

What drives biodiversity patterns? Using long-term multidisciplinary data to discern centennial-scale change

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Abstract

1. Biodiversity plays an important role in ecosystem functioning, habitat recovery following disturbance and resilience to global environmental change. Long-term ecological records can be used to explore biodiversity patterns and trends over centennial to multi-millennial time-scales across broad regions. Fossil pollen grains preserved in sediment over millennia reflect palynological richness and diversity, which relates to changes in landscape diversity. Other long-term environmental data, such as fossil insects, palaeoclimate and archaeologically inferred palaeodemographic (population) data, hold potential to address questions about the drivers and consequences of diversity change when combined with fossil pollen records.
2. This study tests a model of Holocene palynological diversity change through a synthesis of pollen and insect records from across the British Isles along with palaeodemographic trends and palaeoclimate records. We demonstrate relationships between human population change, insect faunal group turnover, palynological diversity and climate trends through the Holocene.
3. Notable increases in population at the start of the British Neolithic (~6,000 calendar years before present [BP]) and Bronze Age (~4,200 BP) coincided with the loss of forests, increased agricultural activity and changes in insect faunal groups to species associated with human land use. Pollen diversity and evenness increased, most notably since the Bronze Age, as landscapes became more open and heterogeneous. However, regionally distinctive patterns are also evident within the context of these broad-scale trends. Palynological diversity is correlated with population while diversity and population are correlated with some climate datasets during certain time periods (e.g. Greenland temperature in the mid-late Holocene).
4. *Synthesis.* This study has demonstrated that early human societies contributed to shaping palynological diversity patterns over millennia within the context of broader climatic influences upon vegetation. The connections between population and palynological diversity become increasingly significant in the later Holocene, implying intensifying impacts of human activity, which may override climatic effects. Patterns

of palynological diversity trends are regionally variable and do not always follow expected trajectories. To fully understand the long-term drivers of biodiversity change on regionally relevant ecological and management scales, future research needs to focus on amalgamating diverse data types, along with multi-community efforts to harmonise data across broad regions.

KEYWORDS

biodiversity, biogeography and macroecology, global change ecology, insects, land-cover change, landscape ecology, land-use change, palaeoecology and land-use history

1 | INTRODUCTION

1.1 | Current biodiversity patterns and potential of long-term environmental data

Biogeographers aim to understand the importance of different factors governing patterns of biodiversity and increasingly recognise the significance of historic dynamics in shaping current diversity patterns (Birks, Felde, & Seddon, 2016; Gaston, 2000). Understanding how climate and human land use shape diversity allows the processes of community assembly to be explored, which can feed into efforts to mitigate the effects of human-driven influences on global biodiversity (Rowan et al., 2019). Biodiversity patterns emerge as a combined result of speciation, extinction and migration, and play an important role in the stability of ecosystems and global climate (Symstad et al., 2003). Environments with higher levels of biodiversity are thought to recover faster following natural disasters, and experiments have demonstrated that biodiverse ecosystems are more productive (Fargione et al., 2007). Recent debate has questioned whether biodiversity patterns are shaped by local or continental-scale factors (Borregaard et al., 2020); global drivers include climate trends, latitudinal gradients, evolutionary processes and speciation while local disturbance factors include agricultural activity, erosion, grazing animals, changes in soil properties and water/nutrient availability. Human impact over the last 3,000 years has been an increasingly important disturbance factor at subcontinental scales, as illustrated in a recent survey of research community opinions (Stephens et al., 2019) and through studies based on empirical data (Roberts et al., 2018). Through analysis of spatially extensive fossil pollen datasets, Giesecke et al. (2019) demonstrated that past human impacts on the latitudinal diversity gradient in Europe had greater impacts on species richness than climate. Long-term multi-millennial scale environmental datasets have been underutilised in research aiming to understand recent biodiversity trends (Willis & Birks, 2006; Willis et al., 2005). Such datasets hold great potential to inform restoration ecology (Fordham et al., 2020; Higgs et al., 2014; Hobbs et al., 2014) through revealing ecological legacies and the influence of past human activities on current biodiversity patterns, which can be problematic to measure in relation to achieving conservation targets (Watts et al., 2020).

Spatial patterns in diversity derived from fossil pollen datasets (Colombaroli et al., 2013; Felde et al., 2016; Matthias et al., 2015; Reitalu et al., 2019) can reveal information about ecological memory, shifting baselines and dynamic equilibrium, that is, the patterns of change in species assemblages that have persisted or changed through millennia. Shifting baseline syndrome (Pauly, 1995; Soga & Gaston, 2018) represents the tendency of modern societies to believe that conditions in recent human memory provide an appropriate reference for a particular environment. Such historical baselines are largely a 'snapshot' of species assemblages that have developed over centuries and millennia of natural and human-induced disturbance. They rarely represent stable or natural 'baselines'. Consideration of the evolutionary and ecological legacies of both the recent and ancient past is key to understanding the forces shaping global patterns of present-day biodiversity (Rowan et al., 2019). This challenges the concept of stable baselines, demonstrating that communities can reassemble through millennia (Edwards et al., 2017). Divišek et al. (2020) incorporated historical processes in modelling current species richness using Holocene species distribution data from central Europe revealing that landscape changes since the Last Glacial Maximum are important predictors of current plant species richness. However, historical effects were found to be habitat specific and often show a nonlinear relationship with species richness due to the impacts of recent environmental conditions and anthropogenic activity. This highlights the importance of using multiple data types to tease apart these relationships over time and space. Relationships and thresholds between diversity and ecosystem functioning operate on regional scales (Brook et al., 2013), therefore the regional vegetation signature captured by fossil pollen datasets provides an ideal data type to explore relationships between land use and diversity change.

1.2 | Identifying the drivers of biodiversity trends

Patterns of change in Holocene plant diversity trends have been summarised by Birks, Felde, and Seddon (2016) in a conceptual schematic for northwest Europe, building on McGill et al.'s (2015) biodiversity classification (summarised in Figure 1). Initial forest development is expected to have involved a period of change from high to lower diversity, which was followed by declining diversity when landscapes

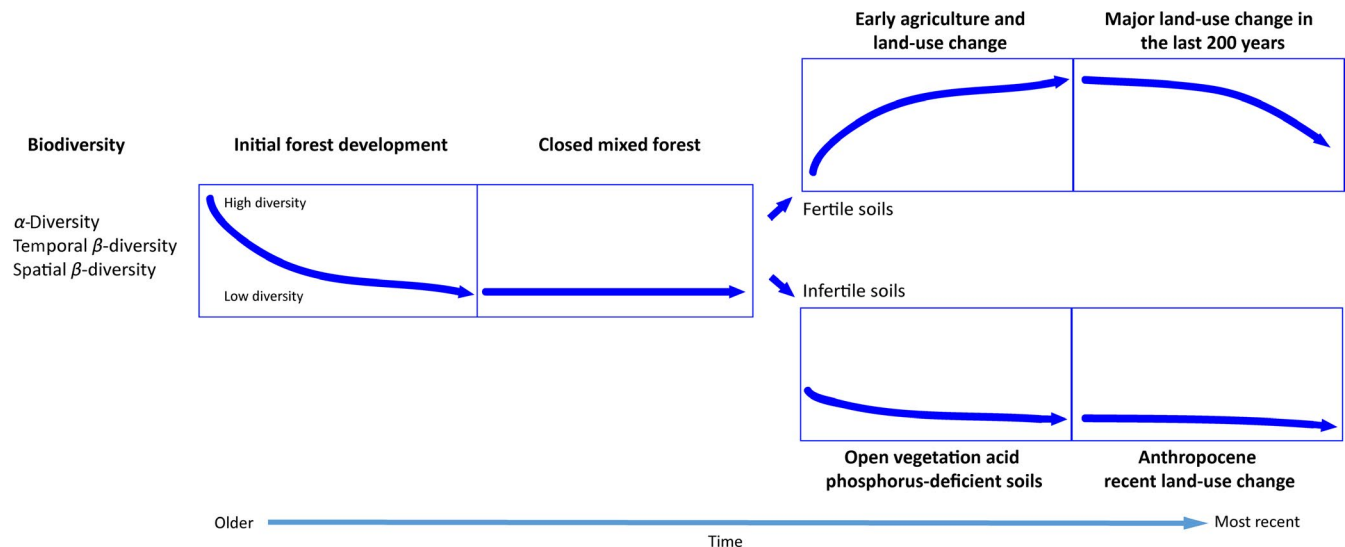


FIGURE 1 Theoretical model of local to meta-community scale diversity and possible drivers of change: summary of trends in biodiversity through the Holocene for fertile and infertile soils (based on Birks, Felde, & Seddon, 2016)

became increasingly dominated by closed mixed forests. An increase in diversity is then predicted on fertile soils linked to early agriculture, land-use change and natural/human-induced disturbance, which is then followed by recent loss of diversity in the last 200 years associated with major land-use intensification. Plant assemblages in areas with infertile soils are expected to show declining or static diversity during these latter periods. This model has not yet been tested for the British Isles, particularly alongside the analyses of how population change and climate interact to affect diversity patterns.

Here we present current understanding of long-term changes in land cover, palynological (pollen) diversity and insect faunal groups through the last 10,000 years (Holocene) via a synthesis of pollen sequences, insect faunal group assemblages, human population inferred from radiocarbon-dated archaeological sites from the British Isles and palaeoclimate records driven by North Atlantic conditions. We aim to test the aforementioned model of Holocene biodiversity trends using pollen datasets. Pollen-derived patterns of vegetation/land-cover change have been established (Fyfe et al., 2013) and these have been compared with archaeologically derived human population estimates (Woodbridge et al., 2014) across the British Isles, but diversity impacts and influence on faunal communities have yet to be investigated.

Periods of human population increase are often associated with major land-cover transformations, such as the loss of woodlands and increasingly open landscapes associated with agriculture (Roberts et al., 2019; Woodbridge et al., 2014). However, deforestation in the British Isles, from the start of the Neolithic around 6,000 years ago, is recognised as occurring slightly earlier than major population increases through evidence of axe production and declining forest vegetation (Schauer et al., 2019). There is no simple correlation between population rise and deforestation; therefore, the way in which people use the land requires investigation as well as understanding of population change. Insect assemblages show a large degree of turnover in lowland Britain

as a consequence of prehistoric field system development, with the open ground and dung-associated 'field fauna' replacing woodland insects (Smith et al., 2019, 2020). Similar evidence is now emerging in other regions (e.g. Schafstall et al., 2020). Insect datasets reflect land-use/cover change on a finer scale than pollen records, which reflect both local (on-site) and catchment vegetation. Goring et al. (2013) tested relationships between pollen and plant richness and suggested that palynological richness cannot be considered a universally reliable proxy for inferring plant richness. However, Matthias et al. (2015) demonstrated that palynological diversity can capture landscape structure and diversity. They found that Shannon index and the number of taxa are highly correlated providing a useful measure of pollen-type diversity that reflects landscape diversity. Insect and pollen data therefore allow complementary scales of analysis on community turnover.

Pollen diversity measures represent both taxa richness and assemblage evenness through estimating particular numerical characteristics of fossil pollen assemblages (Birks, Felde, Bjune, et al., 2016). Quantifying biodiversity trends remains challenging because 'there is no single index that adequately summarises the concept' (Morris et al., 2014). These challenges, along with taxonomic precision, the effects of sample size and pollen representation of different plant types, can result in biases in biodiversity measures (Odgaard, 1994, 2001). Kuneš et al. (2019) demonstrated that ecosystems were most affected by disturbances during the Early Holocene with lower level disturbance in the mid-Holocene. These shifts in disturbance were associated with pronounced changes in pollen richness. However, the relationship between pollen-type richness and plant species richness is not straightforward and reflects pollen population evenness. This is related to vegetation evenness and disturbance (Odgaard, 2001), which reflects the degree of landscape homogeneity or heterogeneity. These factors require consideration when interpreting diversity trends derived from pollen data.

2 | MATERIALS AND METHODS

2.1 | Fossil pollen data

The datasets included in this study (Figure 2) consist of 269 fossil pollen datasets (Table S2) extracted from the European Pollen Database (Leydet, 2007–2020) or provided by data contributors. Pollen datasets were selected based on their radiocarbon dating quality and sample size (Fyfe et al., 2013). Sediment core chronologies were taken from Giesecke et al. (2014) or where necessary established through fitting a new age–depth model using CLAM (Blaauw, 2010). Data have been taxonomically harmonised at two levels of aggregation (233 and 558 taxa groups) and placed on a common chronological time-scale summed into 200-year long time windows, which has been demonstrated in previous studies to be a suitable time resolution over which to investigate vegetation turnover (Woodbridge et al., 2014). The relationships between palynological diversity and plant or vegetation diversity are complex; however, most studies comparing modern pollen richness with contemporary plant richness show good relationships between the two (Birks, Felde, Bjune, et al., 2016). Within this study, we explore pollen (palynological) diversity as opposed to plant or vegetation diversity. Pollen data are also presented as quantified land-cover types transformed using the REVEALS (Regional Estimates of Vegetation Abundance from Large Sites) approach (Sugita, 2007), which converts pollen count data into quantified vegetation using knowledge of the differential pollen productivity, fall speed and pollen dispersal distances characteristic of different plant types (Broström et al., 2008; Fyfe et al., 2013). The pollen productivity estimates (PPEs) and fall speed of pollen for the 25 taxa in Trondman et al. (2015) were used in this study. These

PPEs are derived by investigating relationships between vegetation and pollen abundance in modern landscapes (Broström et al., 2008). A detailed description of the REVEALS method is provided in Fyfe et al. (2013) and Trondman et al. (2015).

There are numerous approaches for estimating diversity from ecological data (Hill, 1973), and most are strongly related (Matthias et al., 2015). Several approaches were provisionally tested within this work, with Shannon diversity and evenness index identified as the most suitable for capturing broad-scale trends alongside rarefaction, which provides a record of species richness accounting for varied sample sizes. Shannon diversity index reflects both taxa richness and evenness, which relates to assemblage heterogeneity and can be analysed as a separate component of the index. These indices were calculated using pollen percentages from taxa count data binned into 200-year time windows. As the REVEALS approach can only be applied to a limited number of taxa for which there are reliable PPEs, we chose to estimate diversity using all 233 or 558 land pollen taxa groups rather than REVEALS transformed data. Felde et al. (2016) found that results based on transformed and untransformed pollen data show the same patterns and pollen richness and diversity estimates generally increase after transformations. This occurs because greater weight is placed on rare taxa as the influence of abundant pollen taxa is reduced. Therefore, we chose not to transform the pollen data in order to retain more information about the assemblage. The R VEGAN package (Oksanen et al., 2019) was used to summarise both species richness and relative abundance (Magurran, 2003) within the entire pollen assemblage. Shannon (H) index provides a useful measure of pollen-type diversity corresponding to landscape diversity (Matthias et al., 2015). The index reflects the proportion of each taxon in the population relative to the total number of taxa

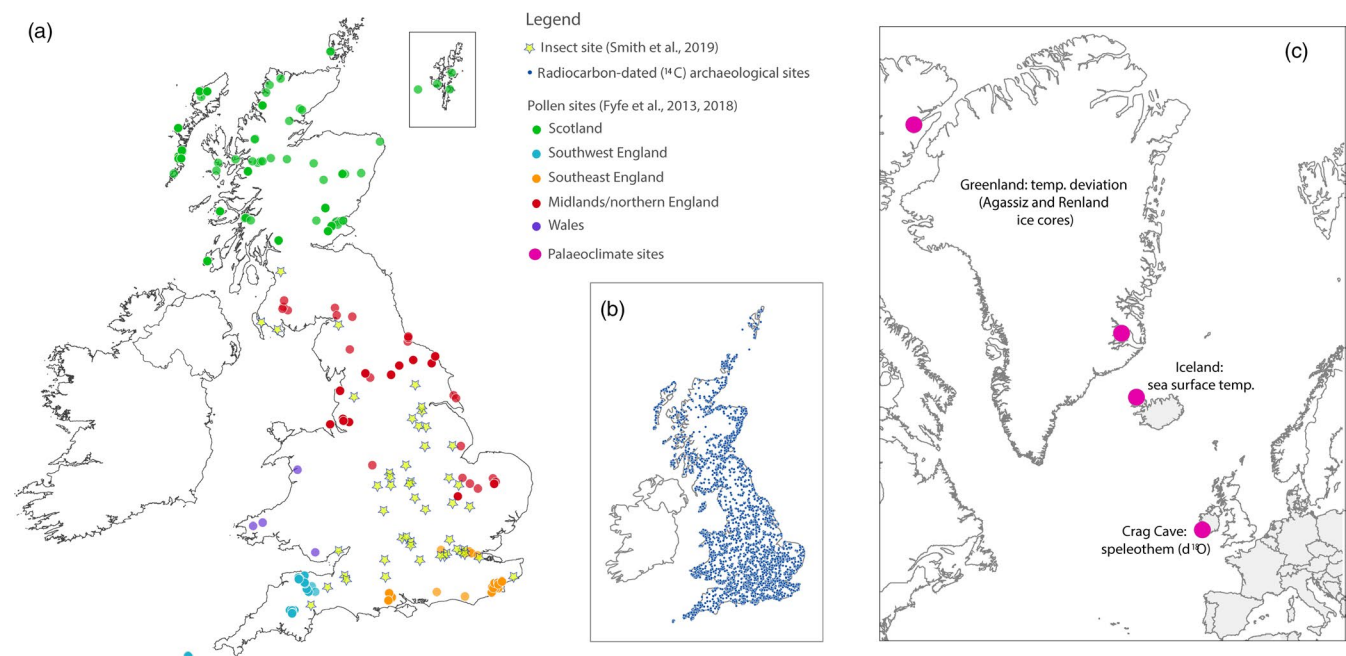


FIGURE 2 (a) Fossil pollen and insect sites, (b) radiocarbon-dated archaeological (palaeodemographic) site distribution and (c) palaeoclimate sites

present. Index values are derived by dividing the number of individuals of each taxon in each sample by the total number of individuals of all taxa. This value is then multiplied by the fraction by its natural logarithm and the results for all taxa are summed together and multiplied by minus 1. A high value of H represents a diverse and equally distributed community while lower values represent less diverse assemblages that are less equally distributed (Gaunle, 2020). The evenness of a community reflects the ratio of observable diversity to maximum diversity. This ranges between 0 and 1, with 1 representing complete evenness (Magurran, 2003). Rarefaction (pollen taxa richness) has been calculated from pollen count data using the R VEGAN package function 'rarefy' (Oksanen et al., 2019) to generate randomly rarefied community data for a given sample size (based on the mean of all samples) producing species richness estimates for each time window. Typically, the minimum of all samples is used; however, the minimum was not suitable for this dataset due to the presence of time windows with zero values; consequently the mean was selected as an alternative measure. The rarefaction trend is identical to pollen richness derived from Hill numbers; therefore this approach is deemed suitable for capturing diversity change that accounts for varied sample sizes.

2.2 | Palaeodemographic data

In total, 22,719 archaeological radiocarbon dates for mainland Britain have been extracted from Bevan et al. (2017) to infer regional-level palaeodemographic changes (Bevan & Crema, 2018; Palmisano et al., 2017). Palaeodemographic trends are inferred using a summed

probability distribution (SPD) approach where the number of radiocarbon dates act as a proxy for human population size for a given time period (Shennan et al., 2013). Potential biases resulting from multiple dates being sampled from the same archaeological phase are accounted for by aggregating uncalibrated radiocarbon dates from the same site within 100 years of one another and dividing by the number of dates in the 'time bin' (Timpson et al., 2014). The resulting SPDs, which represent summed probabilities from each calibrated date, are binned into 200-year time windows to allow multi-proxy comparisons.

2.3 | Fossil insect data

We used the 30 fossil insect beetle (Coleoptera) datasets from archaeological sites summarised in Smith et al. (2019), Smith et al. (2020) to reconstruct insect turnover. Metadata and references for the fossil insect sites are provided in Smith et al. (2020). Insect taxa have been allocated to ecological groups where possible and the relative proportions of these groupings calculated. The ecological groups used are a revision of Robinson (1981, 1983). Insect species are also classified as semi- or fully synanthropic (human-dependent; Smith et al., 2020) and this is represented in Figure 3 by the proportions of Kenward's 'house fauna' recovered for the periods concerned. As the insect data are derived from archaeological sites, it is necessary to aggregate by archaeological period, rather than into time windows that are comparable to the pollen data. Thus, it is not possible to perform detailed statistical comparisons between the insect data and the other proxies presented here.

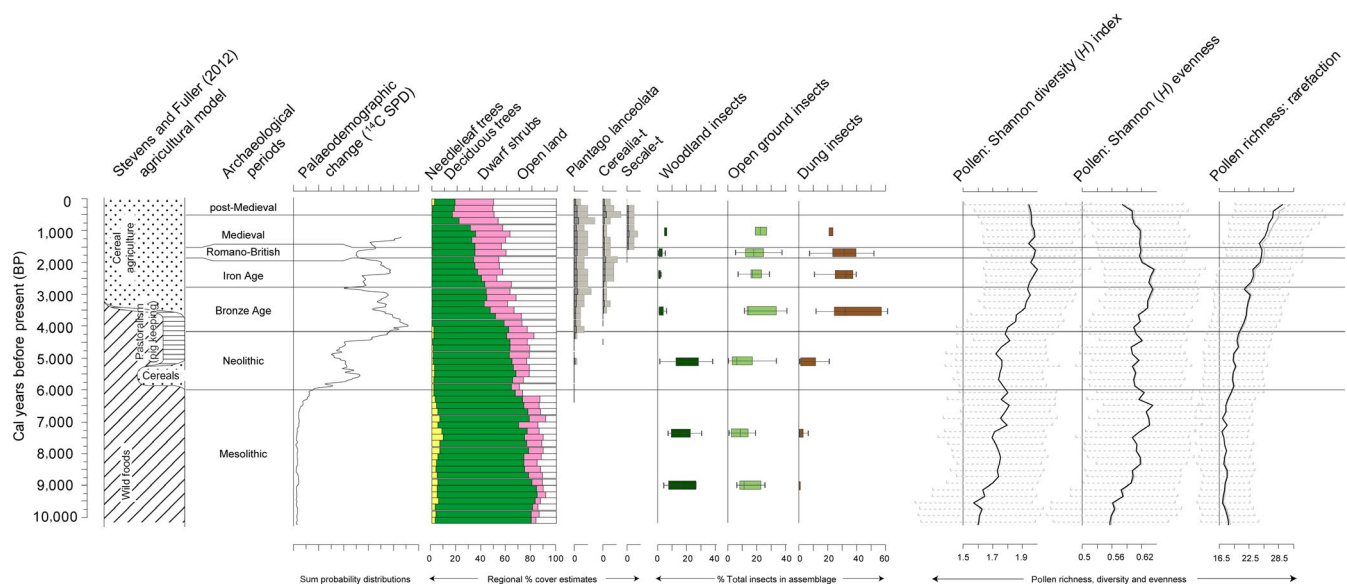


FIGURE 3 Synthesis of pollen and insect records from the British Isles: Stevens and Fuller's (2012) model of agricultural changes in the United Kingdom presented with archaeological periods, radiocarbon-inferred palaeodemographic changes (from Bevan et al., 2017), pollen-based vegetation cover and key land-use indicators (Fyfe et al., 2013), changes in key insect faunal groups (Smith et al., 2019) represented as average, minimum, maximum and interquartile range, and pollen taxa richness and evenness (Shannon diversity and rarefaction) indices averaged for all pollen sites. Dashed grey lines show values based on 233 pollen taxa groups and solid black lines show values for 558 pollen taxa groups and dotted horizontal lines show the standard deviation

2.4 | Climate data

Palaeoclimate datasets (Figure 2) were selected to cover the majority of the Holocene and characterise North Atlantic atmospheric and oceanic climatic patterns. These include:

- A record of sea surface temperature (SST) from northwest Iceland (Moossen et al., 2015). This dataset reflects SSTs reconstructed using the hydrogen isotopic composition of the C29 n-alkane (see Moossen et al., 2015 for further details).
- An ^{18}O isotope speleothem record from Crag Cave (southwest Ireland; McDermott et al., 2001) that provides a regional signal predominantly driven by temperature and North Atlantic Oscillation, but is also influenced by factors such as ice rafting, meltwater input and moisture availability (see McDermott et al., 2001 for further details).
- A Holocene record of deviation from modern temperature derived from Greenland ice cores reconstructed from ^{18}O isotopic data (see Vinther et al., 2009 for further information).
- A cosmogenic isotope and total solar irradiance (TSI) record as a proxy for solar activity (Steinhilber et al., 2012). The reconstruction is based on a combination of different ^{10}Be ice core records from Greenland and Antarctica with the global ^{14}C tree ring record (see Steinhilber et al., 2012 for further information; site locations not displayed in Figure 2).

General Additive Models (GAMs) were fitted to the climate data using the 'gam' function in the `MGCV` R package (Wood, 2017) to smooth and interpolate values in the climate data series for time periods that match the pollen and archaeological datasets. GAMs allow flexible modelling of nonlinear relationships, such as those displayed in climate data series; therefore we used a smoothing function to capture these nonlinear patterns through time.

Spearman's rank correlation coefficient was used to identify relationships between the datasets, as ranked correlation coefficients are most suitable when a proxy indicator is not linearly related to a variable (e.g. SPDs are not linearly related to population, but indicate magnitude of population change). The 'p.adjust' function in R using the 'Bonferroni' method was applied to correct p-values for multiple tests and avoid spurious significant correlations (Benjamini & Yekutieli, 2001). The dataset was divided into periods representing the early (10,000–6,000 BP), mid (6,000–3,000 BP), late (3,000–0 BP) and entire Holocene for correlation analysis to explore differences in relationships between the datasets over time.

2.5 | Site distribution

The fossil pollen sites are generally located within upland regions with data gaps in central England and Wales, while the insect sites are mostly situated in southeast and central England with very few datasets in Scotland. The palaeodemographic archaeological sites are mainly located in England and the coastal regions of Scotland

(Figure 1), which impacts upon the trends identified in the different datasets. We have not included the island of Ireland as it was separate from the British Isles by the start of the Holocene, and therefore might be expected to have different patterns of biodiversity to Britain, which remained connected to continental Europe until several millennia after the start of the Holocene. The pollen and palaeodemographic datasets have been analysed at sub-regional scales to address these spatial biases. Climate records based on sites within the British Isles were explored, but these datasets largely only cover short periods of the Holocene, therefore we selected records from different locations within the North Atlantic that principally reflect temperature variation across the majority of the Holocene epoch.

3 | RESULTS

3.1 | Holocene trends in environmental datasets

Synthesis of the pollen-inferred land cover, fossil insect faunal groups, palaeodemographic trends and pollen-derived diversity measures (Figures 3 and 4) reveals that population increases at the start of the Neolithic, ~6,000 BP (before present), and Bronze Age, ~4,200 BP, coincided with declining deciduous forest and increasing open land. The first appearance of plant types indicative of agriculture, such as cereals and plant species associated with disturbance as a result of human land use, is evident from the start of the Neolithic. Marked increases in these indicators are not apparent until the Bronze Age (Stevens & Fuller, 2012), which marks the first widespread evidence for cereal cultivation with more pronounced increases in the most recent 3,000 years. The transition from the Neolithic to the Bronze Age also saw a significant shift in insect fauna from woodland types to open ground and dung insect types associated with agricultural activity and the presence of grazing animals. See Smith et al. (2019) for further discussion around the site types investigated. We see an increase in palynological diversity from ~9,400 BP, which was followed by a period of stable diversity scores. Shannon diversity index values then increase at the start of the Bronze Age, continue to steadily increase until the Iron Age (~2,700 BP) and remain stable until the most recent part of the record with a slight decline since the Medieval period (~1,000 BP). The palynological evenness component of the Shannon index shows a similar trend to the index scores that incorporate taxa richness, but evenness values decline more from the end of the Iron Age into the Medieval period, showing that these trends are increasingly decoupled during the most recent 2,000 years. Calculating diversity measures at different levels of pollen taxonomic resolution (232 and 558 taxa groupings; e.g. separating or combining pollen taxonomic units) reveals the same trends throughout the Holocene. Rarefaction analysis provides a measure of taxa richness that is independent of evenness, and indicates that palynological richness was lowest during periods of high woodland cover, and increased as landscapes became more open, similar to the Shannon diversity curve. Changes in broad landscape openness are much more subtle after the middle Iron Age.

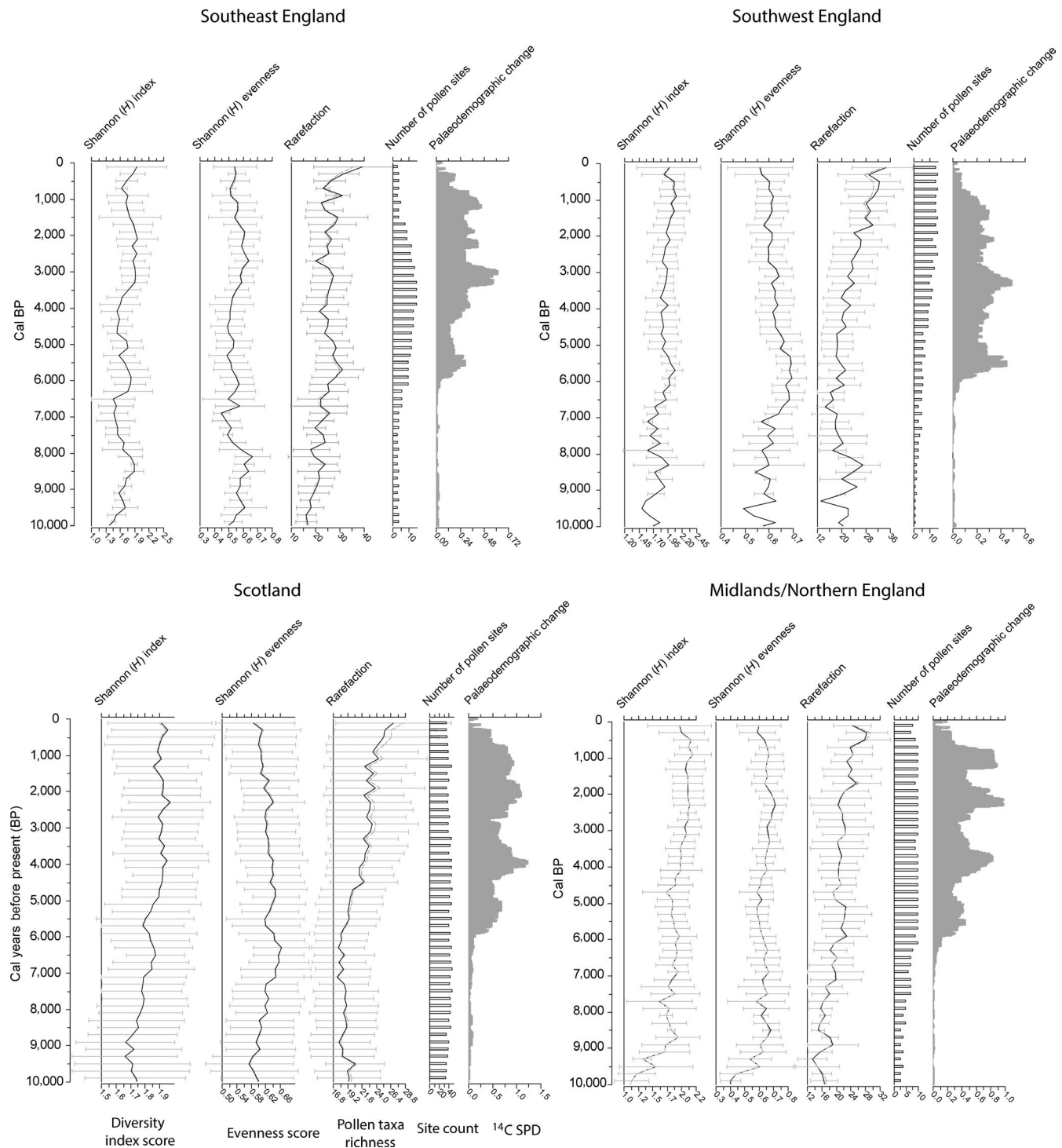


FIGURE 4 Pollen taxon richness and assemblage evenness summarised by Shannon diversity and evenness indices and rarefaction (pollen richness; with standard deviation and number of pollen sites) averaged for four regions of the British Isles: southeast England, southwest England, Scotland and the midlands/northern England. Dashed grey lines show values based on 233 pollen taxa groups and solid black lines show values for 558 pollen taxa groups. Palaeodemographic (population) trends are shown for each region (based on the summed probability distributions (SPDs) of radiocarbon-dated archaeological sites)

Significant relationships between palaeodemographic, climate and pollen data are mostly evident with palynological richness rather than evenness (Table 1). Palaeodemographic (population) trends are also more strongly correlated with pollen diversity in the later Holocene with higher r -values, although the p -values were not

deemed significant after correcting for multiple tests. Some climate datasets show correlations with the pollen datasets in the early Holocene (e.g. Iceland temperature) and others in the later Holocene (e.g. Greenland temperature). The strongest relationships are shown with the Greenland ice core temperature deviation and Iceland SST

TABLE 1 Spearman's rank correlations (r and p -values) between the palaeoclimate records reflecting North Atlantic patterns, pollen taxa richness and evenness (Shannon diversity index and evenness) and taxa richness (rarefaction), and palaeodemographic change (population) inferred from summed probability density (SPD) functions of radiocarbon-dated archaeological sites. Correlation analyses were carried out for the early, mid, late and entire Holocene, and significant relationships are shaded. Dates represent the mid-point of each 200-year time window. Grey shading indicates significant correlations ($p < 0.05$). p -values corrected for multiple comparisons of significantly correlated variables are shown in brackets

	Time period	Pollen: Shannon diversity index	Pollen: Shannon evenness	Pollen taxa richness (rarefaction)	
Palaeodemographic change	9900–1700 BP	0.768 0.00	0.048 0.762	0.88 0.00	
	2900–1700 BP	0.821 0.023 (0.138)	0.036 0.939	0.679 0.094	
	5900–3100 BP	0.532 0.041 (0.246)	0.229 0.413	0.746 0.001 (0.006)	
	9900–6100 BP	0.102 0.668	0.056 0.816	0.299 0.2	
Palaeoclimate records					Palaeodemographic change
Iceland: sea surface temperature	9900–100 BP	–0.547 0.00	–0.249 0.081 (0.486)	–0.669 0.00	(9900–1700 BP) –0.676 0.00
	2900–100 BP	0.446 0.095	–0.411 0.128	0.45 0.092	(2900–1700 BP) 0.5 0.253
	5900–3100 BP	–0.689 0.004 (0.024)	–0.396 0.143	–0.957 0.00	–0.746 0.001 (0.006)
	9900–6100 BP	0.508 0.022 (0.132)	0.484 0.031 (0.186)	0.008 0.975	0.126 0.596
Crag Cave speleothem: ^{18}O	9900–100 BP	–0.227 0.112	0.041 0.779	–0.348 0.013 (0.078)	(9900–1700 BP) –0.584 0.00
	2900–100 BP	–0.257 0.355	0.186 0.508	–0.111 0.694	(2900–1700 BP) –0.214 0.645
	5900–3100 BP	–0.421 0.118	–0.143 0.612	–0.646 0.009 (0.054)	–0.925 0.00
	9900–6100 BP	0.411 0.072	0.295 0.207	0.352 0.128	0.302 0.195
Greenland ice core: temperature deviation	9900–100 BP	–0.848 0.00	–0.291 0.04 (0.240)	–0.94 0.00	9900–100 BP –0.879 0.00
	2900–100 BP	–0.057 0.84	0.743 0.002 (0.012)	–0.882 0.00	(2900–1700 BP) –0.929 0.003 (0.018)
	5900–3100 BP	–0.7 0.004 (0.024)	–0.411 0.128	–0.832 0.00	–0.65 0.009 (0.054)
	9900–6100 BP	0.002 0.995	0.002 0.995	–0.236 0.316	–0.368 0.11
Total Solar Irradiance (TSI)	9300–100 BP	0.124 0.405	0.079 0.596	0.166 0.265	(9300–1700 BP) 0.719 0.00
	2900–100 BP	0.261 0.348	0.571 0.026 (0.156)	–0.471 0.076	(2900–1700 BP) 1 0.00
	5900–3100 BP	0.143 0.612	–0.054 0.85	0.364 0.182	0.375 0.168
	9300–6100 BP	0.044 0.866	–0.123 0.639	0.145 0.58	0.414 0.098

records. Population and climate trends show the strongest significant relationships for the entire Holocene, but this is likely associated with the higher number of samples compared, which leads to lower *p*-values. The climate record from Iceland indicates that the early Holocene was characterised by high air temperatures relative to the later Holocene, but SSTs were dampened by melt water events (Moossen et al., 2015; Figure 5). The middle Holocene saw a peak in SSTs, followed by cooling into the late Holocene (Moossen et al., 2015). The Crag Cave speleothem $\delta^{18}\text{O}$ sequence reflects temperature change with cooling events evident at ~7,730, 7,010, 5,210 and 4,200 BP (McDermott et al., 2001) while the Greenland ice core record reveals a number of abrupt shifts in climate with the most significant at ~7,600, 6,500, 6,300 and 4,300 BP. The TSI record fluctuates through the Holocene with lowest values in the early and late Holocene.

Testing the conceptual diagram presented by Birks, Felde, and Seddon (2016; Figure 1) at the scale of the British Isles indicates that loss of diversity associated with initial forest development is

not reflected in the current dataset in the early Holocene. However, this may be because the transitional phase from late-glacial vegetation to early Holocene forest initiation is not captured by these datasets. Subsequent periods show similar trends to those predicted by the model. Closed mixed forest is characterised by a period of limited change in palynological diversity (~10,000–6,000 BP), which is followed by early agriculture and land-use change associated with a clear increase in diversity, particularly since the beginning of the Bronze Age when agricultural activity increased (Figure 3). The final phase in the model for fertile soils, declining diversity associated with recent land-use change in the last 200 years, is not clearly captured by the Shannon diversity index. The model predicts no change in diversity in the most recent phase on infertile soils, which may be expected in upland regions and in parts of Scotland and Wales with acid infertile soils, a pattern that is supported by the subregional analyses for Scotland and the midlands/northern England where little recent change is evident (Figure 4). This final phase may be indistinguishable at the broad spatial and temporal scale used here (200-year long time windows)

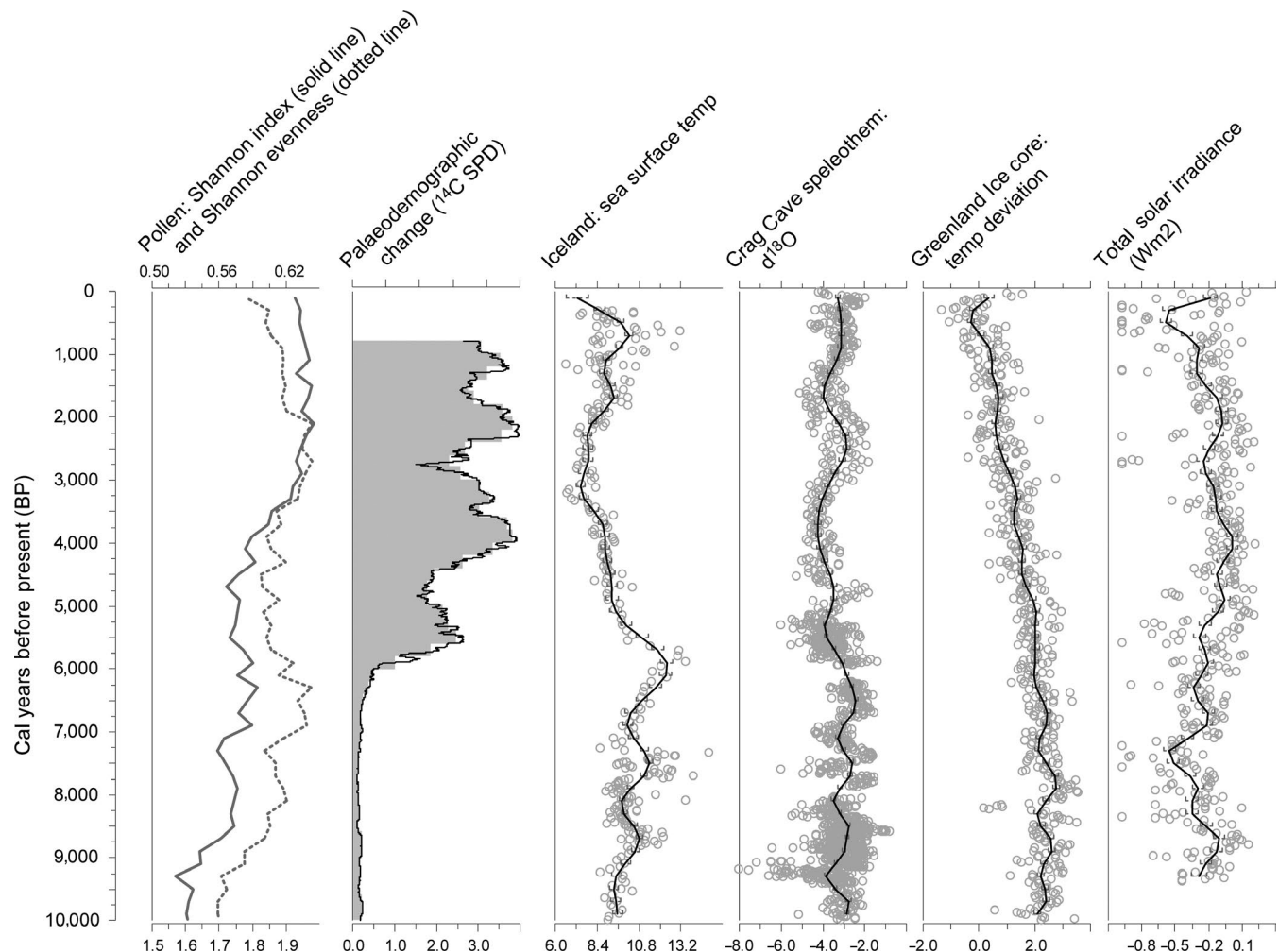


FIGURE 5 Pollen taxa richness and assemblage evenness summarised by Shannon diversity and evenness indices for the British Isles presented with palaeodemographic data for all regions and palaeoclimate datasets: sea surface temperature (SST) from Iceland (Moossen et al., 2015), an $\delta^{18}\text{O}$ isotope speleothem record from Crag Cave (Ireland; McDermott et al., 2001), temperature deviation from the Greenland ice core (Vinther et al., 2009) and total solar irradiance (TSI; Steinhilber et al., 2012). Grey circles represent all data points and black lines represent smoothed data values derived using a general additive model (GAM)

and shows the importance of exploring patterns at smaller subregional and site-specific scales. It may also reflect the lack of pollen data spanning recent decades in the synthesis, which could capture this more recent decline in diversity (e.g. Hanley et al., 2008).

At the subregional scale (Figure 4), some of the patterns predicted by Birks, Felde, and Seddon (2016) model are shown more clearly. For example, the decline in palynological diversity in the last 500 years appears to be reflected in the diversity indices for southwest England and the midlands/northern England pollen sites where a minor recent decline in diversity is evident, but not clearly for sites in southeast England and Scotland. Regional variation is evident when average palynological diversity index scores for the four regions are compared (Figure 4). The large standard deviation in palynological diversity within the pollen datasets from Scotland reflects the greater number of sites capturing the diverse landscapes within this region. Whereas the smaller standard deviation for sites in the southwest, southeast, midlands/northern England show that palynological diversity trends through the Holocene were more similar for sites within these regions, which may represent more similar landscapes or land-use types. Pollen taxa richness (rarefaction) reflects the diversity index and indicates gradually increasing values in all four regions as landscapes became more open. The palaeodemographic curves (SPDs of radiocarbon-dated archaeological sites) for these areas indicate increasing population at the start of the Neolithic with all regions showing a peak ~5,200 BP. This is followed by another population peak ~3,500 BP during the Bronze Age, and further increases in the late Iron Age/early Roman period (~2,000 BP) and in the Medieval period (~1,000 BP; Figure 4).

4 | DISCUSSION

4.1 | Biodiversity trends in the Holocene

The synthesis presented in this study (Figure 3) has demonstrated that people and climate have played important roles in shaping past land-cover change with likely impacts on the changing diversity and abundance of vegetation types, which reflects previous literature demonstrating the impact of people on past vegetation and pollen richness (e.g. Birks & Line, 1992; Iversen, 1949). However, the relationships between human population, climate, land cover and palynological and insect diversity are not straightforward, and consideration of the processes involved in landscape transformation and different species traits, which influence species responses, is key to understanding how modern biodiversity patterns emerged within a long-term context.

Trends identified in the pollen-inferred land-cover types reflect Stevens and Fuller's (2012) agricultural model (Figure 3), which is based on radiocarbon-dated wild and cultivated food plants. The model recognises an initial phase of arable agriculture in the early Neolithic followed by predominantly pastoral practices and evidence of later more pronounced Bronze Age intensification of agriculture. This reflects the patterns shown in Figure 3 and the findings

of Colombaroli et al. (2013) who identified that land clearance promoted diverse open ecosystems, but in the long-term, this led to reduced woodland and forest diversity. In our study, this is reflected by decreased deciduous forest cover from the start of the Neolithic, which became more pronounced from the start of the Bronze Age. This was followed by a clear increase in cereals and a shift from woodland to open ground insect types.

The palynological diversity indices presented here imply that opening of the landscape, associated with early land-use and forest removal, initially led to an increase in the diversity of vegetation types across many sites, which varied regionally (Figure 4). Similar patterns identified by Kuneš et al. (2019) in central Europe show that diversity increased continuously throughout the Holocene with comparable trends between pollen richness and evenness. This pattern is reflected in the rarefaction curves presented here. While the Shannon index also provides a measure of taxa richness, it does not account for varied sample sizes and slight differences in the Shannon and rarefaction figures are apparent (Figure 3). Recent loss of diversity is not clearly reflected by the majority of sites in this study, which is likely the result of pollen records not extending into the most recent period, the amalgamation of pollen data from 200 BP until present, the absence of modern (i.e. datasets spanning recent decades) pollen data in the analyses, and as a result of many sites being located on infertile soils, which Birks, Felde, and Seddon (2016) model predicts should not show a recent decline in diversity. Once landscapes have become predominantly open (i.e. by the start of the historic period in Britain), measures such as woodland cover become insensitive proxies for understanding biodiversity trends and more ecologically detailed interpretations of pollen assemblages are required. This study also demonstrates that vegetation communities are rarely stable over time as assemblages reassemble on centennial to millennial time-scales (Edwards et al., 2017).

Smith et al. (2020) identified distinct phases in the introduction of synanthropic insects in the British Isles. This included an initial group of taxa originating from natural ecosystems during the Mesolithic and Neolithic, followed by a second phase of new insect taxa associated with pasture, fodder production and animal stocking in the Bronze Age and Iron Age. This was proceeded by the appearance of strongly synanthropic insect species, such as grain pests, during following time periods, which were introduced into Britain during Romans times (Smith et al., 2020). The agricultural landscape may have become more even and less diverse in the Roman period as areas became specialised in producing for larger populations. Insect remains can provide a range of information at an intermediate scale on land-use nature and practice, particularly the clearance of forest and the development of pasture, along with indicating the spread and intensity of settlement (Kenward, 1997; Smith, 2012; Smith et al., 2010, 2019, 2020).

The absence of patterns between the palaeodemographic curves and the palynological diversity indices for each region (Figure 4) implies that there are no direct detectable regional-scale relationships between population change and palynological

diversity in this study beyond the initial change at the start of the Neolithic at the onset of agriculture. Therefore, the size of the population may be less important than the way in which people used the land. Within some regions, such as the midlands/northern England, palynological diversity appears to have remained stable during multiple population 'boom and bust' cycles; however, changing palynological diversity patterns may not be easily detectable at this spatial scale. In other regions, such as southwest England, highest levels of palynological diversity occur when population peaks in Neolithic times. This implies that low levels of human-induced disturbance and associated land-use practices may have initially led to an increase in pollen diversity; however, this pattern is not evident for all regions. In a review of biodiversity trends through the Anthropocene, McGill et al. (2015) highlighted human-induced land-cover change as a major factor influencing biodiversity patterns. They identified that land-cover change typically results in decreased species richness in the changed area. They also recognise that by creating more heterogeneous habitat structures, meta-community to biogeographical-scale species richness can increase through integration of edge or open habitat species. This is clearly demonstrated in the pollen-inferred diversity trends presented here (Figure 3), which increase when deciduous forest declines and vegetation becomes more open. During recovery from natural or human-mediated disturbance, species richness often peaks during periods of intermediate disturbance, as demonstrated by McGill et al. (2015). This too is reflected in the pollen-inferred diversity trends, such as from the start of the Bronze Age as landscapes became more open as a result of forest removal and use of land for agriculture. This 'intermediate' land use would have been less intensive than later agriculture and forest removal, which is demonstrated in Figure 3 as woodland/open land cover, increasing cereal crops and insect groups indicative of human activity. McGill et al. (2015) identified 15 categories of biodiversity trends based on a range of data types and highlighted the importance of scale in interpreting diversity indices. Pollen data represent different spatial scales dependent on taxa group and landscape type, such as closed forest or open grassland. The results presented in this study mostly represent meta-community scales (i.e. spatial heterogeneity with dispersal as the dominant process) as opposed to biogeographical and global scales, which are governed by speciation and global extinction (McGill et al., 2015). This study has highlighted that spatial scale plays an important role in understanding human drivers of biodiversity.

The results from this data synthesis indicate that patterns of diversity change are more heterogeneous than the theoretical schema presented by Birks, Felde, and Seddon (2016) and highlight that there is a great deal of regional and temporal variability in palynological diversity trends, although the conceptual model may reflect large (continental)-scale trends. The relationships between population change, land cover and diversity are not straightforward, which implies that the ways in which people managed the land has greater impact on diversity than changing population levels through the Holocene. Detailed information

about the type, scale and intensity of land use is needed to allow diversity patterns to be fully understood in relation to changing human populations over time. The specific combinations of taxa driving diversity change and traits that condition 'success' or 'failure' to persist also require exploration alongside diversity, as interpreting diversity indices alone may mask the decline or loss of key taxa or functional types (e.g. Carvalho et al., 2019; Davies, 2016; Reitalu et al., 2015). More detailed analysis of species characteristics or traits is needed, which will be addressed in future work on the combined analyses of pollen and archaeobotanical data, which provide information about the scale and intensity of land use (Treasure et al., 2019), cultivation practices, cereal and horticultural crops, and the evolution of weed floras. Further work at smaller spatial scales is also needed to explore patterns between demographics, land use and trends in particular taxa or phytosociological groups, which is demonstrated by the high standard deviation in certain subregional patterns indicating dissimilar trends between individual sites. Broad spatial scale macroecological syntheses are valuable for understanding to what extent there are generalisable relationships between human land use and biodiversity trends. However, meta-analyses need to consider subregional patterns and site-specific characteristics along with exploration of the nature of past land use to assess species sensitivity to change. This has potential to provide answers to questions about the way in which these factors shaped plant assemblages, which can facilitate more efficient communication across palaeo- and neo-ecology and conservation.

The majority of the significant correlations appear between climate, palaeodemography and the pollen taxa richness component of diversity rather than evenness. This implies that the significant associations with Shannon diversity mostly depend on the richness component and not evenness. Analyses of palaeoclimate trends can also help to address debates about the relationships between climate, land use and land cover over time (Dark, 2006). The climate datasets analysed within this study provided mixed results with some climate trends showing significant correlations with palynological diversity and population change for specific time periods, but not others. Weak correlations are to be expected during periods of stable Holocene climate when climatic influence on vegetation change would have been minor. However, the significant correlations identified with climate records from Iceland and Greenland demonstrate a strong relationship between pollen diversity trends and climate, suggesting that the climatic optima and ranges of different taxa played an important role in shaping vegetation patterns. The Greenland temperature deviation record shows strongest correlations with population and the diversity indices. Despite the numerous significant correlations between the datasets, we cannot assume that causation directly relates to the variables of interest. Despite statistically significant correlations between population and both Shannon index and rarefaction for the entire time period covered by both records (9,900–1,700 BP), *r*-values indicate that population change is correlated with palynological diversity more clearly in the later Holocene in comparison

with the earlier Holocene. This suggests that people had an increasingly impactful influence on landscapes and palynological diversity, which is reflected by the increase in insect fauna associated with human land use and the increasing abundance of cereals and arable pollen indicators.

5 | CONCLUSIONS

Synthesis of fossil pollen, archaeological and insect datasets from the British Isles has demonstrated that humans played an important role in shaping landscape transformation throughout the Holocene within the context of climatic influences on vegetation change. However, relationships between population change, land cover and palynological diversity in the past are not straightforward. Testing a model of biodiversity change has demonstrated that patterns of palynological diversity trends are regionally variable and may not always follow expected trajectories. Current understanding of environmental change is often focused on recent decades, which only represents a 'snapshot' in time. Exploring trends at smaller spatial scales, and understanding how different types of human-induced disturbance, such as land-use change, lead to loss or increases in diversity, also holds great potential for addressing questions about human impacts on biodiversity change. In order for long-term environmental data to inform modern challenges surrounding land use and biodiversity loss, detailed high-resolution spatial and temporal datasets need to be synthesised through multi-community efforts and large-scale data harmonisation exercises.

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AUTHORS' CONTRIBUTIONS

J.W. wrote the manuscript, carried out analyses and produced the figures; R.F. acquired and amalgamated the fossil pollen datasets, wrote R script to carry out pollen data harmonisation and REVEALS reconstructions and conceptualised Figure 3; R.F., R.P., D.S. and J.W. designed the research while J.W. and R.F. led the conception and design on the manuscript; D.S. acquired and amalgamated the fossil insect datasets; C.R.B. contributed numerous pollen datasets from the London area and A.L.D. contributed several pollen datasets from Scotland; A.B. acquired and amalgamated radiocarbon-dated archaeological data and wrote R script for producing summed probability distributions (SPDs) as a proxy for population change; J.W., R.F., R.P., D.S., A.d.V., C.R.B., A.B. and A.L.D. contributed to the interpretation of data, revised the manuscript critically, made intellectual contributions and approved the final version for publication.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13565>.

DATA AVAILABILITY STATEMENT

The majority of the original pollen datasets used in this study are available from the European Pollen Database (EPD; www.europeanpollendatabase.net/) and can be accessed here: <http://www.europeanpollendatabase.net/fpd-epd/bibli.do> by selecting a country and clicking on a relevant site name (please see Supporting Information for site names, author names and references). The EPD is also available as an Access database, which can be downloaded here: <http://www.europeanpollendatabase.net/data/downloads/>.

The fossil insect datasets are available from BugsCEP (<http://bugscap.com/>). The latest version of the BugsCEP Access database can be downloaded here: <http://bugscap.com/downloads.html>. All radiocarbon dates used for palaeodemographic reconstructions are available within University College London's Discovery database (discovery.ucl.ac.uk/10025178/; <https://doi.org/10.14324/000.ds.10025178>). For a full set of sources and acknowledgements for the radiocarbon data see Bevan et al. (2017).

The climate datasets are available from NOAA (<https://www.noaa.gov/>) and can be accessed using the following links:

- Northwest Iceland Climate Reconstructions: <https://data.noaa.gov/dataset/dataset/noaa-wds-paleoclimatology-northwest-iceland-holocene-biomarker-data-and-climate-reconstruction>
- 18O isotope speleothem record from Crag Cave (southwest Ireland): University of Plymouth PEARL repository: <https://doi.org/10.24382/c7ex-n779>
- Holocene record of deviation from modern temperature derived from Greenland ice cores: <https://www.ncdc.noaa.gov/paleo-search/study/22057>
- Cosmogenic isotope and total solar irradiance (TSI): <https://www.ncdc.noaa.gov/paleo-search/study/12894>
- A modified version of the climate datasets modelled using GAMs (General Additive Models) is available from the University

of Plymouth PEARL data archive: <https://doi.org/10.24382/c7ex-n779>

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