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Agricultural systems regulate plant and insect (beetle) diversity and induce ecosystem novelty

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Highlights

- Integrating past environmental archives informs about land use and diversity change
- Insect and pollen diversity trends reflect disturbance caused by land-use change
- Ecosystem novelty is represented by non-analogue pollen species assemblages
- Novel ecosystems emerged from the cumulative long-term impacts of land-use change

Abstract

Land-use change plays an important role in shaping plant and insect diversity over long time timescales. Great Britain provides an ideal case study to investigate patterns of long-term vegetation and insect diversity change owing to the existence of spatially and temporally extensive environmental archives (lake sediments, peatlands, and archaeological sites) and a long history of landscape transformation through agrarian change. The trends identified in past environmental datasets allow the impacts of land-use change on plant and insect diversity trends to be investigated alongside exploration of the emergence of ecological novelty. Using fossil pollen, insect (beetle), archaeodemographic, archaeobotanical and modern landscape datasets covering Britain, similarities are identified between insect diversity and pollen sample evenness indicating that vegetation heterogeneity influences insect diversity. Changing land use captured by archaeobotanical data is significantly correlated with pollen diversity demonstrating the role of human activity in shaping past diversity trends with shifts towards ecosystem novelty identified in the form of non-analogue pollen taxa assemblages (unique species combinations). Modern landscapes with higher agricultural suitability are less likely to have pollen analogues beyond the last 1000 years, whilst those in areas less suited to agriculture and on more variable topography are more likely to have analogues older than 1000 years. This signifies the role of agriculture in the creation of novel ecosystems. Ecological assemblages characteristic of earlier periods of the Holocene may persist in areas less impacted by agriculture. The last 200 years has witnessed major shifts in novelty in a low number of pollen sites suggesting that novel ecosystems emerged over a longer time period resulting from the cumulative impacts of land-use change.

Key words: *biodiversity, disturbance, beetles, insects, pollen, land-use, paleoecology*

1. Introduction

1.1 Long-term records of diversity change

Biodiversity loss has become of increasing international concern in recent decades with numerous initiatives and targets set with the aim to enhance and protect biodiversity and ecosystem resilience (European Commission, 2021). However, many targets that aim to

protect and restore biodiversity have not been reached globally (Nature, 2020). Much conservation decision making is based on recent understanding only, and restoration studies often only look at single years or aim to maintain existing patterns (Wilson, 2021). Agricultural systems have played a key role in biodiversity change in past (Birks et al., 2016a) and modern systems (Dudley & Alexander, 2017; Outhwaite et al., 2022). Long-term (paleo) environmental records provide insights into the multi-millennial scale patterns and processes that lead to diversity change (Hjelle et al., 2012), for example, fossil pollen datasets can be used as a proxy for land cover and vegetation diversity change, and fossil insect (beetle) records reflect disturbances and human activity. Archaeological records of land use (archaeobotany) and population change (archaeodemography) allow exploration of factors that influence these trends. Such datasets can be analysed alongside modern landscape data allowing long-term patterns to be viewed within the context of contemporary agricultural suitability.

The role of historic environmental change in shaping current diversity patterns has been demonstrated (Gaston, 2000; Birks et al., 2016a; 2016b) with a focus on placing trends identified in recent decades-centuries into the context of the longer-term past. Temperate European vegetation trends have previously been described as characterised by declining biodiversity during initial forest development in the early Holocene (11700-8000 cal. BP) (cal. BP: calibrated years Before Present, where present = AD 1950), stable levels of diversity during periods dominated by closed mixed forest in the mid-Holocene (8000-6000 cal. BP), increasing biodiversity on fertile soils with the emergence of agricultural land use from 6000-4000 cal. BP, and declining biodiversity in the most recent 200 years (Birks et al., 2016a). Subsequent research has identified similar trends for pollen sites across Britain within the context of regional variability and has revealed that a recent decline in biodiversity is not always detectable in fossil pollen datasets (Woodbridge et al., 2021). Novel plant communities represent new combinations of taxa with no previous analogue and result from the arrival or introduction of new species often representing human-driven changes, such as altered land use, or climate change, and may be reflected by increasing 'Rate of Change' in assemblage composition (Finsinger et al., 2017).

Spatial and temporal patterns of changing diversity derived from fossil pollen datasets have been used to infer past biodiversity trends for various regions from temperate and northern Europe to the Neotropics (Odgaard, 1994; Weng et al., 2006; Colombaroli et al., 2013; Felde et al., 2016; Matthias et al., 2015; Reitalu et al., 2015; 2019; Kuneš et al., 2019; Roleček et al., 2021). Similar challenges in elucidating the relationships between pollen diversity and vegetation diversity have been described (Weng et al., 2007; Gosling et al., 2009) due to the impacts of differential pollen dispersal and productivity, the effects of landscape openness and changing pollen concentration on taxa representation in datasets, and the coarser taxonomic resolution of fossil pollen data compared to plant taxonomy (Odgaard et al., 1999; Weng et al., 2006; van der Knaap, 2009; Goring et al., 2013; Pardoe, 2021). Despite these challenges, new methodological developments and suitable analytical approaches are improving understanding of biodiversity change based on fossil pollen data (Roleček et al., 2021). Previous research has paved the way for palynology to go beyond describing patterns

of diversity change and, as a discipline, to play a key role in understanding the processes of change and the relationships between ecosystem characteristics, disturbances, and diversity change. The results of recent palynological studies demonstrate that pollen richness, which reflects the number of taxa, shows good correspondence with plant richness, as well as demonstrating that plant and pollen diversity are significantly related (Meltsov et al., 2011; Felde et al., 2016; Giesecke et al., 2014; 2019; Reitalu et al., 2019; Roleček et al., 2021).

Fossil insect datasets are used to investigate the impacts of changing land use or vegetation cover and are informative about the spread and intensity of human settlement (Kenward, 1997; Smith, 2012; Smith et al., 2010, 2019, 2020). In a recent analysis of fossil insect datasets from across Europe, Pilotto et al. (2022) suggest that the expansion of agriculture 6,000 years ago had as dramatic an impact on insect communities as rising temperatures in the early Holocene. Smith et al. (2020) describe the increased scale of agriculture during the late Bronze Age / early Iron Age (3100-2700 cal. BP; 1150-750 cal. BC) of the British Isles as having a similar drastic effect on insect faunas. Insects include many different groups with dissimilar responses to environmental changes. Within this research the Coleoptera (beetle) insect group is analysed, and datasets are referred to as "insect" records. Exploration of changing insect diversity in response to land-use and land-cover change in the past currently represents a knowledge gap in paleoenvironmental research.

1.2 Diversity-disturbance relationships and ecological novelty

The frequency and type of disturbances in a landscape influence plant and insect communities on local to broad regional scales. Disturbance may include climatic change or altered land-use practices, with differing consequences related to other landscape characteristics, such as elevation and topography. Fossil pollen datasets have been used to identify 'baseline' states, i.e. conditions that predate human disturbance and represent an ecosystem's 'normal' range of variability (Willis et al., 2010; Forbes et al., 2018). The term 'ecological novelty' can be associated with human disturbances (Finsinger et al., 2017) or climatic factors and represents change across different ecological levels from ecosystems to landscapes. When the species represented within a sample and their abundances are uniquely dissimilar to other samples within the same record and those from different sites (i.e. 'non-analogue' assemblages) this can be an indicator of 'ecological novelty'. From the onset of Neolithic farming, significant landscape alterations have been well documented across various global regions (Fyfe et al., 2015; Roberts et al., 2018; Woodbridge et al., 2019), particularly associated with changing land-use practices and the spatiotemporal migration of human populations (Racimo et al., 2020). Applying analytical techniques to pollen and insect datasets, as a proxy for past vegetation and landscape change, allows assessment of relationships between diversity and disturbance, which can be used to signify ecological shifts and the emergence of novel ecosystems (Burke et al., 2019).

1.3 Past land-use, population shifts, and climate change

Archaeobotanical records (plant remains preserved at archaeological sites) provide a wealth of information about past subsistence and land-use strategies (de Vareilles et al., 2021). The main factors that affect the recovery of archaeobotanical evidence are preservation conditions, variations in sampling practices, and the nature and scale of past arable agriculture (van der Veen et al., 2007; Fuller and Stevens, 2012; van der Veen, 2014; Bishop, 2015; Carruthers and Hunter Dowse, 2019). Changes in crops, intensity and scale of production, arable equipment, catchment and population size and structure, will have profoundly altered the character of arable landscapes. Increased scale of arable production is indicated in archaeobotanical records by higher densities of bulk finds of charred plant remains (van der Veen, 2014) as well as features and structures associated with crop storage and processing. Significant arable innovations from the introduction of farming at the start of the Neolithic (~4000 BC) (~6000 cal. BP) to the Agricultural Revolution of the 18th century AD are shown in Table 1. Knowledge of past land-use strategies, including the intensity (i.e. input, such as labour or manure, per unit of soil) and extent of agriculture, allows understanding of how these processes influence plant and insect diversity and the role of people in shaping biodiversity trends over historic timescales.

Archaeological datasets are also used to infer demographic change (Bevan et al., 2017) based on the assumption that the density of radiocarbon-dated sites relates to human population size (Shennan et al., 2013). Demographic trends may influence land requirements to support changing populations and thus affect landscape change. The impacts of land-use changes are also constrained by the climatic tolerances and optima of plant and insect species. Paleoclimate datasets reflecting North Atlantic climatic conditions are summarised in Woodbridge et al. (2021) where significant relationships were identified between palaeoclimate datasets, population change and pollen diversity trends.

Table 1 Summary of key agricultural developments in Britain affecting changes in scale and intensity of land-use. *follows Historic England's Period List, FISH terminology (Historic England, 2022).

Archaeological period*	**Key agricultural events**	**Key references**
Early Neolithic 4000 - 3300 BC (5950 - 5250 BP)	Advent and spread of farming across Britain	Brown (2007); Whittle et al. (2011)
Middle and Late Neolithic 3300 - 2200 BC	Decline in arable agriculture in some areas; shift to predominantly barley cultivation in Scotland/N England	Bishop (2015); Stevens & Fuller (2012; 2015)
Late Early to Middle Bronze Age 1800 - 1200 BC	Co-axial field/reave system; introduction of spelt wheat and pulses; start of the widespread use of the horse; increased scale of and diversity in cultivation	Bradley (2007); Historic England (2018); Marshall et al. (2019); Martin et al. (2012); Treasure and Church (2017)
Late Iron Age to Roman 100 BC to 400 AD	Coulter plough and the cultivation of heavy clay soils; cattle traction (possibly used earlier – Serjeantson 2012); increased scale of cultivation; horticulture developed; hay meadows	Allen et al. (2017); Boothe et al. (2007); Witcher (2013); Van der Veen (2014); Lodwick (2017); Robinson (2011)

Early medieval AD 410 - 1066	Limited evidence for the mouldboard plough from the (7th)9th – 11th century, affecting soil hydrology and field ecology; Open field systems; cultivation becomes more extensive; free-threshing wheat and rye widely cultivated. Temporary land abandonment in the immediate post-Roman period in some areas.	Hamerow et al. (2020); McKerracher (2018); Stevens and Fuller (2018); Dark (2000)
Medieval AD 1066 - 1540	Black Death (AD 1346-1352): 40-60% mortality – significant reduction in agricultural labour and abandonment of arable land/villages	Benedictow (2004)
From AD 1700	Industrial Revolution, mechanised farming and the use of pesticides; improved cereals	

1.4 Investigating patterns of diversity and ecological novelty

This study presents the most extensive integrative research combining fossil pollen and insect (beetle) records of diversity change from sites across Britain, and for the first time couples these with long term land-use patterns inferred from plant macrofossil (archaeobotanical) data. Records from a spatially extensive database spanning the last ~11,000 years are integrated to identify and evaluate the relationships between land-use and plant and insect diversity in addressing the following questions:

a) How does disturbance from land use affect diversity and do pollen and insect diversity trends show the same patterns of change through time?
b) To what extent can ecological novelty be identified in long-term ecological datasets and when do novel ecosystems emerge?

2. Methods

2.1 Data assimilation and harmonisation

297 radiocarbon-dated fossil pollen datasets have been amalgamated from across Britain (Fig. 1 and Supplementary Information 1). BPOL database (an extensive archive of British fossil pollen site information) (Grant et al., 2017) was used to identify datasets and provided information about radiocarbon-dating quality. The pollen datasets partly derive from the European Pollen Database (Leydet et al., 2007-2023) and were gathered within the LandClimI project (Fyfe et al., 2013; Trondman et al., 2015). Additional datasets were provided by data contributors and a small number of datasets have been digitised using Straditize software (Sommer, 2019). Pollen records from individual coring sites have been taxonomically harmonised using the European Pollen Database nomenclature (Leydet et al., 2007-2023) and summed into 200-year time windows for analysis. Total land pollen counts for each taxon were summed and percentages calculated as a proportion of the pollen grain count for the time window. The approach follows Fyfe et al. (2015), Roberts et al. (2018) and

Woodbridge et al. (2019). For digitised datasets, pollen percentages were averaged for each time window. Datasets with at least three radiocarbon dates were selected and chronologies have been constructed using "clam" (Blaauw, 2010) and "rbacon" (Blaauw, 2021) R packages. Information about the ^{14}C dates that underpin the chronologies of the pollen records, and for ^{14}C dates used in the construction of archaeodemographic data, is available from the repository where the original data are archived (Leydet et al., 2007-2023; Bevan et al. 2017). All ^{14}C dates were calibrated using the same parameters with the 'clam' or 'rbacon' R packages using the IntCal13 calibration curve (Reimer et al., 2016). Pollen datasets not derived from archaeological sites (e.g. those from lakes and peatland bogs) were used in the analyses to explore vegetation responses to land-use change.

The pollen datasets have been transformed into quantified land cover using the REVEALS (Regional Estimates of Vegetation Abundance from Large Sites) approach (Sugita, 2007; Fyfe et al., 2013; Marquer et al., 2014). Selection criteria were applied to identify pollen sites suitable for the REVEALS approach based on the model types currently available (Fig. 1c and Supplementary Information 1). The approach uses information about the relative pollen productivity (RPPs) of different plants, the dispersal behaviour (fall speed) of different pollen types, and the site type (lake or peatland/bog) and size, to produce estimates of quantified vegetation cover. RPPs are only available for a sub-set of 23 pollen types (*Abies alba, Alnus glutinosa, Chenopodiaceae, Artemisia, Betula, Calluna vulgaris, Carpinus betulus, Cerealia-type, Corylus avellana, Ericaceae, Fagus sylvatica, Filipendula, Fraxinus, Picea, Pinus, Plantago lanceolata* type*, Poaceae,* deciduous *Quercus, Rumex acetosa*-type*, Salix, Secale, Tilia* and *Ulmus*) within these datasets, therefore quantified vegetation cannot be reconstructed for the entire land pollen assemblage. For this reason, we primarily calculate diversity from pollen percentage data for all land pollen types. The assumptions of the REVEALS model means that it can only be applied to groups of small or medium sized bogs and lakes (Githumbi et al., 2022), therefore REVEALS has not been applied to all sites (Supplementary Information 1). The REVEALS model produces estimates of regional vegetation, which requires pollen sites to be grouped according to site type and size, geographical proximity to other sites, and landscape characteristics. This resulted in 37 sub-regions illustrated in Fig. 1c. See Githumbi et al., (2022) for a detailed description of the REVEALS approach.

572 fossil insect (beetle) assemblages from 117 different sites (Fig. 1) extending back to the Late Glacial period (10,050 BC) (~12,000 cal. BP) have been combined. This includes data from the BugsCEP database (Buckland & Buckland, 2006) and datasets amalgamated by Smith et al. (2010, 2019, 2020). Many of these datasets derive from archaeological sites, so species assemblages may reflect fauna around domestic dwellings or human-made structures. The datasets have been taxonomically harmonised, aggregated by archaeological period and converted to percentages. Insect data are dated by archaeological period according to the site context and the taxon harmonisation process followed the BugsCEP database taxonomy. The pollen sites have a largely uniform distribution across Britain with gaps in the midlands, while the insect datasets are largely located in the south and midlands. An archaeodemographic dataset (Bevan et al., 2017) based on the summed probability

distributions (SPD) of radiocarbon-dated archaeological sites from across Britain is used as a record of population change. Pollen samples from each 200-year time window were assigned a corresponding archaeological period to match the phases assigned to each archaeobotanical and insect sample according to site context to allow comparison between datasets.

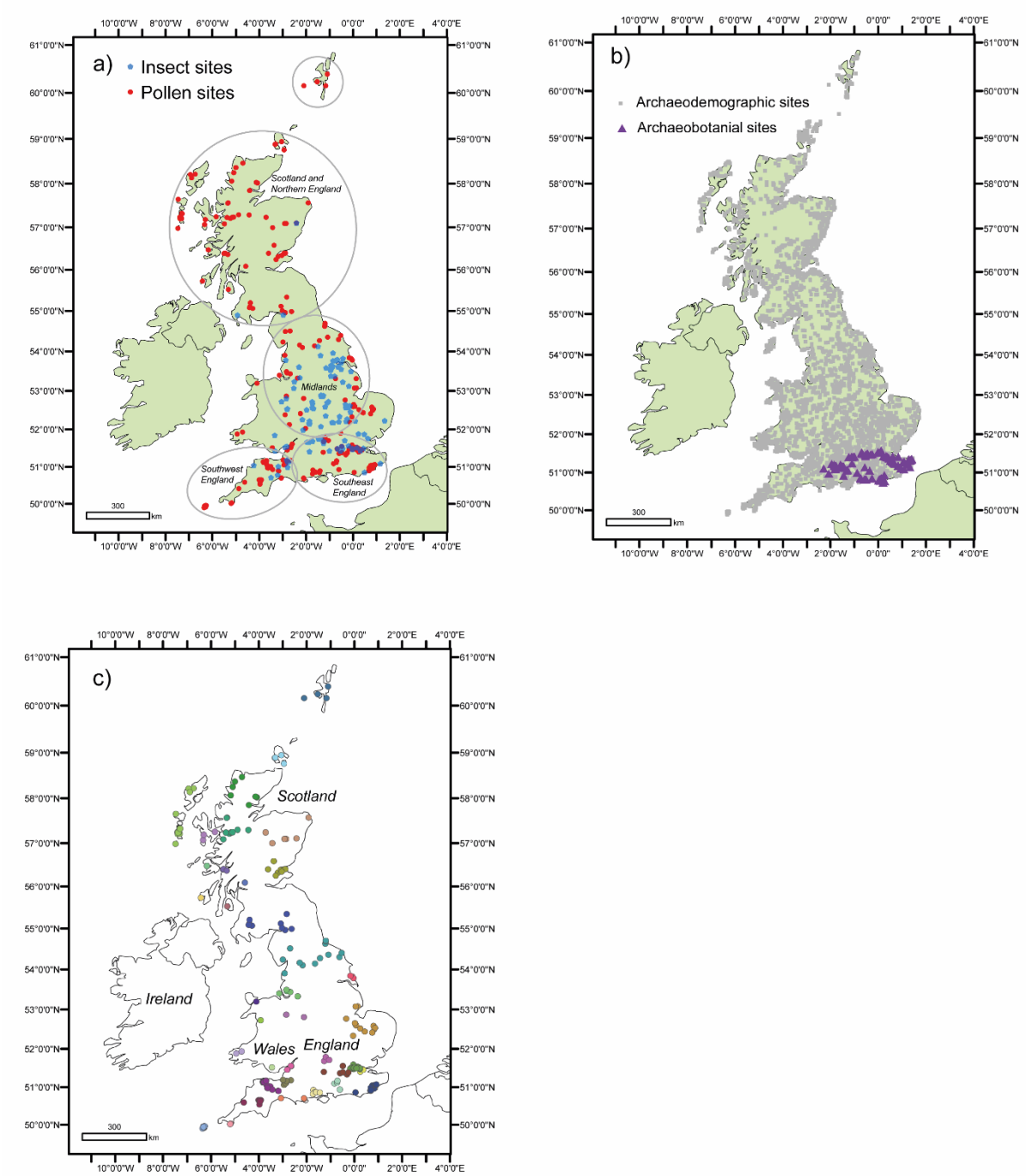


Figure 1. Site locations: a) fossil insect (blue pentagons) and pollen (red circles) datasets covering the Holocene (grey circles represent areas for regional analyses), b) archaeobotanical sites (purple triangles), radiocarbon-dated archaeological sites (grey

squares) (archaeodemography), and c) pollen sites used in the REVEALS model colour coded by site aggregation for regional vegetation reconstruction.

Modern landscape data have been extracted from within a 10 km radius around pollen sites that have a sample in the most recent time window (AD 1750 - present) (200 to -70 cal. BP). The 10 km distance was selected following previous work comparing modern pollen with remote sensed vegetation maps (Woodbridge et al., 2014b), to reflect the average pollen source area of sites, and to capture both local and regional landscape characteristics. Topographic data were obtained from a 1 km resolution dataset using an elevation model for the UK. Agricultural suitability derives from a 100 m resolution dataset obtained from the Macaulay Land Use Research Institute (1991) for which data across England, Scotland and Wales were combined. Agricultural suitability values represent the percentage of land area within 10 km of a pollen site in agricultural suitability classes 1-3 (i.e. land capable of producing 1: a very wide range of crops, 2: a wide range of crops, and 3: a moderate range of crops). The relationship between pollen sample analogues and modern landscape data (topographic roughness, elevation and agricultural suitability) is presented in a ternary plot using the Ternary R package (Smith, 2017), which graphically presents the ratios between three variables as positions within a triangle. Each pollen sample is plotted according to the modern landscape characteristics at the coring site and colour coded by analogue matching. Only sites that have pollen samples in the most recent time window (200 BP - present) were included in the analogue matching exercise for comparison with all 297 pollen sequences.

Plant macrofossil data have been amalgamated from 1718 archaeobotanical samples (charred plant macrofossil remains) from 110 sites across the southeast of England (Fig. 1). The archaeobotanical data were analysed using cluster analysis and an autoecological approach based on modern field observations of individual taxa tolerances to environmental conditions (de Vareilles et al., in review). These datasets have been used to explore changes in the composition and amount of crops and gathered resources to infer land-use scale and range of plant foods (de Vareilles et al., 2021; in review). The bulk density of plant macrofossil remains associated with different types of human land use (crop and cereal cultivation and gathering resources) have been combined and are compared with pollen diversity scores. The 'cereal' macrofossil category includes barley (*Hordeum vulgare*), emmer wheat (*Triticum dicoccum*), spelt wheat (*T. spelta*), free-threshing wheat (*T. aestivum/durum/turgidum*), rye (*Secale cereale*) and oat (*Avena sativa*). The 'gathered' category includes hazelnut (*Corylus avellana*), prunus (*Prunus spp.*), apple/pear (*Malus/Pyrus sp.*), elder (*Sambucus nigra*), berries (*Rubus spp.* and *Fragaria vesca*), hawthorn (*Crataegus monogyna*) and acorn (*Quercus sp.*). However, interpretations based on these taxa groups must take into account that fruits and nuts are likely to have been cultivated by the Roman period, and oats are likely to have been wild until the late Iron Age. Figure 3a is based on these studies and shows a conceptual summary of the changes in land use 'scale' (i.e. production relative to population) and range (i.e. the range of cultivated crops), which includes 0: pre-agriculture, 1: pastoral with limited arable production, 2: subsistence farming, 3: broader spectrum subsistence farming, 4: surplus production with further diversification of crops, 5: further increase in the crop spectrum and scale of production, and 6: change and increase in the crop spectrum and

continued growth of production. Palaeodemographic changes are estimated based on the summed probability distribution (SPD) of 22,719 archaeological radiocarbon (^{14}C) dates for Britain (Bevan et al., 2017). The package 'rcarbon' was used to produce an SPD curve from the ^{14}C dates, which is binned into 200-year time windows and is presented in Woodbridge et al. (2021).

2.2 Data analysis

Disturbance is caused by numerous factors associated with natural and human induced environmental changes. Population change reflects land requirements for agriculture, however, archaeodemographic trends are not likely to be linearly related to disturbance, therefore a pastoral/human activity pollen index is used as an indicator of changing disturbance levels. The index is a sum of untransformed pollen percentage data, which includes Asteraceae subfamily Asteroideae*,* Asteraceae subfamily Lactucoideae*,* Cynareae*,* Rubiaceae*,* Ranunculaceae*, Potentilla, Plantago lanceolata, Plantago major, Plantago media,* Chenopodiaceae*, Rumex, Urtica* and Cerealia. The inclusion of certain taxa within the index has been informed by previous work involving pastoral/human activity pollen indices (Behre, 1986; Berglund, 1991, Mazier et al., 2006; 2009; Fyfe et al. 2010; Araujo et al., 2020). Pollen indices of human activity should be interpreted with recognition that taxa may also occur naturally as well as associated with anthropogenic activity.

The 'Vegan' R package (Oksanen et al., 2019) was used to calculate Shannon diversity (Magurran, 2003) index within the total land pollen assemblage on a 200-year continuous time scale. This index was selected to visualise evenness separately from diversity, as sample evenness is informative about vegetation homogeneity or heterogeneity. The pollen sites were divided into four sub-regions (Fig. 1: grey rings) for exploration of regional diversity trends. The R package 'hillR' (Li, 2018) was used to estimate species richness and diversity (Hill numbers) for the beetle and pollen datasets according to archaeological periods within the insect dataset. A pairwise Wilcox test was used to test the differences between insect and pollen diversity scores by archaeological period after identifying that the data are not normally distributed using a Shapiro test (STHDA, 2022). A diversity index has also been produced using REVEALS transformed pollen data (i.e. data that have been converted to quantified vegetation) (Fig. 3). This allows comparison of diversity based on all land pollen percentage data with diversity from quantified vegetation, which more accurately reflects regional landscape character.

Rate of Change (RoC) calculations followed the method described by Finsinger et al. (2017) where chord distance is used as a measure for dissimilarity between pollen assemblages to estimate within-site RoC between consecutive time windows. RoC values were subsequently averaged across sites for each 200-year time window. Spearman's Rank correlation was used to analyse the relationship between archaeobotanical remains and pollen diversity. An analogue-matching approach (Simpson & Oksanen, 2021) has been applied to the pollen datasets to identify similar and dissimilar assemblages between all 200-year time windows through the Holocene. The closest analogues for each pollen sample from the 297 sequences

have been determined using the 'analog' package with R (Simpson & Oksanen, 2021). Analogue groups are defined according to whether the most recent pollen assemblage (200 cal. BP - present) has a close analogue in the last 1000 years, a close analogue older than 1000 years, or no close analogue through the entire record. Insect samples assigned 'modern' were deemed unsuitable for comparison with insect datasets from earlier archaeological periods using the analogue-matching approach, as the collection methods for modern samples differ from methods applied to paleoenvironmental insect samples leading to certain taxa groups being over-represented.

3. Results

3.1 Diversity and disturbance trends across Britain

When amalgamated for all sites across Britain (Fig. 1), diversity scores derived from the insect and pollen datasets reveal similarities from the Mesolithic (7050 BC) (~9000 cal. BP) to the Bronze Age and distinctive patterns in more recent parts of the records (Fig. 2). The insect datasets show an increase in diversity from the Mesolithic to the Neolithic and Bronze Age. Pollen data also show an increasing trend in diversity during this time, as human land use was a major factor leading to opening of vegetation cover (Woodbridge et al., 2014a). Insect diversity then declined during the Iron Age, while pollen diversity continued to increase during this period. Insect diversity subsequently increased during the Roman period, while pollen diversity appears to decrease slightly during Roman times. This was followed by a decline in insect diversity during the medieval and modern periods; however, this pattern reflects the different number of samples from this period, and the different sampling approach for modern samples. Pollen diversity remained stable during medieval times and declined slightly in the most recent time period. Statistically significant differences are evident in insect and pollen diversity between archaeological periods (Table 2). Greatest differences are observed between the Late Glacial, Mesolithic, Neolithic, and subsequent periods for the insect data, and between all archaeological periods other than the Roman to medieval within the pollen datasets. Reflecting these patterns, highest Rate of Change in the pollen datasets is shown in the most recent 1000 years (Fig. 3). Insect diversity is not statistically related to pollen diversity, but insect diversity is significantly related to pollen sample evenness. However, correlations are influenced by the lower insect sample sizes for some periods and the limited comparison possible with the underlying data (eight archaeological periods).

Decreased insect diversity in the medieval period, which is not reflected by declining pollen diversity, may be captured by declining pollen evenness (Fig. 2) showing that landscapes have become increasingly dominated by certain plant types. These patterns reflect the changing scale and spectrum of land-use practice (Figs. 2 and 3) and population trends inferred from archaeological records (Fig. 3). The larger range in the insect diversity box plots (Fig. 2) indicates significant spread within the data, signalling considerable variability between sites. Diversity scores derived from British Isles pollen datasets using different measures of diversity (Hill Numbers, Shannon diversity, evenness and Rarefaction) have previously revealed very similar trends (Woodbridge et al., 2021). Comparison of diversity

trends after separating lake and peatland site types based on all 153 pollen taxa shows similar patterns with only minor differences, which are most notably in pollen sample evenness in the most recent period (Fig. 3).

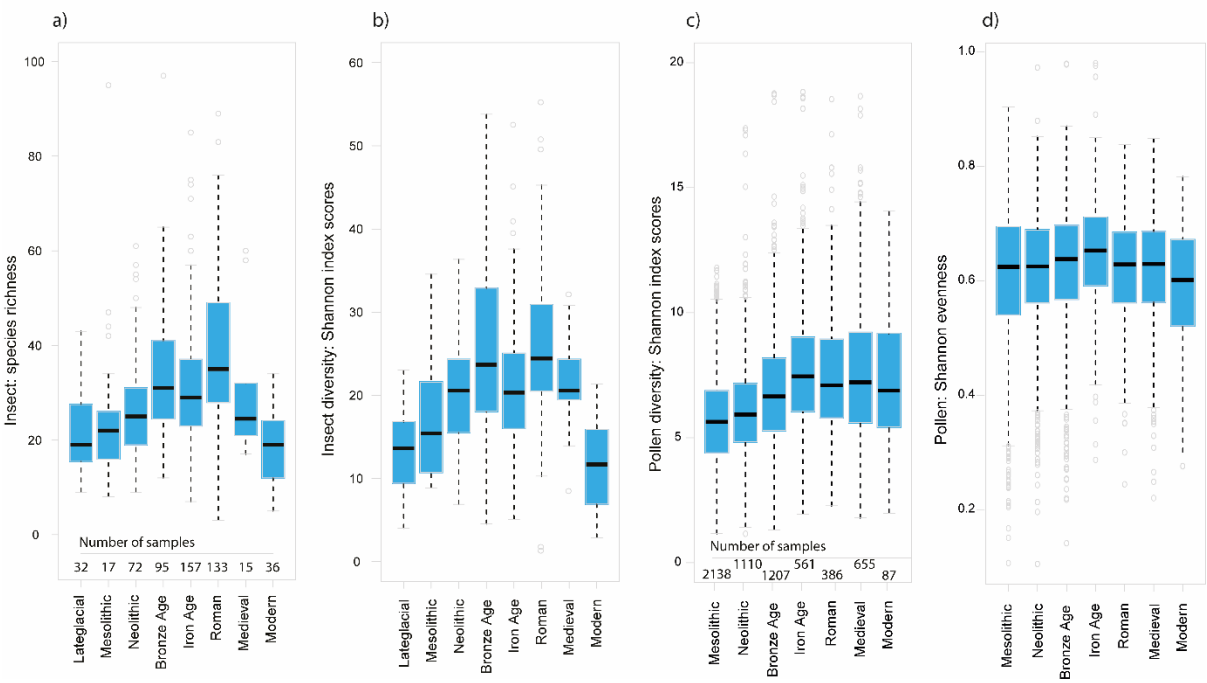


Figure 2. Insect and pollen diversity change through archaeological periods: a) insect species richness, b) insect Shannon diversity index, c) pollen Shannon diversity index and d) pollen Shannon evenness. Box plots show the mean values (black horizontal lines), first and third quartile (blue bars), and "whiskers" show the data range after filtering outliers (circles). 'Modern' in the pollen datasets represents 200 cal. BP - present. 'Number of samples' refers to the number of individual samples within the archaeological period.

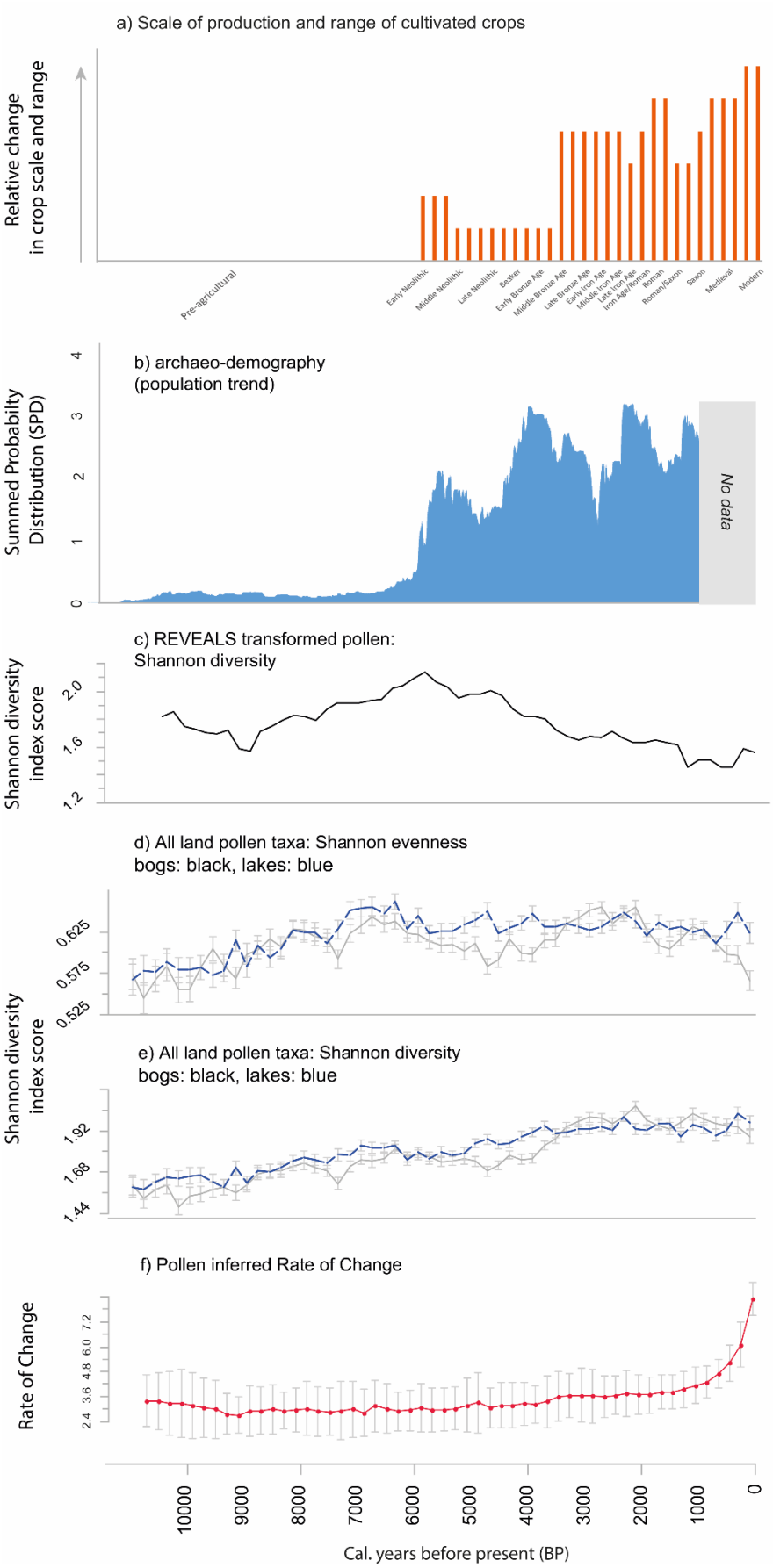
Table 2 Kruskal-Wallis test *p*-values for Shannon diversity change between archaeological time periods: a) fossil pollen datasets, b) fossil insect datasets, c) Spearman's Rank (*r*-value) correlations between pollen diversity (Shannon index) and evenness and land use inferred from archaeobotanical assemblages, and d) Spearman's Rank (*r*-value) correlations between pollen diversity and evenness and insect diversity (Hill Numbers). Shaded cells indicate statistical significance ($p < 0.05$).

a) Pollen	Mesolithic	Neolithic	Bronze Age	Iron Age	Roman	Medieval
Neolithic	0.00					
Bronze Age	0.00	0.00				
Iron Age	0.00	0.00	0.00			
Roman	0.00	0.00	0.00	0.00		
Medieval	0.00	0.00	0.00	0.00	0.51	
Modern	0.02	0.00	0.00	0.00	0.00	0.00

b) Insects	Late glacial	Mesolithic	Neolithic	Bronze Age	Iron Age	Roman	Medieval
Mesolithic	0.01						
Neolithic	0.00	0.45					
Bronze Age	0.00	0.00	0.00				
Iron Age	0.00	0.00	0.00	0.02			
Roman	0.00	0.00	0.00	0.32	0.00		
Medieval	0.00	0.04	0.11	0.26	0.95	0.06	
Modern	0.85	0.00	0.00	0.00	0.00	0.00	0.00

c) Land use and pollen diversity	Cereals	Gathered
Pollen: Shannon diversity index	0.806	-0.806
Pollen: Shannon evenness	0.721	-0.648

d) Insect and pollen diversity	Insects H1	Insects H0	Insects H2
Pollen: Shannon diversity index	0.310	0.238	0.333
Pollen: Shannon evenness	0.762	0.738	0.833


a) Scale of production and range of cultivated crops
Relative change in crop scale and range
Pre-agricultural
Early Neolithic
Middle Neolithic
Late Neolithic
Beaker
Early Bronze Age
Middle Bronze Age
Late Bronze Age
Early Iron Age
Middle Iron Age
Late Iron Age
Iron Age/Roman
Roman
Roman/Saxon
Saxon
Medieval
Modern
b) archaeo-demography (population trend)
Summed Probabilty Distribution (SPD)
0
1
2
3
4
No data
c) REVEALS transformed pollen: Shannon diversity
Shannon diversity index score
1.2
1.6
2.0
d) All land pollen taxa: Shannon evenness bogs: black, lakes: blue
Shannon diversity index score
0.525
0.575
0.625
e) All land pollen taxa: Shannon diversity bogs: black, lakes: blue
1.44
1.68
1.92
f) Pollen inferred Rate of Change
Rate of Change
2.4
3.6
4.8
6.0
7.2
10000
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
Cal. years before present (BP)

449

Figure 3. a) land-use change based on crop spectrum and scale of agriculture using a conceptual interpretive scale (de Vareilles et al., in review), b) summed probability distribution (SPD) of radiocarbon-dated archaeological sites from across Britain (archaeodemographic trend), c) Shannon diversity derived from REVEALS transformed pollen data (based on 23 taxa), d) Shannon evenness for all land pollen types (153 taxa groups) separated according to sample context (peatlands vs. lakes) with standard error, e) Shannon diversity index for all land pollen types (153 taxa groups), f) pollen-inferred Rate of Change for all British sites (solid red line shows average values and the error bars show the standard deviation).

The average pollen diversity scores and average pastoral/human activity pollen index, reflecting land conversion for agriculture, is presented in Fig. 4 for different regions. The dates represent the mid-point of each 200-year time window (e.g. 300 BP on the plot represents the period 400-200 BP). The time periods spanning 2000-1000 cal. BP (950 BC - AD 50) have highest pastoral/human activity index values and diversity, while earlier prehistoric periods are characterised by lower diversity scores, reflecting the low impact on vegetation cover that small-scale, and perhaps irregular (Stevens and Fuller, 2012), agricultural practices would have had. Pollen diversity declines in the 300 and 100 cal. BP (400 cal. BP - present) time windows (Fig. 4) in Scotland, southwest England and for all British sites while the pastoral/human activity index increases. This pattern is shown for all regions other than southeast England and the midlands where 100 cal. BP (200 cal. BP - present) represents a period with higher diversity. Land-use scale and spectrum (i.e. range of crops) shown on the southeast England plot inferred from archaeobotanical records illustrates the increasing intensity of agriculture with highest pollen diversity scores during the Iron Age to Roman transition (~2100 cal. BP) (150 BC) and the late Saxon period (~900 cal. BP) (AD 1050). The impacts of land-use change are illustrated in Fig. 6, which shows that pollen diversity index scores are statistically significantly related to changing land-use practices evidenced in archaeobotanical remains (Table 2c). Pollen diversity is positively related to crop and cereal plant types, particularly during the early Iron Age, Late Bronze Age and Roman period, and negatively related to plant types associated with gathering.

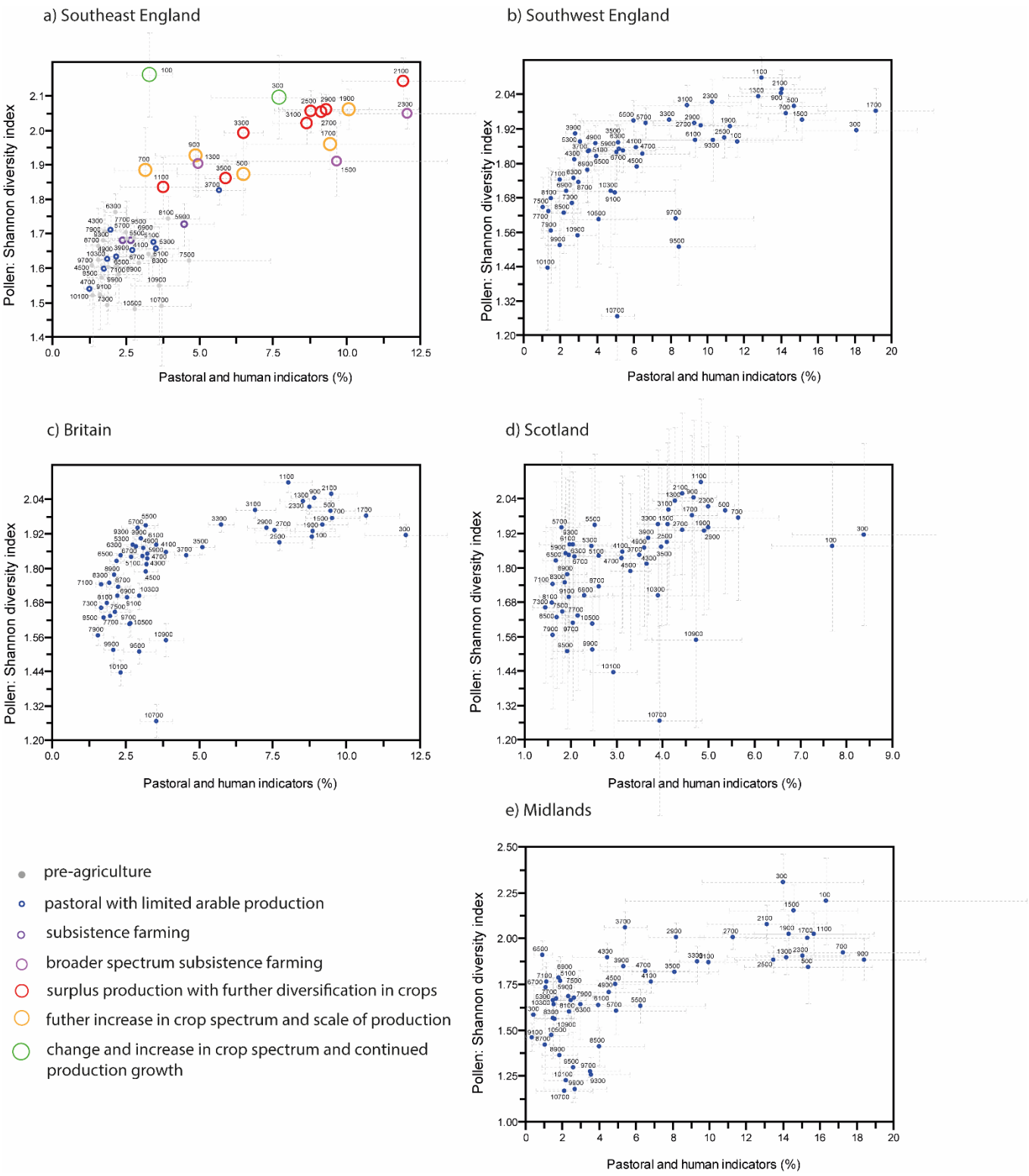


Figure 4. Pastoral/human activity pollen index plotted against Shannon diversity index (pollen derived). Dates in cal. BP (cal. year Before Present) represent the mid-point of a 200-year time window (e.g. 300 represents 400-200 cal. BP). The sub-regional divisions are shown on Fig. 1. The error bars represent the standard deviation within the datasets for each time window. Symbols used in plot a) reflect changing land use in terms of crop spectrum and scale for corresponding time periods.

The spatial distribution of pollen sites in the most recent period (200 cal. BP - present) with matching analogues (i.e. similar species assemblages) in the last 1000 years and the rest of the Holocene (11,700 - 1000 cal. BP) is shown in Fig. 5 in relation to modern landscape data. Sites with a close analogue in the last 1000 years (red circles) are located across the British Isles, which reflects the higher Rate of Change in the pollen assemblage during this time. This is the main analogue match type in the southeast of England where agricultural suitability is highest and topographic roughness is lowest (Fig. 5b). Sites with a close analogue older than 1000 years (grey circles) are largely located in Scotland where topographic roughness is higher (i.e. relating to the distinction between uplands and lowlands). Sites with no analogue (blue squares) have a more mixed distribution and may represent ecological novelty in the last 200 years.

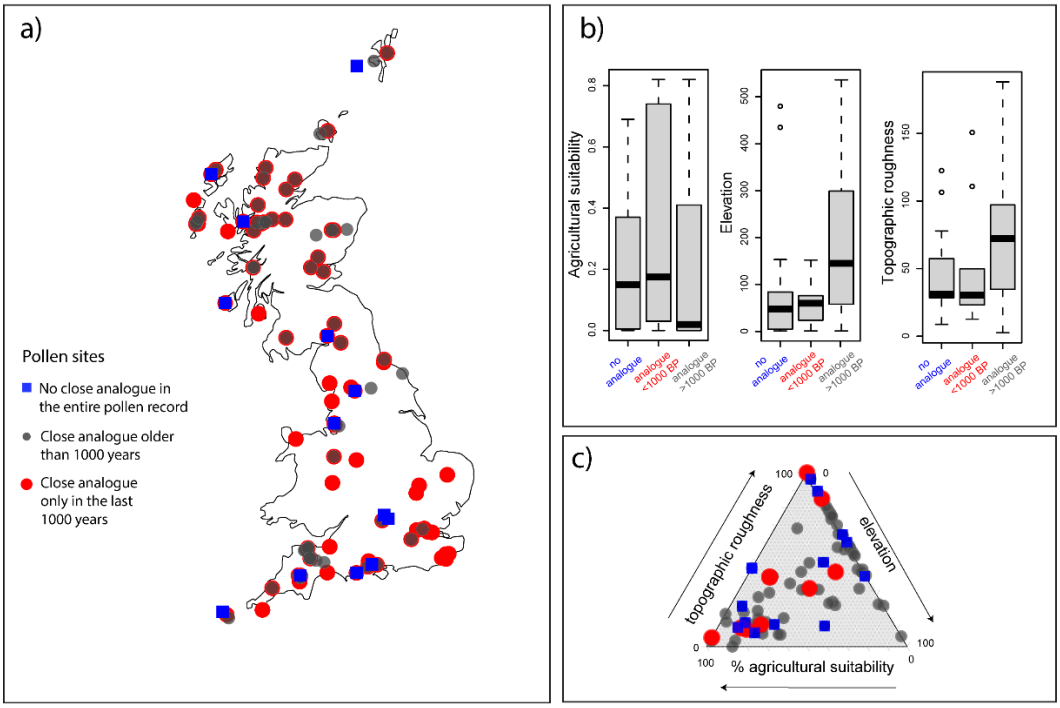


Figure 5 a) Pollen analogue matching between the most recent time period (200 cal. BP - present) and 200-year time windows spanning the Holocene (11700 - 200 cal. BP), b) box plots illustrating the spread of agricultural suitability, elevation and topographic roughness (derived from modern landscape data) across the pollen sites assigned to each analogue matching group, and c) ternary plot illustrating the relationships between pollen assemblage analogue matches and landscape characteristics.

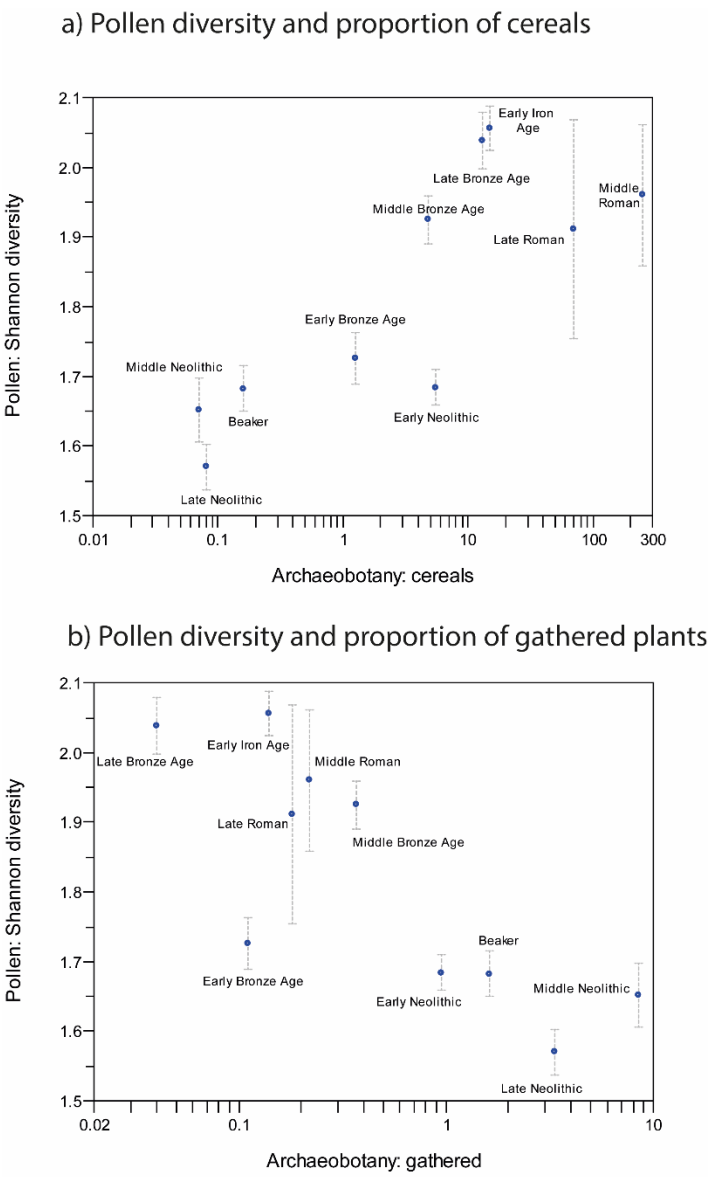


Figure 6 Pollen diversity (Shannon) index scores plotted against plant macrofossil data showing the density of: a) cereals, b) gathered plants (plotted on a logarithmic scale) within bulk archaeobotanical finds.

4. Discussion

4.1 Pollen and insect diversity and disturbance from arable land use

Similar diversity patterns have been identified between the pollen and insect records for certain time periods. However, spatial bias in site locations reduces the comparability of these datasets. Pollen diversity indices imply that land conversion for agriculture, associated with early land-use and woodland removal, initially led to an increase in the diversity of vegetation across many sites. An increase in insect diversity with forest reduction from the Mesolithic to the Bronze Age is to be expected as clearance and disturbance in woodland leads to the 'edge effect' that promotes insect diversity (Guimarães et al., 2014). Insects

associated with agricultural activity and the presence of grazing animals are known to have become more abundant during the Bronze Age as a result of land-use changes associated with agriculture, particularly the emergence of spatially extensive field systems and the niches that emerged around these, which includes, for example, ditches and hedgerows (Smith et al., 2019). Periods of increasing insect diversity are reflected by the creation of early 'fieldscapes' and anthropogenic heathlands (Løvschal, 2021) with large-scale grazing regimes since ~4000 cal. BP (~2050 BC), which were sustained by disturbance, with landscape longevity and resilience varying spatially. The increase in insect diversity from the Mesolithic to the Neolithic and Bronze Age may reflect opening of woodland and diversification of habitats.

Significant relationships between pollen diversity and palaeodemographic change have been demonstrated with *r*-values between 0.5 and 0.8 since the advent of agriculture (Woodbridge et al., 2021), which indicates that land requirements for human populations are linked to pollen diversity change. Through investigating relationships between human activity, as a proxy for disturbance, and diversity change through time, pollen and insect datasets show higher levels of diversity during periods of increasingly varied land use, i.e. during the Bronze Age and Iron Age, in comparison to more recent periods (Fig. 5), and that land-use phases broadly reflect demographic trends (Fig. 3). Higher pollen diversity has also been associated with numerous grassland and wetland taxa, crops and weeds in central Europe (Roleček et al., 2021). The results presented here (Fig. 4) show highest diversity in the land-use phase characterised by 'surplus production with further diversification of crops' from the Late Iron Age into the Roman period and during the late Saxon period. The variation in diversity scores between pollen and insect sites (Fig. 2) may reflect regional variability in land use and demonstrates that the level of disturbance is not the only factor influencing diversity, but the type of disturbance is also relevant, and whether this leads to the creation of new habitats or the removal of key habitats.

Previous analysis of fossil insect datasets has revealed significant assemblage change in lowland Britain resulting from the creation of middle Bronze Age and Iron Age field systems with stenotopic woodland species replaced by eurytopic open and disturbed ground types along with species that are associated with the dung of domestic grazing animals (Smith et al., 2019; 2020). The decline in insect diversity identified during the Iron Age may reflect a reduced range of habitats with a shift towards taxa typical of open disturbed ground and animal dung. Increased settlement and agricultural waste, and the introduction of new insect species into Britain, such as grain pests, also contributed to assemblage change (Smith et al., 2020). The Mesolithic woodland insect faunas include a large number of species represented by low numbers of individuals whereas agricultural faunas are represented by a large number of individuals from a smaller selection of species. The increased scale of cultivation and the development of other land-use activities evident during the Roman period (Table 2) would have led to the creation of new habitats and a higher level of human-induced disturbance. Highest pollen diversity scores are seen in the Iron Age and highest insect diversity values are identified in the Roman period. The slight decrease in pollen diversity scores during the late Roman period may represent the first time in British farming history when land-use

expanded at the expense of vegetation diversity (de Vareilles et al., in review). Archaeological evidence for agricultural productivity during the centuries immediately after the Roman period is scarce (McKerracher, 2018). A resurgence in agricultural productivity into the medieval period is accompanied by higher pollen diversity. This period was followed by increasing abundance of strongly synanthropic insect species, such as grain pests, which were introduced into Britain during Romans times (Smith et al., 2020). Insect assemblage changes identified in earlier studies (Smith et al., 2020) are reflected by significant increases in insect diversity compared to Mesolithic (pre-agricultural) levels (Fig. 2).

Shifts in insect diversity appear more pronounced than shifts in pollen diversity when data are amalgamated at a broad spatial scale. However, differences in how pollen and insect data sense the landscape, how these indicators respond to land use, and the spatial and temporal differences in the distribution of sites, will have affected the patterns observed. The pollen data cover a larger geographical area and include a greater number of sites while the insect data largely cover southern England and the midlands. Regional dissimilarities have been documented previously, for example, pollen evidence suggests that some regions of former Roman Britain (e.g. northern England) experienced an episode of land abandonment (evidenced as woodland regeneration) in the immediate post-Roman period, following an expansion of open land in the late Iron Age/early Roman period (Dark, 2000). Other types of disturbances, such as climatic change or disease (Flynn and Mitchell, 2019; Halsch et al., 2021), affect plant and insect diversity in different ways, and may explain the different trends identified in the most recent part of the records. When considering recognised Holocene climatic events (Vinther et al., 2009), there are no clearly identifiable episodes reflected in the pollen and insect diversity trends. However, statistically significant relationships have previously been identified between paleoclimate records reflecting North Atlantic conditions and pollen diversity trends (Woodbridge et al., 2021) demonstrating that diversity patterns are constrained by species climatic optima within the context of changing land use.

4.2 Identifying patterns of diversity change

Previous research has shown that Rate of Change (i.e. the degree of difference between adjacent samples over a known period of time) in pollen assemblages increased through the Holocene in other European regions (Finsinger et al., 2017) and on a global scale (Mottl et al. 2021b). These broad patterns are reflected within results from analysis of the British pollen datasets in this study, which includes an increase in Rate of Change following the Last Glacial Maximum transition and a more pronounced increase during the late Holocene. Rate of Change analysis allows both periods of perturbation, but also of stability, to be identified. The longest periods of stability (Fig. 3) occurred during the most forested period (~8000 - 6000 cal. BP) and during periods of lower land-use intensity from ~9000 - 1000 cal. BP (~7050 - 950 AD) (Fig. 3). The insect and pollen datasets show similarities in terms of diversity trends, but the timing of episodes of stability differ. There is a clearer late Holocene decline in diversity in the insect datasets, which may reflect differences in the response to land-use change or disparities associated with sampling locations and the lower number of insect sites in this period. Although the pollen datasets do not show a clear decline in

diversity in the most recent period at a broad scale, altered assemblage composition may be captured by the recent decline in pollen sample evenness, indicating the emergence of more homogeneous landscapes, however, this decline is of a relatively small scale compared to other shifts in the record. There are some differences in the pollen diversity trends in the current study and those presented in Woodbridge et al. (2021) due to the addition 100 extra sites to the British Isles pollen dataset, and the exclusion of pollen records from archaeological sites to capture landscape scale vegetation change. For example, the current study shows stronger evidence of a more recent decline in pollen diversity scores.

The increase in pollen assemblage Rate of Change (Fig. 3) is reflected by increasing pastoral/ human activity pollen index values. Diversity change is not only influenced by the scale of agriculture, but reflects the varied use of land, regional characteristics, and different functional relationships. This is indicated by dissimilarities in the results for each region where land-use practices would have varied (Fig. 4). Diversity trends inferred using all terrestrial pollen taxa differ from diversity trends derived from REVEALS quantified vegetation. This index shows a decline in diversity since ~6000 cal. BP (~4050 BC). These datasets capture different aspects of diversity: the former represents palynological diversity (Odgaard, 1999; Woodbridge et al., 2021), and the latter reflects the patterning and structure of landscapes (Matthias et al., 2015). The REVEALS approach incorporates site-type differences into the model when estimating regional land cover (Sugita, 2007). There are more woody than herbaceous taxa with RPPs that are used in the REVEALS approach, which may lead to bias towards woody vegetation in the diversity scores based on REVEALS transformed data, and therefore the pattern (Fig 3c) may reflect loss of woodland, while the 'all land pollen taxa' diversity trend represents the number of pollen types with higher diversity of herbaceous species linked to woodland opening. This has led to an inversed relationship between the 'REVEALS transformed vegetation diversity' and 'all land pollen diversity' curves. When compared with pollen diversity using all 153 land pollen taxa groups (i.e. the percentage data for all terrestrial pollen types), differences are also evident due to the more limited number of taxa, and the correction for production and dispersal differences between taxa in the regional scale vegetation cover estimates produced by REVEALS. The selection of sites that the REVEALS approach was applied to also differs from the sites that were used in the 'all taxa' diversity scores due to the smaller range of site types suited to the REVEALS models available. The difference in pollen sites represented in the two analyses may also explain dissimilates in the index scores. Diversity trends based on all land pollen taxa are therefore deemed more useful for understanding the range of vegetation types in the landscape for comparison with other environmental datasets.

Multiple smaller sites, or combinations of lakes and peat sites can be used to estimate regional vegetation cover in the absence of large lakes (Mazier et al., 2012; Fyfe et al., 2013; Trondman et al., 2016), but it is unclear what impact this has on diversity measures. Separating sites by type (lakes and peatland sites) (Fig. 3) revealed that different site types capture pollen diversity change in a similar way, however, a larger decline in evenness within datasets from peatland sites in recent centuries is evident. This may reflect the individual nature of landscapes from which these datasets are derived. Upland landscapes in particular

have been subject to intense grazing over recent centuries (Yeo and Blackstock, 2002; Davies, 2016), possibly reducing the diversity of these previously more ecologically complex landscapes.

4.3 The emergence of ecological novelty

Within the pollen datasets analysed in this study, increasing Rate of Change and assemblage novelty is evident and reflects changing land use. Similarly, within analysis of Rate of Change and ecological novelty in pollen datasets from across Europe, Finsinger et al. (2017) identified that land-use change had a greater effect on pollen assemblage Rate of Change and novelty than post-glacial climatic changes. They highlight that novelty did not develop as a constant linear function of time from past baseline conditions and the emergence of novelty accelerated with anthropogenic land-cover changes. The distinctions between the insect datasets in different periods may signify ecological novelty and the emergence of non-analogue assemblages through time. Woodland insect faunas were replaced by farmland faunas in the late Bronze Age and early Iron Age, which represented novel assemblages at this time with related shifts in functional diversity signified by changes between stenotypic woodland, eurytopic farmland and synanthropic urban taxa. However, species diversity only reflects one aspect of biodiversity. Functional diversity may have remained constant, as different species can have similar functional characteristics: this is described as 'functional redundancy' (Mayfield et al., 2010). Bronze Age insect assemblages are diverse because this phase includes woodland faunas along with wetland faunas and represents the first agricultural field systems. This may signify a transitional period where several ecotypes (i.e. locally adapted populations) co-existed and indicates that times of change are more diverse. The Bronze Age/Iron Age transition is often interpreted to coincide with a change to drier conditions (e.g. van Geel et al., 1996; Molloy, 2022), so climatic changes may have also influenced change in land use. The decline in insect diversity in the Iron Age reflects the agricultural lands from which these faunas have been derived and the lack of representation of multiple habitats. The rise in insect diversity in the Roman period corresponds to an increase in synanthropic diversity in urban areas. However, the lower number of insect sites in the medieval period and the different sampling methods used for modern samples influences the trends identified in the data.

The 'analogue-matching' analysis has revealed a number of pollen sequences where the most recent time window (200 - present) assemblage does not have equivalent analogues either within the same record, or elsewhere within the collection of datasets, and that there are sequences that only have analogues in the past 1000 years. This implies the development of anthropogenic biomes ('anthromes', *sensu* Ellis, 2015). Considering the characteristics of the pollen samples with close analogues only in the last 1000 years, or those with no analogues, these sites are often located in areas with greater agricultural suitability, implicating intensification of land-use practice in driving ecological novelty. Non-analogue assemblages in the south also include sites in the New Forest, which have been significantly altered by silviculture (Grant & Edwards, 2008). Sites with close analogues older than 1000 years are largely located in the north and west of Britain, and in areas of greater topographical

roughness (Fig. 5). The emergence of novelty in the Bronze Age, for example, where the development of fieldscapes has been shown to increase diversity in both pollen and insect datasets, is not identified, but these spaces may thus have greater conservation value, through the persistence of more stable ecological conditions over millennia.

4.4 Long-term ecology and conservation

Questions concerning what ecosystem characteristics and taxa to conserve, and where to prioritise conservation efforts, are often not straightforward to answer. Within Dornelas et al.'s (2014) global assessment of biodiversity time series data, assemblages were identified as undergoing biodiversity change, but not systematic biodiversity loss, with threats to key habitats emphasised. Therefore, concern should not only focus on biodiversity loss, but also on changing assemblage composition, which is demonstrated through the analysis of past environmental datasets presented in this study. Trends identified correspond with Mayfield et al.'s (2010) findings that species richness and trait diversity change may follow numerous response trajectories after land-use change in different modern landscapes. Land-use changes and intensification are often described as major factors in the emergence of ecological novelty (Jackson, 2013; Finsinger et al., 2017; Mottl et al., 2021a), and therefore decisions about future biodiversity conservation will benefit from improved understanding of the past. In applying long-term environmental data to modern environmental questions, there are challenges in analysing data from different environmental archives and proxies. For example, challenges result from differences in chronological control, the spatial coverage of archives, the complexities in amalgamating datasets, obstacles in linking correlation to causation, and the intricacies of the pollen diversity - plant diversity relationship. Greater communication and data integration is required between branches of paleoecology and archaeology, and conservation ecology, to address these challenges and move towards incorporating long-term understanding into modern planning.

5. Conclusions

Through investigating a) 'how disturbance from land-use change affects diversity trends and whether pollen and insect diversity trends show the same patterns of change through time', this study demonstrates that fossil beetle and pollen records show similar diversity trends in the early to middle Holocene with greater dissimilarities in more recent periods. Insect diversity is only statistically correlated with the pollen diversity evenness index indicating a relationship between vegetation heterogeneity and insect diversity, but comparisons are restricted by the number of insect samples for certain time periods and spatial differences in site locations. There are also periods of stability in the pollen diversity data and accelerated change in both the pollen and beetle diversity trends, particularly associated with changing land-use scale and crop spectrum. Comparing land use from archaeobotanical data with pollen data indicates that disturbance affects diversity change with statistically significant relationships demonstrated between the density of cereals and gathered resources and pollen diversity. In addressing b) 'investigating the extent to which ecological novelty can be identified in long-term ecological datasets and exploring when novel ecosystems emerge', the

pollen datasets show ecological novelty in the form of non-analogue assemblages and increasing Rate of Change. A high proportion of pollen sites only have a matching analogue assemblage in the last 1000 years, modern landscapes with higher agricultural suitability appear more likely to have analogues in the last 1000 years, and those with higher topographic roughness may be more likely to have analogues older than 1000 cal. BP. This indicates that agriculture plays a role in the emergence of novel ecosystems.

The analysis of long-term pollen and insect datasets from across Britain provides evidence of changes in land-cover, disturbance, and diversity through the Holocene and particularly since the onset of farming. Long-term environmental data reveal that change is a normal part of ecosystem functioning. In exploring when and how current patterns of biodiversity emerged and how human actions shaped biodiversity trends, the results of this study indicate that there are no clear baselines for current patterns, which reflect dynamic shifts in land use represented by insect faunal and vegetation responses. Shifts in land use and cultivation broadly follow the same trajectories as those of vegetation and insect diversity. Links between disturbance and diversity have implications for the way in which land-use impacts are understood and prioritised for the sustainable use and management of modern landscapes. Increasing Rate of Change and ecologically distinct assemblages are identified in the more recent past within this study. Nature-based solutions for land management that aim to enhance biodiversity will benefit from awareness of the long-term historic relationships between land cover, which is largely the result of human action, and vegetation and insect diversity change.

Supplementary Information 1 Fossil pollen and insect site metadata for all sites across Britain

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Author contributions

JW, RF, RP, DS and AdV were central to the conception and design, acquisition of data, analysis and interpretation of the data. JW drafted the manuscript and RF, RP, DS and AdV revised the content critically contributing intellectual content. MG, RB, RS, JG, PD, DD, GG, AP, TH, ES, MS, FC, CB and MW contributed pollen data for analysis and commented on the manuscript providing critical feedback. All authors gave final approval of the version to be published.

Data availability statement

The results of the analyses carried out are archived within the open access PANGAEA database. Many of the original pollen datasets used in this study are available from the European Pollen Database (EPD; www.europeanpollendatabase.net/) and can be accessed here: http://www.europeanpollendatabase.net/fpd-epd/bibli.do (please see Supplementary Information for site names, author names and references). The EPD is also available as an Access database, which can be downloaded here: http://www.europeanpollendatabase.net/data/downl oads/ and the same datasets are available via the Neotoma Database: https://www.neotomadb.org/. The majority of the fossil insect datasets are available from BugsCEP (http://bugscep.com/). The latest version of the BugsCEP Access database can be downloaded here: http://bugsc ep.com/downl oads.html. All radiocarbon dates used for Paleodemographic reconstructions are available within University College London's Discovery database (discovery.ucl.ac.uk/10025178/: https://doi.org/10.14324/ 000.ds.10025178). For a full set of sources and acknowledgements for the radiocarbon data see Bevan et al. (2017). Archaeobotanical datasets are stored within ArboDat (https://nihk.de/en/research/current-projects/arbodat-ape) and are available via the ABCD (https://www.intarch.ac.uk/journal/issue1/tomlinson/toc.html).