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Abstract

The Eemian interglacial represents a natural experiment on how past vegetation with negligible human impact responded to amplified temperature changes compared to the Holocene. Here, we assemble 47 carefully selected Eemian pollen sequences from Europe to explore geographical patterns of (1) total compositional turnover and total variation for each sequence and (2) stratigraphical turnover between samples within each sequence using detrended canonical correspondence analysis, multivariate regression trees, and principal curves. Our synthesis shows that turnover and variation are highest in central Europe (47–55°N), low in southern Europe (south of 45°N), and lowest in the north (above 60°N). These results provide a basis for developing hypotheses about causes of vegetation change during the Eemian and their possible drivers.

Keywords Detrended canonical correspondence analysis · Extrinsic and intrinsic processes · Inertia · Last interglacial dataset · Multivariate regression trees · Neutral processes · Principal curves

Introduction

The last interglacial (Eemian, c. 129–116 ka ago) is the most extensively studied pre-Holocene stage of the Quaternary (Tzedakis 2007a). It is characterised during its early part by a strong summer insolation anomaly, peak global mean surface air temperatures of ~ 1 °C above pre-industrial values, reaching 3–11 °C in the Arctic (Fischer et al. 2018), and by a peak sea-level of 6–9 m above present (Dutton et al. 2015).

The duration of the last interglacial represents the interval of reduced ice volume, demarcated at its onset by deglaciation and at its close by glacial inception (Tzedakis et al.

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2012) and is broadly equivalent to Marine Isotope sub-Stage 5e (~ 132–116 ka) and the Eemian interglacial of north-west Europe (Kukla et al. 2002). The term Eemian was introduced by Harting (1874) to describe a subsoil characterised by warm marine molluscs in the Eem valley near Amersfoort in The Netherlands (Tzedakis 2007a). Integrated palaeoceanographic and pollen analyses from the Portuguese margin show that the marine isotopic and terrestrial stage boundaries are not synchronous, with the interval of temperate forest conditions extending from ~ 129 to ~ 111 ka (Shackleton et al. 2003; Tzedakis et al. 2018). Here we use the term 'Eemian' informally to refer to the forested interval (protocratic, mesocratic, and oligocratic/telocratic phases—see Fig. 1a) in last interglacial pollen sequences across Europe. While the long duration (~ 18,000 years) of the forest interval in southern Europe is supported by independent chronologies (Brauer et al. 2007), a shorter duration (~ 11,000 years) has generally been applied to north-central European pollen sequences on the basis of a partially annually laminated record at Bispingen, Germany at 53°N (Müller 1974). However, recent joint palaeoceanographic pollen
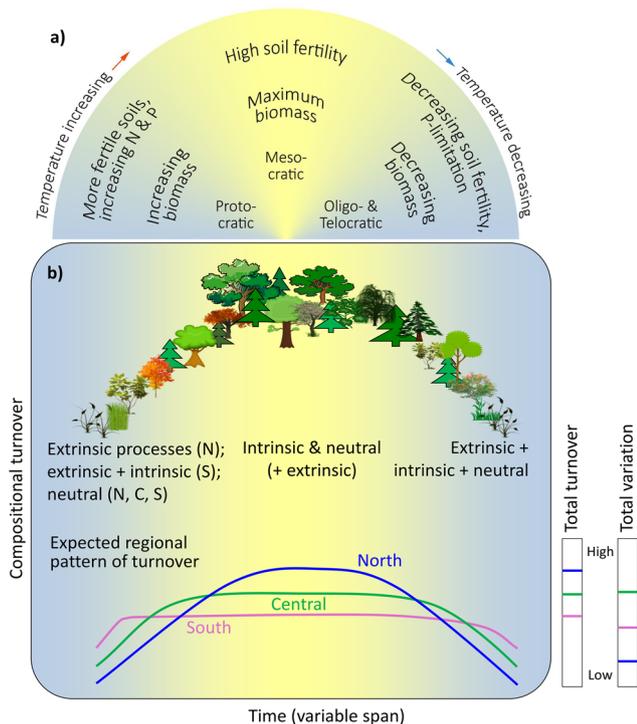
Fig. 1 Hypothetical responses of an ecosystem in the last interglacial (Eemian) in terms of biomass and fertility (modified from Birks and Birks 2004). **a** The three phases of Eemian vegetation history, namely protocratic, mesocratic, and oligocratic plus telocratic, in response to changing temperature (outer arc). **b** Hypothetical model of compositional change (turnover) within an Eemian pollen sequence with expected patterns of turnover in each geographical region and an indication of total palynological turnover and total palynological variation expected in north (above 60°N), central (45–60°N), and south (below 45°N) Europe. The turnover axis can be, for example, an ordination axis

analyses from the Bay of Biscay (Sánchez Goñi et al. 2012) and comparisons with pollen sequences in southern France and southern Germany indicate a long Eemian duration (~ 18,000 years) at least as far north as 48°N. It is possible that the unlaminated upper part of the Bispingen sequence represents a longer time interval than presently assumed and that the duration of the forested interval in northern Germany was approximately as long as farther south. In the absence of any independent chronology and duration estimates, the length of the Eemian in Fennoscandia remains unclear.

Ever since the pioneering studies in Denmark and Germany by Jessen and Milthers (1928), many Eemian pollen sequences have been analysed, focussing mainly on sedimentary settings, stratigraphies, pollen assemblages, vegetation histories, dating, and climate (e.g. Zagwijn 1996; Kühl 2003; Tzedakis 2007a). Eemian pollen records present a valuable opportunity to study vegetation patterns across broad spatial and temporal scales without extensive human impact

(Kühl 2003; Tzedakis 2007a; Milner et al. 2013). Ecological questions abound about the Eemian. For example, are Eemian inferred vegetation patterns similar to Holocene patterns prior to human influence? How similar are Eemian pollen stratigraphies across Europe? Are there consistent temporal patterns in the appearance, expansion, and decline of major arboreal taxa across Europe? What are the spatial variations in pollen compositional change ("turnover") and total variation across Europe?

To answer such questions and to study vegetation patterns and trends during the Eemian in Europe, we compile an Eemian dataset based on 47 representative pollen sequences. Here, we consider what the spatial patterns are in pollen turnover and total variation across Europe. We use compositional turnover and variation to estimate change in pollen-assemblage composition over time and space (Andersen 1994; Birks and Birks 2004; Birks 2007). With these explorative analyses presented here, we address the following two questions. (Q1) How does compositional turnover change within Eemian pollen sequences? (Q2) What are the spatial variations in total pollen compositional turnover and total variation across Europe?

As the concept of turnover is rarely used in pollen analysis (see Birks 2007), we summarise what this concept is. In community ecology, turnover is used to describe and possibly to quantify the replacement of one species by another in an assemblage in space or time or both. In pollen analysis, turnover is used to refer to the amount of compositional change of all pollen taxa within a stratigraphical sequence, namely along a temporal gradient (Birks 2007). Although the concept of turnover is widely used in ecology (e.g. Baselga 2010; Descombes et al. 2017) and biogeography (e.g. Buckley and Jetz 2008), little appears to be known about how turnover within an assemblage changes with time (e.g. Jarzyna et al. 2014). Pollen sequences provide a means of studying biotic turnover over long time periods. We use compositional turnover (one type of β-diversity *sensu* Anderson et al. 2011) as estimates of change in pollen-assemblage composition along the temporal gradient in a pollen sequence. This is "directional turnover" (Anderson et al. 2011) or "compositional gradient length" (Tuomisto 2010). We avoid referring to β-diversity because it now has so many meanings (e.g. Tuomisto 2010; Anderson et al. 2011) in ecology, biogeography, and palaeoecology.

Variation in pollen-stratigraphical data is simply the total amount of variation in a sequence. In the case of linear-based methods of data-analysis (ter Braak and Prentice 1988), it is estimated by the classical variance statistic. In non-linear unimodal-based methods (ter Braak and Prentice 1988), as here, it is estimated as total inertia (Šmilauer and Lepš 2014). There are many causes of variation in a pollen sequence, for example stratigraphical changes, inherent statistical variation in pollen counts, and differential pollen

preservation in different sediment types within sequences (see Maher et al. 2012).

Based on previous studies of vegetation development during interglacials spanning part of one precession cycle (e.g. Andersen 1994; Birks and Birks 2004; Tzedakis 2007b; Helmens 2014), we expect all sequences to show a generally unimodal pattern of compositional change or turnover within the Eemian reflecting the protocratic, mesocratic, and oligocratic plus telocratic phases (Q1, Fig. 1a). Additionally, we predict the total amount of turnover to have been highest in northern Europe, intermediate in central, and lowest in southern Europe, whereas total variation may have been highest in central Europe and lowest in the north (Q2, Fig. 1b). These hypotheses are based on the assumption that a different mix of extrinsic, intrinsic, and neutral processes play out in the different regions. At the beginning of the Eemian, most taxa would have already been present in the south and compositional change was likely driven primarily by extrinsic and/or intrinsic processes (sensu Williams et al. 2011a), such as climatic shifts, competition, and facilitation, along with neutral processes such as historical legacies and location of glacial-stage refugia (Jackson and Blois 2015). In the north, turnover may reflect species spread as driven by extrinsic and neutral processes. In the mesocratic phase, changes in all regions may have been a result primarily of intrinsic and neutral processes (e.g. Iversen 1960; Birks 1986) with some extrinsic processes, whereas changes in the oligocratic/telocratic phase may have been driven by an interaction of extrinsic, intrinsic, and neutral processes (e.g. Wardle et al. 2008).

Dataset and methods

Answering the two questions above (Q1, Q2) requires three major components—(1) representative Eemian pollen data across Europe, (2) critical screening to ensure they lack pre- or post-Eemian pollen spectra or hiatuses, are of comparable analytical standard, and have a consistent pollen nomenclature, and (3) robust numerical tools for consistent data analysis. Here we describe the methodology followed to address these components. See Electronic Supplementary Materials (ESM) 1 for details of the numerical methods and software.

Compiling a European Eemian pollen dataset

We implemented four criteria to select Eemian pollen sequences from different sources, including Pangaea, the European Pollen Database, and the Polish Pleistocene Pollen Database (Kupryjanowicz et al. 2018) (see ESM 2 for details). These criteria are (1) they must cover the entire

Eemian and display signals of protocratic, mesocratic, and oligocratic/telocratic phases of an interglacial, allowing for differences in how these phases are reflected in different parts of Europe (Birks 1986); (2) the sequences must have at least 15 analysed samples; (3) there must be no clear evidence for any major hiatuses; and (4) the sequences should have consistent pollen identifications of reasonable analytical standard. For sequences in geographically critical areas with few complete Eemian sequences and the primary data no longer available, published Eemian diagrams were digitised. Pollen values are expressed as percentages of total pollen excluding pollen of aquatics and all spores.

Because samples in sequences are in stratigraphical order, numerical analysis should, when appropriate, take account of this data-property and be constrained by sample order. Ideally, this constraint should be sample age but age estimates are not available for almost all Eemian sequences. In the absence of age estimates, we have used depth which reflects sample order within a sequence. Birks (2007) discusses using either age or depth as an external constraint in the ordination of Holocene sequences and obtains almost identical results irrespective of the type of constraint imposed.

As in any quantitative pollen-analytical study, there are palynological and numerical assumptions behind our study. There are nine major assumptions: five are palynological and four are numerical. The palynological assumptions are:

1. all the sequences are Eemian, are complete with no discernible hiatuses, and have roughly constant or at least monotonic sediment accumulation rates.
2. a minimum number of 15 samples in a sequence is adequate to assess variability and turnover (our numbers of samples range from 16 to 213; mean = 60; median = 52).
3. pollen taxonomy is of a comparable and consistent standard for all sequences, with all major non-arboreal taxa identified and recorded for each sequence (our taxa range from 13 to 99; mean = 48; median = 47).
4. in the absence of independent chronologies from northern Europe, we assume that the duration of the forested interval across Europe was approximately similar.

The numerical assumptions are:

1. detrended canonical correspondence analysis (DCCA) provides robust estimates of turnover and variation (see also ESM 1)
2. multivariate regression trees (MRT) and associated cross-validation are robust in identifying the optimal partition tree, even with small numbers of samples (Simpson and Birks 2012) and hence in accessing the amount of palynological variation in a sequence (see ESM 1)

3. the numerical results are not overly affected by pollen-count size and hence number of taxa.
4. the numerical results are not overly affected by the number of samples in a sequence.

These assumptions are discussed and assessed more fully in ESM 3.

Estimating compositional turnover within each sequence and total turnover for each pollen sequence

Compositional turnover is estimated using DCCA constrained by depth (or order) plus depth^2 (Birks 2007; ter Braak and Šmilauer 2012) and principal curves (PCs) (Simpson and Birks 2012). DCCA directly scales variables' (in our case pollen taxa) ordination scores such that their average within-sample standard deviation is unity along the ordination axes which are here constrained by sample depth or order. The change in weighted average (WA) sample scores (CaseR *sensu* ter Braak and Šmilauer 2012) reflects compositional change or turnover in standard deviation (SD) units. PCs are more "neutral" than DCCA in that they make fewer assumptions of the data than DCCA does. In the PC approach, a PC is fitted to the entire Eemian dataset of 2,840 samples. Sample locations along the final PC are determined and scaled to 0–1. Maximum difference of sample scores within a sequence is a relative turnover measure (Simpson and Birks 2012). For each sequence, total compositional turnover is estimated and within each sequence we explore patterns of turnover. Emphasis here is placed on the DCCA results for both total turnover and changes within a sequence because they are expressed in ecologically interpretable SD units of taxon turnover (Figs. 2, 3; ESM 4). The PC results for total turnover are summarised in Fig. 3b.
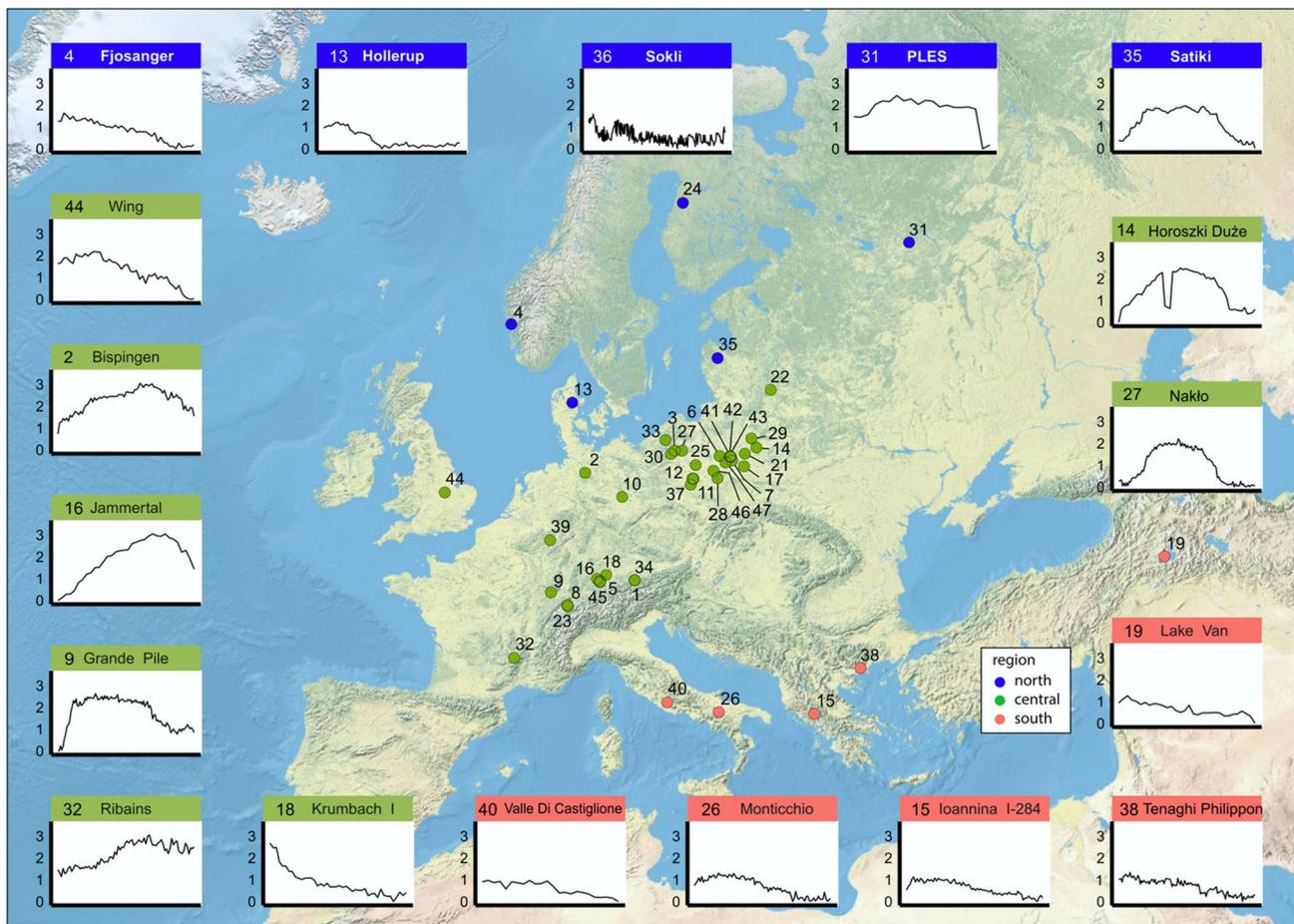

Fig. 2 Map of the 47 analysed Eemian pollen sequences and individual sample scores (standard deviation units) of selected detrended canonical correspondence analysis (DCCA) axis 1 plots for 18 sequences (the remaining 29 sequences are in ESM 8). Colours of locations indicate assigned region (blue = north; green = central; salmon = south). The number at each location corresponds with sequence numbers in ESM 2. The sample scores are plotted with the oldest (bottom) at the far left and the youngest (top) at the far right. The individual sample scores are weighted averages of the response (pollen taxa) variable scores (also applies to ESM 8)

Fig. 3 Total compositional turnover in each sequence plotted against latitude estimated by **a** detrended canonical correspondence analysis (DCCA; in standard deviation units) and **b** principal curves (PC; proportional distance); **c** total inertia or variation for each sequence estimated by DCCA; and **d** the proportions of optimal partitions to total number of samples in a sequence for each region. The fitted lines in **a, b,** and **c** are a fitted generalised linear model with a Gaussian distribution with a second-order polynomial (grey shading is the 95% confidence interval). The DCCA-based turnover for each sequence is estimated as the range in sample scores (weighted averages of the taxon scores) within the sequence
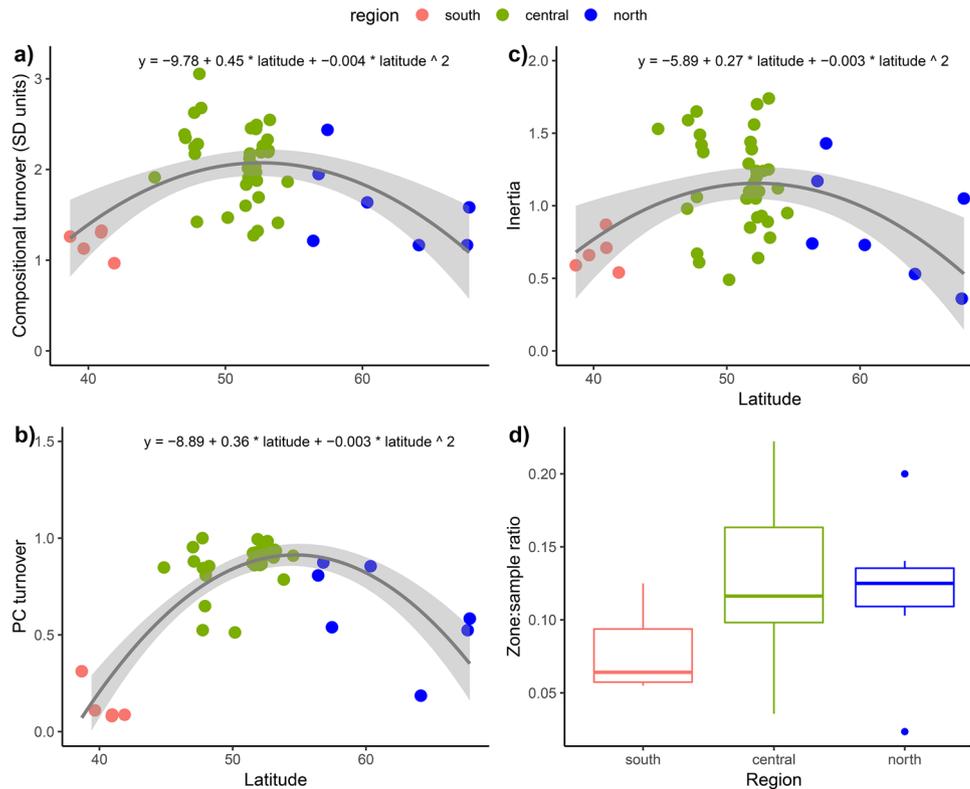
Estimating total variation for a sequence

Two contrasting numerical approaches are used to estimate total variation for each sequence: (1) total inertia (= weighted variance) estimated by correspondence analysis for each sequence in the absence of any external constraints (ter Braak and Šmilauer 2012) and (2) sequence partitioning using multivariate regression trees (MRTs) (Simpson and Birks 2012) and cross-validation to estimate the optimal number of partitions ("zone boundaries"). Optimal partition number depends on the number of samples in a sequence. We thus express the number of optimal partitions as a proportion of the number of samples. This reflects the amount of palynological variation within a sequence. Estimates of variation are summarised in Fig. 3c, d and ESM 4.

Results

We assemble 47 suitable sequences from 14 countries grouped into three regions (above 60°N, 45–60°N, below 45°N; Fig. 2; ESM 2). Full analytical results are given in ESM 4–7. The sequences range from 16 to 213 samples and 13–99 pollen taxa after basic taxonomic harmonisation. The dataset is chosen to cover as much of Europe as possible and to contain representative (but not all) Eemian sequences from Europe. Some areas, however, have many more Eemian

sequences than others (e.g. N Germany and Poland compared with Scandinavia).

There is a distinct temporal pattern of compositional change within each sequence over geographical space displayed by the individual sample scores (SD units) on DCCA axis 1 (Figs. 2, 3; ESM 8). The observed patterns naturally reflect site-specific changes, but it is possible to identify two general patterns where the DCCA sample values show either a gradually changing linear trend or a unimodal pattern where it reaches a peak and then slowly declines. Of the 31 sequences with a unimodal pattern, 27 occur in central Europe. Four northern sequences show a unimodal pattern and no southern sequence shows such a pattern. Linear trends are found in all regions (3 in northern, 8 in central, 5 in southern Europe) (Fig. 2; ESM 8, 9).

The greatest Eemian turnover and variation are in central Europe, whereas the southern and northern regions show less change (Fig. 3; ESM 8, 9). Total compositional turnover (DCCA, Fig. 3a; PC, Fig. 3b) and inertia (weighted variance) (Fig. 3c) have peaks between 47 and 55°N. Lowest values are above 60°N and are low south of 45°N. In contrast, the proportion of optimal partitions has highest values in central and north Europe (Fig. 3d). The null hypothesis that the mean change in optimal partitions does not differ between regions is not rejected. An analysis of variance indicates a probability > 0.05 that the null hypothesis is true ($F = 2.575$, $p = 0.088$).

Discussion

We compiled an Eemian pollen sequence dataset from across Europe, based on a set of predefined criteria and assumptions, to explore the magnitude of compositional turnover and total variation in Eemian pollen sequences. We show that there is substantial spatial variation in both variables, presumably reflecting responsiveness to various degrees of extrinsic, intrinsic, and neutral processes at local and regional scales during the Eemian (Birks 1986; Williams et al. 2011a; Jackson and Blois 2015).

Our Eemian dataset shows that there are important geographical voids of complete Eemian pollen sequences—none in Ireland and Iberia, few in Britain and France, and, not surprisingly, very few in much of Scandinavia that was heavily glaciated after the Eemian. Studies focussing on interglacial dynamics in comparison to the Holocene would benefit from a better geographical coverage of Eemian sequences to assess all vegetation types and climate conditions of the continent.

Pollen sequences in central Europe display the expected unimodal pattern (Fig. 2), but surprisingly, several sequences from across Europe, especially in the north and the south, show a gradually changing linear trend (cf. Fig. 1b). Less palynological change in the south and the north (Fig. 3) could imply that the taxa are shifting abundances between a few equally abundant taxa, thereby displaying a gradual changing pattern of turnover instead of a unimodal pattern (Q1).

We show that the greatest Eemian variation and turnover are in central Europe (Fig. 3), whereas there are fewer compositional changes in the southern and the northern regions (Q2). This is only partly consistent with the prior expectation of a unimodal trend in turnover during the entire Eemian (Fig. 1b). One possible explanation for the greatest change in central Europe is that during the Eemian there was a great variety and replacement of forest trees and shrubs (e.g. *Carpinus, Corylus, Quercus, Taxus, Tilia, Ulmus*) contributing to the regional pollen deposition, thereby providing a greater potential for palynological compositional turnover to be detected by a technique such as DCCA. Such pollen taxa have high N2 values where N2 (ter Braak and Verdonschot 1995) is the effective number of occurrences of a given taxon. DCCA is based on weighted averages, and N2 is effectively determined by taxa with high abundances (ter Braak and Verdonschot 1995).

An alternative and more convincing hypothesis to explain differences between the predicted (Fig. 1b) and observed (Figs. 2, 3; ESM 8, 9) patterns is that in southern Europe many taxa were already present at the onset of the Eemian (Bennett et al. 1991; Tzedakis et al. 2013).

The observed pollen-stratigraphical changes there may be mostly a result of intrinsic processes such as facilitation and competition between species and of neutral processes leading to a gradual shift from a landscape dominated by evergreen sclerophyll and deciduous-*Quercus* and *Ulmus* to a vegetation with later expansion of *Carpinus, Ostrya*, and *Abies* into locally favourable habitats. Such changes may be recorded palynologically as relatively low turnover (Fig. 3).

An additional related hypothesis for the observed contrasting patterns in southern and central Europe (Fig. 3; ESM 8, 9) involves a detailed consideration of the pollen records. While a number of southern European pollen sequences show a pattern of early, middle, and late expanding taxa not dissimilar to that of central Europe (Tzedakis et al. 2001), the main taxa (e.g. deciduous-*Quercus, Ulmus*) tend to persist through most of the Eemian with later expansions of *Carpinus, Ostrya*, and *Abies* superimposed on the existing assemblages. In central Europe, by comparison, there is a replacement of the early dominant taxa by later arrivals (similar to a relay), leading to a more accentuated and greater turnover. These patterns (relay vs expansion plus persistence of early taxa) may reflect climate differences. As climate shifted towards cooler temperatures during the course of the Eemian (Fig. 1a), the early thermophilous taxa may have declined in central Europe, while in the south, temperature (and precipitation) may not have become limiting, allowing the persistence of these taxa (e.g. Bennett et al. 1991), resulting in reduced turnover and variation.

The low palynological turnover and variation in northern Europe (Fig. 3) may reflect the relatively low pollen richness with few abundant taxa of restricted competitive abilities, especially trees, in the Eemian. The restricted arboreal flora may simply have been a result of climatic limitations. The detailed study at Sokli in northern Finland (Salonen et al. 2018) suggests, however, that thermophilous taxa such as *Corylus* were present and persisted in the north until the close of the Eemian, perhaps because of a major decrease in seasonality in the late Eemian with increase in winter insolation.

An alternative, more general and simpler hypothesis (and hence more attractive) for the observed patterns in turnover is 'silent palynological turnover'. North of the Alps today there are only two native *Quercus* species, one native *Pinus* species, one native *Abies* species, and one native *Juniperus* species. In contrast, in southern Europe all of these genera comprise several, if not many (e.g. *Quercus*), species. The pollen, however, of the various species within these genera cannot generally be distinguished. This pollen species-morphological limitation may result in compositional turnover at the species level not being detected palynologically. In central and northern Europe with only one or two species in these genera,

turnover is at or near the species level and is thus more visible palynologically. Such silent turnover could thus contribute, at least in part, to the observed patterns within Europe as a whole (Fig. 3; ESM 8, 9). It also suggests that the apparent persistence of some genera in southern European sequences may result in a potentially misleading record of the amount of ecological turnover that actually took place during the Eemian.

The hypothetical model of turnover and variation (Fig. 1b) is largely refuted by the patterns detected in this study (Fig. 3; ESM 8, 9). The contrasting hypotheses as explanations for the observed patterns highlight how much there is to be discovered about the palaeoecology and vegetation dynamics of the Eemian.

The DCCA compositional turnover for the Eemian is higher than for the Holocene (11 ka) in over 40 sites in Scandinavia and Britain (Birks, unpublished data; Birks 2007). Future studies include extending the geographical coverage of Holocene turnover estimates into central and southern Europe so as to compare Eemian and Holocene turnover for nearby sites.

Conclusions

We have compiled a dataset of 47 representative Eemian pollen sequences from across Europe. We have consistently analysed the sequences using multivariate numerical methods to estimate total pollen compositional change (turnover) and total variation for each sequence and to explore how turnover changes within each sequence and between sequences. The turnover and variation estimates show coherent but unexpected geographical and temporal patterns. They provide a basis for developing hypotheses about palynological changes during the Eemian and their possible causes. This demonstration that numerical analysis of our Eemian dataset produces robust and ecologically interpretable patterns gives confidence in our dataset. Further questions about Eemian vegetation dynamics and history will be explored using this dataset in subsequent studies.

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