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

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

3  
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## 44 **Highlights**

45

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

51

52

## 53 **Abstract**

54

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

76

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

78

79

## 80 **1. Introduction**

81

### 82 ***1.1 Long-term records of diversity change***

83

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

87 protect and restore biodiversity have not been reached globally (Nature, 2020). Much  
88 conservation decision making is based on recent understanding only, and restoration studies  
89 often only look at single years or aim to maintain existing patterns (Wilson, 2021).  
90 Agricultural systems have played a key role in biodiversity change in past (Birks et al.,  
91 2016a) and modern systems (Dudley & Alexander, 2017; Outhwaite et al., 2022). Long-term  
92 (paleo) environmental records provide insights into the multi-millennial scale patterns and  
93 processes that lead to diversity change (Hjelle et al., 2012), for example, fossil pollen datasets  
94 can be used as a proxy for land cover and vegetation diversity change, and fossil insect  
95 (beetle) records reflect disturbances and human activity. Archaeological records of land use  
96 (archaeobotany) and population change (archaeodemography) allow exploration of factors  
97 that influence these trends. Such datasets can be analysed alongside modern landscape data  
98 allowing long-term patterns to be viewed within the context of contemporary agricultural  
99 suitability.

100

101 The role of historic environmental change in shaping current diversity patterns has been  
102 demonstrated (Gaston, 2000; Birks et al., 2016a; 2016b) with a focus on placing trends  
103 identified in recent decades-centuries into the context of the longer-term past. Temperate  
104 European vegetation trends have previously been described as characterised by declining  
105 biodiversity during initial forest development in the early Holocene (11700-8000 cal. BP)  
106 (cal. BP: calibrated years Before Present, where present = AD 1950), stable levels of  
107 diversity during periods dominated by closed mixed forest in the mid-Holocene (8000-6000  
108 cal. BP), increasing biodiversity on fertile soils with the emergence of agricultural land use  
109 from 6000-4000 cal. BP, and declining biodiversity in the most recent 200 years (Birks et al.,  
110 2016a). Subsequent research has identified similar trends for pollen sites across Britain  
111 within the context of regional variability and has revealed that a recent decline in biodiversity  
112 is not always detectable in fossil pollen datasets (Woodbridge et al., 2021). Novel plant  
113 communities represent new combinations of taxa with no previous analogue and result from  
114 the arrival or introduction of new species often representing human-driven changes, such as  
115 altered land use, or climate change, and may be reflected by increasing 'Rate of Change' in  
116 assemblage composition (Finsinger et al., 2017).

117

118 Spatial and temporal patterns of changing diversity derived from fossil pollen datasets have  
119 been used to infer past biodiversity trends for various regions from temperate and northern  
120 Europe to the Neotropics (Odgaard, 1994; Weng et al., 2006; Colombaroli et al., 2013; Felde  
121 et al., 2016; Matthias et al., 2015; Reitalu et al., 2015; 2019; Kuneš et al., 2019; Roleček et  
122 al., 2021). Similar challenges in elucidating the relationships between pollen diversity and  
123 vegetation diversity have been described (Weng et al., 2007; Gosling et al., 2009) due to the  
124 impacts of differential pollen dispersal and productivity, the effects of landscape openness  
125 and changing pollen concentration on taxa representation in datasets, and the coarser  
126 taxonomic resolution of fossil pollen data compared to plant taxonomy (Odgaard et al., 1999;  
127 Weng et al., 2006; van der Knaap, 2009; Goring et al., 2013; Pardoe, 2021). Despite these  
128 challenges, new methodological developments and suitable analytical approaches are  
129 improving understanding of biodiversity change based on fossil pollen data (Roleček et al.,  
130 2021). Previous research has paved the way for palynology to go beyond describing patterns

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

137

138 Fossil insect datasets are used to investigate the impacts of changing land use or vegetation  
139 cover and are informative about the spread and intensity of human settlement (Kenward,  
140 1997; Smith, 2012; Smith et al., 2010, 2019, 2020). In a recent analysis of fossil insect  
141 datasets from across Europe, Pilotto et al. (2022) suggest that the expansion of agriculture  
142 6,000 years ago had as dramatic an impact on insect communities as rising temperatures in  
143 the early Holocene. Smith et al. (2020) describe the increased scale of agriculture during the  
144 late Bronze Age / early Iron Age (3100-2700 cal. BP; 1150-750 cal. BC) of the British Isles  
145 as having a similar drastic effect on insect faunas. Insects include many different groups with  
146 dissimilar responses to environmental changes. Within this research the Coleoptera (beetle)  
147 insect group is analysed, and datasets are referred to as “insect” records. Exploration of  
148 changing insect diversity in response to land-use and land-cover change in the past currently  
149 represents a knowledge gap in paleoenvironmental research.

150

### 151 ***1.2 Diversity-disturbance relationships and ecological novelty***

152

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

171

### 172 ***1.3 Past land-use, population shifts, and climate change***

173

174 Archaeobotanical records (plant remains preserved at archaeological sites) provide a wealth  
 175 of information about past subsistence and land-use strategies (de Vareilles et al., 2021). The  
 176 main factors that affect the recovery of archaeobotanical evidence are preservation  
 177 conditions, variations in sampling practices, and the nature and scale of past arable  
 178 agriculture (van der Veen et al., 2007; Fuller and Stevens, 2012; van der Veen, 2014; Bishop,  
 179 2015; Carruthers and Hunter Dowse, 2019). Changes in crops, intensity and scale of  
 180 production, arable equipment, catchment and population size and structure, will have  
 181 profoundly altered the character of arable landscapes. Increased scale of arable production is  
 182 indicated in archaeobotanical records by higher densities of bulk finds of charred plant  
 183 remains (van der Veen, 2014) as well as features and structures associated with crop storage  
 184 and processing. Significant arable innovations from the introduction of farming at the start of  
 185 the Neolithic (~4000 BC) (~6000 cal. BP) to the Agricultural Revolution of the 18<sup>th</sup> century  
 186 AD are shown in Table 1. Knowledge of past land-use strategies, including the intensity (i.e.  
 187 input, such as labour or manure, per unit of soil) and extent of agriculture, allows  
 188 understanding of how these processes influence plant and insect diversity and the role of  
 189 people in shaping biodiversity trends over historic timescales.

190  
 191 Archaeological datasets are also used to infer demographic change (Bevan et al., 2017) based  
 192 on the assumption that the density of radiocarbon-dated sites relates to human population size  
 193 (Shennan et al., 2013). Demographic trends may influence land requirements to support  
 194 changing populations and thus affect landscape change. The impacts of land-use changes are  
 195 also constrained by the climatic tolerances and optima of plant and insect species.  
 196 Paleoclimate datasets reflecting North Atlantic climatic conditions are summarised in  
 197 Woodbridge et al. (2021) where significant relationships were identified between  
 198 palaeoclimate datasets, population change and pollen diversity trends.

199  
 200 **Table 1** Summary of key agricultural developments in Britain affecting changes in scale and  
 201 intensity of land-use. \*follows Historic England’s Period List, FISH terminology (Historic  
 202 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 (7 <sup>th</sup> ), 9 <sup>th</sup> – 11 <sup>th</sup> 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	

203

204

#### 205 ***1.4 Investigating patterns of diversity and ecological novelty***

206

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

213

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

218

## 219 **2. Methods**

220

### 221 ***2.1 Data assimilation and harmonisation***

222

223 297 radiocarbon-dated fossil pollen datasets have been amalgamated from across Britain (Fig.  
 224 1 and Supplementary Information 1). BPOL database (an extensive archive of British fossil  
 225 pollen site information) (Grant et al., 2017) was used to identify datasets and provided  
 226 information about radiocarbon-dating quality. The pollen datasets partly derive from the  
 227 European Pollen Database (Leydet et al., 2007-2023) and were gathered within the  
 228 LandClimI project (Fyfe et al., 2013; Trondman et al., 2015). Additional datasets were  
 229 provided by data contributors and a small number of datasets have been digitised using  
 230 Straditize software (Sommer, 2019). Pollen records from individual coring sites have been  
 231 taxonomically harmonised using the European Pollen Database nomenclature (Leydet et al.,  
 232 2007-2023) and summed into 200-year time windows for analysis. Total land pollen counts  
 233 for each taxon were summed and percentages calculated as a proportion of the pollen grain  
 234 count for the time window. The approach follows Fyfe et al. (2015), Roberts et al. (2018) and

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

245

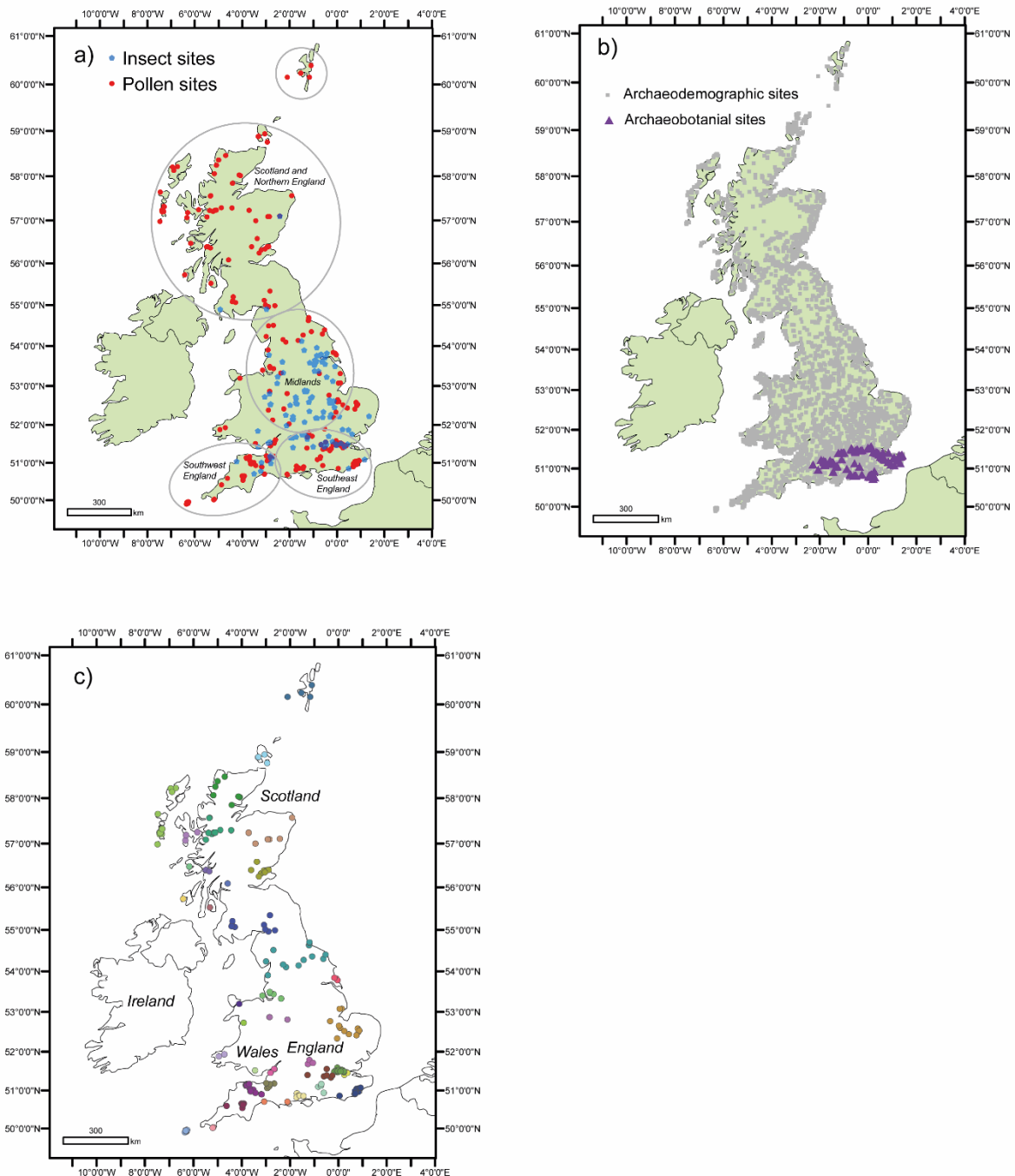
246 The pollen datasets have been transformed into quantified land cover using the REVEALS  
247 (Regional Estimates of Vegetation Abundance from Large Sites) approach (Sugita, 2007;  
248 Fyfe et al., 2013; Marquer et al., 2014). Selection criteria were applied to identify pollen sites  
249 suitable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

267

268 572 fossil insect (beetle) assemblages from 117 different sites (Fig. 1) extending back to the  
269 Late Glacial period (10,050 BC) (~12,000 cal. BP) have been combined. This includes data  
270 from the BugsCEP database (Buckland & Buckland, 2006) and datasets amalgamated by  
271 Smith et al. (2010, 2019, 2020). Many of these datasets derive from archaeological sites, so  
272 species assemblages may reflect fauna around domestic dwellings or human-made structures.  
273 The datasets have been taxonomically harmonised, aggregated by archaeological period and  
274 converted to percentages. Insect data are dated by archaeological period according to the site  
275 context and the taxon harmonisation process followed the BugsCEP database taxonomy. The  
276 pollen sites have a largely uniform distribution across Britain with gaps in the midlands,  
277 while the insect datasets are largely located in the south and midlands. An  
278 archaeodemographic dataset (Bevan et al., 2017) based on the summed probability



279 distributions (SPD) of radiocarbon-dated archaeological sites from across Britain is used as a  
 280 record of population change. Pollen samples from each 200-year time window were assigned  
 281 a corresponding archaeological period to match the phases assigned to each archaeobotanical  
 282 and insect sample according to site context to allow comparison between datasets.  
 283  
 284



285  
 286  
 287 **Figure 1.** Site locations: a) fossil insect (blue pentagons) and pollen (red circles) datasets  
 288 covering the Holocene (grey circles represent areas for regional analyses), b)  
 289 archaeobotanical sites (purple triangles), radiocarbon-dated archaeological sites (grey

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

292

293 Modern landscape data have been extracted from within a 10 km radius around pollen sites  
294 that have a sample in the most recent time window (AD 1750 - present) (200 to -70 cal. BP).  
295 The 10 km distance was selected following previous work comparing modern pollen with  
296 remote sensed vegetation maps (Woodbridge et al., 2014b), to reflect the average pollen  
297 source area of sites, and to capture both local and regional landscape characteristics.

298 Topographic data were obtained from a 1 km resolution dataset using an elevation model for  
299 the UK. Agricultural suitability derives from a 100 m resolution dataset obtained from the  
300 Macaulay Land Use Research Institute (1991) for which data across England, Scotland and  
301 Wales were combined. Agricultural suitability values represent the percentage of land area  
302 within 10 km of a pollen site in agricultural suitability classes 1-3 (i.e. land capable of  
303 producing 1: a very wide range of crops, 2: a wide range of crops, and 3: a moderate range of  
304 crops). The relationship between pollen sample analogues and modern landscape data  
305 (topographic roughness, elevation and agricultural suitability) is presented in a ternary plot  
306 using the Ternary R package (Smith, 2017), which graphically presents the ratios between  
307 three variables as positions within a triangle. Each pollen sample is plotted according to the  
308 modern landscape characteristics at the coring site and colour coded by analogue matching.  
309 Only sites that have pollen samples in the most recent time window (200 BP - present) were  
310 included in the analogue matching exercise for comparison with all 297 pollen sequences.

311

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

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

339

## 340 **2.2 Data analysis**

341

342 Disturbance is caused by numerous factors associated with natural and human induced  
343 environmental changes. Population change reflects land requirements for agriculture,  
344 however, archaeodemographic trends are not likely to be linearly related to disturbance,  
345 therefore a pastoral/human activity pollen index is used as an indicator of changing  
346 disturbance levels. The index is a sum of untransformed pollen percentage data, which  
347 includes Asteraceae subfamily Asteroideae, Asteraceae subfamily Lactucoideae, Cynareae,  
348 Rubiaceae, Ranunculaceae, *Potentilla*, *Plantago lanceolata*, *Plantago major*, *Plantago*  
349 *media*, Chenopodiaceae, *Rumex*, *Urtica* and Cerealia. The inclusion of certain taxa within the  
350 index has been informed by previous work involving pastoral/human activity pollen indices  
351 (Behre, 1986; Berglund, 1991, Mazier et al., 2006; 2009; Fyfe et al. 2010; Araujo et al.,  
352 2020). Pollen indices of human activity should be interpreted with recognition that taxa may  
353 also occur naturally as well as associated with anthropogenic activity.

354

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

369

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

378 have been determined using the ‘analog’ package with R (Simpson & Oksanen, 2021).  
379 Analogue groups are defined according to whether the most recent pollen assemblage (200  
380 cal. BP - present) has a close analogue in the last 1000 years, a close analogue older than  
381 1000 years, or no close analogue through the entire record. Insect samples assigned ‘modern’  
382 were deemed unsuitable for comparison with insect datasets from earlier archaeological  
383 periods using the analogue-matching approach, as the collection methods for modern samples  
384 differ from methods applied to paleoenvironmental insect samples leading to certain taxa  
385 groups being over-represented.

386

### 387 **3. Results**

388

#### 389 *3.1 Diversity and disturbance trends across Britain*

390

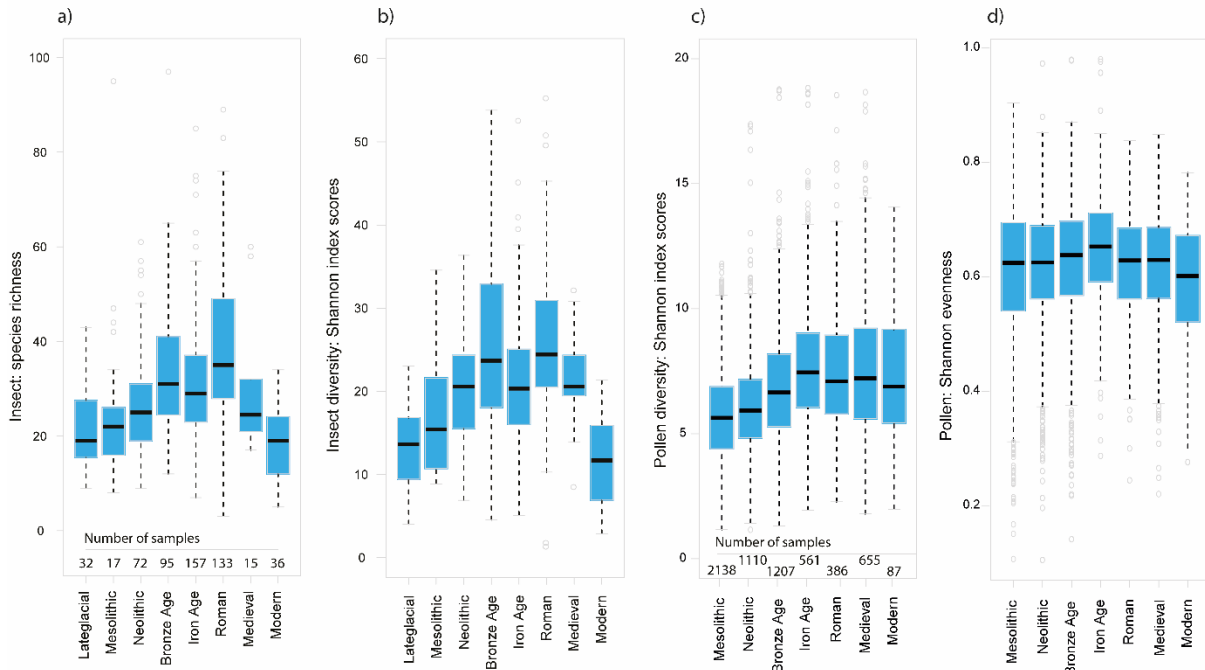
391 When amalgamated for all sites across Britain (Fig. 1), diversity scores derived from the  
392 insect and pollen datasets reveal similarities from the Mesolithic (7050 BC) (~9000 cal. BP)  
393 to the Bronze Age and distinctive patterns in more recent parts of the records (Fig. 2). The  
394 insect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

412

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

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

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

435

436 **Table 2** Kruskal-Wallis test *p*-values for Shannon diversity change between archaeological  
 437 time periods: a) fossil pollen datasets, b) fossil insect datasets, c) Spearman’s Rank (*r*-value)  
 438 correlations between pollen diversity (Shannon index) and evenness and land use inferred  
 439 from archaeobotanical assemblages, and d) Spearman’s Rank (*r*-value) correlations between  
 440 pollen diversity and evenness and insect diversity (Hill Numbers). Shaded cells indicate  
 441 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

442

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

443

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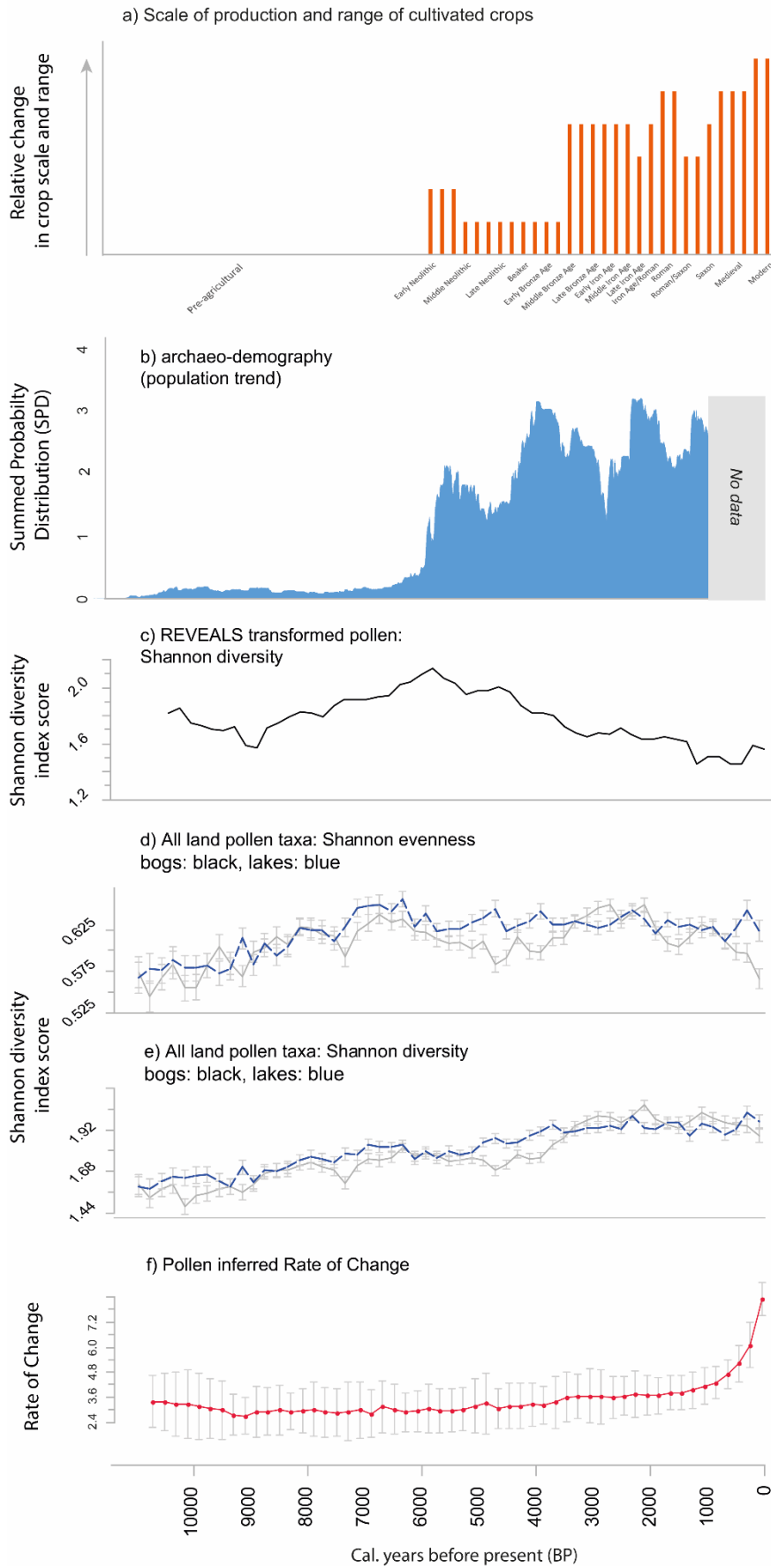
d) Insect and pollen diversity	Insects H1	Insects H0	Insects H2
Pollen: Shannon diversity index	0.310	0.238	0.333
Pollen: Shannon evenness	0.762	0.738	0.833

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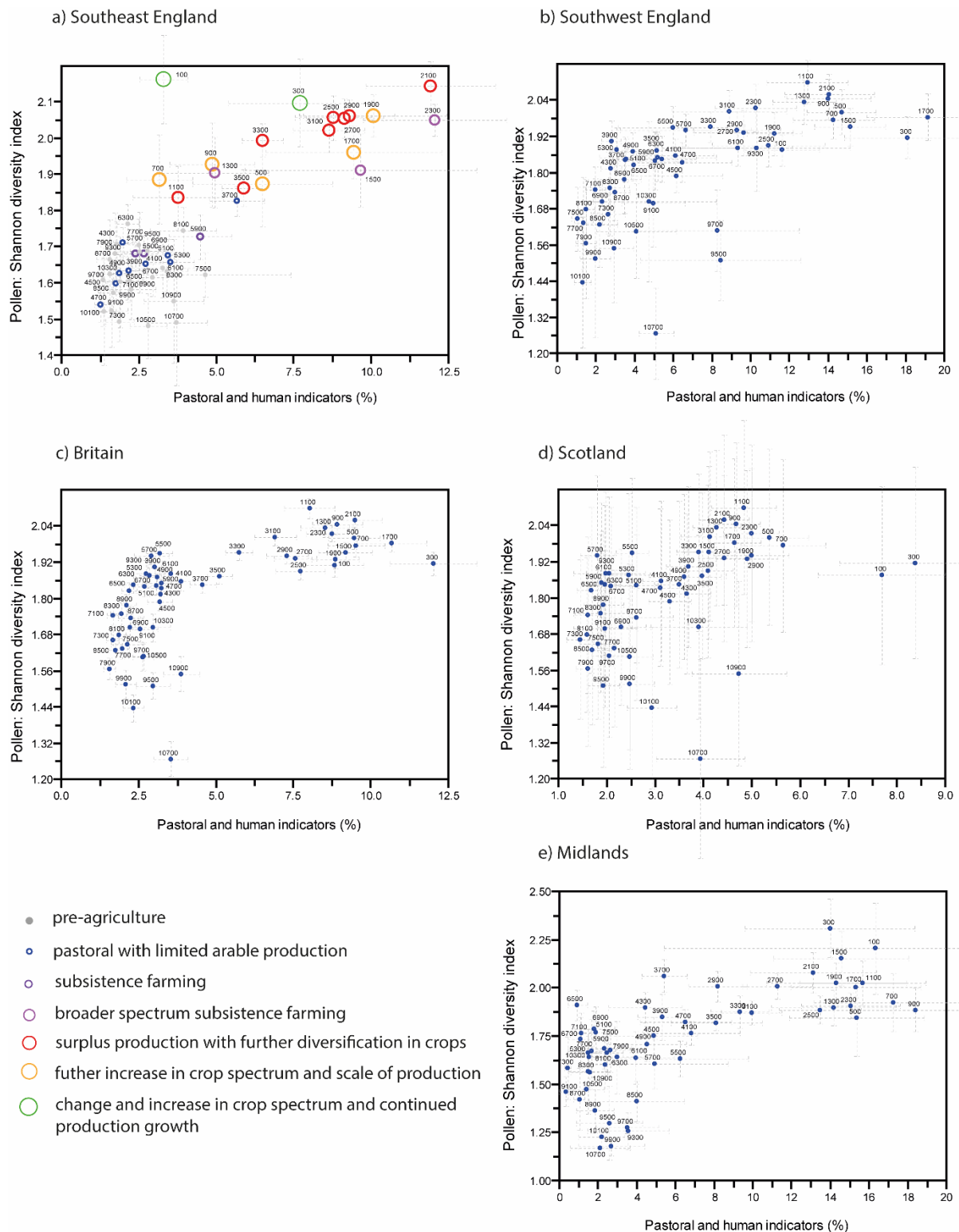


450 **Figure 3.** a) land-use change based on crop spectrum and scale of agriculture using a  
451 conceptual interpretive scale (de Vareilles et al., in review), b) summed probability  
452 distribution (SPD) of radiocarbon-dated archaeological sites from across Britain  
453 (archaeodemographic trend),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

459

460 The average pollen diversity scores and average pastoral/human activity pollen index,  
461 reflecting land conversion for agriculture, is presented in Fig. 4 for different regions. The  
462 dates represent the mid-point of each 200-year time window (e.g. 300 BP on the plot  
463 represents the period 400-200 BP). The time periods spanning 2000-1000 cal. BP (950 BC -  
464 AD 50) have highest pastoral/human activity index values and diversity, while earlier  
465 prehistoric periods are characterised by lower diversity scores, reflecting the low impact on  
466 vegetation cover that small-scale, and perhaps irregular (Stevens and Fuller, 2012),  
467 agricultural practices would have had. Pollen diversity declines in the 300 and 100 cal. BP  
468 (400 cal. BP - present) time windows (Fig. 4) in Scotland, southwest England and for all  
469 British sites while the pastoral/human activity index increases. This pattern is shown for all  
470 regions other than southeast England and the midlands where 100 cal. BP (200 cal. BP -  
471 present) represents a period with higher diversity. Land-use scale and spectrum (i.e. range of  
472 crops) shown on the southeast England plot inferred from archaeobotanical records illustrates  
473 the increasing intensity of agriculture with highest pollen diversity scores during the Iron Age  
474 to Roman transition (~2100 cal. BP) (150 BC) and the late Saxon period (~900 cal. BP) (AD  
475 1050). The impacts of land-use change are illustrated in Fig. 6, which shows that pollen  
476 diversity index scores are statistically significantly related to changing land-use practices  
477 evidenced in archaeobotanical remains (Table 2c). Pollen diversity is positively related to  
478 crop and cereal plant types, particularly during the early Iron Age, Late Bronze Age and  
479 Roman period, and negatively related to plant types associated with gathering.



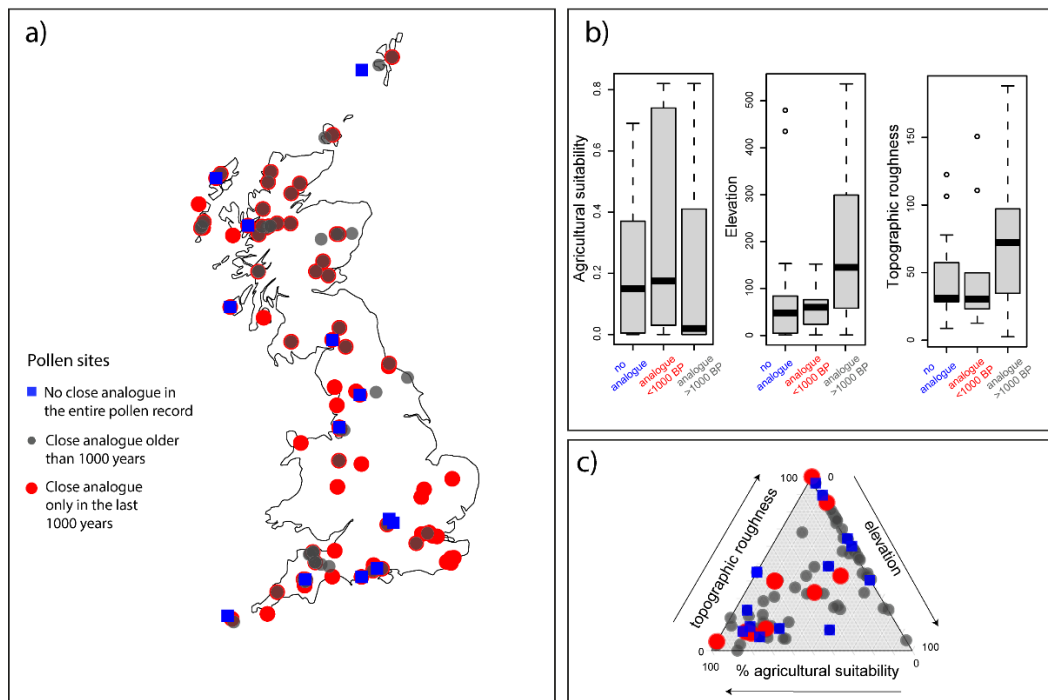


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**Figure 4.** Pastoral/human activity pollen index plotted against Shannon diversity index (pollen derived). Dates in cal. BP (cal. year Before Present) represent the mid-point of a 200-year time window (e.g. 300 represents 400-200 cal. BP). The sub-regional 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.

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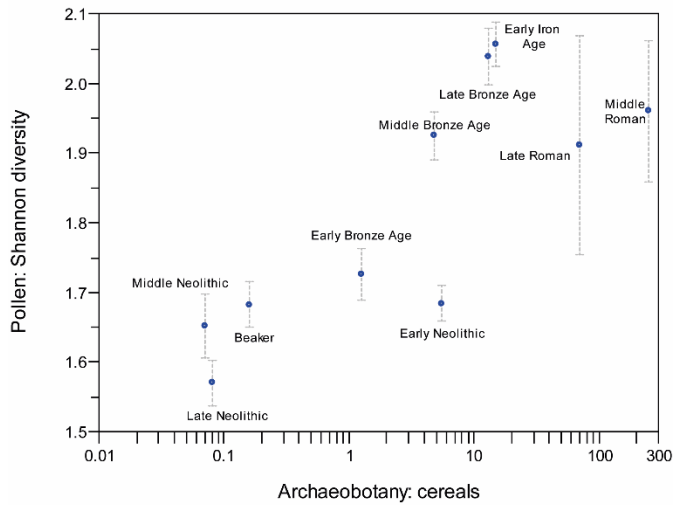
The spatial distribution of pollen sites in the most recent period (200 cal. BP - present) with matching analogues (i.e. similar species assemblages) in the last 1000 years and the rest of the Holocene (11,700 - 1000 cal. BP) is shown in Fig. 5 in relation to modern landscape data. Sites with a close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



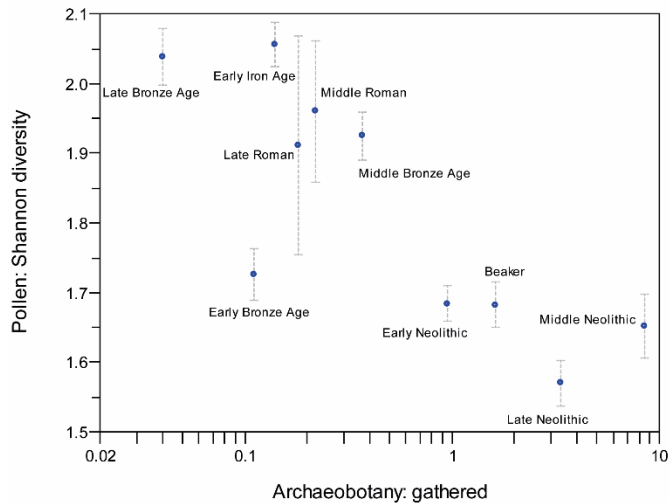
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**Figure 5** a) Pollen analogue matching between the most recent time period (200 cal. BP - present) and 200-year time windows spanning the Holocene (11700 - 200 cal. BP), b) box plots illustrating the spread of agricultural suitability, elevation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



511

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

515

516

517 **4. Discussion**

518

519 **4.1 Pollen and insect diversity and disturbance from arable land use**

520

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

528 associated with agricultural activity and the presence of grazing animals are known to have  
529 become more abundant during the Bronze Age as a result of land-use changes associated with  
530 agriculture, particularly the emergence of spatially extensive field systems and the niches that  
531 emerged around these, which includes, for example, ditches and hedgerows (Smith et al.,  
532 2019). Periods of increasing insect diversity are reflected by the creation of early  
533 ‘fieldscapes’ and anthropogenic heathlands (Løvschal, 2021) with large-scale grazing  
534 regimes since ~4000 cal. BP (~2050 BC), which were sustained by disturbance, with  
535 landscape longevity and resilience varying spatially. The increase in insect diversity from the  
536 Mesolithic to the Neolithic and Bronze Age may reflect opening of woodland and  
537 diversification of habitats.

538

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

555

556 Previous analysis of fossil insect datasets has revealed significant assemblage change in  
557 lowland Britain resulting from the creation of middle Bronze Age and Iron Age field systems  
558 with stenotopic woodland species replaced by eurytopic open and disturbed ground types  
559 along with species that are associated with the dung of domestic grazing animals (Smith et  
560 al., 2019; 2020). The decline in insect diversity identified during the Iron Age may reflect a  
561 reduced range of habitats with a shift towards taxa typical of open disturbed ground and  
562 animal dung. Increased settlement and agricultural waste, and the introduction of new insect  
563 species into Britain, such as grain pests, also contributed to assemblage change (Smith et al.,  
564 2020). The Mesolithic woodland insect faunas include a large number of species represented  
565 by low numbers of individuals whereas agricultural faunas are represented by a large number  
566 of individuals from a smaller selection of species. The increased scale of cultivation and the  
567 development of other land-use activities evident during the Roman period (Table 2) would  
568 have led to the creation of new habitats and a higher level of human-induced disturbance.  
569 Highest pollen diversity scores are seen in the Iron Age and highest insect diversity values  
570 are identified in the Roman period. The slight decrease in pollen diversity scores during the  
571 late Roman period may represent the first time in British farming history when land-use

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

580

581 Shifts in insect diversity appear more pronounced than shifts in pollen diversity when data are  
582 amalgamated at a broad spatial scale. However, differences in how pollen and insect data  
583 sense the landscape, how these indicators respond to land use, and the spatial and temporal  
584 differences in the distribution of sites, will have affected the patterns observed. The pollen  
585 data cover a larger geographical area and include a greater number of sites while the insect  
586 data largely cover southern England and the midlands. Regional dissimilarities have been  
587 documented previously, for example, pollen evidence suggests that some regions of former  
588 Roman Britain (e.g. northern England) experienced an episode of land abandonment  
589 (evidenced as woodland regeneration) in the immediate post-Roman period, following an  
590 expansion of open land in the late Iron Age/early Roman period (Dark, 2000). Other types of  
591 disturbances, such as climatic change or disease (Flynn and Mitchell, 2019; Halsch et al.,  
592 2021), affect plant and insect diversity in different ways, and may explain the different trends  
593 identified in the most recent part of the records. When considering recognised Holocene  
594 climatic events (Vinther et al., 2009), there are no clearly identifiable episodes reflected in  
595 the pollen and insect diversity trends. However, statistically significant relationships have  
596 previously been identified between paleoclimate records reflecting North Atlantic conditions  
597 and pollen diversity trends (Woodbridge et al., 2021) demonstrating that diversity patterns are  
598 constrained by species climatic optima within the context of changing land use.

599

#### 600 *4.2 Identifying patterns of diversity change*

601

602 Previous research has shown that Rate of Change (i.e. the degree of difference between  
603 adjacent samples over a known period of time) in pollen assemblages increased through the  
604 Holocene in other European regions (Finsinger et al., 2017) and on a global scale (Mottl et al.  
605 2021b). These broad patterns are reflected within results from analysis of the British pollen  
606 datasets in this study, which includes an increase in Rate of Change following the Last  
607 Glacial Maximum transition and a more pronounced increase during the late Holocene. Rate  
608 of Change analysis allows both periods of perturbation, but also of stability, to be identified.  
609 The longest periods of stability (Fig. 3) occurred during the most forested period (~8000 -  
610 6000 cal. BP) and during periods of lower land-use intensity from ~9000 - 1000 cal. BP  
611 (~7050 - 950 AD) (Fig. 3). The insect and pollen datasets show similarities in terms of  
612 diversity trends, but the timing of episodes of stability differ. There is a clearer late Holocene  
613 decline in diversity in the insect datasets, which may reflect differences in the response to  
614 land-use change or disparities associated with sampling locations and the lower number of  
615 insect sites in this period. Although the pollen datasets do not show a clear decline in

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

624

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

652

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

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

663

### 664 *4.3 The emergence of ecological novelty*

665

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

692

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

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

708

#### 709 ***4.4 Long-term ecology and conservation***

710

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

731

#### 732 **5. Conclusions**

733

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



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

754

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

770

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

773

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775

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785

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1182  
 1183 **Author contributions**

1184

1185 JW, RF, RP, DS and AdV were central to the conception and design, acquisition of data,  
1186 analysis and interpretation of the data. JW drafted the manuscript and RF, RP, DS and AdV  
1187 revised the content critically contributing intellectual content. MG, RB, RS, JG, PD, DD, GG,  
1188 AP, TH, ES, MS, FC, CB and MW contributed pollen data for analysis and commented on  
1189 the manuscript providing critical feedback. All authors gave final approval of the version to  
1190 be published.

1191

### 1192 **Data availability statement**

1193

1194 The results of the analyses carried out are archived within the open access PANGAEA  
1195 database. Many of the original pollen datasets used in this study are available from the  
1196 European Pollen Database (EPD; [www.europeanpollendatabase.net/](http://www.europeanpollendatabase.net/)) and can be accessed  
1197 here: <http://www.europeanpollendatabase.net/fpd-epd/bibli.do> (please see Supplementary  
1198 Information for site names, author names and references). The EPD is also available as an  
1199 Access database, which can be downloaded  
1200 here: <http://www.europeanpollendatabase.net/data/downloads/> and the same datasets are  
1201 available via the Neotoma Database: <https://www.neotomadb.org/>. The majority of the fossil  
1202 insect datasets are available from BugsCEP (<http://bugscep.com/>). The latest version of the  
1203 BugsCEP Access database can be downloaded here: <http://bugsc ep.com/downloads.html>.  
1204 All radiocarbon dates used for Paleodemographic reconstructions are available within  
1205 University College London's Discovery database ([discovery.ucl.ac.uk/10025178/](http://discovery.ucl.ac.uk/10025178/):  
1206 <https://doi.org/10.14324/000.ds.10025178>). For a full set of sources and acknowledgements  
1207 for the radiocarbon data see Bevan et al. (2017). Archaeobotanical datasets are stored within  
1208 ArboDat (<https://nihk.de/en/research/current-projects/arbodat-ape>) and are available via the  
1209 ABCD (<https://www.intarch.ac.uk/journal/issue1/tomlinson/toc.html>).