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Woodbridge, J

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Highlights

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

Abstract

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

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

1. Introduction

1.1 Long-term records of diversity change

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

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

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

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

1.2 Diversity-disturbance relationships and ecological novelty

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

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

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 18th 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 (7th)9th – 11th century, affecting soil hydrology and field ecology; Open field systems; cultivation becomes more extensive; free-threshing wheat and rye widely cultivated. Temporary land abandonment in the immediate post-Roman period in some areas.	Hamerow et al. (2020); McKerracher (2018); Stevens and Fuller (2018); Dark (2000)
Medieval AD 1066 - 1540	Black Death (AD 1346-1352): 40-60% mortality – significant reduction in agricultural labour and abandonment of arable land/villages	Benedictow (2004)
From AD 1700	Industrial Revolution, mechanised farming and the use of pesticides; improved cereals	

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 ^{14}C dates that underpin the chronologies of the pollen
239 records, and for ^{14}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 ^{14}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

distributions (SPD) of radiocarbon-dated archaeological sites from across Britain is used as a record of population change. Pollen samples from each 200-year time window were assigned a corresponding archaeological period to match the phases assigned to each archaeobotanical and insect sample according to site context to allow comparison between datasets.
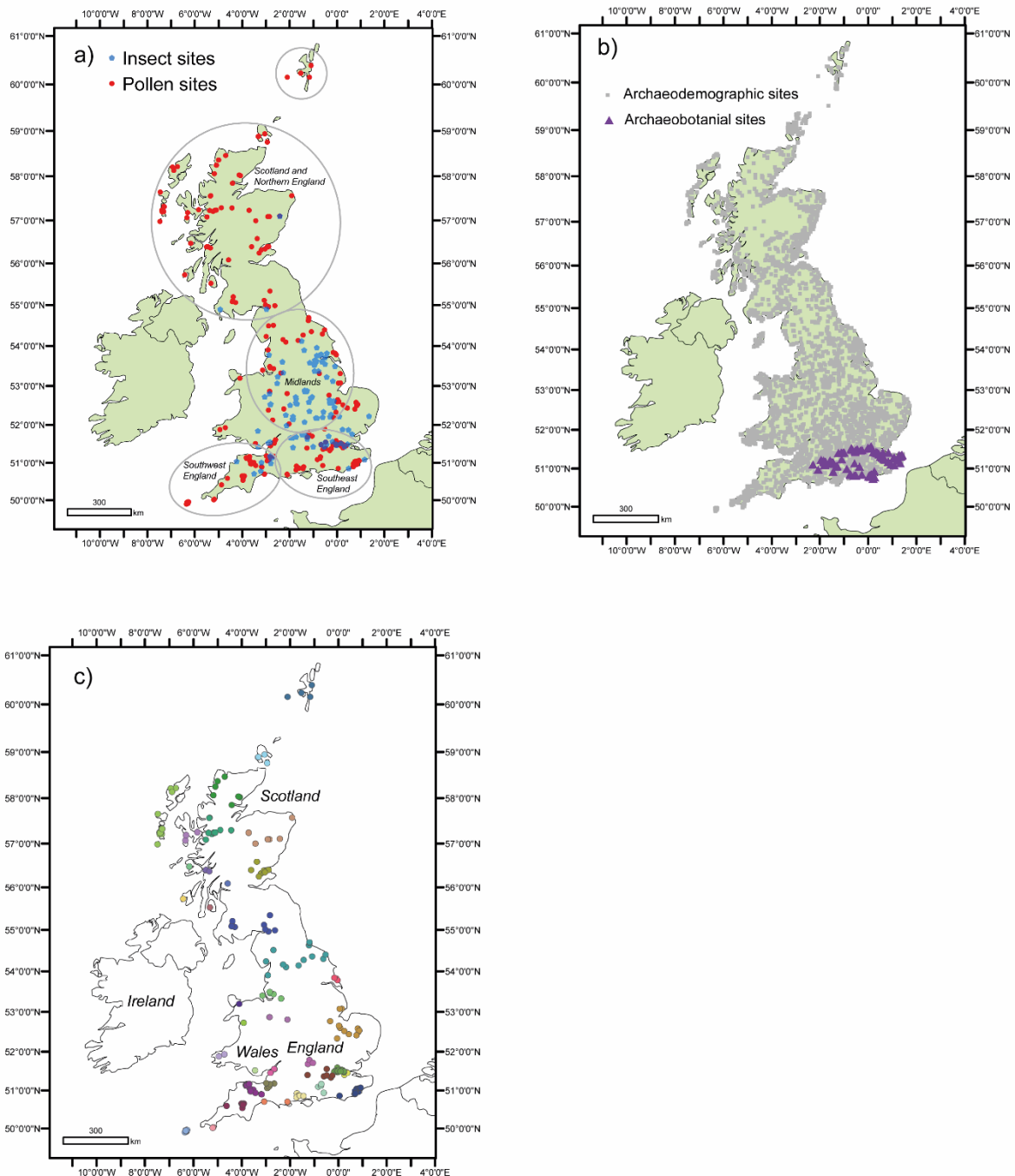
Figure 1. Site locations: a) fossil insect (blue pentagons) and pollen (red circles) datasets covering the Holocene (grey circles represent areas for regional analyses), b) archaeobotanical sites (purple triangles), radiocarbon-dated archaeological sites (grey

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}C) dates for
336   Britain (Bevan et al., 2017). The package 'rcarbon' was used to produce an SPD curve from
337   the ^{14}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

trends after separating lake and peatland site types based on all 153 pollen taxa shows similar
patterns with only minor differences, which are most notably in pollen sample evenness in
the most recent period (Fig. 3).
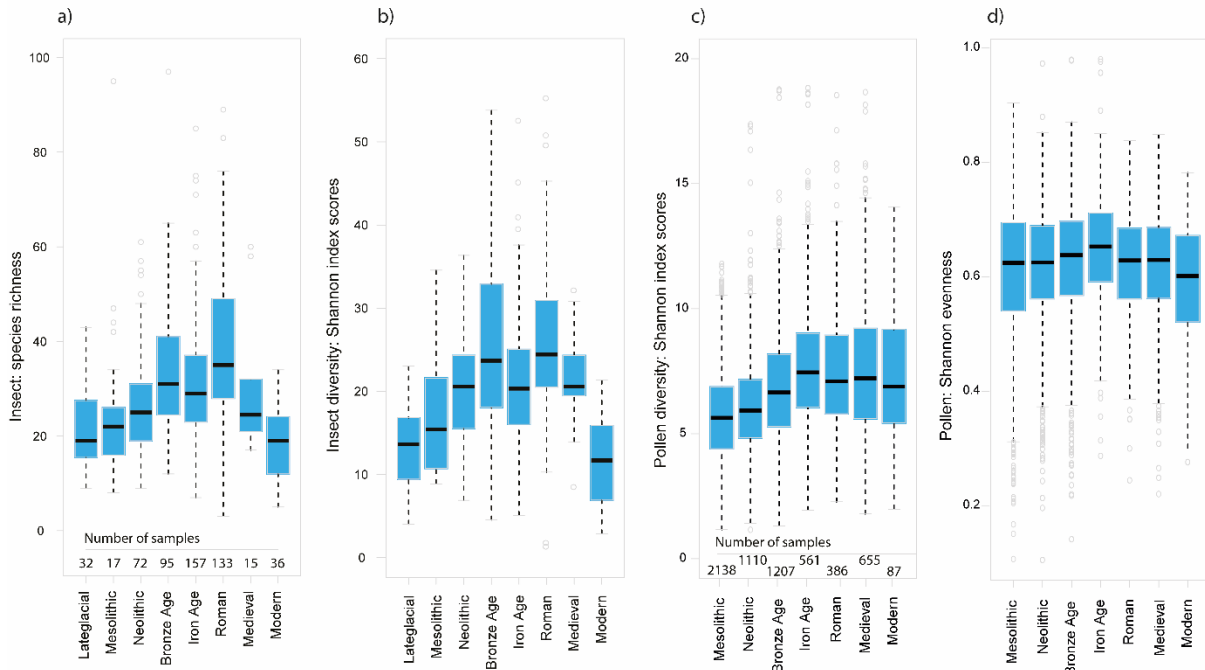
Figure 2. Insect and pollen diversity change through archaeological periods: a) insect species
richness, b) insect Shannon diversity index, c) pollen Shannon diversity index and d) pollen
Shannon evenness. Box plots show the mean values (black horizontal lines), first and third
quartile (blue bars), and "whiskers" show the data range after filtering outliers (circles).
'Modern' in the pollen datasets represents 200 cal. BP - present. 'Number of samples' refers
to the number of individual samples within the archaeological period.

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

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

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

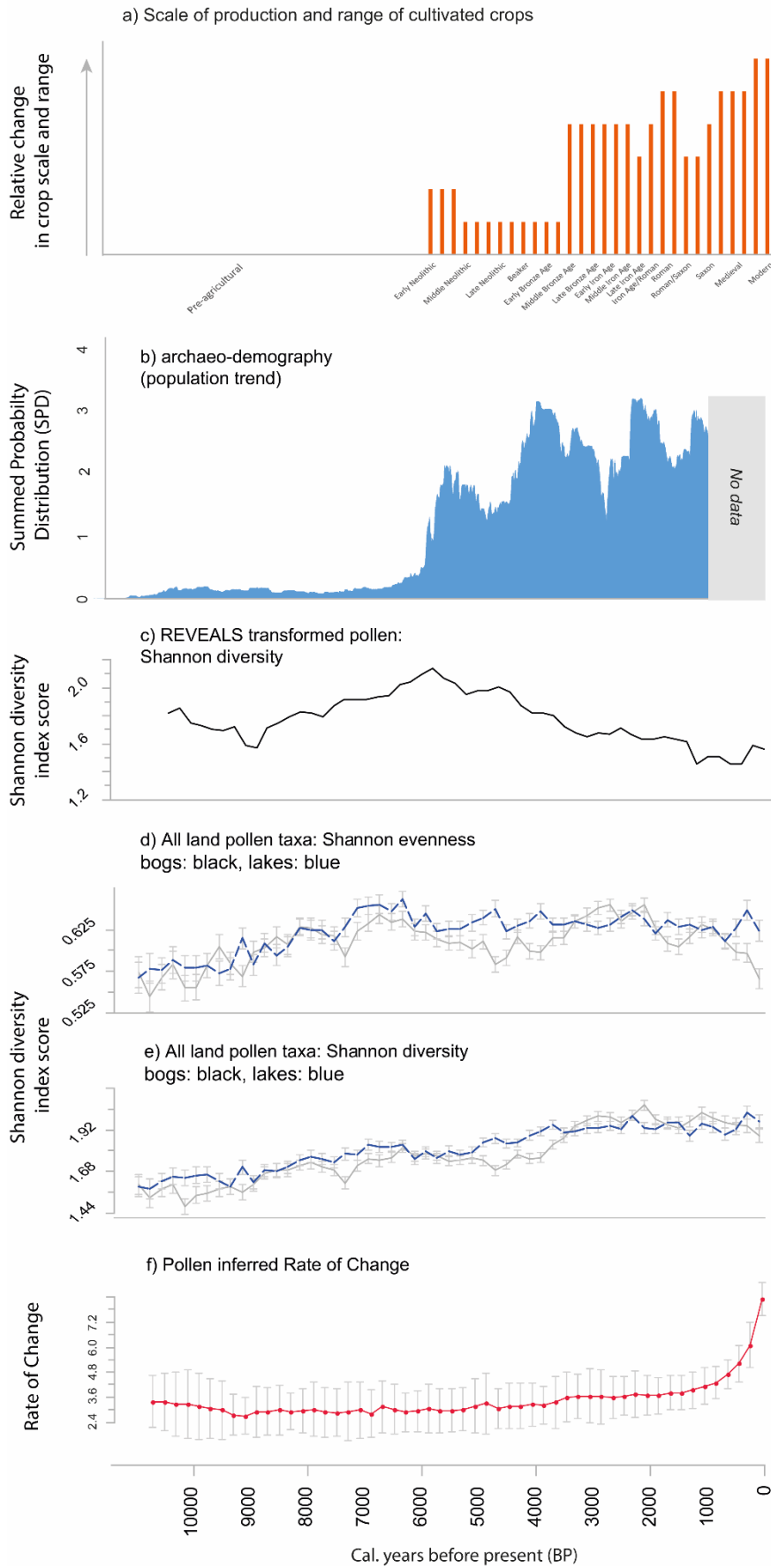| c) Land use and pollen diversity	Cereals	Gathered
Pollen: Shannon diversity index	0.806	-0.806
Pollen: Shannon evenness	0.721	-0.648

444

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

445

446

447

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a) Scale of production and range of cultivated crops

Relative change in crop scale and range

Pre-agricultural | Early Neolithic | Middle Neolithic | Late Neolithic | Beaker | Early Bronze Age | Middle Bronze Age | Late Bronze Age | Early Iron Age | Middle Iron Age | Late Iron Age | Iron Age/Roman | Roman | Roman/Saxon | Saxon | Medieval | Modern

b) archaeo-demography
(population trend)

Summed Probabilty Distribution (SPD)

No data

c) REVEALS transformed pollen:
Shannon diversity

Shannon diversity index score

d) All land pollen taxa: Shannon evenness
bogs: black, lakes: blue

Shannon diversity index score

e) All land pollen taxa: Shannon diversity
bogs: black, lakes: blue

f) Pollen inferred Rate of Change

Rate of Change

Cal. years before present (BP)

449

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

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

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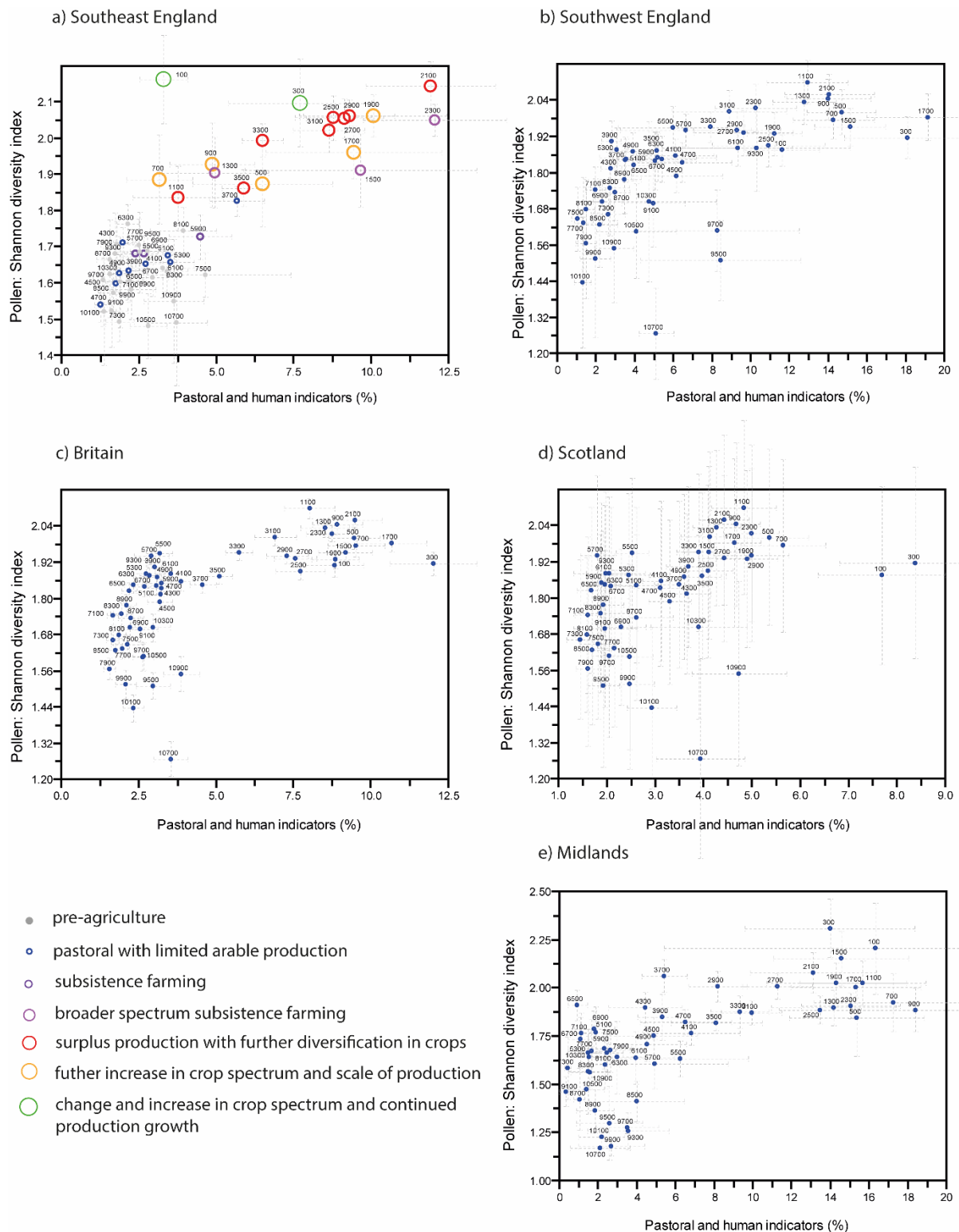
Figure 4. Pastoral/human activity pollen index plotted against Shannon diversity index (pollen derived). Dates in cal. BP (cal. year Before Present) represent the mid-point of a 200-year time window (e.g. 300 represents 400-200 cal. BP). The sub-regional divisions are shown on Fig. 1. The error bars 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.

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

500

501
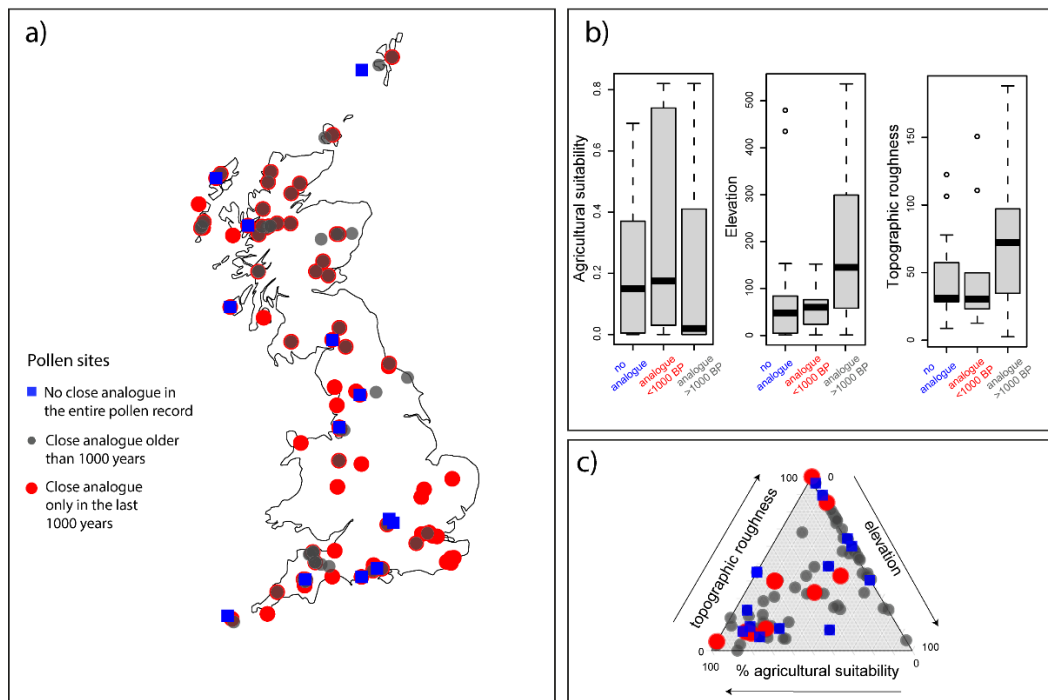
503 **Figure 5** a) Pollen analogue matching between the most recent time period (200 cal. BP -
504 present) and 200-year time windows spanning the Holocene (11700 - 200 cal. BP), b) box
505 plots illustrating the spread of agricultural suitability, elevation and topographic roughness
506 (derived from modern landscape data) across the pollen sites assigned to each analogue
507 matching group, and c) ternary plot illustrating the relationships between pollen assemblage
508 analogue matches and landscape characteristics.

509

510

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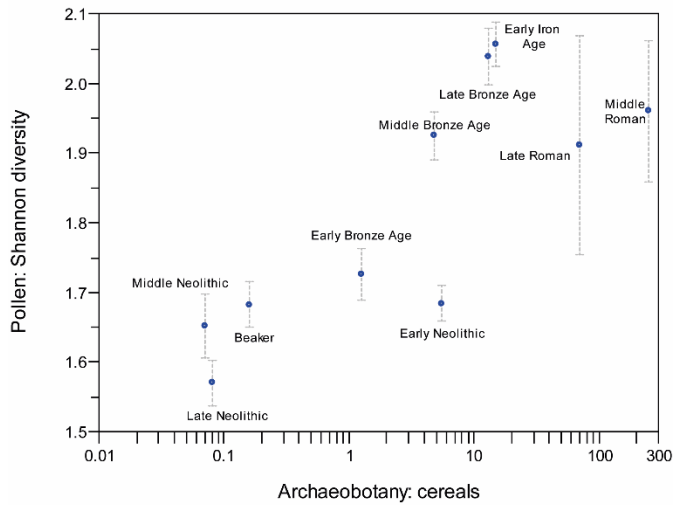
b) Pollen diversity and proportion of gathered plants
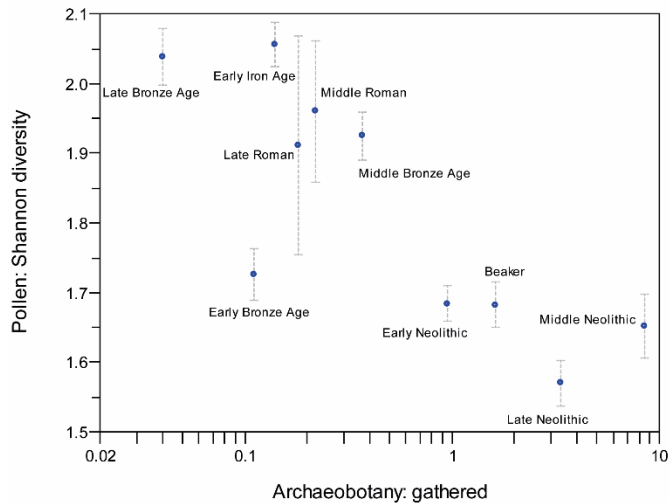
Figure 6 Pollen diversity (Shannon) index scores plotted against plant macrofossil data showing the density of: a) cereals, b) gathered plants (plotted on a logarithmic scale) within bulk archaeobotanical finds.

4. Discussion

4.1 Pollen and insect diversity and disturbance from arable land use

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

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

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

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

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

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

4.2 Identifying patterns of diversity change

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

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.

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 dissimilates 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.

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

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

4.4 Long-term ecology and conservation

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

5. Conclusions

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

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

Acknowledgements

775
785

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787
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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.

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1192 **Data availability statement**

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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/) 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/downl oads/ 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/downl oads.html.
1204 All radiocarbon dates used for Paleodemographic reconstructions are available within
1205 University College London's Discovery database (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).