

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

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

Abstract

Land-use change plays an important role in shaping plant and insect diversity over long time scales. 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), a long history of landscape transformation through agrarian change, and physical isolation from the European landmass since the early Holocene (11,700 calibrated years before present). 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).

44 Agricultural systems have played a key role in biodiversity change in past (Birks et al.,
45 2016a) and modern systems (Dudley & Alexander, 2017; Outhwaite et al., 2022). Long-term
46 (paleo) environmental records provide insights into the multi-millennial scale patterns and
47 processes that lead to diversity change (Hjelle et al., 2012), for example, fossil pollen datasets
48 can be used as a proxy for land cover and vegetation diversity change, and fossil insect
49 (beetle) records reflect disturbances and human activity. Archaeological records of land use
50 (archaeobotany) and population change (archaeodemography) allow exploration of factors
51 that influence these trends. Such datasets can be analysed alongside modern landscape data
52 allowing long-term patterns to be viewed within the context of contemporary agricultural
53 suitability.

54

55 The role of historic environmental change in shaping current diversity patterns has been
56 demonstrated (Gaston, 2000; Birks et al., 2016a; 2016b) with a focus on placing trends
57 identified in recent decades-centuries into the context of the longer-term past. Temperate
58 European vegetation trends have previously been described as characterised by declining
59 biodiversity during initial forest development in the early Holocene (11700-8000 cal. BP)
60 (cal. BP: calibrated years Before Present, where present = AD 1950), stable levels of
61 diversity during periods dominated by closed mixed forest in the mid-Holocene (8000-6000
62 cal. BP), increasing biodiversity on fertile soils with the emergence of agricultural land use
63 from 6000-4000 cal. BP, and declining biodiversity in the most recent 200 years (Birks et al.,
64 2016a). Subsequent research has identified similar trends for pollen sites across Britain
65 within the context of regional variability and has revealed that a recent decline in biodiversity
66 is not always detectable in fossil pollen datasets (Woodbridge et al., 2021). Novel plant
67 communities represent new combinations of taxa with no previous analogue and result from
68 the arrival or introduction of new species often representing human-driven changes, such as
69 altered land use, or climate change, and may be reflected by increasing 'Rate of Change' in
70 assemblage composition (Finsinger et al., 2017).

71

72 Spatial and temporal patterns of changing diversity derived from fossil pollen datasets have
73 been used to infer past biodiversity trends for various regions from temperate and northern
74 Europe to the Neotropics (Odgaard, 1994; Weng et al., 2006; Colombaroli et al., 2013; Felde
75 et al., 2016; Matthias et al., 2015; Reitalu et al., 2015; 2019; Kuneš et al., 2019; Roleček et
76 al., 2021). Similar challenges in elucidating the relationships between pollen diversity and
77 vegetation diversity have been described (Weng et al., 2007; Gosling et al., 2009) due to the
78 impacts of differential pollen dispersal and productivity, the effects of landscape openness
79 and changing pollen concentration on taxa representation in datasets, and the coarser
80 taxonomic resolution of fossil pollen data compared to plant taxonomy (Odgaard et al., 1999;
81 Weng et al., 2006; van der Knaap, 2009; Goring et al., 2013; Pardoe, 2021). Despite these
82 challenges, new methodological developments and suitable analytical approaches are
83 improving understanding of biodiversity change based on fossil pollen data (Roleček et al.,
84 2021). Previous research has paved the way for palynology to go beyond describing patterns
85 of diversity change and, as a discipline, to play a key role in understanding the processes of
86 change and the relationships between ecosystem characteristics, disturbances, and diversity
87 change. The results of recent palynological studies demonstrate that pollen richness, which

88 reflects the number of taxa, shows good correspondence with plant richness, as well as
89 demonstrating that plant and pollen diversity are significantly related (Meltsov et al., 2011;
90 Felde et al., 2016; Giesecke et al., 2014; 2019; Reitalu et al., 2019; Roleček et al., 2021).

91

92 Fossil insect datasets are used to investigate the impacts of changing land use or vegetation
93 cover and are informative about the spread and intensity of human settlement (Kenward,
94 1997; Smith, 2012; Smith et al., 2010, 2019, 2020). In a recent analysis of fossil insect
95 datasets from across Europe, Pilotto et al. (2022) suggest that the expansion of agriculture
96 6,000 years ago had as dramatic an impact on insect communities as rising temperatures in
97 the early Holocene. Smith et al. (2020) describe the increased scale of agriculture during the
98 late Bronze Age / early Iron Age (3100-2700 cal. BP; 1150-750 cal. BC) of the British Isles
99 as having a similar drastic effect on insect faunas. Insects include many different groups with
100 dissimilar responses to environmental changes. Within this research the Coleoptera (beetle)
101 insect group is analysed, and datasets are referred to as “insect” records. Exploration of
102 changing insect diversity in response to land-use and land-cover change in the past currently
103 represents a knowledge gap in paleoenvironmental research.

104

105 ***1.2 Diversity-disturbance relationships and ecological novelty***

106

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

125

126 ***1.3 Past land-use, population shifts, and climate change***

127

128 Archaeobotanical records (plant remains preserved at archaeological sites) provide a wealth
129 of information about past subsistence and land-use strategies (de Vareilles et al., 2021). The
130 main factors that affect the recovery of archaeobotanical evidence are preservation
131 conditions, variations in sampling practices, and the nature and scale of past arable

132 agriculture (van der Veen et al., 2007; Fuller and Stevens, 2012; van der Veen, 2014; Bishop,
 133 2015; Carruthers and Hunter Dowse, 2019). Changes in crops, intensity and scale of
 134 production, arable equipment, catchment and population size and structure, will have
 135 profoundly altered the character of arable landscapes. Increased scale of arable production is
 136 indicated in archaeobotanical records by higher densities of bulk finds of charred plant
 137 remains (van der Veen, 2014) as well as features and structures associated with crop storage
 138 and processing. Significant arable innovations from the introduction of farming at the start of
 139 the Neolithic (~4000 BC) (~6000 cal. BP) to the Agricultural Revolution of the 18th century
 140 AD are shown in Table 1. Knowledge of past land-use strategies, including the intensity (i.e.
 141 input, such as labour or manure, per unit of soil) and extent of agriculture, allows
 142 understanding of how these processes influence plant and insect diversity and the role of
 143 people in shaping biodiversity trends over historic timescales.

144
 145 Archaeological datasets are also used to infer demographic change (Bevan et al., 2017) based
 146 on the assumption that the density of radiocarbon-dated sites relates to human population size
 147 (Shennan et al., 2013). Demographic trends may influence land requirements to support
 148 changing populations and thus affect landscape change. The impacts of land-use changes are
 149 also constrained by the climatic tolerances and optima of plant and insect species.
 150 Paleoclimate datasets reflecting North Atlantic climatic conditions are summarised in
 151 Woodbridge et al. (2021) where significant relationships were identified between
 152 palaeoclimate datasets, population change and pollen diversity trends.

153
 154 **Table 1** Summary of key agricultural developments in Britain affecting changes in scale and
 155 intensity of land-use. *follows Historic England’s Period List, FISH terminology
 156 <http://www.heritage-standards.org.uk/chronology/>

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 (7 th)9 th – 11 th century, affecting soil hydrology and field ecology; Open field systems; cultivation becomes more extensive; free-threshing wheat and rye widely cultivated.	Hamerow et al. (2020); McKerracher (2018); Stevens and Fuller (2018); Dark (2000)

	Temporary land abandonment in the immediate post-Roman period in some areas.	
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	

157

158

159 ***1.4 Investigating patterns of diversity and ecological novelty***

160

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

167

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

172

173 **2. Methods**

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175 ***2.1 Data assimilation and harmonisation***

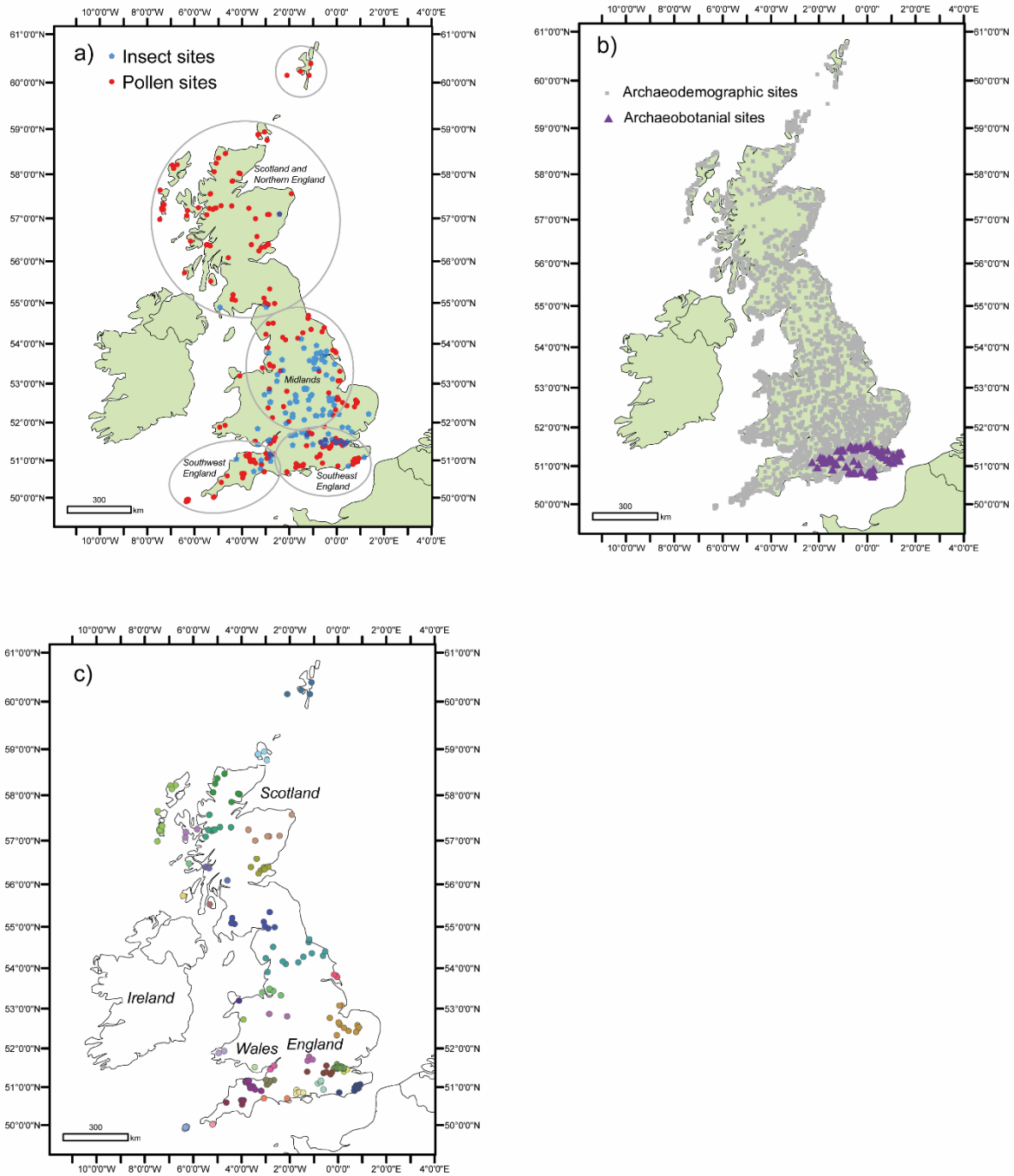
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177 297 radiocarbon-dated fossil pollen datasets have been amalgamated from across Britain (Fig.
 178 1 and Supplementary Information 1). BPOL database (an extensive archive of British fossil
 179 pollen site information) (Grant et al., 2017) was used to identify datasets and provided
 180 information about radiocarbon-dating quality. The pollen datasets partly derive from the
 181 European Pollen Database (Leydet et al., 2007-2023) and were gathered within the
 182 LandClimI project (Fyfe et al., 2013; Trondman et al., 2015). Additional datasets were
 183 provided by data contributors and a small number of datasets have been digitised using
 184 Straditize software (Sommer, 2019). Pollen records from individual coring sites have been
 185 taxonomically harmonised using the European Pollen Database nomenclature (Leydet et al.,
 186 2007-2023) and summed into 200-year time windows for analysis. Total land pollen counts
 187 for each taxon were summed and percentages calculated as a proportion of the pollen grain
 188 count for the time window. The approach follows Fyfe et al. (2015), Roberts et al. (2018) and
 189 Woodbridge et al. (2019). For digitised datasets, pollen percentages were averaged for each
 190 time window. Datasets with at least three radiocarbon dates were selected and chronologies
 191 have been constructed using “clam” (Blaauw, 2010) and “rbacon” (Blaauw, 2021) R
 192 packages.

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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.



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234

235 **Figure 1.** Site locations: a) fossil insect (blue pentagons) and pollen (red circles) datasets
 236 covering the Holocene (grey circles represent areas for regional analyses), b)
 237 archaeobotanical sites (purple triangles), radiocarbon-dated archaeological sites (grey
 238 squares) (archaeodemography), and c) pollen sites used in the REVEALS model colour
 239 coded by site aggregation for regional vegetation reconstruction.

240

241 Modern landscape data have been extracted from within a 10 km radius around pollen sites
 242 that have a sample in the most recent time window (AD 1750 - present) (200 to -70 cal. BP).
 243 The 10 km distance was selected following previous work comparing modern pollen with
 244 remote sensed vegetation maps (Woodbridge et al., 2014b), to reflect the average pollen

245 source area of sites, and to capture both local and regional landscape characteristics.
246 Topographic data were obtained from a 1 km resolution dataset using an elevation model for
247 the UK. Agricultural suitability derives from a 100 m resolution dataset obtained from the
248 Macaulay Land Use Research Institute (1991) for which data across England, Scotland and
249 Wales were combined. Agricultural suitability values represent the percentage of land area
250 within 10 km of a pollen site in agricultural suitability classes 1-3 (i.e. land capable of
251 producing 1: a very wide range of crops, 2: a wide range of crops, and 3: a moderate range of
252 crops). The relationship between pollen sample analogues and modern landscape data
253 (topographic roughness, elevation and agricultural suitability) is presented in a ternary plot
254 using the Ternary R package (Smith, 2017), which graphically presents the ratios between
255 three variables as positions within a triangle. Each pollen sample is plotted according to the
256 modern landscape characteristics at the coring site and colour coded by analogue matching.
257 Only sites that have pollen samples in the most recent time window (200 BP - present) were
258 included in the analogue matching exercise for comparison with all 297 pollen sequences.

259
260 Plant macrofossil data have been amalgamated from 1718 archaeobotanical samples (charred
261 plant macrofossil remains) from 110 sites across the southeast of England (Fig. 1). The
262 archaeobotanical data were analysed using cluster analysis and an autoecological approach
263 based on modern field observations of individual taxa tolerances to environmental conditions
264 (de Vareilles et al., in review). These datasets have been used to explore changes in the
265 composition and amount of crops and gathered resources to infer land-use scale and range of
266 plant foods (de Vareilles et al., 2021; in review). The bulk density of plant macrofossil
267 remains associated with different types of human land use (crop and cereal cultivation and
268 gathering resources) have been combined and are compared with pollen diversity scores. The
269 ‘cereal’ macrofossil category includes barley (*Hordeum vulgare*), emmer wheat (*Triticum*
270 *dicoccum*), spelt wheat (*T. spelta*), free-threshing wheat (*T. aestivum/durum/turgidum*), rye
271 (*Secale cereale*) and oat (*Avena sativa*). The ‘gathered’ category includes hazelnut (*Corylus*
272 *avellana*), prunus (*Prunus spp.*), apple/pear (*Malus/Pyrus sp.*), elder (*Sambucus nigra*),
273 berries (*Rubus spp.* and *Fragaria vesca*), hawthorn (*Crataegus monogyna*) and acorn
274 (*Quercus sp.*). However, interpretations based on these taxa groups must take into account
275 that fruits and nuts are likely to have been cultivated by the Roman period, and oats are likely
276 to have been wild until the late Iron Age. Figure 3a is based on these studies and shows a
277 conceptual summary of the changes in land use ‘scale’ (i.e. production relative to population)
278 and range (i.e. the range of cultivated crops), which includes 0: pre-agriculture, 1: pastoral
279 with limited arable production, 2: subsistence farming, 3: broader spectrum subsistence
280 farming, 4: surplus production with further diversification of crops, 5: further increase in the
281 crop spectrum and scale of production, and 6: change and increase in the crop spectrum and
282 continued growth of production. Palaeodemographic changes are estimated based on the
283 summed probability distribution (SPD) of 22,719 archaeological radiocarbon (^{14}C) dates for
284 Britain (Bevan et al., 2017). The package ‘rcarbon’ was used to produce an SPD curve from
285 the ^{14}C dates, which is binned into 200-year time windows and is presented in Woodbridge et
286 al. (2021).

287 288 **2.2 Data analysis**

289

290 Disturbance is caused by numerous factors associated with natural and human induced
291 environmental changes. Population change reflects land requirements for agriculture,
292 however, archaeodemographic trends are not likely to be linearly related to disturbance,
293 therefore a pastoral/human activity pollen index is used as an indicator of changing
294 disturbance levels. The index is a sum of untransformed pollen percentage data, which
295 includes Asteraceae subfamily Asteroideae, Asteraceae subfamily Lactucoideae, Cynareae,
296 Rubiaceae, Ranunculaceae, *Potentilla*, *Plantago lanceolata*, *Plantago major*, *Plantago*
297 *media*, Chenopodiaceae, *Rumex*, *Urtica* and Cerealia. The inclusion of certain taxa within the
298 index has been informed by previous work involving pastoral/human activity pollen indices
299 (Behre, 1986; Berglund, 1991, Mazier et al., 2006; 2009; Fyfe et al. 2010; Araujo et al.,
300 2020). Pollen indices of human activity should be interpreted with recognition that taxa may
301 also occur naturally as well as associated with anthropogenic activity.

302

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

317

318 Rate of Change (RoC) calculations followed the method described by Finsinger et al. (2017)
319 where chord distance is used as a measure for dissimilarity between pollen assemblages to
320 estimate within-site RoC between consecutive time windows. RoC values were subsequently
321 averaged across sites for each 200-year time window. Spearman’s Rank correlation was used
322 to analyse the relationship between archaeobotanical remains and pollen diversity. An
323 analogue-matching approach (Simpson & Oksanen, 2021) has been applied to the pollen
324 datasets to identify similar and dissimilar assemblages between all 200-year time windows
325 through the Holocene. The closest analogues for each pollen sample from the 297 sequences
326 have been determined using the ‘analog’ package with R (Simpson & Oksanen, 2021).
327 Analogue groups are defined according to whether the most recent pollen assemblage (200
328 cal. BP - present) has a close analogue in the last 1000 years, a close analogue older than
329 1000 years, or no close analogue through the entire record. Insect samples assigned ‘modern’
330 were deemed unsuitable for comparison with insect datasets from earlier archaeological
331 periods using the analogue-matching approach, as the collection methods for modern samples

332 differ from methods applied to paleoenvironmental insect samples leading to certain taxa
333 groups being over-represented.

334

335 **3. Results**

336

337 *3.1 Diversity and disturbance trends across Britain*

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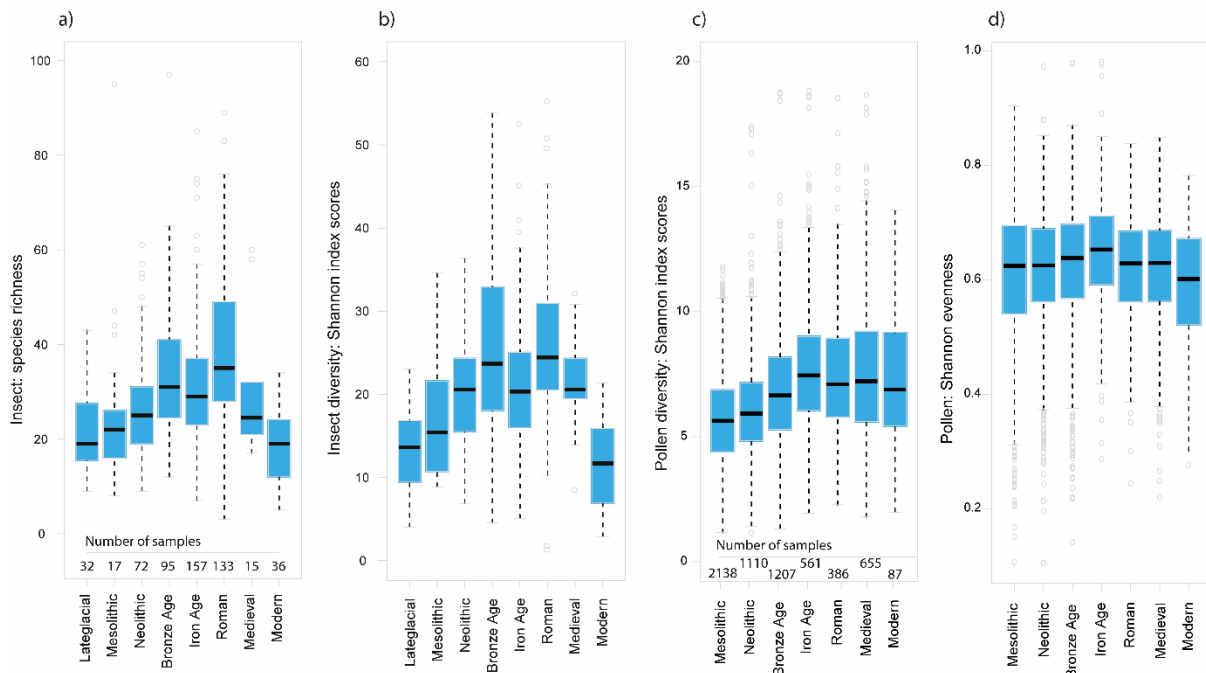
339 When amalgamated for all sites across Britain (Fig. 1), diversity scores derived from the
340 insect and pollen datasets reveal similarities from the Mesolithic (7050 BC) (~9000 cal. BP)
341 to the Bronze Age and distinctive patterns in more recent parts of the records (Fig. 2). The
342 insect datasets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

360

361 Decreased insect diversity in the medieval period, which is not reflected by declining pollen
362 diversity, may be captured by declining pollen evenness (Fig. 2) showing that landscapes
363 have become increasingly dominated by certain plant types. These patterns reflect the
364 changing scale and spectrum of land-use practice (Figs. 2 and 3) and population trends
365 inferred from archaeological records (Fig. 3). The larger range in the insect diversity box
366 plots (Fig. 2) indicates significant spread within the data, signalling considerable variability
367 between sites. Diversity scores derived from British Isles pollen datasets using different
368 measures of diversity (Hill Numbers, Shannon diversity, evenness and Rarefaction) have
369 previously revealed very similar trends (Woodbridge et al., 2021). Comparison of diversity
370 trends after separating lake and peatland site types based on all 153 pollen taxa shows similar
371 patterns with only minor differences, which are most notably in pollen sample evenness in
372 the most recent period (Fig. 3).

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

383

384 **Table 2** Kruskal-Wallis test p -values for Shannon diversity change between archaeological
385 time periods: a) fossil pollen datasets, b) fossil insect datasets, c) Spearman’s Rank (r -value)
386 correlations between pollen diversity (Shannon index) and evenness and land use inferred
387 from archaeobotanical assemblages, and d) Spearman’s Rank (r -value) correlations between
388 pollen diversity and evenness and insect diversity (Hill Numbers). Shaded cells indicate
389 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

390

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

391

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

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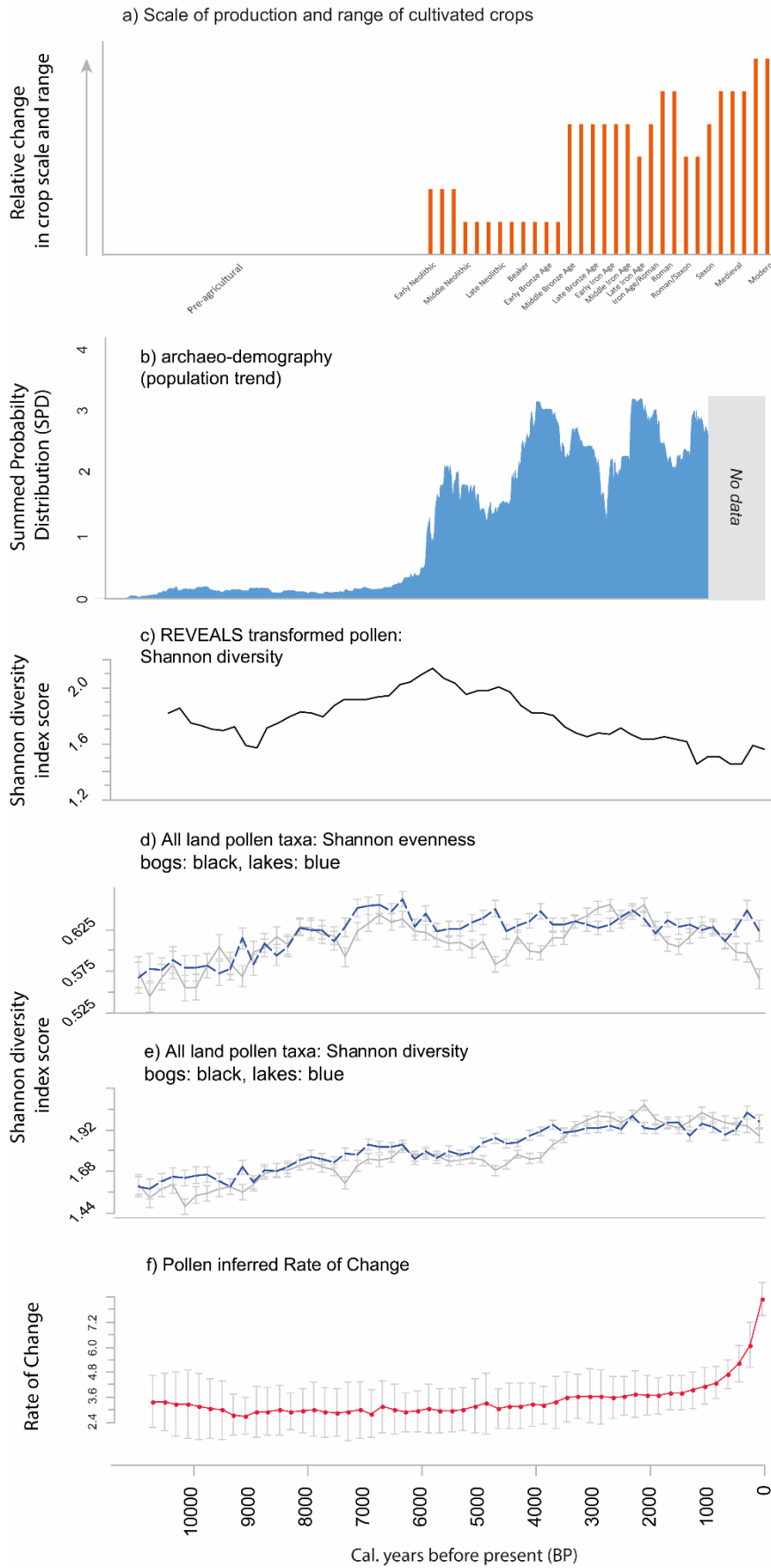
d) Insect and pollen diversity	Insects H1	Insects H0	Insects H2
Pollen: Shannon diversity index	0.310	0.238	0.333
Pollen: Shannon evenness	0.762	0.738	0.833

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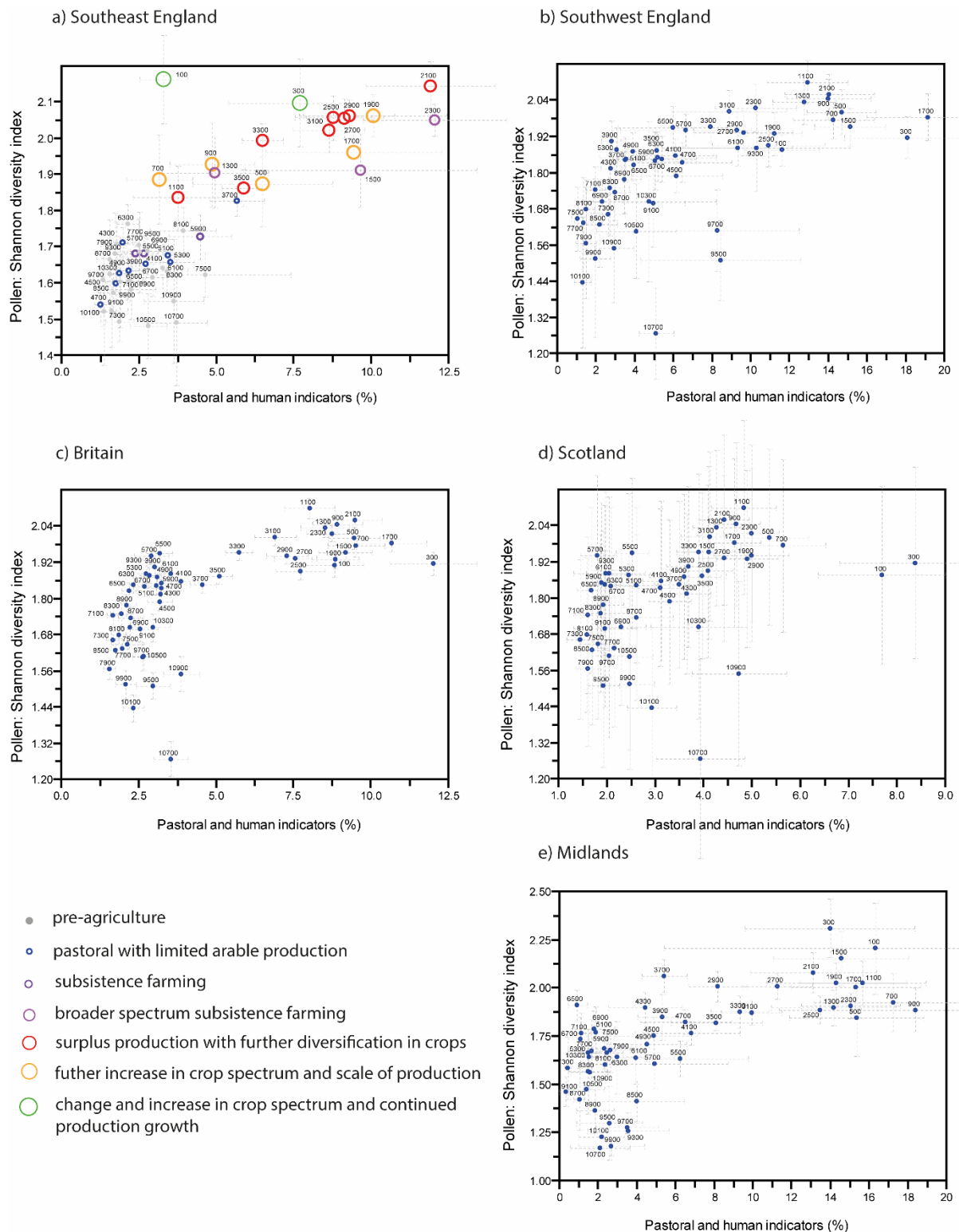
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398 **Figure 3.** a) land-use change based on crop spectrum and scale of agriculture using a
399 conceptual interpretive scale (de Vareilles et al., in review), b) summed probability
400 distribution (SPD) of radiocarbon-dated archaeological sites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

407

408 The average pollen diversity scores and average pastoral/human activity pollen index,
409 reflecting land conversion for agriculture, is presented in Fig. 4 for different regions. The
410 dates represent the mid-point of each 200-year time window (e.g. 300 BP on the plot
411 represents the period 400-200 BP). The time periods spanning 2000-1000 cal. BP (950 BC -
412 AD 50) have highest pastoral/human activity index values and diversity, while earlier
413 prehistoric periods are characterised by lower diversity scores, reflecting the low impact on
414 vegetation cover that small-scale, and perhaps irregular (Stevens and Fuller, 2012),
415 agricultural practices would have had. Pollen diversity declines in the 300 and 100 cal. BP
416 (400 cal. BP - present) time windows (Fig. 4) in Scotland, southwest England and for all
417 British sites while the pastoral/human activity index increases. This pattern is shown for all
418 regions other than southeast England and the midlands where 100 cal. BP (200 cal. BP -
419 present) represents a period with higher diversity. Land-use scale and spectrum (i.e. range of
420 crops) shown on the southeast England plot inferred from archaeobotanical records illustrates
421 the increasing intensity of agriculture with highest pollen diversity scores during the Iron Age
422 to Roman transition (~2100 cal. BP) (150 BC) and the late Saxon period (~900 cal. BP) (AD
423 1050). The impacts of land-use change are illustrated in Fig. 6, which shows that pollen
424 diversity index scores are statistically significantly related to changing land-use practices
425 evidenced in archaeobotanical remains (Table 2c). Pollen diversity is positively related to
426 crop and cereal plant types, particularly during the early Iron Age, Late Bronze Age and
427 Roman period, and negatively related to plant types associated with gathering.

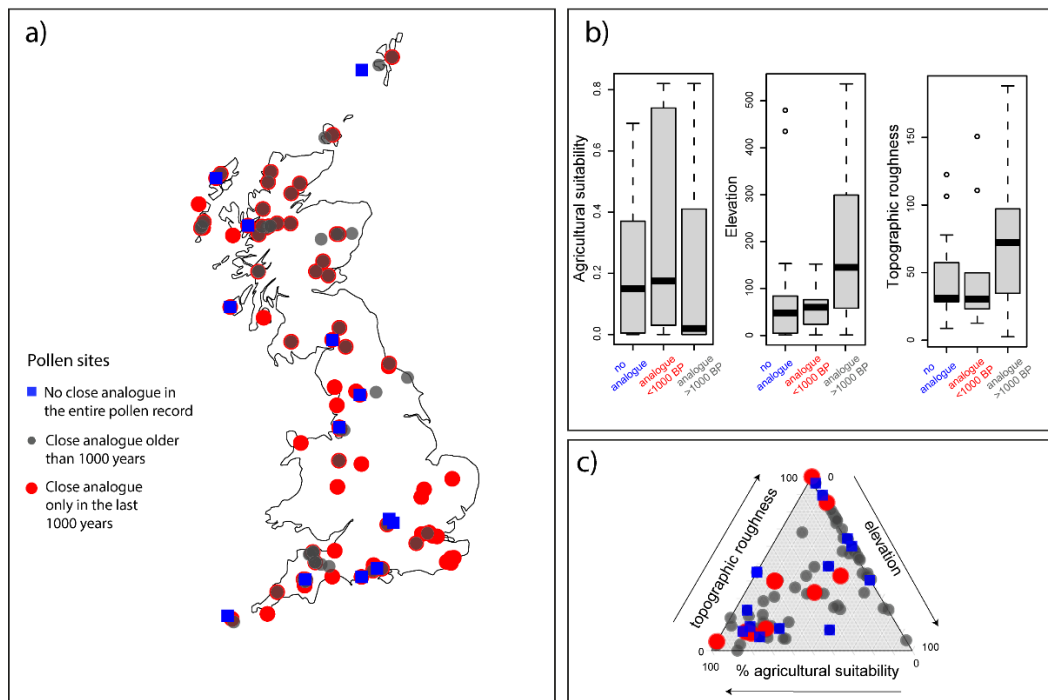


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430 **Figure 4.** Pastoral/human activity pollen index plotted against Shannon diversity index
 431 (pollen derived). Dates in cal. BP (cal. year Before Present) represent the mid-point of a 200-
 432 year time window (e.g. 300 represents 400-200 cal.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

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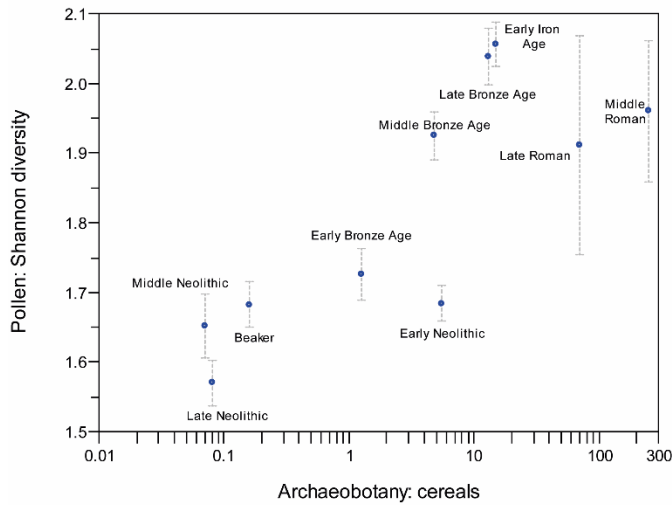
The spatial distribution of pollen sites in the most recent period (200 cal. BP - present) with matching analogues (i.e. similar species assemblages) in the last 1000 years and the rest of the Holocene (11,700 - 1000 cal. BP) is shown in Fig. 5 in relation to modern landscape data. Sites with a close 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.



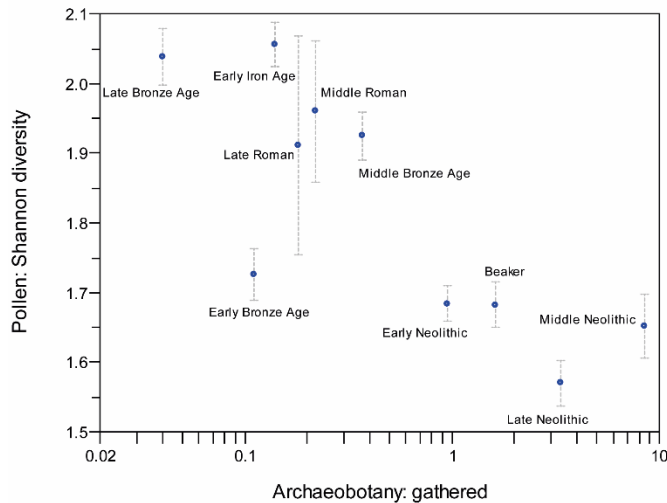
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Figure 5 a) Pollen analogue matching between the most recent time period (200 cal. BP - present) and 200-year time windows spanning the Holocene (11700 - 200 cal. BP), b) box plots illustrating the spread of agricultural suitability, elevation and 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.

a) Pollen diversity and proportion of cereals



b) Pollen diversity and proportion of gathered plants



459

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

463

464

465 **4. Discussion**

466

467 **4.1 Pollen and insect diversity and disturbance from arable land use**

468

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

476 associated with agricultural activity and the presence of grazing animals are known to have
477 become more abundant during the Bronze Age as a result of land-use changes associated with
478 agriculture, particularly the emergence of spatially extensive field systems and the niches that
479 emerged around these, which includes, for example, ditches and hedgerows (Smith et al.,
480 2019). Periods of increasing insect diversity are reflected by the creation of early
481 ‘fieldscapes’ and anthropogenic heathlands (Løvschal, 2021) with large-scale grazing
482 regimes since ~4000 cal. BP (~2050 BC), which were sustained by disturbance, with
483 landscape longevity and resilience varying spatially. The increase in insect diversity from the
484 Mesolithic to the Neolithic and Bronze Age may reflect opening of woodland and
485 diversification of habitats.

486

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

503

504 Previous analysis of fossil insect datasets has revealed significant assemblage change in
505 lowland Britain resulting from the creation of middle Bronze Age and Iron Age field systems
506 with stenotopic woodland species replaced by eurytopic open and disturbed ground types
507 along with species that are associated with the dung of domestic grazing animals (Smith et
508 al., 2019; 2020). The decline in insect diversity identified during the Iron Age may reflect a
509 reduced range of habitats with a shift towards taxa typical of open disturbed ground and
510 animal dung. Increased settlement and agricultural waste, and the introduction of new insect
511 species into Britain, such as grain pests, also contributed to assemblage change (Smith et al.,
512 2020). The Mesolithic woodland insect faunas include a large number of species represented
513 by low numbers of individuals whereas agricultural faunas are represented by a large number
514 of individuals from a smaller selection of species. The increased scale of cultivation and the
515 development of other land-use activities evident during the Roman period (Table 2) would
516 have led to the creation of new habitats and a higher level of human-induced disturbance.
517 Highest pollen diversity scores are seen in the Iron Age and highest insect diversity values
518 are identified in the Roman period. The slight decrease in pollen diversity scores during the
519 late Roman period may represent the first time in British farming history when land-use

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

528

529 Shifts in insect diversity appear more pronounced than shifts in pollen diversity when data are
530 amalgamated at a broad spatial scale. However, differences in how pollen and insect data
531 sense the landscape, how these indicators respond to land use, and the spatial and temporal
532 differences in the distribution of sites, will have affected the patterns observed. The pollen
533 data cover a larger geographical area and include a greater number of sites while the insect
534 data largely cover southern England and the midlands. Regional dissimilarities have been
535 documented previously, for example, pollen evidence suggests that some regions of former
536 Roman Britain (e.g. northern England) experienced an episode of land abandonment
537 (evidenced as woodland regeneration) in the immediate post-Roman period, following an
538 expansion of open land in the late Iron Age/early Roman period (Dark, 2000). Other types of
539 disturbances, such as climatic change or disease (Flynn and Mitchell, 2019; Halsch et al.,
540 2021), affect plant and insect diversity in different ways, and may explain the different trends
541 identified in the most recent part of the records. When considering recognised Holocene
542 climatic events (Vinther et al., 2009), there are no clearly identifiable episodes reflected in
543 the pollen and insect diversity trends. However, statistically significant relationships have
544 previously been identified between paleoclimate records reflecting North Atlantic conditions
545 and pollen diversity trends (Woodbridge et al., 2021) demonstrating that diversity patterns are
546 constrained by species climatic optima within the context of changing land use.

547

548 *4.2 Identifying patterns of diversity change*

549

550 Previous research has shown that Rate of Change (i.e. the degree of difference between
551 adjacent samples over a known period of time) in pollen assemblages increased through the
552 Holocene in other European regions (Finsinger et al., 2017) and on a global scale (Mottl et al.
553 2021b). These broad patterns are reflected within results from analysis of the British pollen
554 datasets in this study, which includes an increase in Rate of Change following the Last
555 Glacial Maximum transition and a more pronounced increase during the late Holocene. Rate
556 of Change analysis allows both periods of perturbation, but also of stability, to be identified.
557 The longest periods of stability (Fig. 3) occurred during the most forested period (~8000 -
558 6000 cal. BP) and during periods of lower land-use intensity from ~9000 - 1000 cal. BP
559 (~7050 - 950 AD) (Fig. 3). The insect and pollen datasets show similarities in terms of
560 diversity trends, but the timing of episodes of stability differ. There is a clearer late Holocene
561 decline in diversity in the insect datasets, which may reflect differences in the response to
562 land-use change or disparities associated with sampling locations and the lower number of
563 insect sites in this period. Although the pollen datasets do not show a clear decline in

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

572

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

600

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

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

611

612 *4.3 The emergence of ecological novelty*

613

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

640

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

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

656

657 ***4.4 Long-term ecology and conservation***

658

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

679

680 **5. Conclusions**

681

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

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

702

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

718

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

721

722 **Acknowledgements**

723

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732 the use of Straditize software.

733

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1122 **Author contributions**

1123

1124 JW, RF, RP, DS and AdV were central to the conception and design, acquisition of data,
1125 analysis and interpretation of the data. JW drafted the manuscript and RF, RP, DS and AdV
1126 revised the content critically contributing intellectual content. MG, RB, RS, JG, PD, DD, GG,
1127 AP, TH, ES, MS, FC, CB and MW contributed pollen data for analysis and commented on
1128 the manuscript providing critical feedback. All authors gave final approval of the version to
1129 be published.

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1131 **Data availability statement**

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1133 The results of the analyses carried out are archived within the open access PANGAEA
1134 database. Many of the original pollen datasets used in this study are available from the
1135 European Pollen Database (EPD; www.europeanpollendatabase.net/) and can be accessed
1136 here: <http://www.europeanpollendatabase.net/fpd-epd/bibli.do> (please see Supplementary
1137 Information for site names, author names and references). The EPD is also available as an
1138 Access database, which can be downloaded
1139 here: <http://www.europeanpollendatabase.net/data/downloads/> and the same datasets are
1140 available via the Neotoma Database: <https://www.neotomadb.org/>. The majority of the fossil
1141 insect datasets are available from BugsCEP (<http://bugscep.com/>). The latest version of the
1142 BugsCEP Access database can be downloaded here: <http://bugscep.com/downloads.html>.
1143 All radiocarbon dates used for Paleodemographic reconstructions are available within
1144 University College London's Discovery database (discovery.ucl.ac.uk/10025178/:
1145 <https://doi.org/10.14324/000.ds.10025178>). For a full set of sources and acknowledgements
1146 for the radiocarbon data see Bevan et al. (2017). Archaeobotanical datasets are stored within
1147 ArboDat (<https://nihk.de/en/research/current-projects/arbodat-ape>) and are available via the
1148 ABCD (<https://www.intarch.ac.uk/journal/issue1/tomlinson/toc.html>).