled at 100 m resolution for England, and summarised at the scale of 10 x 10 km grid squares. The survival or extinction of 1,082 species that retracted their range over the past four decades was then modelled as a function of the environmental properties in each square that were hypothesised to influence refugium potential.

After controlling for the effects of recorder effort and agricultural intensity, there were strong indications that rates of local population persistence were influenced both by rates of climatic change, and by environmental properties hypothesised to influence refugium potential. Across all species, local extinctions were higher in areas experiencing greater climatic change, but these effects were buffered by the existence of heterogeneous microclimatic conditions. However, there were consistent differences in the responses of six different taxonomic groups (higher plants; lower plants; beetles; butterflies and moths; all other insects; and other arthropod groups) to different properties of landscape and climatic change. Plant persistence tended to be reduced in regions of greater summer warming, with an indication that this negative effect of warming was buffered by heterogeneity in incoming solar radiation. Beetles showed stronger responses than the other taxa to changes in rainfall, and to modelled topographic variability in moisture levels. Persistence in the other invertebrate groups showed stronger relationships with trends in summer temperature. The models of species persistence were used to provide maps of refugium potential at 10 km scale in England, shown for: i) all modelled variables, including geology and agricultural intensity; ii) climatic change and microclimatic effects; iii) microclimatic variables. Maps depicting microclimatic variables have been included as colour backgrounds to the figures in the present study, indicating where palaeoecological data have been collected.

The importance of long-term ‘refugia’ to conservation ecology has been emphasised by various authors (e.g. Huntley 1991a; Stewart 2009). The term ‘refugia’ (singular refugium) has been used in conservation ecology in different, although related, ways (e.g. ‘thermal refugia’, ‘island refugia’, ‘mountain refugia’, ‘microrefugia’). Samways (1990), for example, uses the term when referring to shorter term population contractions due to climatic change or other influences. An overview of refugial terminology is provided in Box 2. In the context of recent ecological responses to climatic change, variation in topography or vegetation structure at much finer spatial scales leads to marked variation in the climates experienced by organisms. These areas, often referred to as refugia in the ecological literature, are likely to be key determinants of species’ survival in particular regions (Ashcroft 2010; Suggitt *et al.* 2011; Gillingham *et al.* 2012).

In the palaeoecological literature, the term ‘refugia’ is most frequently used to refer to regions in which a species persisted during those phases of glacial-interglacial cycles when conditions generally were unfavourable and the species’ range was as a result relatively spatially restricted. Although when unqualified the term is most often used to refer to areas to which species with wide interglacial distributions were restricted during the cold extremes of glacial stages, the term ‘interglacial refugia’ has more recently been coined to refer to areas occupied during interglacial stages by species with wide glacial ranges. In this report we use the term refugia in the context of climatic change and use it to describe an area in which species have, or are likely to have, persisted despite unsuitable regional climate. We make no assumptions about the length of time over which the species are likely to have persisted or will persist, but instead qualify this explicitly when it is appropriate to do so. We use the term microrefugia to explicitly refer to small areas, less than 1 km^2 in size, in which populations have persisted or are likely to persist in the face of an adverse regional climate.

Box 2. Refugial terminology

In recent years, there has been a rapid increase of refugia-related terms. *Palaeorefugia* and *neorefugia* have been used to distinguish whether the areas that support populations not found elsewhere in the landscape were formed before or after the surrounding matrix (Nekola 1999). The terms *macrorefugium* and *microrefugium* have been used to distinguish between the main distribution area of a species and small areas in which small populations can survive outside the main distribution area protected from unfavourable regional environmental conditions (Rull 2009). In ecological and conservation literature, the term ‘*refugia’* often refers to microrefugia, whereas in the palaeoecological literature, the term is generally used to refer to macrorefugia. In Europe, classic and cryptic glacial or interglacial refugia have been used to distinguish, for different types of species, areas that probably hosted small populations that cannot be easily detected in palaeoecological records from larger areas in which the species almost certainly occurred (Stewart *et al*. 2010). Nunataks, peripheral, lowland, *in situ* and *ex situ* have been used to describe different types of glacial refugia for alpine species. Bennett & Provan (2008) proposed to replace the term ‘refugium’ with ‘bottleneck’, where change in abundance is being considered.

While these qualifiers may in some instances add precision to the term, it has been argued that many of these terms are superfluous and do not have a clearly definable meaning (Tzedakis *et al.* 2013). Another source of confusion is the timescales over which refugia are assumed to operate. Perhaps unsurprisingly, palaeoecologists typically think of refugia in terms of persistence over glacial-interglacial cycles whereas, when used in the context of applied ecology and conservation, the term is often used to describe persistence over much shorter timescales.

It has been claimed that some species may have survived previous periods of generally unfavourable climatic conditions in areas offering (micro-)climatic conditions atypical of the regional climate, but without to-date having been detected in the fossil record (‘cryptic refugia’; Stewart & Lister 2001; Provan & Bennett 2008; Hampe & Jump 2011; Keppel & Wardell-Johnson 2012). Others, however, have contested this claim, particularly for glacial refugia for temperate trees in northern Europe (Tzedakis *et al*. 2013). Whether or not ‘cryptic refugia' have existed in the past, the capacity for a landscape to function as a refugium is believed to be enhanced by topographic diversity, although in the context of current climatic change there is little empirical information on the topoclimatic or other fine-scale environmental features that may promote population stability (Dobrowski 2010; Keppel & Wardell-Johnson 2012). It is widely accepted, however, that regions where concentrations of temperate species currently reach their low-latitude range limits are also centres of inter- and intra-specific diversity precisely because they acted as refugia for temperate species during glacial stages (Hampe & Jump 2011). It is therefore vital to understand the impacts of past climatic changes in shaping extant species, both: 1) in order better to understand the threat(s) posed by climatic change to biodiversity; and 2) to validate conservation measures proposed in response to climatic change.

4.2. Influence of palaeoclimate on present day ecological communities

It is clear that past climatic events have had profound influences on present ecological communities. The Last Glacial Period had a substantial limiting effect on biodiversity in what we now call the temperate and boreal zones. Reaching its peak around 26.5 ka cal BP (thousand calibrated radiocarbon years before present – see Box 3) and persisting to 19 ka cal BP – the Last Glacial Maximum (LGM) (Clark *et al*. 2009), the advance of the ice sheets and onset of cooler conditions had substantial implications for species, which were extirpated from parts of their ranges, shifting their distributions to persist either extensively in unglaciated areas or with spatially limited distributions in refugia within or outside the glaciated areas. This is evidenced across all taxa for which reliable records exist. For example, patterns of phylogeography and genetic diversity in European temperate and boreal mammals reflect their southern distributions during the LGM (Willis & Whittaker 2000; Edwards *et al.* 2012; Ruiz-González *et al.* 2013). The English biota is a mix of species from multiple refugial sources, and even individual species can have several refugial source populations (Ferris *et al*. 1995).

Box 3. A note on dating palaeoecological data

Many of the published studies referred to in this report base their ages on radiocarbon dates. Radiocarbon dating is a technique that uses the decay of unstable carbon-14 (^{14}C) to estimate the age of organic materials. The Earth's atmosphere contains three isotopes of carbon in roughly constant proportions, with the stable ^{12}C isotope being much the most abundant. When plants photosynthesise, they absorb ^{14}C (and other carbon isotopes), and when plants (or other organisms) die, they contain a ratio of ^{14}C to ^{12}C determined principally by the ratio of the two isotopes in the atmosphere. However, with no possibility of replenishment, the proportion of ^{14}C decreases at a known constant rate due to radioactive decay. Dating is based on the amount of ^{14}C left after this radioactive decay. Radiocarbon years differ from true "calendar" years because the amount of radiocarbon produced in the atmosphere changes over time, as does the rate that carbon is exchanged between the ocean, atmosphere, and biosphere, and because of a historical inaccuracy in the determination of the half-life of ^{14}C that is used to calculate radiocarbon ages. Calibrations are based on comparisons between radiocarbon years and true calendar year by dating samples of known age (such as wood samples dated by counting annual growth rings) and comparing the apparent radiocarbon age to the true age. Calibration methods have been improved and refined over the past few decades. Where possible, we report dates as calibrated radiocarbon years before present using recent calibration methods (approximately the true age). However, because our report refers to studies published many years ago, many of the original publications give only uncalibrated radiocarbon dates, some used radiocarbon calibration systems that are now obsolete, and others infer dates using alternative approaches. In order to make all of these dates truly comparable, we would need to have developed and applied new age models for many of the studies. Doing so was beyond the scope of this project and it should thus be noted that not all of the dates summarising the findings of individual studies are directly comparable.

For more recent samples, there are several other dating techniques such as the decay of lead-210 (^{210}Pb) or caesium-137 (^{137}Cs). ^{210}Pb is ideal for dating depositional environments in which changes have occurred during the last century and sedimentation rates can be quantified. It relies on the presence of radon-222, which escapes into the atmosphere at a known rate and decays quickly to ^{210}Pb. This process produces excess lead-210 in the atmosphere and subsequently the hydrosphere and then into particulate material within on-going depositional systems. This produces excess lead-210 over that expected and it is the measurement and interpretation of this excess ^{210}Pb that enables age assessment (see Sanchez-Cabeza & Ruiz-Fernández 2012 for a review of methods). ^{137}Cs dating exploits the injection of radioisotopes into the atmosphere, which occurred during atmospheric nuclear testing, mainly in the late 1950s and mid-1960s. It uses this injection as a marker to identify soil and sediment particles laid down at that time.

For those species that survived the cold extremes of the last glacial stage and the extreme cold of the Younger Dryas (13.0-11.7 ka cal BP), the warming after the LGM and during the Lateglacial (14.6 – 11.7 ka cal BP – see Box 4), and the onset of the Holocene (11.7 ka cal BP), brought newly available areas of climatic conditions suitable for temperate species in the mid–high latitudes, including England, and a rapid reduction in the extent of areas suitable for Arctic–Alpine taxa. Spreading north from more extensive southern refugia, and possibly also in multiple directions from more spatially-restricted northern 'cryptic refugia' (Mosblech *et al*. 2011), temperate species colonised the newly suitable areas at varying rates and to varying extents, in a manner that can often be established via DNA (phylogeographic) analysis (e.g. Qiu *et al*. 2011). Colonisation routes are often reflected in modern day distribution patterns. In addition, many current hybridisation zones are artefacts of colonisation routes, physical barriers and commonalities in the locations of glacial refugia (Hewitt 2000). However, palaeoecological studies have also demonstrated the long-term persistence of various cold-adapted plant species in upland areas of England. In Upper Teesdale, for example, species of the Arctic–Alpine element (Matthews 1937) such as dwarf birch (*Betula nana*), starry saxifrage (*Saxifraga stellaris*) and yellow mountain saxifrage (*S. aizoides*) were present throughout the post-glacial in relatively widespread upland habitats, whereas other species, such as the spring gentian (*Gentiana verna*), a member of the Alpine element, maintained their presence by occupying suitable micro-habitats (Turner *et al.* 1973).

Box 4. The climates of the Holocene and Pleistocene

The Pleistocene is the geological epoch which lasted from about 2,600 ka cal BP to 11.7 ka cal BP, spanning the world's recent period of glaciations. The Holocene is the epoch that followed the Pleistocene (c. 11.7 ka cal BP), continuing to the present day. The modern continents were largely in their present day configuration throughout the Pleistocene; therefore, climatic changes that occurred during these epochs are not due to shifts in the position of land masses.

Glaciation during the Pleistocene proceeded differently across regions, depending on latitude, terrain and climate. The overriding factor causing these variations is believed to be Milankovitch variations, which have periodicities of c. 20,000, 41,000 and 100,000 years, with glacial-interglacial cycles corresponding to the 100,000 year periodicity (Imbrie *et al.* 1992). These are periodic variations in regional and planetary solar radiation reaching the Earth, caused by slight, repetitive changes in the Earth's orbital motions. In addition to, and superimposed on the Milankovich climatic change, are the climate oscillations of shorter duration. Of relevance to the temporal coverage of this study is the geologically brief (1,300 ± 70 years) period of cold climatic conditions and drought known as the Younger Dryas, which occurred at the end of the Pleistocene (onset at around 13 ka cal BP, Muscheler *et al.* 2008) and followed a period of much warmer conditions that began 14.6 ka cal BP. Following this, the temperature trend was one of predominant warming until ~ 8 ka cal BP, after which the climate has remained relatively stable. The coolest temperatures of the last 2,000 years occurred during the Little Ice Age (c. 200 years ago). This cooling was particularly pronounced in the North Atlantic area, where temperatures dropped by 2^{o}C (Marcott *et al.* 2013). In the present warming episode, global temperatures have not yet exceeded peak interglacial values, but are now warmer than during most of the Holocene. Notably, IPCC climate model projections for 2100 substantially exceed the highest temperatures estimated via palaeoclimatic techniques not only for the Holocene (Marcott *et al.* 2013), but probably for the entire Pleistocene.

4.3. Interactions between palaeoclimate and human activities

Past habitat management has also offered warm refugia for species during cold spells. Land management in Britain over the last 6,000 years has created a continuing presence of early successional habitats that would otherwise have matured into closed habitats. This shorter, more open vegetation provides a warmer daytime microclimate (Rosenberg 1974), particularly in terms of maximum temperature (Suggitt *et al.* 2012), leading to faster development in insects such as butterflies (Bryant *et al.* 2002). Already present in Britain circa 7 ka BP, many butterflies are hypothesised to have moved into the warmer microclimates of anthropogenic downland and heathland as the climate cooled during the Holocene, and some are now dependent upon these habitats for their survival (Thomas 1993). Supporting this idea, the cessation of land management practices such as grazing that lead to the development and maintenance of open habitats has been identified as the primary cause of declines in many open habitat butterflies, such as the large blue (*Maculinea arion*, Thomas 1980). Similar findings for plants add weight to this idea: Bennett & Provan (2008) report some herbs that are now commonplace in Britain, which were, however, patchy, scarce or even absent prior to Neolithic agricultural practises. Conversely, however, several palaeoecological studies (e.g. Hibbert & Switsur 1976) also highlight the importance of open habitats for permitting taxa that characterise the colder Younger Dryas (Box 4) species assemblages to persist into the warmer Holocene (e.g. Hibbert & Switsur 1976). Nonetheless, persistence is not always without turnover in the genetic population in question (Meiri et al 2013).

4.4. Outline of report

- In the remainder of this report, the method adopted for data search and analysis is described (Chapter 5) and we summarise the availability of Holocene (and Lateglacial) palaeoecological data across England to determine three geographic regions of England from which high quality evidence is available (Chapter 6).
- For each region, we then provide a more detailed summary of the availability of palaeoecological evidence, outline the vegetation history and discuss the extent to which the palaeoecological data from these regions could be used to help identify the locations of potential refugia, and the opportunities for and constraints on ecological restoration (Chapter 7).
- In Chapter 8, we discuss how palaeoecological data can be used to identify climatic change refugia and areas for ecological restoration. We first discuss the scope for using palaeoecological data to identify areas with the potential for ecological restoration (Section 8.1), before discussing their potential use in identifying refugia from climatic change (Section 8.2). We go on to propose methodologies that are likely to identify the locations of climatic change refugia and potential areas for ecological restoration (Section 8.3), and propose ways in which future data collection could be fruitfully targeted (Section 8.4).
- Finally we provide some concluding remarks (Chapter 9) on the extent to which palaeoecological data can be used to identify the characteristics of refugia and opportunities for and constrains on ecological restoration.

5. Methods

5.1. Focus of data search

Prior to carrying-out the analyses, it was anticipated that data from sediment cores (Figure 5.1) on which pollen analysis had been conducted would be the most useful in terms of investigating the characteristics of climatic change, and for identifying refugia and potential areas for ecological restoration. In order to be informative, sufficient palaeoecological data must be available, both in terms of the geographic extent of the data, and the spatial and temporal density of the data. Data from vertebrates do not easily allow reconstruction of changing ecological communities because continuous records of their fossils are rare to non-existent. While occurrence data may be of use eventually in this context, it provides a poor record relative to pollen data. The vertebrate record may include many errors due to over ambitious identifications and this is particularly the case with avian records (Stewart 2002). Data for some invertebrate groups are more consistently available and some insect groups (e.g. Coleoptera) are well-suited to understanding ecological changes. However, even data for these groups are not as abundant as those available from pollen cores. Given this, and the finite time available to search the literature, our efforts were thus deliberately biased towards palynological studies.

Figure 5.1. *A core taken from lake sediments for palaeoecological analysis, with the sediment – water interface at the top. (Ann Power/University of Exeter)*

5.2. Literature search methods

In order to identify areas of England in which palaeoecological data are most abundant, we systematically conducted a search of the scientific literature. We used the search engine Web of Science and searched for literature using a number of relevant search terms (Appendix 1). We examined the literature cited in each relevant paper and used that as a source for finding additional literature. We also used the search engine Google Scholar with the same search terms applied. Because Google Scholar searches the entire content of a document, using such searched terms returned more literature than it was feasible to search through (e.g. > 75,000 documents for 'holocene' + 'pollen'). Google Scholar allows documents to be sorted by relevance, however. Consequently we sorted the documents in this way and restricted our further interrogation of the documents to the 100 most relevant. The use of Google Scholar has the advantage of returning non-peer reviewed literature, and we were able to source a number of research reports in this manner. Any additional studies known to the project team were also included, and in excess of 100 additional studies were identified in this way. This database (Appendix 3) is provided as a separate excel spreadsheet and is summarised below.

5.3. Selection of geographic regions from which high quality evidence is available

Based on the information compiled nationally, and our assessment of the quality of the palaeoecological data, three geographic regions were selected on the basis of having high quality data that could potentially be used to inform the identification of climatic change refugia and suitable areas for ecological restoration. Our assessment of data quality was made using the following criteria:

(1) The length (duration) of the pollen record.
Ideally data were available for the entire Holocene from a single site, thus maximising the likelihood that the record appears continuous. This was rare for more recently studied sites, and in some instances information from neighbouring sites was amalgamated to produce as complete a record as possible.

(2) The temporal resolution of the pollen record(s).
An ideal temporal record was one in which data resolution was at least sub-centennial and preferably decadal or bi-decadal, enabling rates of change and periods of stability in terms of the vegetation present to be assessed. For most long profiles, temporal resolution varies through the cores, due largely to changes in deposition/sedimentation rate. Where adjacent sites were amalgamated there was inevitably some variation in resolution.

(3) The degree of chronological control in terms of number(s) of dates.
There were many sites with high quality, taxonomically sound data, but with poor or absent well-calibrated radiometric or other dating control. For more recent deposits, it is often assumed that the top of the profile is 0 years BP when this may in fact not be the case, but because the temporal precision of radiocarbon makes dating very recent deposits problematic, constructing rigorous chronologies is difficult. Some degree of temporal uncertainty is therefore inevitable, although the availability of a good range and large numbers of dates from other sites sometimes provided an opportunity for cross-referencing.

(4) The spatial resolution of data: i.e. how many cores were available from the area.
Generally the more cores there are from a geographically restricted area, the better the potential spatial resolution of the data. However a small number of high quality sites in a region was considered preferable to a larger number of lower quality sites, especially if the few high quality sites came from locations topographically closer to the types of environments identified by the parallel project as being likely locations for refugia.

(5) The number of pollen grains and spores counted from each sample.
Typical pollen counts have varied systematically through time as methodologies have evolved and also vary according to the specific study aims. Low counts of 250+ in each sample may be suitable for identifying dominant anemophilous (wind pollinated) taxa and their variability through time (e.g. key arboreal taxa). However, entomophilous (insect pollinated) taxa, including many rarer herbaceous taxa, are found much less frequently, leading to a requirement for counts in excess of 1000 if the consistency of their presence is to be evaluated. For some taxa that produce larger and/or more obvious pollen grains (e.g.

cereal type grasses), an approach involving scanning for the presence of such taxa can be applied, but this is not an option for most native herbaceous taxa.

(6) The level of taxonomic resolution to which pollen/spores are identified.
The taxonomic resolution with which pollen grains or spores of members of the British Flora can potentially be identified varies. Although a minority of species produce distinctive pollen grains/spores (e.g. cornflower (*Centaurea cyanus*), western oakfern (*Gymnocarpium dryopteris*)), more frequently identification is possible only to generic level, as is the case for the majority of arboreal taxa (e.g. oak (*Quercus*) and birch (*Betula*)), or to the sub-family level (e.g. Asteraceae subfamily Cichorioideae). In a few cases identification is predominantly possible only to the level of the family (e.g. most members of the grasses (Poaceae) and sedges (Cyperaceae)). The realised taxonomic resolution with which pollen data are recorded has changed little through time, although some advances have enabled discrimination amongst taxa where this was not initially considered possible (e.g. dwarf birch from tree birches) whilst others have allowed the recognition of pollen taxa that were initially overlooked (e.g. juniper (*Juniperus*) and poplar (*Populus*)).

Some studies include lists of occasional occurrences, or portray these on the pollen diagram using symbols or codes; these can be useful for tracking rare species. Some more recent papers, however, only include major taxa. The paper by Turner *et al*. (1973) discussed above is one of the few specifically to track rare taxa and to discuss their pollen taxonomy for a potentially important region, although it would not meet many of the preceding criteria, especially in terms of dating control. Nonetheless, it provides an excellent model for future research in terms of pollen taxonomic resolution and the tracking of rare taxa.

On the basis of an assessment of the geographic regions identified using these six criteria, three regions were selected for more detailed analyses. These were: (i) the East of England, containing parts of Norfolk, Suffolk and Cambridgeshire; (ii) North East England, which encompasses the North Pennines, parts of Northumberland, Tyne & Wear, Durham and North Yorkshire; and (iii) North West England, which includes Cumbria and parts of North Lancashire (Figure 5.2). For each study area, a more detailed overview of data quality is provided, along with descriptions of the vegetation character of the sites and a brief account of the potential for data from each site to be used to inform identification of potential climatic change refugia and areas for ecological restoration. We also compare and contrast data availability among all three geographic regions.

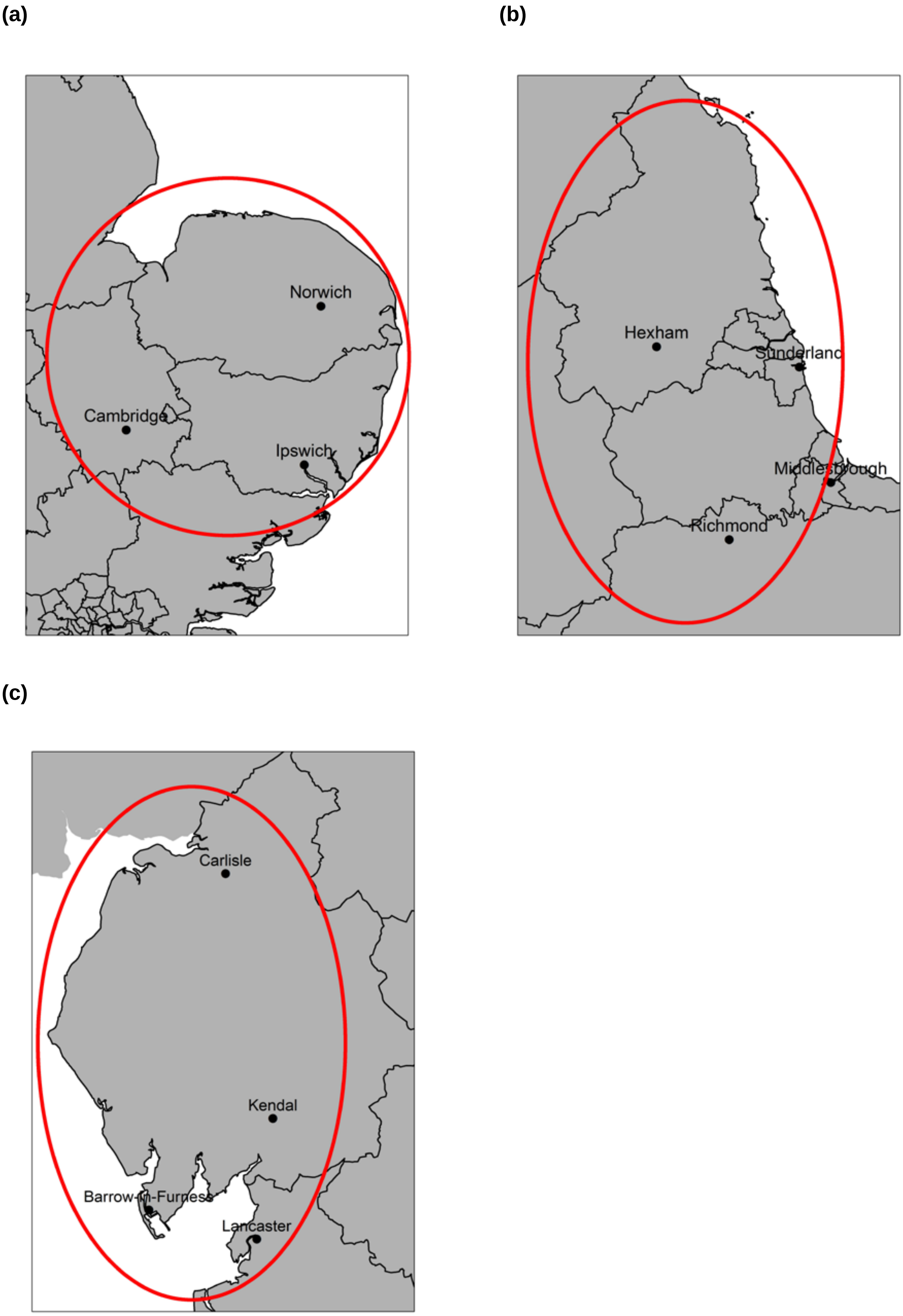


Figure 5.2. *The geographic extents of three study regions selected for more detailed analyses are contained within the red boundary. These regions were: (i) the East of England, containing parts of Norfolk, Suffolk and Cambridgeshire (panel a); (ii) North East England, which encompasses the North Pennines, parts of Northumberland, Tyne & Wear, Durham and North Yorkshire (panel b); and (iii) North West England, which includes Cumbria and parts of North Lancashire (panel c).*

6. Assessing the availability of palaeoecological data in England

6.1. Geographical summary of palaeoecological data

A total of 273 palaeoecological studies were identified through the systematic literature search. These studies represented 763 locations from which palaeoecological data were obtained. Appendix 3). The majority of these (>90%) were sediment cores upon which pollen analyses had been performed, but other types of evidence, such as plant macrofossil (preserved plant remains large enough to be visible without a microscope) and faunal records, were also identified. The number of individual pollen samples examined from a site ranges widely (from 3 to almost 200), but very few sites had more than a small number of plant macrofossil or faunal records. One crucial component of palaeoecological studies, particularly of lake sediment or peat deposits, is the establishment of accurate and reliable chronologies for the pollen records. Radiocarbon dating is the predominant technique used in establishing independent chronologies for such records (Box 3), and without such methods, dating errors can make the establishment of trustworthy chronologies difficult, and can introduce considerable unquantifiable uncertainty into studies of palaeoclimatic events. That is particularly so for those events that are short-lived, such as regional deglaciations (Brown *et al.* 2006; Box 3). For this reason, our syntheses are restricted to dated samples. The locations of sites, together with the number of dated samples associated with each site, are shown in Figures 6.1a-b. There are large variations in the number of sites in different regions of the country, largely in line with a combination of the availability of deposits, adopted research questions and researcher interests. There are particularly abundant data from North East England (especially the North Pennines), Cumbria, the North York Moors and the Humber Estuary area. There is also a moderate amount of data from the Welsh Marches, Dartmoor, Exmoor and areas in the Breckland and Fens. Data from elsewhere are scarce or entirely non-existent, principally due to a lack of suitable deposits rather than untapped resources.

6.2. Overlap with potential refugia identified in the parallel study.

Figure 6.2 shows the location of microclimatic refugia at 10 km grid cell resolution as identified in the parallel project (Box 1) overlain by the locations of dated palaeoecological records. It can be seen that there is a moderately high degree of overlap between geographic regions identified as climatic refugia in the parallel project and those from which large volumes of palaeoecological data exist. In Chapter 7, we outline how the locations and existence of climatic change refugia could be better investigated using existing (as well as additional) palaeoecological data. The overlap between geographic regions with high concentrations of dated palaeoecological records and those identified as refugia in the parallel project, thus offers potential in terms of investigating refugia from a palaeoecological perspective. In particular, understanding of whether the landscape features that promote species persistence are the same over recent and palaeoecological timeframes is facilitated by presenting the data in this way. Areas with a high concentration of dated palaeoecological records and high refugial scores include Cumbria, North East England, Breckland, and (to a lesser extent) Dartmoor.

(a) (b)

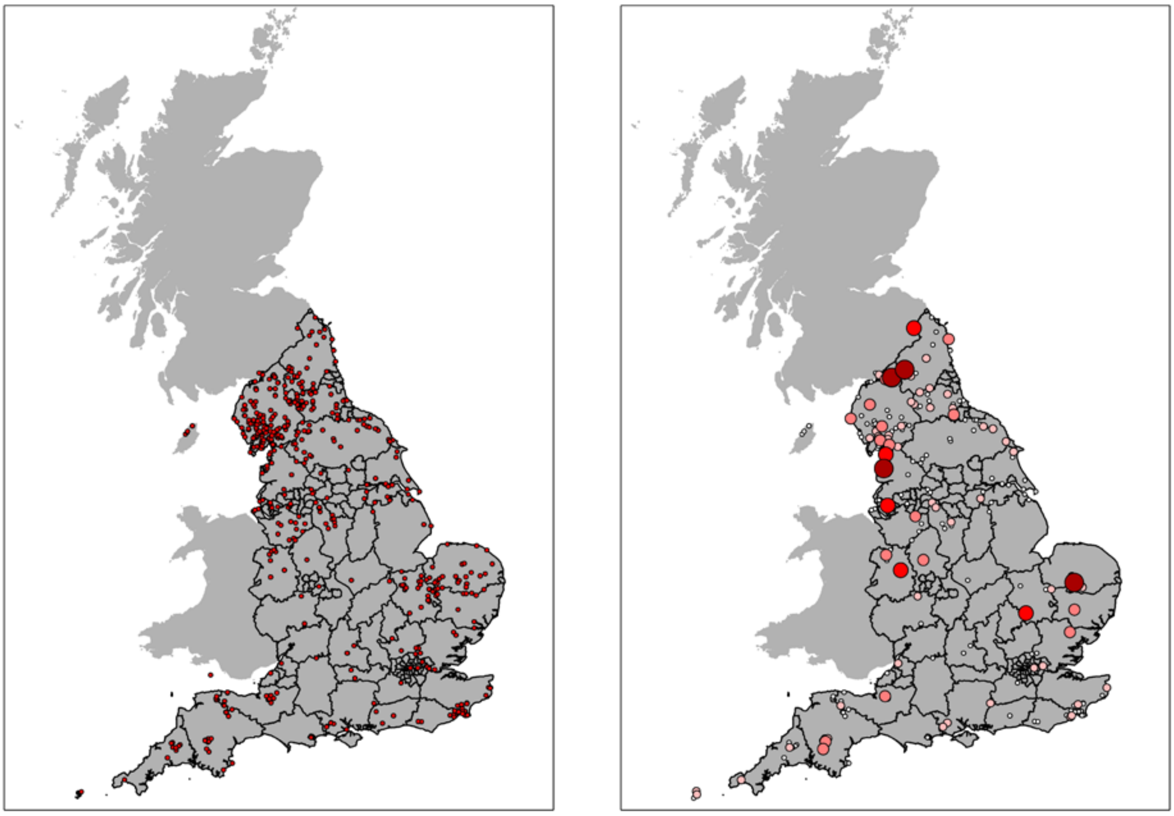


Figure 6.1. *Location of palaeoecological records derived from literature obtained by systematic searching of Web of Knowledge and Google Scholar or from the personal knowledge of project team members. The location of all dated and undated sites is shown in (a). The number of dated samples at each site is shown in (b).*

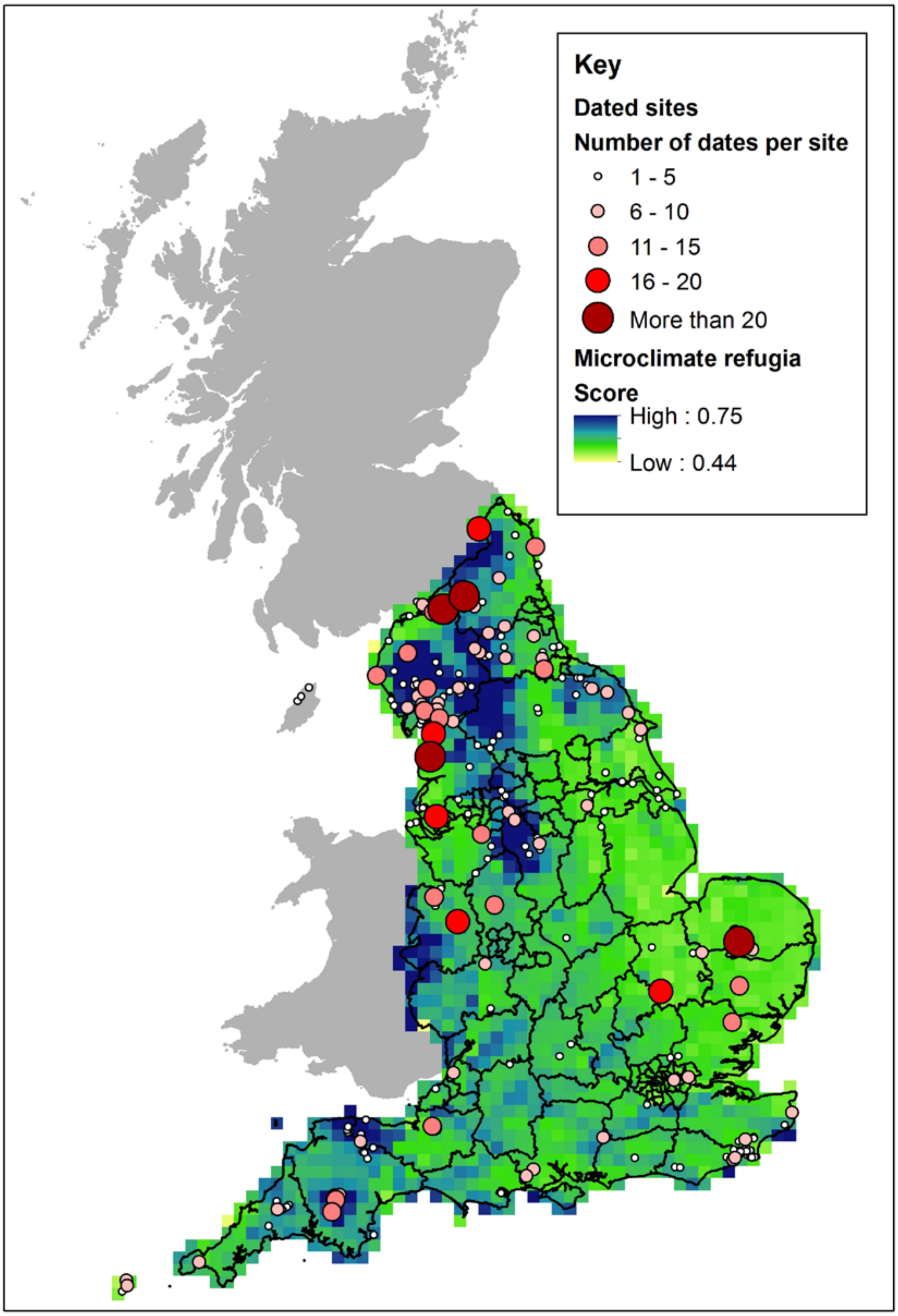


Figure 6.2. *Geographical overlap between all palaeoecological data and microclimatic refugia. Circles denote the locations of dated palaeoecological records in England and the total number of dated samples at each site. Coloured shading of the 10 km grid squares indicates their refugium potential score. Further details of how refugial potential was calculated are given in Suggitt et al. (2014) and Box 2.*

6.3. Temporal summary of palaeoecological data

Most records are confined to the Holocene, with only thirty studies providing data from the terminal stage of the Pleistocene (~15.0 – 11.7 ka cal BP; Figure S2.1 in Appendix 2; Appendix 3). The longest pollen record was estimated as beginning 17.4 ka cal BP (Bennett 1988), although the validity of the older dates from this site (Saham Mere in Norfolk) has been questioned. Palaeoecological studies have been undertaken in England, and more widely in Great Britain and Ireland, since before World War II. Seminal early syntheses were provided by Jessen (1949) of late Quaternary deposits and the floral-history of Ireland, Godwin (1956) of the history of British flora (a subsequent more widely used edition was published in 1975) and Pennington (1969) of the history of British vegetation. Many early studies were focused specifically on aspects of vegetation history, rather than the use of pollen and macrofossils to infer climatic and/or anthropogenic impacts. For instance, there was a sporadic series of papers under the overall title of 'Studies in the post-glacial history of British vegetation' in a range of journals including *Philosophical Transactions of the Royal Society* and *New Phytologist*, the first appearing in 1938 (Godwin & Clifford 1938). By the 1970s there was a growing understanding of vegetation history that included studies of plant colonisation in the early Holocene and thereafter, including work from areas with specialised flora such as Upper Teesdale (Turner *et al.* 1973). These pioneering works provide a rich potential seam for refugial studies but, despite good taxonomic resolution in some instances, suffer from one major drawback in that they preceded the widespread use of radiocarbon dating. They were instead dated by correlation with Godwinian pollen zones, constructed on a very small sample of radiocarbon dates. Nevertheless, the availability of these studies, of which the work of Turner *et al.* (1973) is a prime example, offers an opportunity to evaluate potential sites for re-analysis with more modern overall approaches. As the available database of pollen sites expanded, so they became used for a number of broad scale studies seeking to elucidate patterns of change within the flora, especially for key species and not just for England but for the whole of the British Isles (Birks 1989) and for Europe as a whole (Huntley & Birks 1983).

From the mid-1970s onwards, studies tended to be more hypothesis driven, looking at specific problems. These included human impacts on the landscape from the Mesolithic through to recent historical changes, with a special interest in the earliest agriculture, or climatic change, particularly during the Lateglacial. Greater numbers of radiocarbon dates were often obtained for individual sites, resulting in better dated records than previously, and sequences were often analysed with higher temporal resolution, although with a tendency to focus on specific periods rather than to examine the entire Holocene. As a result, we have a good knowledge of vegetation history across a range of regions from which suitable sites have been analysed, although the data are in some cases rather isolated in time and space, especially where there are severe restrictions on the availability of lake or peat sediments. This is particularly true of England when compared to Wales, Scotland or Ireland. In these latter countries, the greater proportion of uplands and the glacial history result in greater numbers of sites where sediments suitable for analysis have accumulated.

It should be noted that there are relatively few sites from England on any national or international open-access databases that include raw data, hence accessing original data may depend on the availability through authors rather than being available publically. This will also mean that more recent analyses, where researchers are still active, may be preferred (because it is more likely that the researchers are still contactable) and they have the additional advantage of being the best dated.

Thus, although in terms of the present review it has been possible to trace a large number (>750) of individual sites from which palaeoecological data have been obtained and published, in order for these to have value in terms of assessing likely refugial aspects or potential in terms of identifying areas for ecological restoration, it has been necessary to develop a relatively rigorous selection protocol to enable concentration on the most fruitful areas/sites. Subsequent sections of this report describe the protocols that have enabled us to identify some areas with reasonably well known and chronologically accurate vegetation histories for the entire Holocene (although having an accurate chronology for the entire Holocene record is in itself uncommon).

7. Key geographic regions for which high quality palaeoecological data are available

7.1. East of England

7.1.1. Sites – number and quality

The East Anglian Breckland was one of the first parts of England to be studied using pollen analysis, thanks to the pioneering work of Sir Harry Godwin that began in the 1930s and that is perhaps best represented by Godwin and Clifford's (1938) work on Woodwalton Fen from the east of the area. The importance of the University of Cambridge for palaeoecological studies is then reflected in a concentration of studies following World War II and through to the end of the century utilising the high quality sites found in various depressions in the terrain of East Anglia. Some of the sites originally examined by Godwin and others were re-cored and subjected to very detailed analyses in the 1980s and 1990s (Appendix 3). Although over 50 sites in the broader region south of The Wash have been analysed, there is a clear concentration of excellent records centred on Hockham Mere, including Saham Mere, Sea Mere, Old Buckenham Mere, Quidenham Mere, Diss Mere and The Mere, Stow Bedon. The temporal coverage of sites is shown in Figure S2.2a in Appendix 2. To highlight the potential for further examination of the landscape features that promote species persistence, the spatial coverage of all sites overlaid on a map of refugial potential is shown in Figure 7.1. These sites have relatively high temporal resolution; several have records extending back into the Lateglacial and most have good radiocarbon control (Figure S2.2b in Appendix 2), although otherwise important sites such as Diss Mere and Sea Mere lack such dating control because of their calcareous nature. The spatial coverage of sites with radiocarbon dating overlaid on a map of refugial potential is shown in Figure 7.2 and summary statistics for all sites are shown in Table 5.1. At Diss Mere, important parts of the record have laminations that have been shown to be annual in nature; by correlating the pollen record with those from proximal sites with radiocarbon chronologies it has been possible to locate the records in time with a reasonable degree of confidence. In summary, therefore, there is a relatively high density of well dated records that have been analysed in detail covering the entire Holocene and extending back into the later parts of the Lateglacial, especially the Younger Dryas, providing a very good vegetation record for the region. One or two of the oldest radiocarbon dates, however, should be treated with caution and are likely to be too old, e.g. at Saham Mere. Comparison of the location of the sites with areas of refugial potential shows broad coincidence between the pollen records and some of highest potential values, although average refugial potential in the area is not particularly high.

7.1.2. Vegetation character from records

Earliest records - the best dated site with the longest complete record, especially for the Holocene, is at Hockham Mere. It has a sediment core of 11 m with 23 radiocarbon dates, all of which appear to be reliable; this is probably one of the most complete Holocene pollen records for a site from the British Isles. The site was originally studied by Godwin (1941) and Godwin & Tallantire (1951). This record has become the 'standard' sequence for the region, although with local variations between this and neighbouring sites. The earliest pollen samples analysed probably represent the early Younger Dryas. Evidence of the nature of the regional vegetation before that time is provided by the record from Sea Mere, 10km from Hockham Mere, where open vegetation typical of the earlier part of the Lateglacial period is recorded. Several taxa recorded from pre-Holocene sediments at these sites are not recorded from the Holocene and are certainly absent in the region today. This is typical for most areas of the British Isles where Lateglacial sediments have been analysed, although Godwin commented in early papers (Godwin 1941; 1956) that some taxa characteristic of the Lateglacial reappear in the disturbed agricultural landscapes of the Neolithic, a phenomenon since recorded across additional parts of Europe.

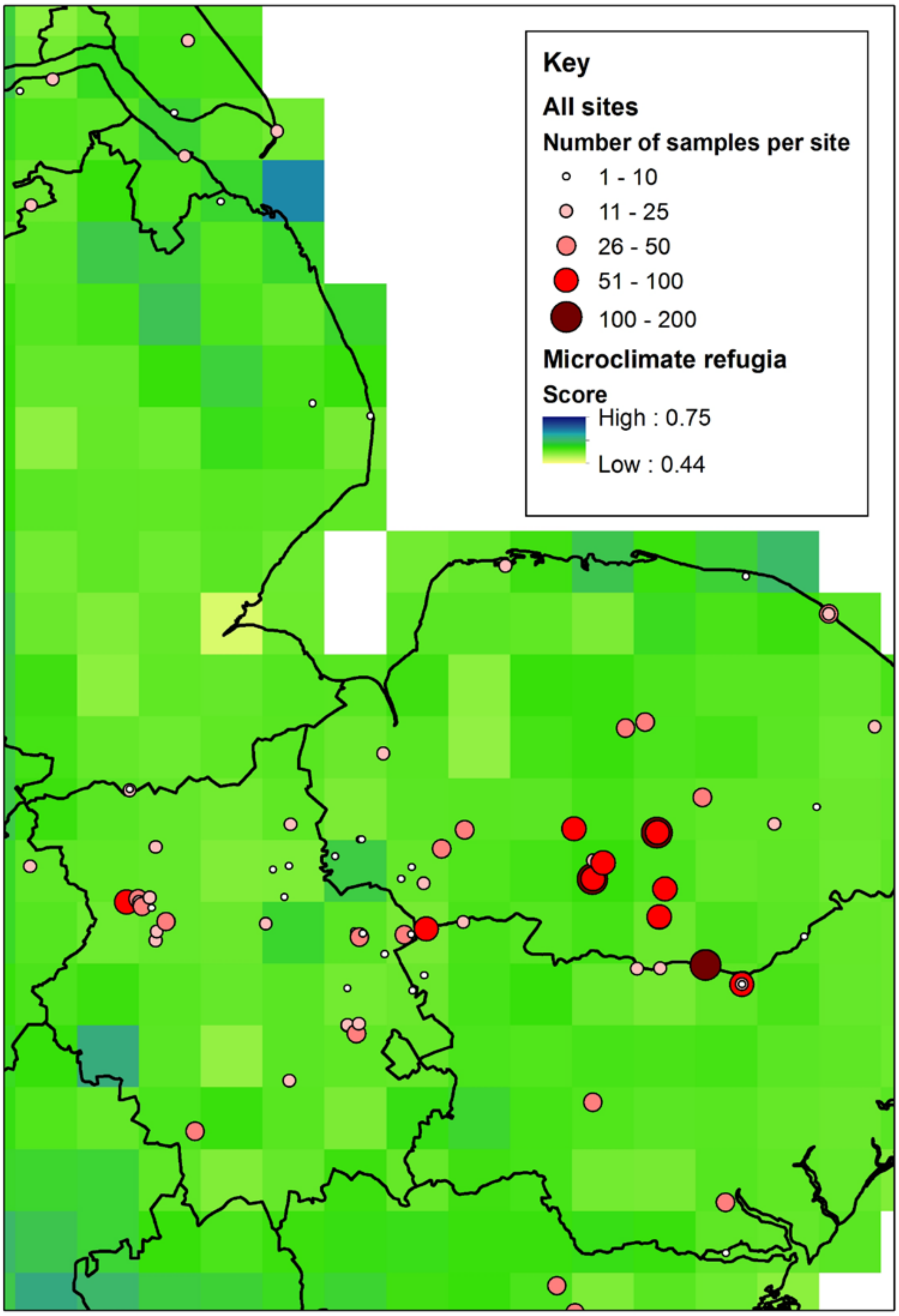


Figure 7.1. *Map showing the locations of sites in (or near) the East of England study area for which palaeoecological data are available. Circles denote the locations of palaeoecological records and the total number of samples analysed at each site. Coloured shading of the 10 km grid squares indicates their refugial potential score. Further details of how refugial potential was calculated are given in Suggitt et al. (2014) and Box 2.*

Woodland development - with the onset of the Holocene, woodland development began, initially of open birch woodland followed by pine (*Pinus*) and then hazel (*Corylus*), elm (*Ulmus*) and oak. Interpreting the pollen diagrams, Bennett (1983) argues for a persistence of oak likely representing both sessile oak (*Q. petraea*) and English oak (*Q. robur*) on different geologies (the pollen of the two species is indistinguishable), and for a likely dominance of a mixture of wych elm (*Ulmus glabra*) and field elm (*U. minor*) (with no common elm (*U. procera*)), contrasting with the absence of wych elm from eastern England at present (species separation of elm spp. is often not attempted, although there are systematic differences in the frequency of different numbers of pores on pollen, which permit a degree of probabilistic differentiation). It is generally difficult to assess the density and nature of the understorey shrubs from pollen evidence because many of them are entomophilous (pollinated by insects), whereas many canopy trees are anemophilous (wind pollinated). Nonetheless, the high pollen counts from Hockham Mere record the early-Holocene presence of a suite of understorey taxa considered typical of lowland mixed oak woodland, including elder (*Sambucus nigra*), guilder rose (*Viburnum opulus*) and common holly (*Ilex aquifolium*), as well as of less frequent components of the canopy, such as poplars, rowan (*Sorbus aucuparia*) and whitebeam (*S. aria*), ivy (*Hedera helix*) and mistletoe (*Viscum album*). Small-leaved lime (*Tilia cordata*) arrived around 7.6 ka cal BP, a few centuries after common alder (*Alnus glutinosa*); the latter persisted with low frequency for *ca*. 1400 years before its main increase, which occurred at markedly different dates even at sites within the study area. European ash (*Fraxinus excelsior*) also appeared at a similar time, whilst there is evidence for the local presence of English yew (*Taxus baccata*) only after 4.5 ka cal BP. Finally, European beech (*Fagus sylvatica*) and common hornbeam (*Carpinus betulus*) appear within the last 2-3000 years. Thus by around 6 ka cal BP, all the main elements of classic Holocene mixed oak woodland could be found in the area. Although a few trees and shrubs arrived later as climatic conditions changed in their favour, the principal feature of the later Holocene is the progressive loss of woodland cover that reflects the impacts of agricultural development by Neolithic and later cultures.

On the basis of the pollen records it is apparent that forest composition not only changed through time at any one location throughout the Holocene, but also that it was at no time uniform across the region. It is thus not possible to think in terms of any particular forest community as representing the 'climax' woodland of the region during the Holocene, or even at any particular time. A telling observation made by Bennett (1988, p.251) when discussing the East Anglian palaeoecological record in a British context, is relevant here; he stated: 'At some time in the early post-glacial of the British Isles, somewhere, almost every conceivable combination of birch, Scot's pine (*Pinus sylvestris*), elm, oak, hazel and common alder has existed (with the added complexity of small-leaved lime in the southeast). The highly variable nature of forest composition in space and time makes it difficult to produce a coherent picture of Holocene forest history on these islands.'

Clearance and management - because of the local density of sites, the available pollen data have provided the basis for reviews examining woodland dynamics (Bennett, 1986) and the impact of fire (Bennett *et al*. 1990). While it has long been suggested that English early post-glacial woodlands, particularly those dominated by hazel, were a fire-climax vegetation type, Bennett *et al*. (1990) suggest that early post-glacial woodlands were not fire-climax types. Instead, they propose that the frequent occurrence of charcoal in lake sediments from this interval reflects human occupation of lake shores, whereas the increased rate of charcoal deposition after c. 5000 years ago reflects increased use of fire as an agent in forest clearance after that time. Diss Mere was also analysed at very high resolution through the elm decline (Peglar 1993a), whilst the data from Quidenham Mere were amongst the first to be analysed using numerical analyses designed to seek recurrent groups and rarefaction (Peglar 1993b). These types of approaches are very useful in the context of reconstructing how vegetation may have responded to human influence and thus provide some context for understanding ecological restoration. Sims (1973; 1978) in two book chapters also used evidence from the area to develop ideas about the nature of early anthropogenic impacts on vegetation.

Persistence of non-arboreal taxa - there is evidence for the Holocene occurrence in the region of a wide range of non-arboreal taxa, although few can be assigned to individual species. This range of taxa is again typical for the British Isles, representing principally species of open and/or early successional habitats, including species that occur as weeds of arable and pastoral agriculture. Peglar *et al.* (1989) discuss in particular the records of pollen of hemp (*Cannabis sativa*) and Cannabaceae undiff. (indistinguishable pollen of either hemp or common hop (*Humulus lupulus*)) from Diss Mere that began after about 1500 years ago. Given that at least half of the Cannabaceae pollen could be identified with confidence as that of hemp and that the abundance of this pollen in the sediments exceeded 20% in some samples, they infer that this reflects the practice of hemp retting either in Diss Mere itself "or, more likely, in nearby pits that drained into the mere" (Peglar *at al*. 1989, p. 219). Early studies paid particular attention to attempting to identify pollen to species level wherever possible with the aim of elucidating the histories of individual species, especially of the calcicolous communities. Although Godwin (1968) reviews a range of Lateglacial records, and comments on the histories of individual taxa, demonstrating the continuous presence of such taxa throughout the Holocene is extremely difficult. As Bennett further comments (1983, p.482), "None of the rare plants of Breckland has been recognised either palynologically or through macrofossils at this [Hockham Mere], or any other, post-glacial site in the area."

7.1.3. Potential

Within the East of England, The Breckland area offers a relatively high concentration of sites with sediments that provide excellent sources of palaeoecological data for the Holocene and Lateglacial, especially those sites with non-calcareous catchments whose sediments thus can be radiocarbon dated. The deep sediments and relatively small size of the sites make them ideal for vegetation reconstructions that will reflect principally the vegetation of the local landscape around the sites. Although mostly studied more than two decades ago, it is possible that raw data would be available if required from the authors, especially Bennett. The available records for this area have good potential for investigating the persistence of taxa, including those of open communities, throughout the period of maximum Holocene woodland development. Sporadic occurrences of rare pollen taxa are recorded from some of the published sites (e.g. Quidenham Mere: Peglar 1993b), but there are few specific comments in papers regarding unusual taxa or particular aspects of the published evidence that examine long-term persistence of the wide variety of taxa that could be seen as characteristic of either forest or non-forest habitats in lowland England.

7.2. North East England

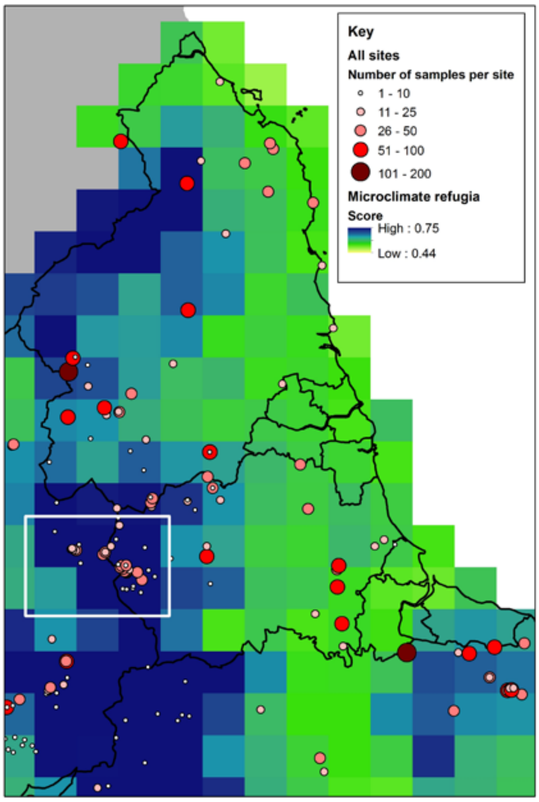
7.2.1. Sites – number and quality

Pollen analyses have been carried out on sediments from a relatively large number of sites in the North East England geographic region (Figure 7.3a), although these sites are unevenly distributed across the region, forming relatively discrete groups that broadly overlap with areas of high refugial potential as identified in the parallel study (Figure 7.3b). Consequently there would be some scope for future work to examine whether the landscape features that promote species persistence in the context of recent climatic change are similar to those that may have promoted persistence over palaeo-timescales. Since the high quality work by Turner and her co-workers in the 1960s and 1970s (Turner 1962; Turner *et al.* 1973), the region has continued to be a focus for palaeoecological research, principally exploiting the opportunities offered by the extensive blanket peat cover of the uplands, although lowland wetlands have also been used in some studies. Studies have examined both vegetation and climatic history, as well as the evidence of human impacts. The geological diversity of the Pennines, and the resulting mosaic of peatlands and heathlands on more acid rocks with grasslands on limestone (some of the latter being of particular botanical interest) has offered opportunities to explore the history of the areas of greater floristic diversity. The location of Durham University, long an important centre for UK palaeoecological research within the area, also has undoubtedly contributed to the intensity with which the region has been studied. Previous studies have compiled and reviewed data from this region, including Pratt (1996) in her PhD thesis and Huntley (2011) in an English Heritage report that identified over 100 sites within the Northern Pennines AONB. A previous English Nature Report by Chambers *et al*. (2007) also included sites from the region. The first two of these publications include unpublished material from a number of sites, some reported in PhD/MSc theses, to which we did not have access.

As with other areas of England, the proportion of sites that have adequate dating control and the overall temporal coverage are both limited, despite the large number of sites that have been studied (Figures S2.3 and 7.4). Few of the pollen records that cover the Early and Middle Holocene extend to the last two millennia, whereas those covering this more recent period are usually from studies that have only examined the more recent past, albeit often with high temporal resolution (e.g. Hendon & Charman 2004; Mighall *et al*. 2004). The latter studies, however, often have excellent chronological control, especially for the last few centuries through the use of ^{210}Pb, ^{137}Cs and/or spheroidal carbonaceous particle (SCP) dating (Box 3), as well as radiocarbon dating. The dominant blanket peat sites extend only to the early or even mid-Holocene; only a few sites have records that extend into pre-Holocene time, these mostly being topogenous mires or kettle holes in eastern parts of the region or in the Eden valley. Thus while it is possible to delimit both the overall regional spatio-temporal vegetation patterns for the Holocene, and with greater uncertainty, the Lateglacial, as well as local vegetation histories for specific sites, the general level of chronological robustness is not high and the quality of the pollen records is highly variable.

One area within the region stands out and has been highlighted in Figure 7.3b; this area of the higher Northern Pennines has the highest spatial density of sites. The most detailed and high quality studies in this core area were those undertaken by Turner *et al*. (1973); furthermore, these studies concentrated on the species of biogeographical interest found principally in Upper Teesdale, and upon questions of their persistence, rather than simply aiming to document the general vegetation and climatic history. Unfortunately, however, few of the sites studied have the level of chronological control that would be expected today, reflecting the fact that these studies took place more than 40 years ago, although broad, approximate ages of many of the deposits may be suggested from the pollen sequences. In terms of refugial interest, it is not surprising that the 1973 study by Turner *et al*., which concentrated on Upper Teesdale, remains the best source of information, despite its lack of a robust chronology. For the purposes of the detailed analyses below, this area of the Northern Pennines has been chosen as the core area for North East England due to its concentration of sites and their juxtaposition with some of the highest values for refugial potential (Figure 7.3a-b). This includes the site of Valley Bog examined by Chambers (1978) that is similarly highlighted by Huntley (2011).

(a)



(b)

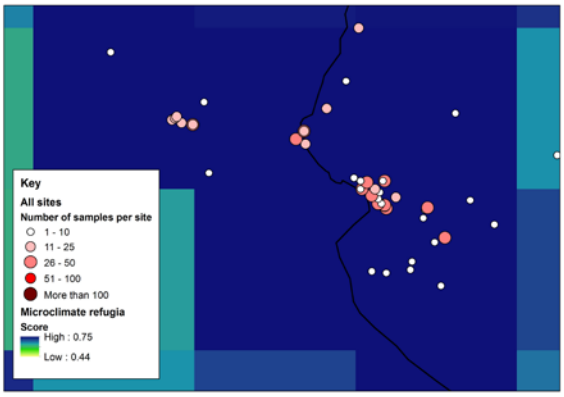


Figure 7.3. *Maps showing the locations of sites in the North East England study region for which palaeoecological data are available (a) and the Northern Pennine sub-region (outlined in white), in which there is a particularly high density of sites (b) Circles denote the locations of palaeoecological records and the total number of samples analysed at each site. Coloured shading of the 10 km grid squares indicates their refugial potential score (see Suggitt et al. 2014 and Box 2 for details).*

It is relevant to discuss these early attempts at examining refugial issues using palaeoecological data in the North East England geographic region. Turner was particularly interested in exploring the history of a number of the rarer and/or more geographically restricted plant species of Upper Teesdale in order to establish whether or not they had persisted there throughout the Holocene. Of the 75 biogeographically interesting and/or rare species identified by Pigott (1956), Turner specifically sought evidence for 16 that are effectively identifiable to species level in the pollen record. Of these, 11 were found in the pollen records she studied – thrift (*Armeria maritime*), dwarf birch, mountain avens (*Dryas octopetala*), spring gentian, hoary rockrose (*Helianthemum canum*), sea plantain (*Plantago maritime*), Jacob's ladder (*Polemonium caeruleum*), Alpine bistort (*Polygonum viviparum*), cloudberry (*Rubus chamaemorus*), yellow mountain saxifrage and starry saxifrage. Their presence, however, was by no means continuous at sites; most were represented only by occasional finds. However, Turner *et al*. (1973) argued that even these occasional records from throughout the Holocene were from generally forested areas. They suggested that large parts of the Northern Pennines, with the exception only of the highest summits, were forested, indicating that suitable conditions for the persistence of these shade-intolerant herbaceous species must have been present at least locally within this forested landscape throughout the Holocene. Such inference, however, raises an important issue regarding the conceptual basis for identifying persistence from palaeoecological data; this is discussed below.

In a subsequent publication entitled '*Conservation in Upper Teesdale: Contributions from the Palaeoecological Record*', Squires (1978) further developed the ideas put forward by Turner *et al*. (1973). He highlighted a number of key points relating to the conditions under which the shade-intolerant species had persisted, suggesting that they may have survived either in open canopied woodlands or in woodlands of varying density but with persistent presence of canopy gaps. He also emphasised the potential importance of the generation of habitats during the Holocene comparable to the earlier cold climatic conditions of disturbed open ground, and especially the importance of conditions that generated or maintained instabilities in the landscape, noting that "*the rarities are more widespread now than at any other time in their Flandrian [Holocene] history because many of their present habitats are recent, at most 5000 years old*" (Squires, 1978, p.146). Although it is probably true that some of the rarities have expanded their ranges in the Northern Pennines since 5 ka BP, the evidence to support a contention that this is more generally true is lacking. Whilst for some of the shade-intolerant species new areas of suitable habitat undoubtedly have become available as Squires (1978) suggests (e.g. cloudberry will potentially have benefitted from the increased extent of blanket mires during the later Holocene; thrift and sea plantain both have colonised spoil heaps around some heavy-metal mines), others remain quite strictly limited to the grassland and/or calcareous heath habitats associated with areas of saccharoidal ('sugar') limestone overlying the dolerite intrusion of the Great Whin Sill (e.g. hoary rockrose, mountain avens).

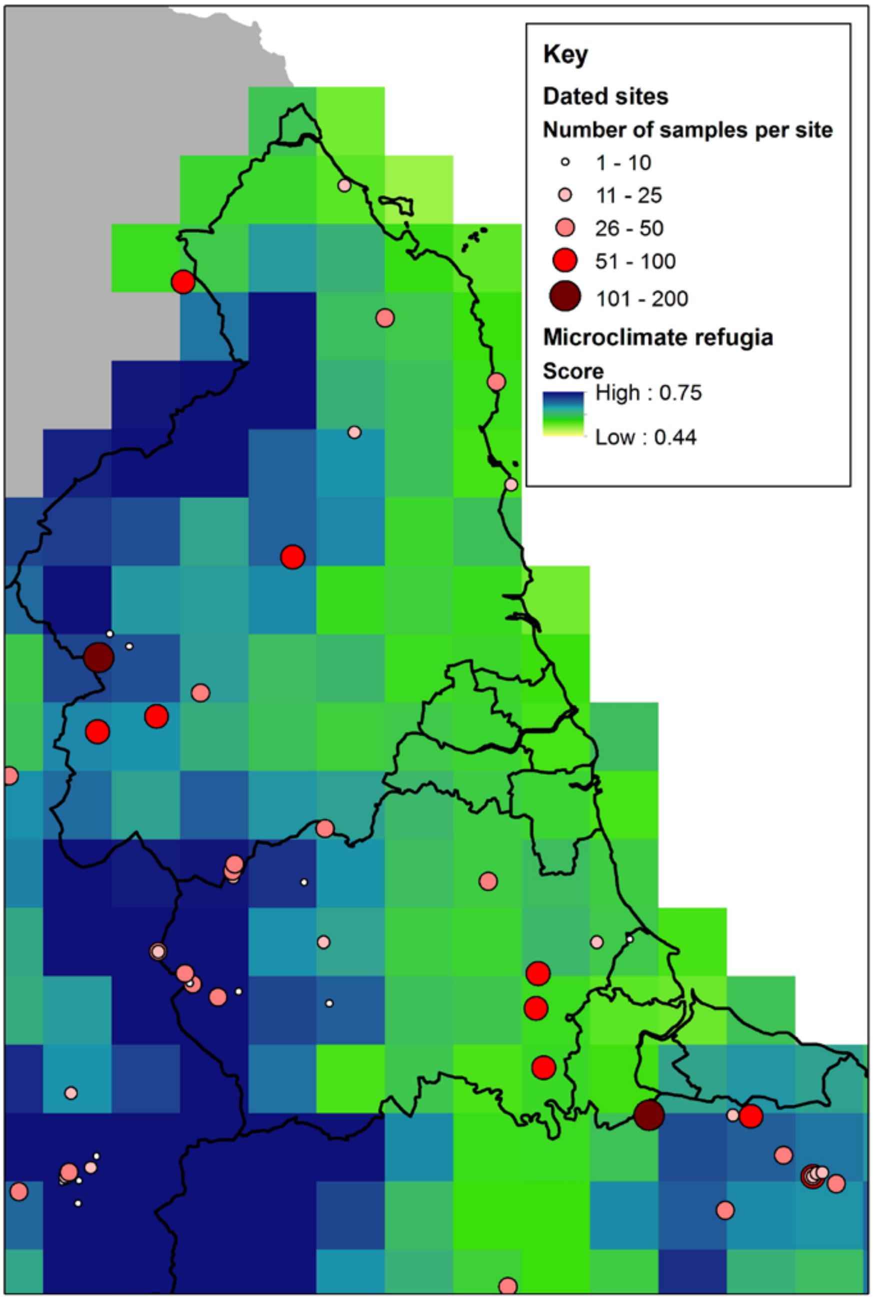


Figure 7.4. Map showing the locations of sites in the North East England study region for which dated palaeoecological data are available. Circles denote the locations of palaeoecological records and the total number of samples analysed at each site. Coloured shading of the 10 km grid squares indicates their refugial potential (see Suggitt *et al.* 2014 and Box 2 for details).

7.2.2. Vegetation character from records

Earliest records - Notwithstanding the lack of records with pre-Holocene radiocarbon dates, the evidence indicates that it is likely that a large number of the open habitat taxa that characterise Younger Dryas pollen assemblages persisted in the region's uplands at the opening of the Holocene, thus providing the basis for their Holocene survival (e.g. Hibbert & Switsur 1976). Species that are rare in the uplands today, but likely to have persisted throughout the Holocene, as discussed above, were almost certainly amongst those present.

Forest development - Although it is possible to discern a 'typical' pattern of forest expansion and development during the early Holocene, details of this are not well dated. There were also variations between sites in species' relative abundances. Elm, in particular, was more abundant at sites in areas dominated by limestone bedrocks, whereas at the Pow Hill site (Turner & Hodgson 1981) on the eastern flanks of the Pennine uplands, pine was locally dominant for an extended period, probably reflecting local geological and edaphic conditions, just as seems to have been the case with respect to the persistence of juniper near High Force in Upper Teesdale (Huntley 1991a). During the early Holocene, the tree line in the Northern Pennines is inferred to have been above 750 m.a.s.l. (Turner & Hodgson 1979). Squires (1978) highlights some of the uncertainties with respect to the pre-clearance patterns in forest composition; without the application of recent modelling developments to determine likely patterns in the composition of the forest cover (e.g. Fyfe *et al*. 2013) it is difficult to assess the spatial patterns of forest community types. The generally weak dating control also renders it difficult to determine any patterns in the temporal changes in forest communities.

Clearance and management - Since the onset of forest clearance during the Mesolithic (c. 10-5 ka cal BP), and especially since clearance intensified with the arrival of Neolithic agriculture, the interplay between different forms of land use and management regimes, changing climatic conditions, and soil formation, has resulted in the landscape and vegetation seen today. Burning and grazing regimes have been especially important influences, excluding longer-lived trees and shrubs and favouring the development of various types of grasslands, as well as of dwarf-shrub heathlands, especially the ling (*Calluna vulgaris*) dominated moorlands now typical of the Pennine uplands. Ling pollen is generally present throughout most of the Holocene in records from the core area of the Northern Pennines, although it increases in abundance in the later Holocene, and especially over the last two millennia, as management at lower elevations (within the region) intensified. Prior to this, the blanket peats, characteristic of the flat and gently sloping areas at higher elevations, gave rise to a blanket mire vegetation, with hare's-tail cottongrass (*Eriophorum vaginatum*) a key component (ling, cross-leaved heath (*Erica tetralix*), and various *Sphagnum* moss spp. also featured). Chambers *et al*. (2006) specifically focused on the question of the persistence and age of moorland communities, building on studies originally undertaken 50 years ago (Johnson & Dunham 1963). This work showed that despite claims to the contrary, ling-dominated moorland in the region has developed only from the time of the industrial revolution, thus making the case for on-going works (grip-blocking) to restore the blanket mire to its former condition at higher elevations within this geographic region (see also Box 5).

7.2.3. Potential

The core area of the Northern Pennines highlighted here has very high potential for several reasons. It is an area of high refugial potential in which a number of shade intolerant plant species of open habitats, that were widespread in the British Isles during the Lateglacial period, have persisted throughout the Holocene (Hibbert & Switsur 1976). There is a high density of published palaeoecological records, some providing evidence of this persistence of open habitat elements of the flora (e.g. Huntley 1991a). There are, however, weaknesses with the palaeoecological data, notably a lack of well-dated sites and of lacustrine sites. Although the widespread blanket and valley peats have great potential in principle, detecting more sparsely distributed and especially non-peatland taxa in these records is difficult. Further work in the area around Valley Bog, a focus for early studies close to the Cow Green Reservoir (Chambers 1978) and a location with a high refugial potential, might provide valuable new insights and would be supported by several published sites from the area with good Holocene coverage. The only available lacustrine records are outside the core area, e.g. Talkin Tarn to the north, in areas that do not have the density of sites or potential records to complement a single new record.

7.3. North West England

7.3.1. Sites – number and quality

The North West of England, especially Cumbria, represents one of the most intensively studied regions of England in terms of sites where pollen analyses have been performed (Figure 7.5, S2.5 in Appendix 2). The wealth of lakes and bogs scattered across the varied habitats of the uplands, lowlands and coastal areas of the region, combined with a rich archaeological history (e.g. McCarthy 1995), provides a particularly favourable context for the study of post-glacial vegetation development. Much of the early pollen work in the Lake District was carried out by Winifred Pennington (Mrs W G Tutin), working first with Sir Harry Godwin in the Sub-Department of Quaternary Research at Cambridge University and later at the Freshwater Biological Association (FBA), Windermere. Her work on sediments from Windermere (Pennington 1943; 1947) is widely regarded as the starting point for palaeolimnological studies in the UK. Working with William Pearsall, she produced the first ecological history of the Lake District (Pearsall & Pennington 1947), using the pollen record from Windermere to explore the long-term factors that had influenced post-glacial vegetation development (e.g. climatic change and human impact), building on ideas first put forward by Pearsall over 25 years earlier (Pearsall 1921).

During a career spanning more than 40 years, Pennington published 16 papers reporting pollen records from lakes and bogs throughout the central massif of the Lake District. Furthermore, she was not working in isolation at this time; several other leading pollen analysts of the period were also working in Cumbria, reflecting the wealth of high quality sites across the county. Key publications included Donald Walker's study on the Late Quaternary vegetation history of the Cumberland Lowlands (Walker 1966) and Frank Oldfield's papers on the use of pollen analysis to investigate the role of human activity in vegetation development, based on his work around Lowland Lonsdale and the Morecambe Bay area (Oldfield & Statham 1963; Oldfield 1969). By the time Pennington published her paper '*Vegetation history in the North-West of England: a regional synthesis*' (1970), a total of 210 pollen records had been published from the region, the highest concentration for any region of England.

After the peak of activity in the 1950s and 60s, the rate of publication of new pollen records decreased, with just 34 studies published during the 1970s and only 25 more since the 1980s. In the late 1990s, however, there was an increased interest in Holocene peat records from the region. Work on records from Bolton Fell Moss and Walton Moss in northern Cumbria (e.g. Dumayne-Peaty & Barber 1994; Hughes *et al.* 2000; Mauquoy *et al.* 2002; Barber *et al.* 2013), and on the Mosses in the Lyth Valley (e.g. Wimble *et al.* 2000) and around the Leven Estuary (Coombes *et al*. 2008) in southern Cumbria, have provided some of the highest resolution pollen and plant macrofossil records available for the Mid and Late Holocene. These studies focused especially upon exploring the potential of these records for palaeoclimatic reconstruction.

During the last decade several studies (e.g. Wimble *et al.* 2000; Chiverrell *et al.* 2006; Harkness & Wilson 2006; Coombes *et al.* 2008) have re-examined some of the classic Cumbrian sites, in part reflecting efforts to improve upon the often very limited age control typical of most pollen records published before 1980. Of all the sites discussed by Pennington (1970), only Blea Tarn (Figure 7.5) and Blelham Tarn had any radiocarbon dates (Harkness & Wilson 2006). The chronology of the Lateglacial and Early Holocene remains problematic, with Blelham Tarn and Windermere remaining two of the best dated sequences. The pollen record for the Mid and Late Holocene has greater spatial resolution, although the spatial distribution of well-dated sites remains uneven (Figures 7.6, 7.7). Thus, despite the high quality of many of the individual pollen records, considerable uncertainty remains with respect to the spatio-temporal patterns of Lateglacial and Holocene vegetation development in the region. The spatial distribution of sites with palaeovegetation records shows a clear north–south trend in the density of investigated sites (Figures 7.6, 7.7), with a much higher density of sites in the southern part of the Lake District mountains and the lowlands of south Cumbria than in the north of the region. The area in the south, with a higher density of sites, includes areas of high refugial potential, in particular in the area from greater Langdale to Burnmoor Tarn (Figures 7.6, 7.7). North of Langdale the density of sites is markedly less, particularly in the area of high refugial potential east of the M6 corridor that runs northwards from Tebay to Carlisle. The western coastal strip also has relatively few investigated sites and offers limited numbers of potential sites for study; this is probably less important, however, as the area has generally low refugial potential. Sites with well-dated palaeo-faunal records are also sparse in this region (Figures 7.7-7.9, S2.5), with no records from the Lake District mountains despite the high refugial potential of this area.

Figure 7.5. *Coring the lake sediments at Blea Tarn SSSI, Langdale, Cumbria, a key site for palaeoenvironmental studies, providing critical evidence on upland conditions during Devensian late-glacial and early and mid-Holocene times. (Ray Wilson).*

7.3.2. Vegetation Character from records

Earliest records - although no continuous high resolution record from the region spans the entire Lateglacial and Holocene, the wealth of data from the region provides a detailed history of vegetation change, albeit with limited dating control. Lowland Lateglacial sites such as Windermere (Pennington 1943; Bonny 1976), Blelham Tarn (Pennington 1965; 1970) Hawes Water (Oldfield 1960) and those examined by Walker (1966), point to a multi-stage transition from the last glacial stage to the Holocene. This transition period, sometimes referred to in England as the Windermere Interstadial, was characterised by the presence of a range of plant communities that are absent from the region today. Communities characterised by the presence of cold-tolerant species, including dwarf willow (*Salix herbacea*), dwarf birch and a range of Arctic–Alpine herbs able rapidly to colonise fresh skeletal soils, are recorded at Blelham Tarn and Windermere *ca*. 14 ka cal BP. Many of the Arctic–Alpine species prevalent across the region at that time are today restricted to higher altitude areas or absent entirely.

Woodland development - as the climate continued to warm, juniper scrub expanded, particularly across the lowlands. This scrub was subsequently replaced by open birch woodland at most lowland sites. The high relative abundance of juniper pollen in the early part of this sequence is of particular interest because such high values are not found in modern pollen samples from the region. The Lateglacial vegetation was also characterised by the presence of sea-buckthorn (*Hippophäe*), especially early in the interval, of *Artemisia* (mugworts and wormwoods), that reached peak abundance during the Younger Dryas cold interval, and of rock roses (*Helianthemum*); these Lateglacial plant communities are without analogues in Britain today. Sea buckthorn, in particular, is today restricted to just a few locations along the Cumbrian coast (Pennington 1970; 1977), whereas during the Lateglacial it was widely present both in the lowlands and uplands, extending to the catchments of sites such as Blea Tarn and Burnmoor Tarn. However, this extensive Lateglacial pattern of occurrence is less surprising when its wider European range today is considered; the species occurs widely in Central Europe both above the treeline and on unstable areas of river floodplains, its combination of shade-intolerance and nitrogen fixing root nodules meaning that it is well adapted to act as a pioneer species on mineral soils. With the onset of the Younger Dryas (Loch Lomond) Stadial, arboreal taxa most likely disappeared completely from North West England. Shade-intolerant herbaceous taxa often associated with disturbance (e.g. plants of the genus *Artemisia*, and carnations (Caryophyllaceae) and crucifers (Brassicaceae)) dominate the record at this time, although total pollen concentrations generally are very low, probably indicating only sparse vegetation cover.

Pollen records for the Early Holocene reflect the classic sequence recorded at sites throughout England as various tree taxa expanded their ranges across Europe and the British isles from the restricted areas in southern Europe where they had persisted during the LGM. By *ca*. 6 ka cal BP, most of the trees and shrubs today considered native to the UK were present in North West England, small-leaved lime having by that time reached its Holocene northern limit that extended across northern England from mid-Cumbria to mid-Durham. Oak was most prevalent in the lowlands, whereas elm was more abundant at intermediate altitudes and birch reached greatest relative abundance in the uplands (Pennington 1969). Detailed reconstructions of lowland forest composition, such as that for Roudsea Wood (Birks 1982), indicate species-rich mixed lowland forests in the early-Holocene, the composition of which included several species that today reach or approach their northern limits in the region (e.g. field maple (*Acer campestre*) and wild service tree (*Sorbus torminalis*)). Pollen records from the uplands indicate that many taxa that were widespread during the Lateglacial persisted in upland habitats well into the Holocene. Indeed, Pennington (1997) suggests that widespread Lateglacial taxa such as meadow rue (*Thalictrum minus*) and meadowsweet (*Filipendula ulmaria*), which are found today on cliff edges at high altitudes in the Lake District mountains, most likely persisted in these habitats throughout the Holocene.

Clearance and management - pollen records for the last 5000 years from the region are generally interpreted principally as providing evidence of anthropogenic activities. The rapid development of Neolithic farming practices is reflected in numerous pollen records by successive 'Landnam' events (the time when land and islands in this area were first populated) at both lowland and upland sites. Subsequent anthropogenic activity, acting in combination with changing climatic conditions, has resulted in marked changes in the spatial patterning and composition of vegetation across the region during the late Holocene. Dating control for vegetation changes during the mid and late Holocene periods is much better than for the Lateglacial and early Holocene, principally as a result of the publication since 2000 of several well-dated, high-resolution records (e.g. Wimble *et al.* 2000; Chiverrell *et al.* 2006; Coombes *et al.* 2008).

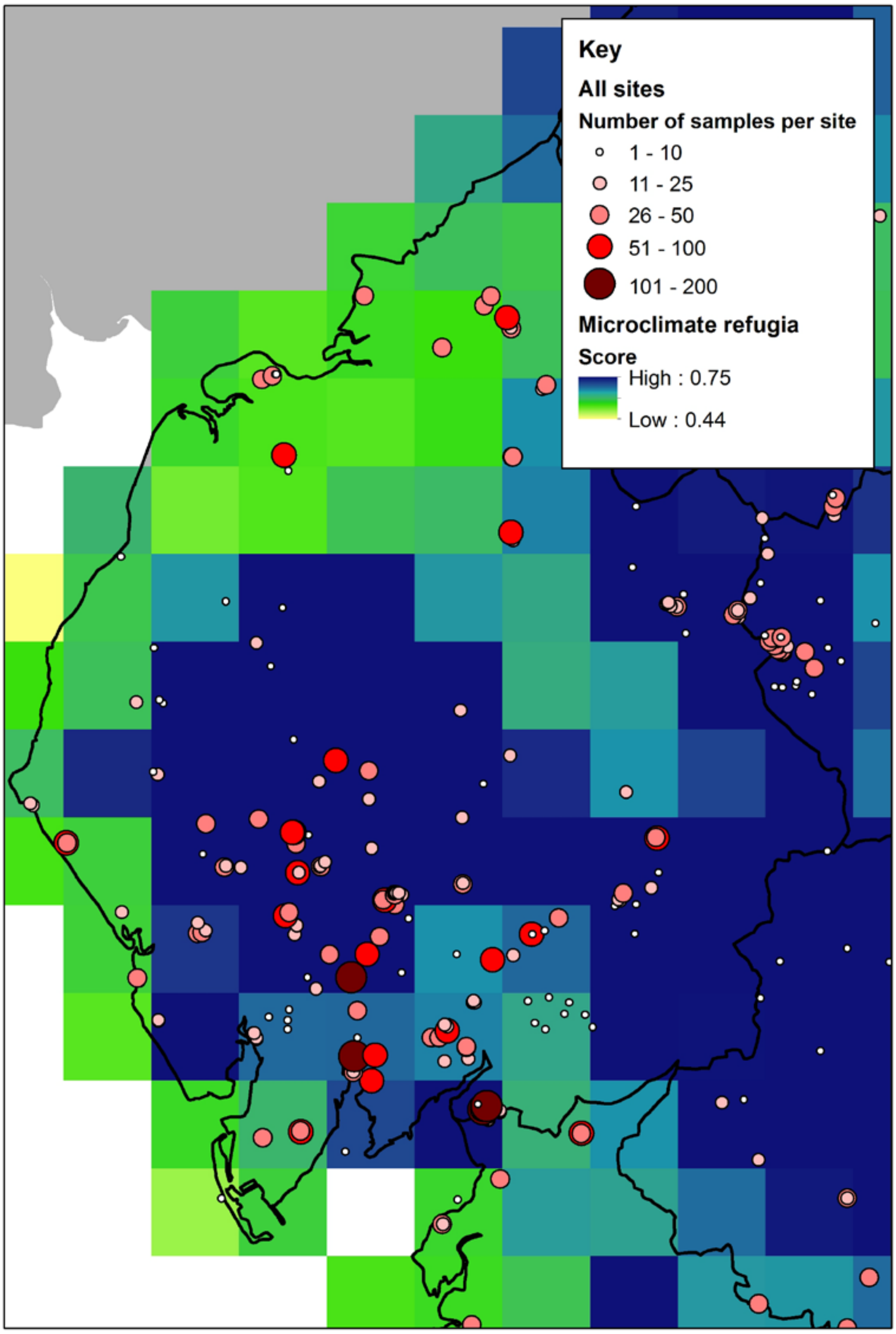


Figure 7.6. *Map showing the locations of sites in the North West England study region for which palaeovegetation data are available. Circles denote the locations of palaeovegetation records and the total number of samples analysed at each site. Coloured shading of the 10 km grid squares indicates their refugial potential (see Suggitt et al. 2014 and Box 2 for details).*

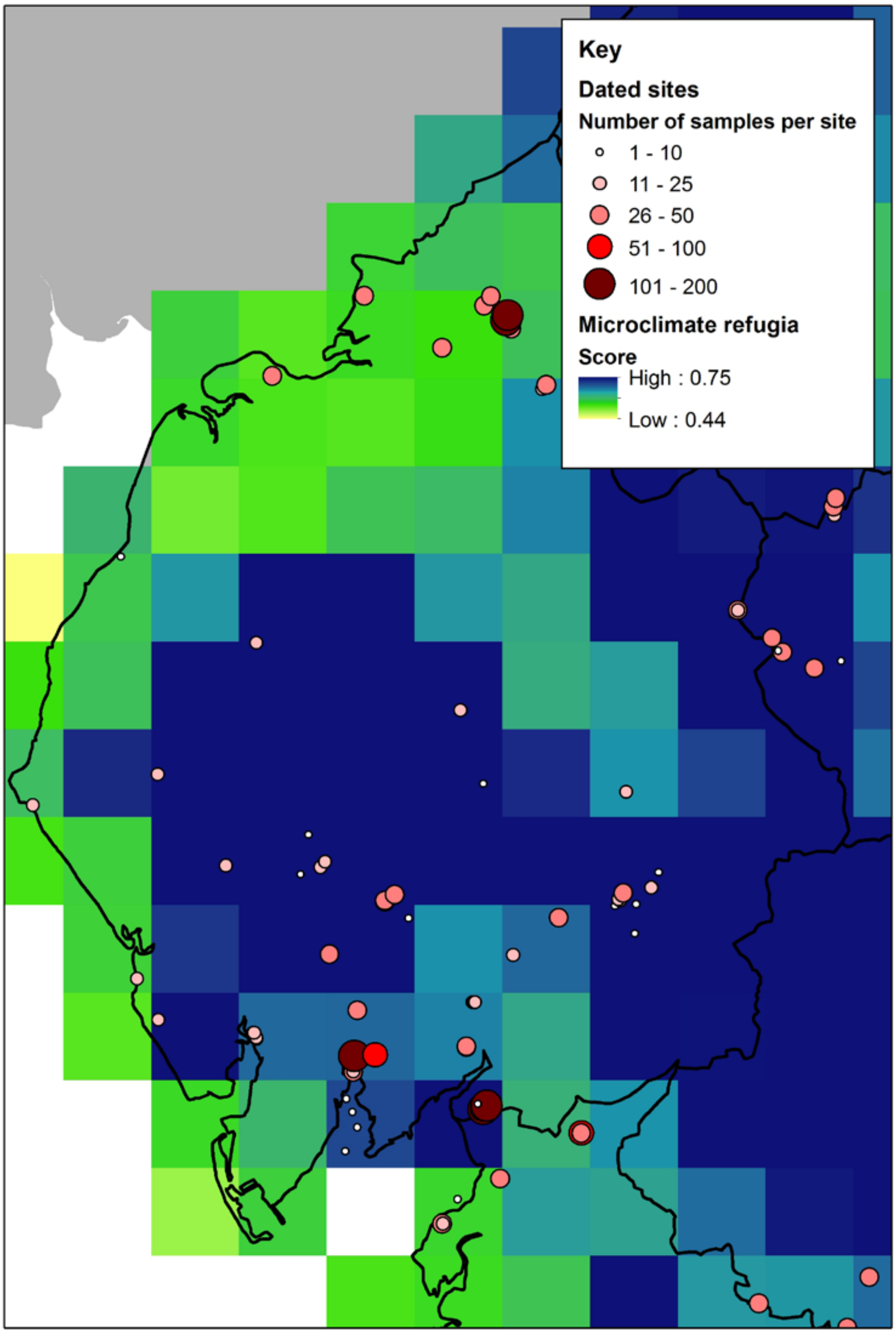


Figure 7.7. *Map showing the locations of dated sites in the North West England study region for which palaeovegetation data are available. Circles denote the locations of palaeovegetation records and the total number of samples analysed at each site. Coloured shading of the 10 km grid squares indicates their refugial potential (see Suggitt et al. 2014 and Box 2 for details).*

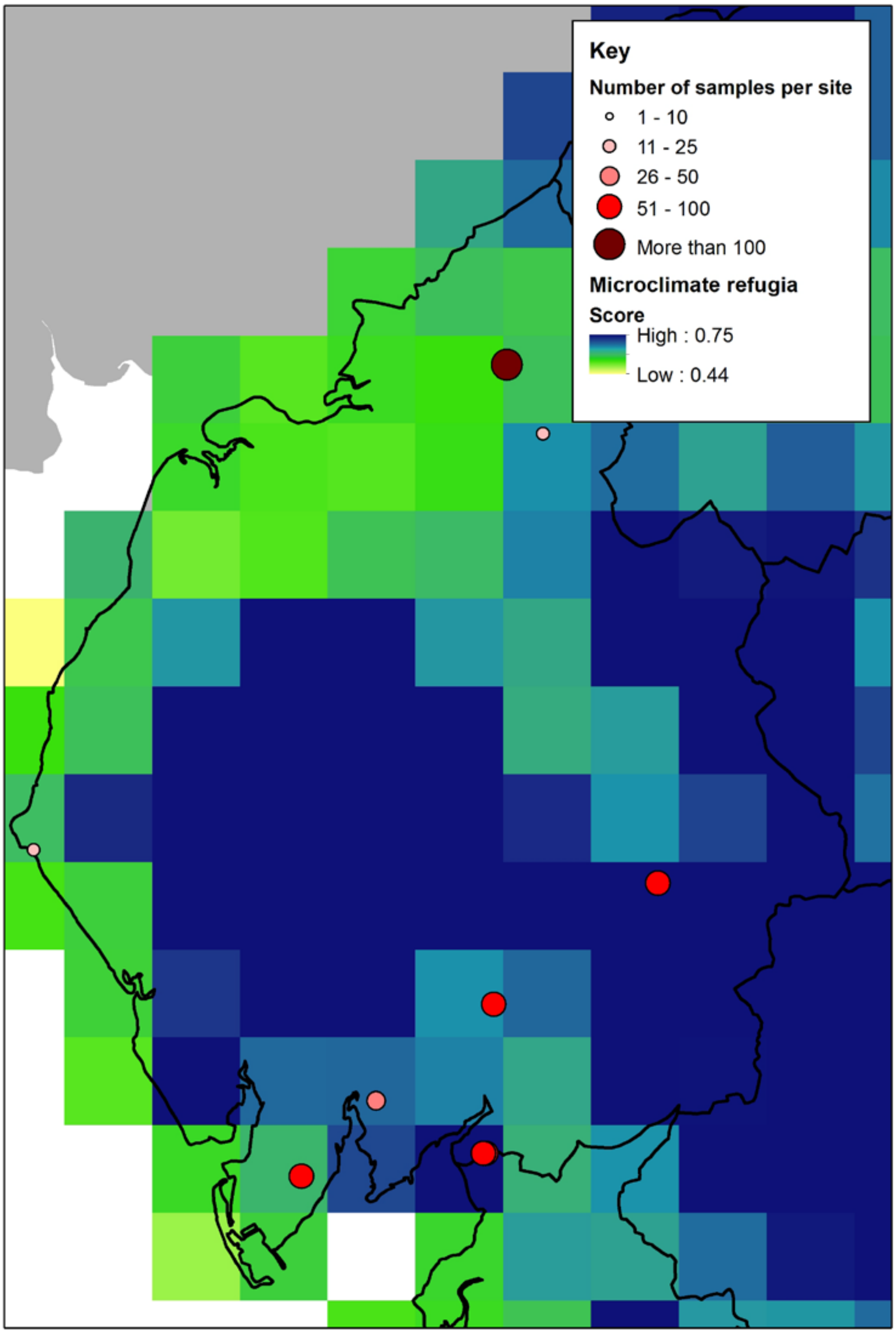


Figure 7.8. *Map showing the locations of sites in the North West England study region for which palaeofaunal data are available. Circles denote the locations of palaeofaunal records and the total number of samples analysed at each site. Coloured shading of the 10 km grid squares indicates their refugial potential (see Suggitt et al. 2014 and Box 2 for details).*

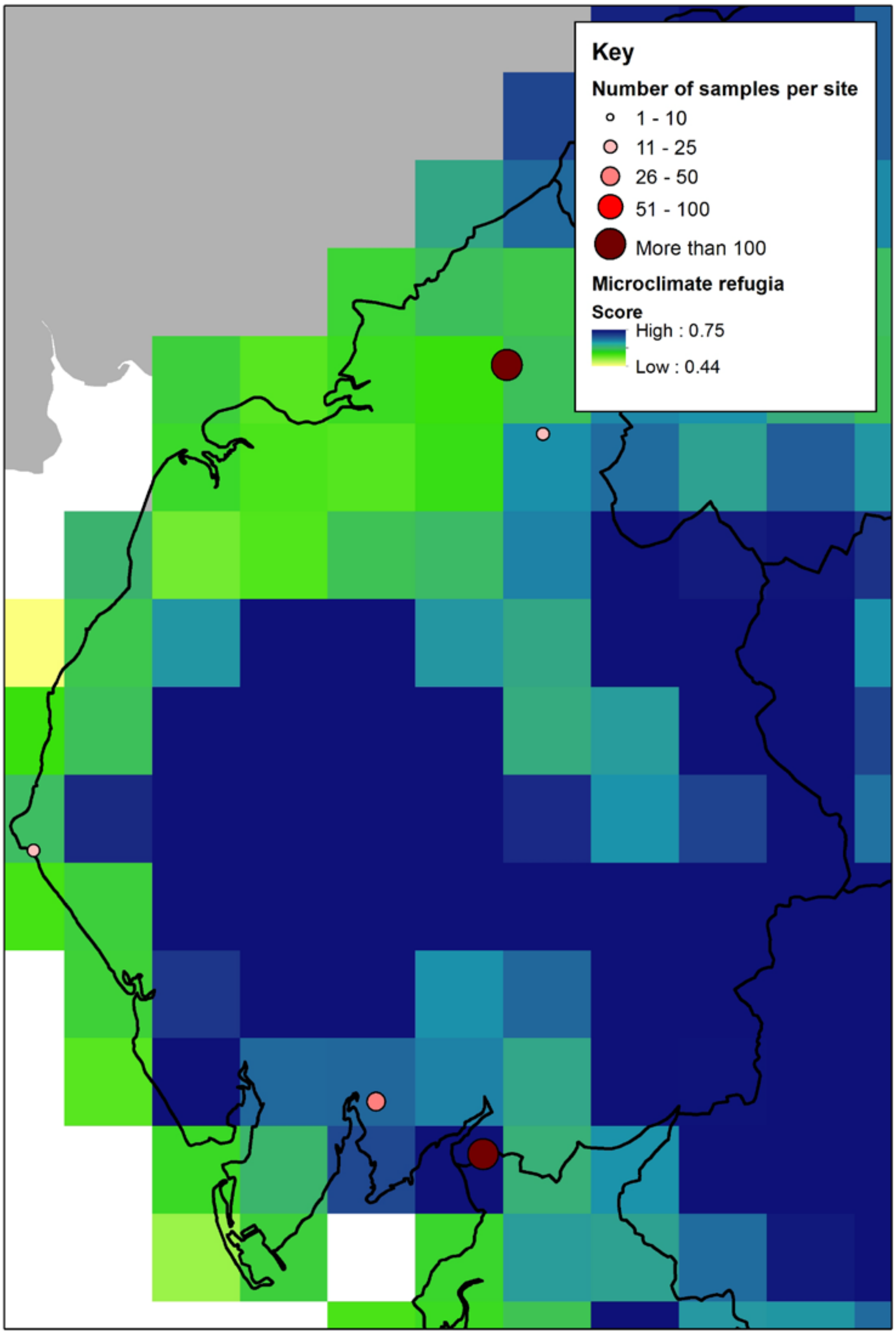


Figure 7.9. *Map showing the locations of dated sites in the North West England study region for which palaeofaunal data are available. Circles denote the locations of palaeofaunal records and the total number of samples analysed at each site. Coloured shading of the 10 km grid squares indicates their refugial potential (see Suggitt et al. 2014 and Box 2 for details).*

7.3.3. Potential

Despite problems with chronological control in earlier time periods, North West England remains a key region for palaeoenvironmental research. The wide variety of local habitats and wealth of high quality sedimentary records make it an ideal location for studies of palaeovegetation, as well as for palaeolimnological investigations and studies aiming to reconstruct palaeoenvironmental conditions. Although a lack of adequate chronological control is an issue with many of the records published prior to 1980, this is generally not an insurmountable problem. Limestone bedrock is of relatively restricted occurrence, being found principally in the south of the region, around Morecambe Bay, and in the east on the flanks of the Northern Pennines, although at some sites (e.g. Hawes Water, Oldfield 1960) Lateglacial and early Holocene sediments are biogenic marls. Most sites thus offer suitable organic remains for radiocarbon dating. The wide range of habitats present in the region is of interest from the perspective of studies of potential refugia as it would facilitate comparison between features hypothesised to promote species persistence with those that have not. Furthermore, comparison of the site locations in North West England with the distribution of refugia identified in the parallel project highlights that this area coincides with some of highest values for refugial potential (Figures 7.7, 7.8). Consequently, there is potential to investigate further the extent to which persistence over palaeoecological timescales is promoted by landscape features that also enhance species persistence over the much shorter timescales associated with recent climatic change. Upland sites such as Blea Tarn, Red Tarn, Burnmoor Tarn and Langdale Coomb provide excellent Holocene records (see Pennington 1970 for a regional synthesis). Lowland sites are equally plentiful, with Lateglacial/Holocene records from the limestone region of southernmost Cumbria (Hawes Water, Cunswick Tarn etc.), in particular, offering insight into palaeovegetation changes in this somewhat karstic setting, albeit with associated dating problems.

7.4. Comparison of geographic regions

7.4.1. Sites – number and quality

A summary of the total number of sites (and dated sites) in each of the study areas is shown in Table 7.1. Breckland, in the East of England, was one of the first areas to be studied using pollen analysis. Some sites within this area have relatively high temporal resolution; several have records extending back into the Lateglacial and some have good radiocarbon control. The Breckland area offers a relatively high concentration of sites ideal for vegetation reconstructions. Most of the species dominating the pollen record are widespread and thus not ideal for determining the locations of refugia. Sporadic occurrences of pollen taxa with more restricted distributions are recorded from some of the published sites, but there are few specific comments in papers regarding the long-term persistence of these. In the North East England region, pollen analyses have been carried out on the sediments from a relatively large number of sites, although these sites are unevenly distributed across the region and fewer have adequate dating control and sufficiently high temporal coverage. North West England, especially the Lake District, represents one of the most intensively studied regions of England. As with other regions, dating control is problematic, but during the last decade several studies have re-dated some of the classic Cumbrian sites.

Table 7.1. *Summary of the number of palaeoecological records in each of the study areas.*

	North East England	East of England	North West England
Total sites	133	83	223
Total dated sites	38	11	73

7.4.2. Vegetation character from records

In the East of England, the onset of the Holocene was characterised by woodland development, initially of open birch woodland followed by pine and then hazel, elm and oak, although the composition at any given time was not uniform across the region. In North East England, it is likely that a large number of the open habitat taxa that characterise Younger

Dryas pollen assemblages persisted in the region's uplands at the beginning of the Holocene. In North West England, lowland Lateglacial sites point to a multi-stage transition from the last glacial stage to the Holocene characterised by the presence of a range of plant communities that are absent from the region today.

In the East of England, by around 6 ka cal BP, all the main elements of classic Holocene mixed oak woodland could be found in the area, although a few tree and shrub species arrived later as climatic conditions changed in their favour. The principal feature of the later Holocene was the progressive loss of woodland cover that reflects the impacts of agricultural development. In North East England, the Northern Pennines are likely to have served as an area of high refugial potential in which a number of shade intolerant plant species of open habitats that were widespread in the British Isles during the Lateglacial period may have persisted throughout the Holocene. In North West England, communities characterised by the presence of cold-tolerant species, including dwarf willow and a range of Arctic–Alpine herbs, persisted across the region, although their ranges gradually declined such that today they are restricted to higher altitude areas or absent entirely.

7.4.3. Potential for using palaeoecological data

The Breckland in the East of England offers a relatively high concentration of sites with sediments that permit robust reconstruction of Holocene vegetation history. At a number of sites, the available records have good potential for investigating the persistence of taxa, but while sporadic occurrences of rare pollen taxa are sometimes recorded, there are few specific comments in papers regarding unusual taxa or particular aspects of the published evidence that examine long-term persistence. In North East England, a core area of the Northern Pennines has very high potential for further investigation of refugial issues, as there is a high density of published palaeoecological records, which documents the persistence throughout the Holocene of plant species widespread in the British Isles during the Lateglacial. North West England remains a key region for palaeoenvironmental research and thus has high potential for detailed reconstructions of vegetation history. Although a lack of adequate chronological control is an issue with many of the records published prior to 1980, many sites offer suitable organic remains for radiocarbon dating. The wide range of habitats present in the region is of interest from the perspective of studies of potential refugia.

8. Potential use of existing palaeoecological data and focus of future work.

In this section, we demonstrate how palaeoecological data can be used to investigate the characteristics and locations of potential climatic change refugia and identify suitable areas for ecological restoration. We start by summarising how palaeoecological data could help to identify areas with the potential for ecological restoration. We then go on to describe how palaeoecological data could be used to investigate the location and characteristics of climatic change refugia. We argue that, while palaeoecological data can provide an important context for discussions relating to ecological restoration and refugia, in most instances the focus of palaeoecological studies has been to characterise vegetation history. Most of the studies we found did not set out specifically to contribute to refugial or restoration debates. However, we identify several ways in which palaeoecological data could be used to investigate these issues in more detail, although this would often require additional data. We summarise the issues that should be taken into account in so doing, and highlight the types of data that it would be most advantageous to collect.

8.1. Palaeoecological data and ecological restoration

8.1.1. Overview

There is no doubt that palaeoecological data can provide an important context for discussions relating to ecological restoration and/or the appropriate management of degraded habitats (Seddon *et al.* 2014). In some cases palaeoecological data may establish the long-term relict status of a community or habitat (e.g. the juniper woodlands around High Force in Upper Teesdale, Huntley 1991a) and provide evidence of the 'baseline' conditions that management/restoration targets might set. For example, sessile oak woodlands characterised by a rich bryophyte community, found commonly in parts of western England, were historically considered close to 'wildwood'. A pollen sequence from the Lake District, however, reveals that bryophyte rich sessile oak is a relatively recent community that results from human disturbance. For much of the Holocene prior to the influence of humans, this woodland was a mixed deciduous type dominated by hazel, birch, alder, holly and rowan (Birks 1996). A further example is provided in Box 5.

More generally, the Holocene palaeoenvironmental record shows that over the last 11,700 years plant species have responded to changing environmental conditions, whether climatic conditions, pressures arising from human activities, edaphic (soil) conditions or interactions with other ecosystem components (e.g. large herbivores). The principal response has been to shift their distributions to track the conditions to which they are adapted (Huntley & Webb 1989). Such distribution shifts are likely to have occurred at all spatial scales, from the well-documented and extensive Holocene 'migrations' of European tree taxa to less clearly demonstrated localised shifts between microsites within a landscape. Thus, even if it is not possible to predict exactly what responses to future environmental conditions are going to be, the palaeoecological record provides an excellent basis for developing management actions designed either to restore habitats or to facilitate ecological responses to environmental change. For example, pollen and plant and faunal macrofossil records from the Yorkshire Wolds (Bush and Flenley 1987) demonstrated that grazing is an important factor in the maintenance of chalk grassland diversity; the cessation of grazing leads to dominance of a few grasses, and even to incursions by shrubs or other woody species.

Furthermore, palaeoecological data have shown that many important communities of present landscapes, considered to be of high conservation value, are relatively recent (centuries to a few millennia) developments rather than having persisted over longer time periods (many millennia or the entire Holocene). More generally, the palaeoecological record has clearly demonstrated the individualism of species' responses to environmental changes. Such insights should inform discussions over what and why to restore; especially relevant to such considerations is the evidence of the ephemeral nature of communities (Huntley 1996). Restoration ecology has traditionally entailed identifying sources of damage and appropriate restoration targets, often the state of the ecosystem before disruption. Palaeoecological reconstructions have contributed to a revision of this approach. Firstly, the concept of “natural” is being redefined based on increasing awareness that humans have, throughout much of the latter Holocene, exerted substantial influence on ecosystems, from simple hunting/harvesting to fire management and direct vegetation alteration (Peglar *et al.* 1989; Bennett *et al.* 1990). Our synthesis of the literature suggests that the nature, duration, and intensity of these impacts varied by region and in time, but few terrestrial ecosystems appear to have escaped some effects of human activity.

Box 5. Example of how of palaeoecological data can be used to inform ecological restoration (see Davies & Bunting 2010 for further details).

As specified in Section 41 of the Natural Environment and Rural Communities Act (2006), upland heathlands in the UK are considered a habitat of principle importance in England. However, they are also threatened by widespread erosion. The high conservation value of this habitat, the threat to it, and the risk of non-reversible damage provide strong justification for ecological restoration (Davies and Bunting 2006). Palaeoecological reconstructions using pollen, plant macrofossil, peat stratigraphy, radiocarbon-dating and the occurrence of soot particles has helped to establish that degradation is associated with strong directional shifts in the competition balance between dominant taxa and species impoverishment (Chambers 2007; 2011). Drivers of this shift include changes in grazing regime, in burning patterns and in atmospheric nitrogen deposition, which may be continuing to favour grass dominance (Chambers et al. 1979, 1999). Palaeoecological data suggest that efforts to restore this habitat type by reducing purple moor grass (*Molinia caerulea*) growth are justified, since the shift in dominance is recent and unprecedented. However, in northern England and South Wales, ling-dominated communities are a relatively recent phenomenon, suggesting that the conservation preference often given to this vegetation type is, perhaps, unwarranted.

8.1.2. Restoration under climatic change

Ecosystems have experienced climatic changes throughout their existence (Box 4), owing to natural causes and more recently to human activities. This situation has led some to argue (e.g. Jackson & Hobbs 2009) that, for many ecosystems, restoration to a historic standard is chronologically inconsistent. The environment has drifted, and so too have the targets, which may be unsustainable under an early 21st-century climate.

Conventional wisdom has seen references to the range core (e.g. Lawton 1993), range margin (Travis & Dytham 2004) or connectivity (Fahrig & Merriam 1985) of populations as key to their continued survival under climatic change. However, evidence from the Quaternary shows that species have exhibited major shifts in their distributions in response to the glacial-interglacial cycles that characterise this period (Huntley & Webb 1989). Thus, most species found today principally in the Nemoral (temperate deciduous forest) zone of Europe were absent from this area during at least the coldest phases of glacial stages, surviving in areas of relative warmth at least principally in the three southern European peninsulas (e.g. Bennett *et al.* 1991; Thomas 1993; Hampe & Jump 2011). Even in those regions, however, temperate species were far from ubiquitous during glacial stages, being instead restricted to intermediate altitudes in mountain ranges for much of each glacial stage (Willis 1994). This suggests that availability of suitable microclimates and microhabitats was key to their survival. Complementary evidence shows that many Boreal and Arctic–Alpine species were widespread in Europe north of the main mountain chains during glacial stages, in some cases their ranges extending as far south as northern Spain. Today many of these species have relict populations in areas of favourable microclimate and/or microhabitats (sometimes referred to as ‘interglacial refugia’ – see Box 2) well to the south of their main area of distribution i.e. the Pyrenees and the Alps.

Many species of conservation concern in the UK, notably invertebrate species, have abrupt northern limits to their ranges that correlate closely with some measure of summer warmth, often a particular mean monthly temperature isotherm (Thomas 1993). Within their UK range these species also often exhibit a preference for the warmest microhabitats within the landscapes where they are found (Suggitt *et al.* 2012), although some other invertebrates with more northerly distributions, such as ground beetles, are more likely to be found in the coldest microhabitats available (Gillingham *et al.* 2012). Southern plant species exhibit a similar pattern to butterflies, their restriction to the warmest microhabitats becoming increasingly marked as their northern limits are approached (e.g. Pigott 1968, 1975). Most of these warm microhabitats are characterised by short, herbaceous vegetation of shade-intolerant species; many are ephemeral because they represent early stages of a succession towards closed woodland or forest communities.

Palaeoecological data (as well as contemporary ecological studies) indicate that many species owe their origins and/or persistence to some form of human activity because of the microclimatic conditions created by such activity. As a consequence, restoring habitats for these species often requires the creation and maintenance of early successional stages. Historically such communities were maintained by traditional land-use practices; maintaining them today thus requires active management that replicates the effects of the appropriate historic land use (Sutherland 2008). Palaeoecological data can potentially provide insight into the nature of the habitats in which these species persisted prior to the development of habitats dependent upon human land use, and especially during the Holocene thermal optimum. In turn, such insights can inform the development of conservation management practices that might be effective in the face of future climatic change. The palaeoecological data presently available, however, would not provide the basis for the required insights for all species of conservation concern in all their varied habitat types. Additional targeted data collection might be possible in some cases where existing data do not suffice, although this is unlikely to be a panacea for all species of concern. We discuss the taxonomic groups, habitat types and types of additional data that would need to be collected in section 8.3 at the end of this chapter.
investigate these issues in more detail, although this would often require additional data. We summarise the issues that should be taken into account in so doing, and highlight the types of data that it would be most advantageous to collect.

8.2. Investigating potential refugia using palaeoecological data

8.2.1. Methodologies

There are a number of ways in which a palaeoecological approach could be used to investigate issues relating to refugia. Some of these have already been applied, while others utilise new ideas or techniques:

(1) Demonstrating persistence of taxa – the intuitive approach.

In their work on the northern Pennines, Turner *et al*. (1973) adopted a classic intuitive approach. They argued that, in the case of open habitat taxa only ever likely to be represented by occasional finds of pollen, their sporadic presence in a pollen record for the Holocene was likely to indicate both their persistence and the persistence of the open habitats that they require, even if the plant communities of those habitats were palynologically silent at times. This argument is especially persuasive if these occasional finds continue throughout a record that otherwise indicates dominance of the local landscape by forest or woodland communities. Thus, whilst such records cannot generally provide details of past community composition in the open habitats, nor of the specific whereabouts of these open habitats at any time, they can demonstrate that particular taxa, and hence suitable open habitats, persisted locally. Few palynologists would argue with the underlying rationale behind this approach. Of course, in upland areas some open and/or unstable environments, such as cliffs or fine scree slopes, may remain unforested without any requirement for special local conditions, thus potentially providing habitats for some open habitat species. Since the mid and late Holocene, human activities may also have provided new areas of open habitats suitable for some taxa. Some taxa may also have been able to exploit areas of disturbance, their location in the landscape varying through time. However, at least some of the species in the area examined by Turner *et al*. (1973) have such specialised habitat requirements (e.g. *Minuartia stricta*, *Viola rupestris*) that their persistence would only be possible where particular local conditions enabled their habitats to persist throughout the Holocene without ever becoming covered by forest.

(2) Demonstrating persistence of taxa – new techniques.
Rather than perform complete pollen counts for all samples, one potential way to seek evidence for persistence of individual taxa would be to scan samples for pollen grains of these designated taxa (see section 8.3.1 at end of this chapter). This would ideally be carried out for taxa that have pollen that is not dispersed by wind as these are less likely to be contaminants. Thus, in theory, several thousand pollen grains would be viewed, but not identified or counted, with only occurrences of the designated but very rare taxa being noted. In practice, this could be time-consuming, because of the large numbers of pollen grains to be viewed, but also because confident identification of pollen grains of the target taxa might require careful examination of a substantial proportion of the pollen grains viewed. Although some potential targets (e.g. thrift, Jacob's ladder) have readily identifiable and relatively large pollen grains, others (e.g. mountain avens, saxifrage (*Saxifraga* spp) and bird's-eye primrose (*Primula farinosa*)) have less readily identifiable and/or relatively small pollen grains. Recent developments in automated pollen counting, especially with very pure pollen samples (e.g. Tennant *et al.* in press) and with targeted taxa, may make this feasible for peats or lake sediments guaranteed to have good pollen preservation and concentration. However, the required conditions may be met at only very few sites, and the not inconsiderable difficulties of automated recognition of the critical pollen taxa that often will be the targets, along with the computational demands of any system that adequately will take into account the three-dimensional form of pollen grains, suggest that this approach requires further testing before its feasibility can be assured.

If such an approach did prove feasible, and resulted in pollen grains of the target taxa being encountered much more regularly throughout the Holocene, it is worth cautioning that this is likely to yield less detailed insight into the composition of the communities represented, and whether target species occupied different habitats and/or were components of different communities at different times during the Holocene, than the more labour-intensive traditional approach. Furthermore, persistence of individual species could be demonstrated only where those species produce distinctive pollen, enabling them to be discriminated from congeners or even other members of the same family. Similarly, even identifications of particular species would not in themselves provide sufficient evidence to infer the composition of past communities. However, many of these issues are limitations in traditional pollen analyses, albeit that the traditional approach provides more reliable identification of a greater number of species. Nonetheless, given sufficient records of a number of individual taxa, the nature of the communities can potentially be inferred from recurrent groups of taxa. However, given the evidence of species' individualistic responses to environmental changes (Huntley 1991b), as well as of changing climatic conditions throughout the Holocene, it is to be expected that present plant communities are of relatively recent origin and that the communities of which any target species has been a component will have changed in composition and character throughout the Holocene. For example, at lowland Lateglacial sites such as Windermere (Pennington 1943; Bonny 1976), Blelham Tarn (Pennington 1965; 1970) Hawes Water (Oldfield 1960) and those examined by Walker (1966), a multi-stage transition from the last glacial stage to the Holocene is evident. Many of the Arctic–Alpine species prevalent across the region at that time are today restricted to higher altitude areas or absent entirely.

(3) Modelling palaeovegetation patterns from pollen data.
Developments over the last two decades offer opportunities to produce quantitative estimates of the extents of open/closed communities (e.g. Hellman *et al*. 2008; Soepboer *et al*. 2010) and of their likely locations within a landscape. However, the highly disturbed character of present British vegetation means that there have been few published studies from the British Isles, although Fyfe *et al*. (2013) recently examined patterns of openness at the national scale, demonstrating that the British Isles had a greater degree of landscape/woodland openness at the regional scale than areas on the European mainland. Nonetheless, for a landscape with palaeovegetation records from a sufficient number of suitable peat and lake sites, it would now in principle be possible to propose hypotheses with respect to likely community types and structures and to test those hypotheses using palaeoecological data from those sites. A potential hypothesis worthy of further investigation is provided in the next section. It should, however, be noted that even with this approach it would remain difficult to demonstrate a direct relationship between a particular landscape characteristic and species' survival/persistence; there would still be a significant degree of hypothesis generation involved in inferring the most likely location(s) for persistence of any particular species.

A principal requirement for any palaeoecological investigation, whether of potential refugia or with some other aim, is the existence of sediments of suitable quality spanning the appropriate interval, with well-preserved pollen and/or fossils, with the potential for radiocarbon or other appropriate dating methods. In lowland areas of England, such as the Breckland, isolated sites of high quality are present, although some lack dating potential. In upland areas there are contrasts between areas with respect to the types of site available. Blanket peats provide the majority of records from North East England, especially from the Northern Pennines where evidence for persistence of rarer open habitat taxa is, however, perhaps strongest, whereas the Lake District of Cumbria offers excellent lake sediment archives to complement peats found elsewhere in North West England, but has more limited evidence for persistence of open habitat taxa, especially rarer species.

As with issues associated with ecological restoration, there is thus no doubt that palaeoecological data can provide an important context for any discussion regarding likely refugial status, establishing 'baseline' conditions and providing evidence as to where open habitat taxa may have persisted during the peak development of Holocene forest cover. By their very nature, however, they are less informative about possible future trends, especially given the future context of climatic conditions unlike any during the Holocene. Nonetheless, palaeoecological data can provide important insights into the mechanisms of species' persistence and the characteristics of landscapes that will favour persistence under changing climatic conditions. Overall, as with any type of evidence, the usefulness of palaeoecological data will depend principally upon the nature of the specific questions being asked, whether of the available published data or of potential new data. This will be especially important when considering how a palaeoecological approach may be able to contribute to answering any broader questions relating to future refugial potential.

summarise the issues that should be taken into account in so doing, and highlight the types of data that it would be most advantageous to collect.

8.2.2. A hypothesis related to refugial potential that may be worthy of investigation using palaeoecological data

Based on the findings presented in this report, and those of the parallel project (Suggitt *et al*. 2014; Box 1), we propose the following hypothesis that we feel is worthy of further investigation:

Landscapes with high refugial potential (i.e. having relatively high geological, edaphic and topographic, and hence microclimatic, heterogeneity) have, throughout the Holocene, *supported more stable and qualitatively different assemblages of plant species from those found in surrounding regions of lower physical heterogeneity. Allied to this is the question of why the co-occurrences of some species persist through time (Seddon et al. 2014).*

The extent to which this hypothesis might be addressed for any given landscape will be constrained by the availability and character of sites with stratified Holocene sediment accumulations that feature well-preserved palaeoenvironmental remains. Careful selection of multiple sites within a landscape would be required in most cases, ensuring that records are obtained from a range of microclimatically contrasting locations. Given the paucity of plant macrofossils found in most sites, and the usually even sparser records of terrestrial faunal groups, it is likely to be possible to address this hypothesis only for higher plants.

8.3. Protocols for future data collection

8.3.1. Taxonomic groups

In order usefully to inform the process of identifying potential refugia from future climatic change, any new palaeoecological data collected must target taxonomic groups that fulfil several criteria. Firstly, the taxonomic group must include at least some species that reach climatic limits within the UK, preferably also species with relatively narrow geographical ranges, thus ensuring that changes in their range and/or abundance in the UK during the Holocene can be attributed principally to climatic changes. Species within many taxonomic groups are likely to fulfil this criterion. Secondly, the taxon must include species with a range of distribution patterns and responses to climatic conditions, such that at least some are more likely to have persisted in areas where the principal micro- or meso-scale climates differ from regional average climate in the direction opposing climatic change (i.e. cool meso- and microclimates when the regional climate is warming, and *vice versa*). Thirdly, in order to be informative, sufficient palaeoecological data must be available for the group, both in terms of the spatial coverage of the data and the spatial and temporal density of the data. Without adequate replication, it is difficult to infer statistically meaningful patterns of change. Data from vertebrates do not easily allow reconstruction of changing ecological communities because continuous records of their fossils are rare to non-existent. While occurrence data may be of use eventually in this context, it provides a comparatively poor record compared to pollen data. The vertebrate record may include errors due to over ambitious identifications, and this is particularly the case with avian records (Stewart 2002). Although data for most invertebrate groups are also generally scarce, molluscs, some insect groups (e.g. Coleoptera) and especially higher plants appear particularly suited to the identification of refugia in relation to Holocene as well as recent climatic changes (Suggitt *et al.* 2014). However, the vast majority of available palaeoecological data are derived from palynological studies. Even for those other taxonomic groups for which some palaeoecological data exist, the number of sites studied, and hence the spatial and temporal density of data, is insufficient for meaningful analysis. Thus, higher plants are likely to be by far the most informative in terms of identifying potential refugial areas in relation to Holocene climatic changes.

In terms of informing the process of ecological restoration, adequate geographic coverage, as well as the spatial and temporal density of data, are again issues that limit the usefulness of all palaeoecological data except pollen data.

8.3.2. Habitats

Although climatic refugia can potentially be found in most habitat types, those habitats associated with more topographically diverse landscapes, particularly those associated with upland areas, are likely to be particularly important in the context of contemporary and future warming for cold-adapted species (Suggitt *et al.* 2014). Similarly, most habitats in the UK have suffered at least some degree of ecological degradation as a result of human activities (and would therefore be the focus of restoration effort), although lowland semi-natural grasslands and heathlands have been especially severely impacted with resultant strong declines in recent years of species associated principally with these habitats (State of Nature 2013).

In the context of the potential use of palaeoecological data to provide evidence of Holocene refugial areas, however, by far the greatest constraint is that imposed by the distribution of the lakes and peatlands from which such records can be obtained. Although as a result very few if any palaeoecological records may be obtainable for some habitats, the concentration of lakes and peatlands in the uplands coincides with landscapes likely to have offered the greatest potential for Holocene refugia for cold-adapted species. Furthermore, modelling approaches have developed rapidly over the past two decades such that it is now possible to provide robust quantitative estimates of the likely spatial patterns of distribution and abundance of individual pollen taxa (and by inference the plant communities of which they are a component), although this is possible only in areas with at least the potential to provide a high density of records from suitable lake or peatland sites.

8.3.3. Additional data

Perhaps the two greatest limitations on the use of existing palaeoecological data to help identify refugia from climatic change, or areas for ecological restoration, are the limited spatial density of sites with data, and the inadequate dating of many of the existing records. Realistically, in order to identify climatic change refugia using palaeoecological data, it would be necessary to compare changes in the pollen records from localities hypothesised to have climatic refugia sufficiently close for the species that they harboured to contribute to these pollen records with changes in the pollen records from other localities in the same region remote from hypothetic climatic refugia. Several considerations are important in the context of acquiring additional data. Firstly, it would also be necessary to obtain a sufficient number of such paired-site comparisons to enable tests of the statistical significance of the differences observed. The sample size required would depend on both within-site variation and on the magnitude of difference that one may wish to detect, so it is difficult to provide guidance on what sample size would be required without first conducting data analysis to assess both within-site variability and the magnitude of between-site differences. However, pollen records from individual sites are likely to exhibit temporal as well as between-site variations in species composition for a number of reasons, so it is likely that large sample sizes would be needed. Secondly, relatively large pollen records, in terms of both the number of pollen samples counted at each site and the overall size of the pollen counts, would be needed to discern signals of climatic refugia, such as the persistence of cold-adapted species, from inherent variability. Lastly, given the constraint in habitat types from which such pollen records can be obtained, a considered approach to site selection would be necessary.

9. Concluding remarks

In summary, palaeoecological data can provide an important context for discussions relating to climatic change refugia and the appropriate management and restoration of degraded habitats. In some cases these data could be used to establish the long-term relict status of a community or habitat, provide evidence of the 'baseline' conditions that management/restoration targets might set, or provide evidence as to where Arctic–Alpine and other species associated with open habitats may have persisted during the peak development of Holocene forest cover. Overall, it has been possible to describe the landscape history and the long-term ecological processes operating in key geographic regions, and to identify the natural and human drivers of these changes. However, constraints on the habitats from which palaeoecological data can be collected, inadequate spatial density of data, and problems associated with chronological control, make it very difficult to demonstrate using palaeoecological data how ecological networks and habitats have changed over time (at least in spatially explicit ways).

We have compiled an extensive database of studies conducted in England from which palaeoecological data are available (see Appendix 3). This database highlights the landscapes from which palaeoecological data already exist. We also propose a key hypothesis related to climatic change refugia that would be worthy of testing in one or more landscape(s). Given careful consideration of this hypothesis, a small number of areas of high potential for furthering such work could be identified. With careful application of well-established field and laboratory methods in appropriate landscapes, palaeoecological research could provide new insights into the potential for ecological restoration and help identify where species are most likely to persist in the face of climatic change (see also Seddon *et al.* 2014). There is also some potential for future developments of new methods that would enable such work to be achieved with less researcher effort. In England, a study designed to test this hypothesis would of necessity be centred either in North West or North East England, more specifically either in the Lake District or the Northern Pennines. It should also be noted, however, that numerous sites in Scotland, Wales and the Republic of Ireland may also lend themselves well to such a study. Whichever area was selected, the study would require a relatively large number of new high-resolution pollen analyses, combined with a sufficient number of radiometric dates to enable an accurate and precise chronology to be derived for the samples analysed from each of the sites investigated.

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Appendix 1. List of search terms used to find palaeoecological data

(1) ‘holocene’ + ‘pollen’
(2) ‘quaternary’ + ‘pollen’
(3) ‘pleistocene + ‘pollen’
(4) ‘holocene’ + ‘palynolog*
(5) ‘quaternary’ + ‘palynolog*
(6) ‘pleistocene’ + ‘palynolog*
(7) ‘holocene’ + ‘fossil’
(8) ‘quaternary’ + ‘fossil’
(9) ‘pleistocene + ‘fossil’
(10) ‘paleoecologic*’
(11) ‘palaeo* + refug*’,
(12) ‘palaeoecolog* + climat* change’
(13) ‘pollen’ + ‘England’
(14) ‘fossil’ + ‘England’
(15) ‘palynolog + ‘England’
(16) ‘glacial ref*’.

Appendix 2. Temporal coverage and density of palaeoecological records

In this section graphical representations of (1) the temporal coverage (earliest date to latest date obtained from the record) and (2) the density of dated palaeoecological records as a function of sample resolution are shown for England as a whole (Figure S2.1), and each of the geographic regions for which more detailed syntheses of the data were conducted, namely the East of England (Figure S2.2), North East England (Figure S2.3) and North West England. For North West England, we provide summaries for both floral (Figure S2.4) and faunal (Figure S2.5) records. Where a site has been cored more than once, to avoid ambiguity, the respective studies are quoted in brackets following the site name (Lead author, year). A number of dating methods were employed in the collection of these data. Higher temporal resolutions are achievable for the more recent past using isotopes with a relatively short half-life (e.g. ^{210}Pb), whilst markers that record particular short-lived events (e.g. ^{137}Cs peaks associated with peak atmospheric testing of nuclear weapons and with the Chernobyl accident; tephra layers associated with particular well-dated volcanic eruptions such as Hekla 4) provide a basis for dating and synchronising records. Radiocarbon dating generally offers lower temporal precision, yet the longer half-life enables dating from earlier in the Holocene. Note that although the latest date of any record may fall before the present day, many samples will offer a record extending to the present (it may be possible to correlate this undated record to samples from other sites).

(a)

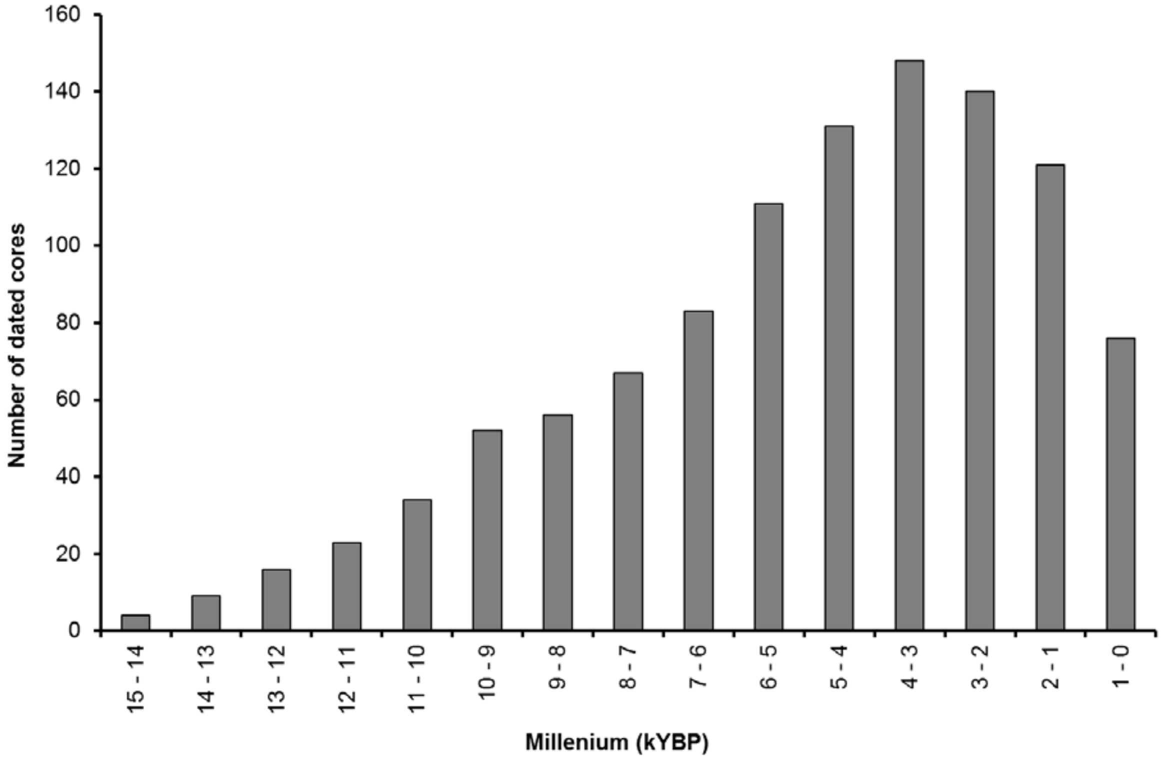
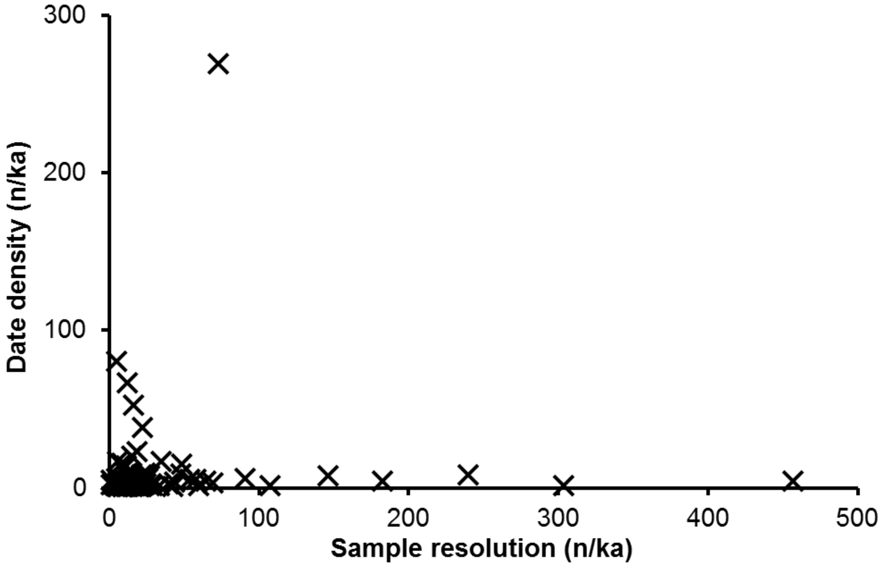


Figure S2.1. *Panel (a) shows the number of (English) dated cores available for each millennium over the last 15,000 years.*

(b)



(c)

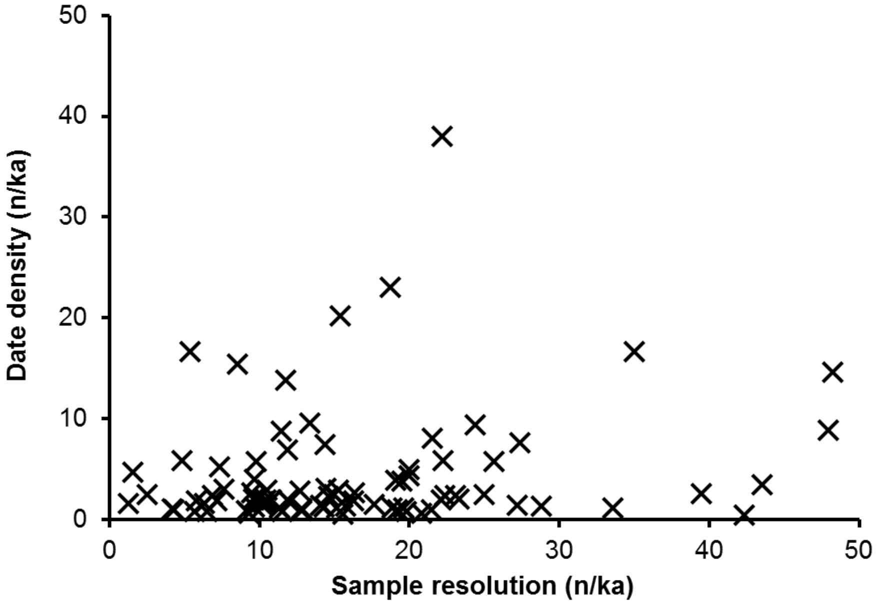


Figure S2.1. *Panel (b) plots the density of dated English palaeoecological records against their sample resolution. Panel (c) is similar to (b), but with values of > 50 excluded. Density and resolution metrics are given as number of samples per 1000 years. (Note that higher densities of both samples and dates generally reflect high resolution studies of short intervals or particular events, e.g. the* lime (Tilia) *decline, and do not indicate that such high resolution is available throughout the Holocene.)*

(a)

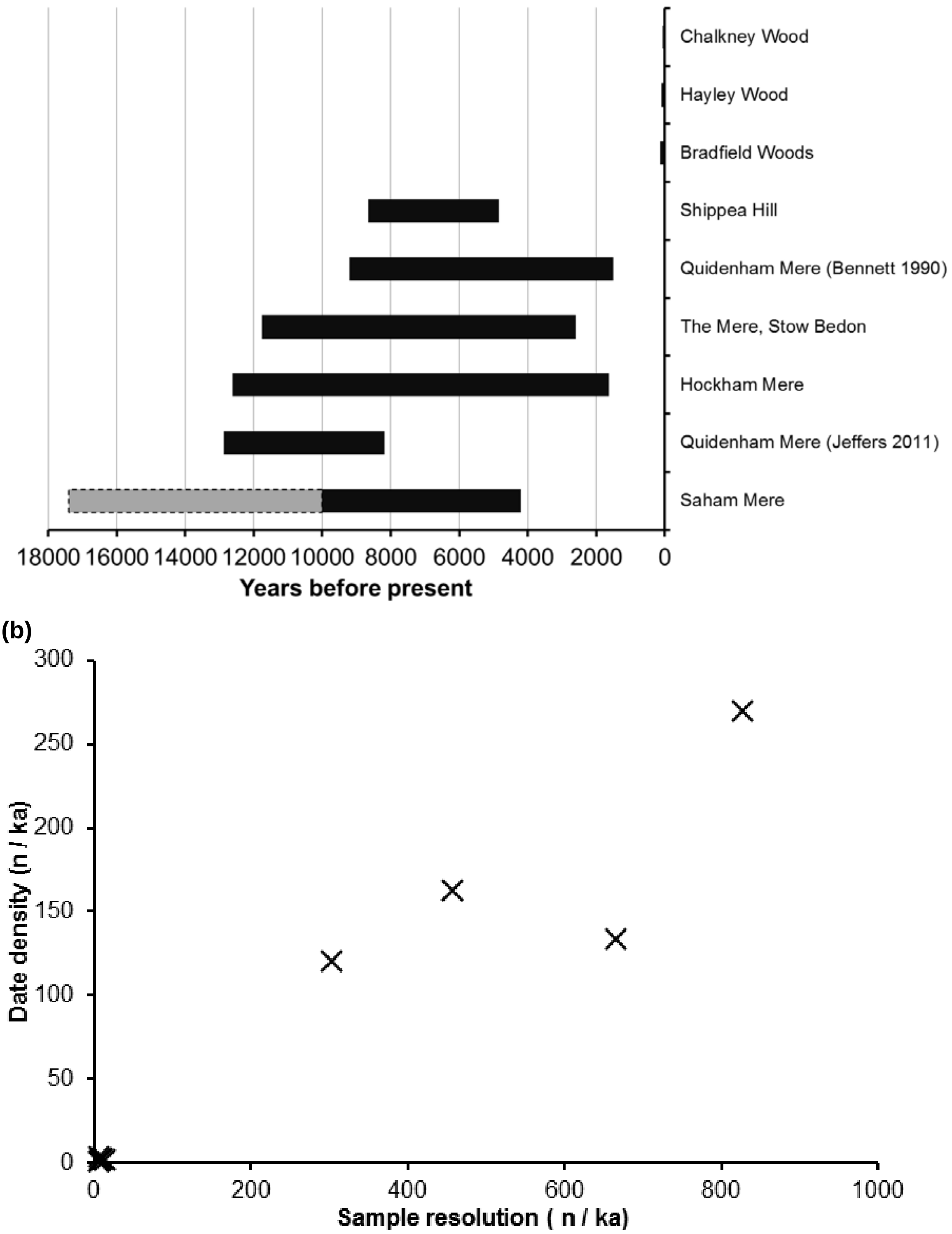


Figure S2.2. *Panel (a) shows the temporal coverage of dated palaeovegetation records in the East of England study region. Panel (b) plots the density of dated records against their sample resolution for this region.*

(c)

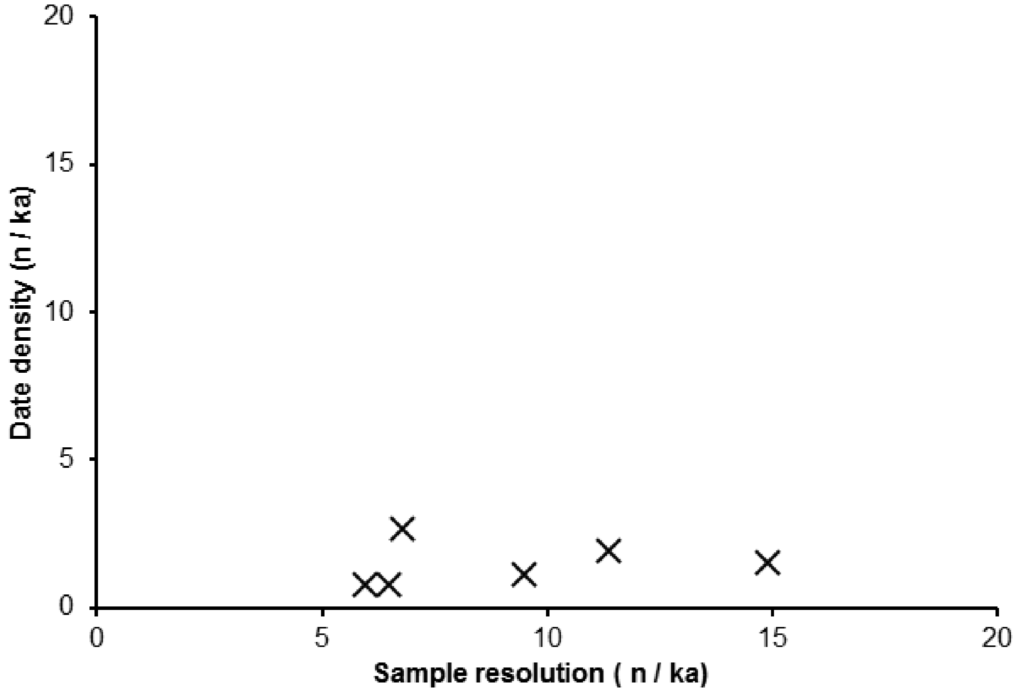
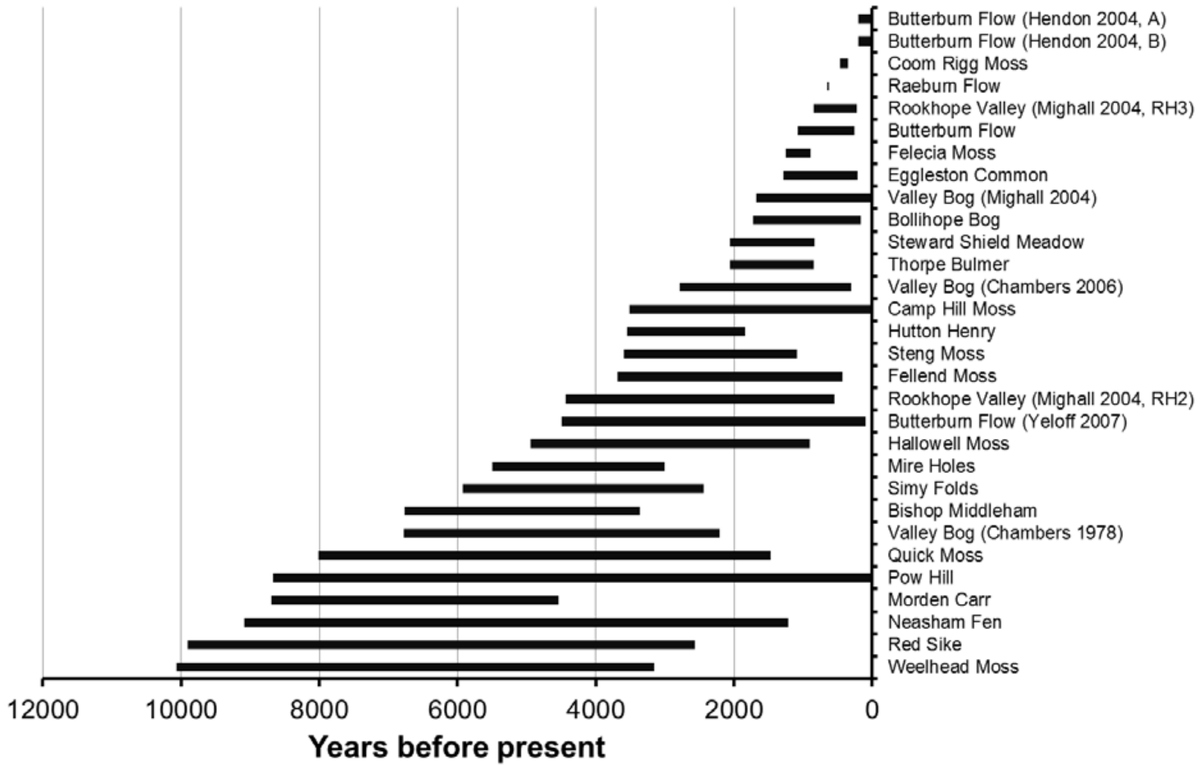


Figure S2.2. *Panel (c) is similar to (b), but with values of > 20 excluded. Density and resolution metrics are given as number of samples per 1000 years. Note that records for Chalkney Wood, Hayley Wood and Bradfield Woods (Waller et al. 2012) cover only the period 150 years BP to present. The earlier dates from Saham Mere have been questioned; this uncertainty is denoted by the grey colouring prior to 10 ka BP.*

(a)



(b)

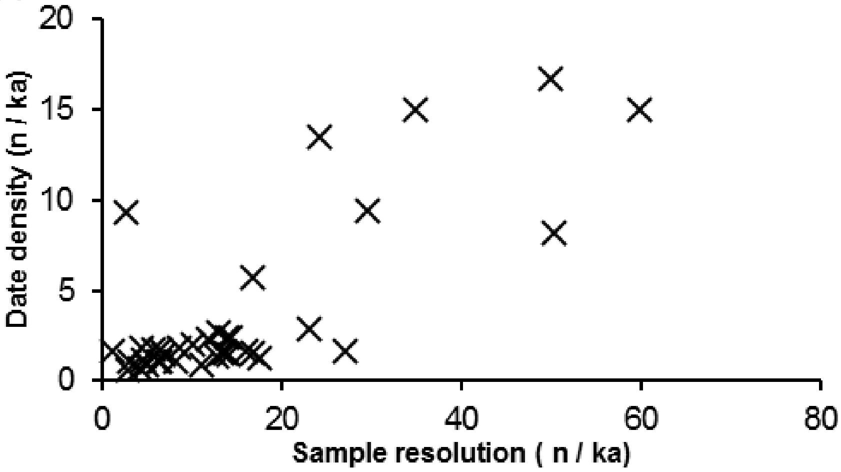


Figure S2.3. *Panel (a) shows the temporal coverage of dated palaeovegetation records in the North East England study region. Panel (b) plots the density of dated records against their sample resolution for this region. Density and resolution metrics are given as number of samples per 1000 years. (One result omitted- Raeburn Flow, Mauquoy 1999. Apparently very high values for resolution at this site were caused by the two radiocarbon samples from different depths in the profile giving very similar dates ~ 25 years apart).*

(a)

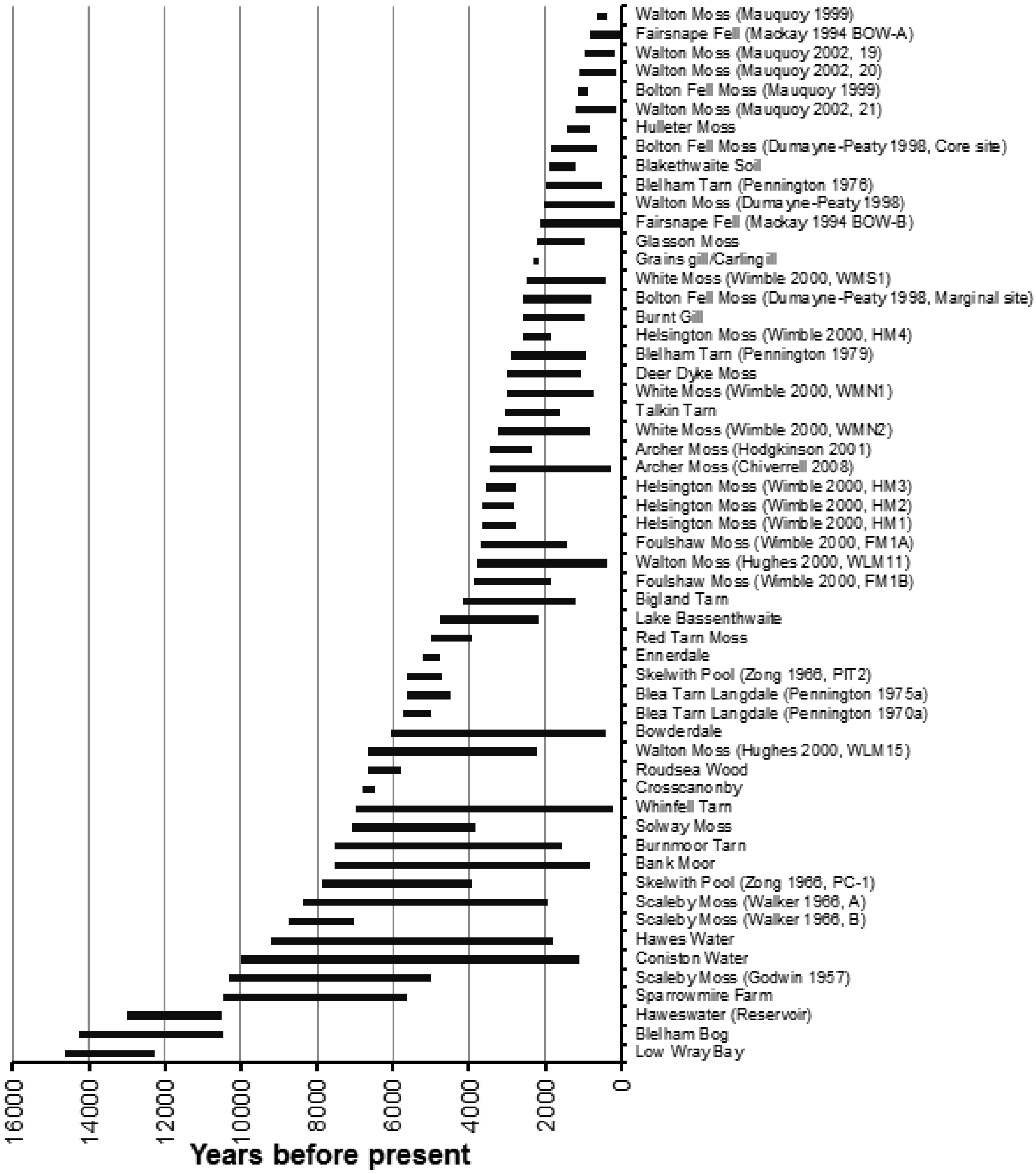


Figure S2.4. *Panel (a) shows the temporal coverage of dated palaeovegetation records in the North West England study region.*

(b)

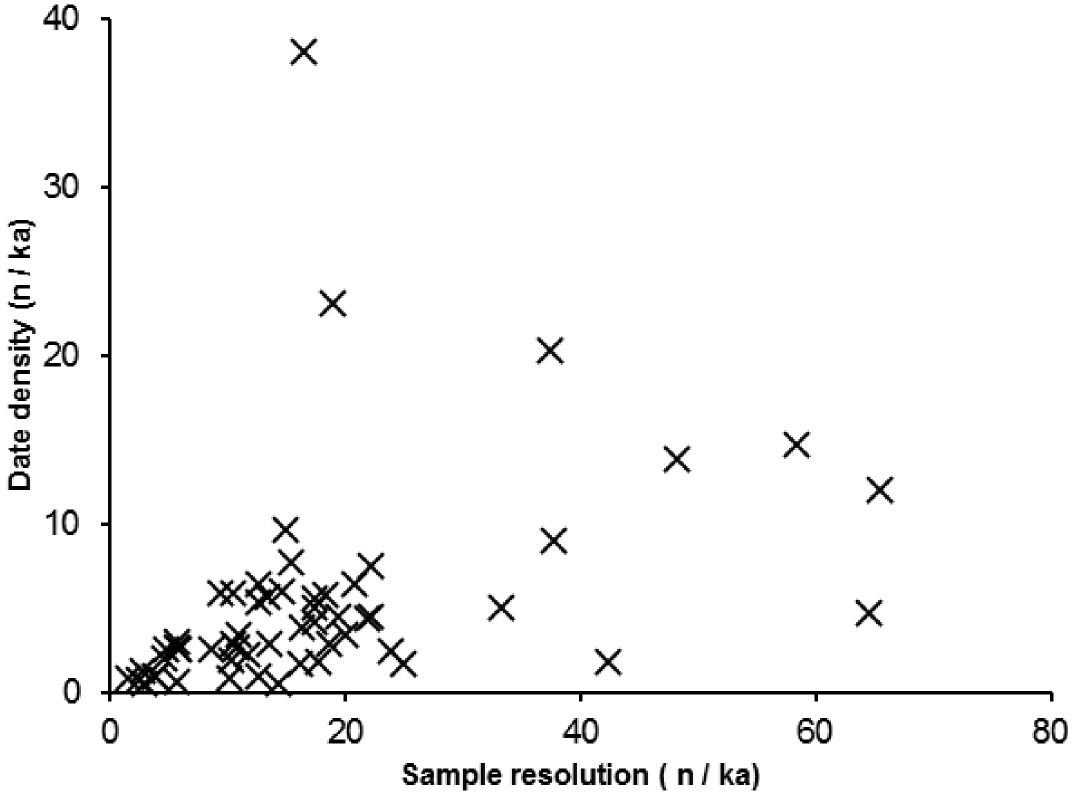
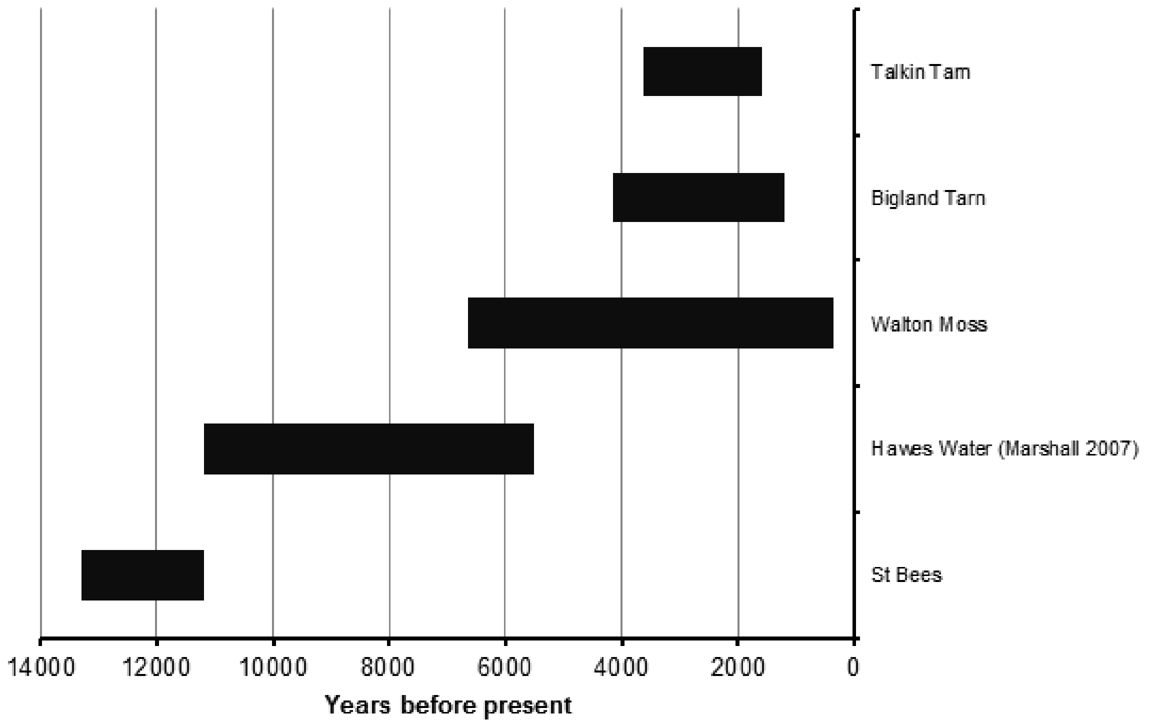


Figure S2.4. *Panel (b) plots the density of dated records against their sample resolution for this region. Density and resolution metrics are given as number of samples per 1000 years.*

(a)



(b)

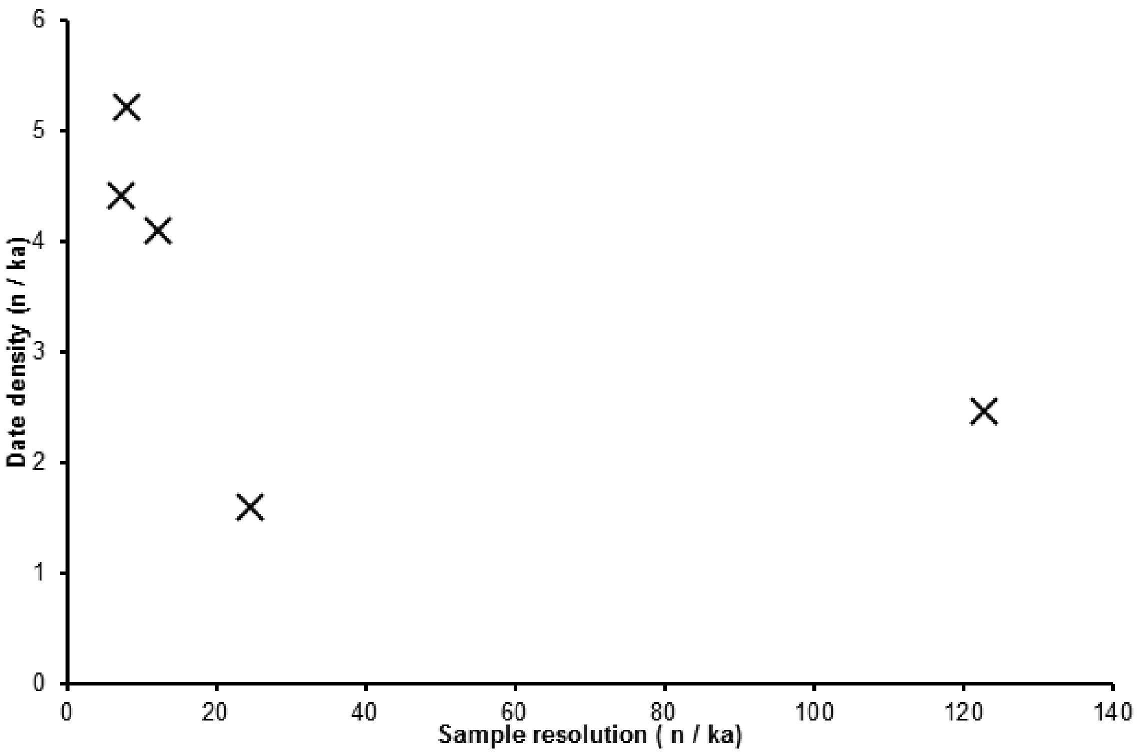


Figure S2.5. *Panel (a) shows the temporal coverage of dated palaeofaunal records in the North West England study region. Panel (b) plots the density of dated palaeofaunal records against their sample resolution for this region. Density and resolution metrics are given as number of samples per 1000 years.*

Appendix 3. Full list of palaeoecological studies

A database, provided as a Microsoft Excel spreadsheet accompanying this report, provides details of all studies from which data were extracted. The geographic location, duration of the record (i.e. interval between the oldest and youngest radiometric or other date for the record), the total number of samples and the number of dates is listed for each record.