Compositional turnover and variation in Eemian pollen sequences in Europe

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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 i) total compositional turnover and total variation for each sequence and ii) 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.

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63   **Keywords**: detrended canonical correspondence analysis, extrinsic processes, inertia, intrinsic
64   processes, last interglacial dataset, multivariate regression trees, neutral processes, principal curves

Introduction

The last interglacial (Eemian, c. 129–116 thousand years ago (ka)) is the most extensively studied pre-Holocene stage of the Quaternary (Tzedakis 2007a). It is characterised during its early part by a stronger 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. 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 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?

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

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

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

137 oligocratic/telocratic phase may have been driven by an interaction of extrinsic, intrinsic, and neutral
138 processes.

Dataset and methods

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

Compiling a European Eemian pollen dataset

147 We implemented four criteria (Box 1) to select Eemian pollen sequences from different sources,
148 including Pangaea, the European Pollen Database, and the Polish Pleistocene Pollen Database
149 (Kupryjanowicz et al. 2018a) (see ESM 2 for details). For sequences in geographically critical areas with
150 few complete Eemian sequences and the primary data no longer available, published Eemian diagrams
151 were digitised. Pollen values are expressed as percentages of total pollen excluding pollen of aquatics
152 and all spores.

Box 1.

Criteria for including sequences in the Eemian dataset
1. 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. Have at least 15 analysed samples
3. Have no clear evidence of major hiatuses
4. Have consistent pollen identifications of reasonable analytical standard

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Box 2.

Assumptions (see also ESM 3)

Palynological

i) Sequences are all Eemian, are complete with no discernible hiatuses, and have roughly constant monotonic sediment accumulation rates

ii) A minimum number of 15 samples in a sequence is adequate to assess variability and turnover. Range of sample numbers is 16–213 (mean = 60; median = 52)

iii) Pollen taxonomy is of a comparable and consistent standard for all sequences, with all major non-arboreal taxa identified and recorded for each sequence. Range of taxa is 13–99 (mean = 48; median = 47)

iv) Digitised data are complete and of sufficient quality for analysis

v) In the absence of independent chronologies from northern Europe, we assume that the duration of the forested interval across Europe was approximately similar

Numerical

vi) DCCA provides robust estimates of turnover and variation (see also ESM 1)

vii) Multivariate regression trees (MRT) and associated cross-validation are robust in identifying the optimal

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154   Because samples in sequences are in stratigraphical order, numerical analysis should, when

155 appropriate, take account of this data-property and be constrained by sample order. Ideally, this

156 constraint should be sample age but age estimates are not available for almost all Eemian sequences. In

157 the absence of age estimates, we have used depth which reflects sample order within a sequence. Birks

158 (2007) discusses using either age or depth as external constraints in the ordination of Holocene

159 sequences and obtains almost identical results irrespective of the type of constraint imposed. The

160 palynological and numerical assumptions behind our study are summarised in Box 2 and are discussed

161 more fully in ESM 3.

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

164 Compositional turnover is estimated using detrended canonical correspondence analysis (DCCA;

165 constrained by depth (or order) plus depth^2) (Birks 2007; ter Braak and Šmilauer 2012) and principal

166 curves (PCs) (Simpson and Birks 2012).

167   DCCA directly scales variables' (in our case pollen taxa) ordination scores such that their average

168 within-sample standard deviation is unity along the ordination axes which are here a mix of sample

169 depth or order. The change in weighted average (WA) sample scores (*CaseR sensu* ter Braak and

170 Šmilauer 2012) reflects compositional change or turnover in standard deviation (SD) units. PCs are

171 more "neutral" than DCCA in that they make fewer assumptions of the data than DCCA does. In the

172 PC approach, a PC is fitted to the entire Eemian dataset of 2840 samples. Sample locations along the

173 final PC are determined and scaled to 0–1. Maximum difference of sample scores within a sequence is

174 a relative turnover measure (Simpson and Birks 2012). For each sequence, total compositional

175 turnover is estimated and within each sequence we explore patterns of turnover. Emphasis here is

176 placed on the DCCA results for both total turnover and changes within a sequence because they are

177 expressed in ecologically interpretable units of standard deviation (SD) of taxon turnover (Figs. 2–3;

178 ESM 8). The PC results for total turnover are summarised in Fig. 3b.

179 Estimating total variation for a sequence

180 Two contrasting numerical approaches are used to estimate total variation for each sequence: 1) total

181 inertia (=weighted variance) estimated by correspondence analysis for each sequence in the absence of

182 any external constraints (ter Braak and Šmilauer 2012) and 2) sequence partitioning using multivariate

183 regression trees (MRTs) (Simpson and Birks 2012) and cross-validation to estimate the optimal

184 number of partitions ("zone boundaries"). Optimal partition number depends on the number of

185 samples in a sequence. We thus express the number of optimal partitions as a proportion of the

186   number of samples. This reflects the amount of palynological variation within a sequence. Estimates of

187   variation are summarised in Fig. 3c and d.

Results

189   We assemble 47 suitable sequences from 14 countries grouped into three regions (above 60°N, 45–

190   60°N, below 45°N; Fig. 2; ESM 2). The sequences range from 16–213 samples and 13–99 pollen taxa

191   after basic taxonomic harmonisation (ESM 4). The dataset is chosen to cover as much of Europe as

192   possible and to contain representative (but not all) Eemian sequences from Europe. Some areas,

193   however, have many more Eemian sequences than others (e.g. N Germany and Poland compared with

194   Scandinavia).

195   There is a distinct temporal pattern of compositional change within each sequence over

196   geographical space displayed by the individual sample scores (SD units) on DCCA axis 1 (Figs. 2–3;

197   ESM 8). The observed patterns indicate site-specific changes, but it is also possible to identify two

198   general patterns where the DCCA sample values show either a gradually changing linear trend or a

199   unimodal pattern where it reaches a peak and then slowly declines. Of the 31 sequences with a

200   unimodal pattern, 27 occur in central Europe. Four northern sequences show a unimodal pattern and

201   no southern sequence shows such a pattern. Linear trends are found in all regions (3 in northern, 8 in

202   central, 5 in southern Europe) (Fig. 2; ESM 8).

203   The greatest Eemian turnover and variation are in central Europe, whereas the southern and

204   northern regions show less change (Fig. 3; ESM 9). Total compositional turnover (DCCA, Fig. 3a; PC,

205   Fig 3b) and inertia (Fig. 3c) have peaks between 47 and 55°N. Lowest values are above 60°N and are

206   low south of 45°N. In contrast, the proportion of optimal partitions has highest values in central and

207   north Europe (Fig. 3d). The null hypothesis that the mean change in optimal partitions does not differ

208   between regions is not rejected. An analysis of variance indicates a probability >0.05 that the null

209   hypothesis is true ($F = 2.575$, $p = 0.088$). Full analytical results are given in ESM 4–7.

Discussion

211   We compiled an Eemian pollen sequence dataset from across Europe, based on a set of predefined

212   criteria and assumptions, to explore the magnitude of compositional turnover and total variation in

213   Eemian pollen sequences. We show that there is substantial spatial variation in both variables,

214   presumably reflecting responsiveness to various degrees of extrinsic, intrinsic, and neutral processes at

215   local and regional scales during the Eemian (Birks 1986; Williams et al. 2011a; Jackson and Blois 2015).

216   Our Eemian dataset shows that there are important geographical voids of complete Eemian

217   pollen sequences – none in Ireland and Iberia, few in Britain and France, and, not surprisingly, very

218   few in much of Scandinavia that was heavily glaciated after the Eemian. Studies focusing on interglacial

219   dynamics in comparison to the Holocene would benefit from a better geographical coverage of
220   Eemian sequences to assess all vegetation types and climate conditions of the continent.

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

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

236   An alternative and more convincing hypothesis is that in southern Europe many taxa were already
237   present at the onset of the Eemian (Bennett et al. 1991; Tzedakis et al. 2013), and the observed pollen-
238   stratigraphical changes there may be mostly a result of intrinsic processes such as facilitation and
239   competition between species and of neutral processes leading to a gradual shift from a landscape
240   dominated by evergreen sclerophyll and deciduous-*Quercus* and *Ulmus* to a vegetation with later
241   expansion of *Carpinus, Ostrya,* and *Abies* into locally favourable habitats. Such changes may be recorded
242   palynologically as relatively low turnover (Fig. 3).

243   An additional related hypothesis for the observed contrasting patterns in southern and central
244   Europe (Fig. 3) involves a detailed consideration of the pollen records. While a number of southern
245   European pollen sequences show a pattern of early, middle, and late expanding taxa not dissimilar to
246   that of central Europe (Tzedakis et al. 2001), the main taxa (e.g. deciduous-*Quercus, Ulmus*) tend to
247   persist through most of the Eemian with later expansion of *Carpinus, Ostrya,* and *Abies* superimposed
248   on the existing assemblages. In central Europe, by comparison, there is a replacement of the early
249   dominant taxa by later arrivals (similar to a relay), leading to a more accentuated and greater turnover.
250   These patterns (relay vs expansion plus persistence of early taxa) may reflect climate differences. As
251   climate shifted towards cooler temperatures during the course of the Eemian (Fig. 1a), the early
252   thermophilous taxa may have declined in central Europe, while in the south, temperature (and
253   precipitation) may not have become limiting, allowing the persistence of these taxa (e.g. Bennett et al.
254   1991), resulting in reduced turnover and variation.

255   The low palynological turnover and variation in northern Europe (Fig. 3) may reflect the relatively

256   low pollen richness with few abundant taxa of restricted competitive abilities, especially trees, in the

257   Eemian. The restricted arboreal flora may simply have been a result of climatic limitations. The

258   detailed study at Sokli in northern Finland (Salonen et al. 2018) suggests, however, that thermophilous

259   taxa such as *Corylus* were present and persisted in the north until the close of the Eemian, perhaps

260   because of a major decrease in seasonality in the late Eemian with increase in winter insolation.

261   An alternative general hypothesis for the observed patterns in turnover is "silent palynological

262   turnover". North of the Alps today there are only two native *Quercus* species, one native *Pinus* species,

263   one native *Abies* species, and one native *Juniperus* species. In contrast, in southern Europe all of these

264   genera comprise several, if not many (e.g. *Quercus*), species. The pollen, however, of the various species

265   within these genera cannot generally be distinguished. This pollen species-morphological limitation

266   may result in compositional turnover at the species level not being detected. In central and northern

267   Europe with only one or two species in these genera, turnover is at or near the species level and is thus

268   more visible palynologically. "Silent turnover" could thus contribute, at least in part, to the observed

269   patterns within Europe as a whole (Fig. 3). It could also suggest the apparent persistence of some

270   genera in southern European sequences and result in a potentially misleading record of the amount of

271   ecological turnover that actually took place during the Eemian.

272   These contrasting hypotheses as explanations for the patterns detected in our study (Fig. 3)

273   highlight how much there is to be discovered about the palaeoecology and vegetation dynamics of the

274   Eemian.

275   The DCCA compositional turnover for the Eemian is higher than for the Holocene (11 ka) in

276   over 40 sites in Scandinavia and Britain (Birks, unpublished data; Birks 2007). Future studies include

277   extending the geographical coverage of Holocene turnover estimates into central and southern Europe

278   so as to compare Eemian and Holocene turnover for nearby sites.

Conclusions

280   We have compiled a dataset of 47 representative Eemian pollen sequences from across Europe. We

281   have consistently analysed the sequences using multivariate numerical methods to estimate total pollen

282   compositional change (turnover) and total variation for each sequence and to explore how

283   composition turnover changes within each sequence and between sequences. The turnover and

284   variation estimates show coherent but unexpected geographical and temporal patterns. They provide a

285   basis for developing hypotheses about palynological changes during the Eemian and their possible

286   causes. This demonstration that numerical analysis of our Eemian dataset produces robust and

287   ecologically interpretable patterns gives confidence in our dataset. Further questions about Eemian

288   vegetation dynamics and history will be explored using this dataset in subsequent studies.

289   _____

290   Data sources. See ESM 2.

291   Author contributions. Ideas – VAF, HJBB, BB; data compilation, digitising – SGAF, CRJ; data

292   management, harmonisation, screening – VAF, BB, HJBB, SGAF; computing – VAF, BB; discussion

293   and/or detailed comments –J-LdB, WG, BH, PK, DM, BR, CJFtB; writing and editing – HJBB, VAF,

294   PCT, SGAF, CRJ; data contributions –JRMA, J-LdB, WG, KH, BH, LK, OK, PK, MK, MM, AMM,

295   MN, BN, IAP, MR, JSS, VS, PCT, HW

296   All authors read and commented on the manuscript, and gave final approval for publication.

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References

308   Andersen ST (1994) History of the terrestrial environment in the Quaternary of Denmark. Bulletin
309   of the Geological Society of Denmark 41:219-228
310   Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV,
311   Comita LS, Davies KF, Harrison SP, Kraft NJB, Stegen JC, Swenson NG (2011) Navigating the
312   multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters
313   14:19-28. doi:10.1111/j.1461-0248.2010.01552.x
314   Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Global
315   Ecology and Biogeography 19 (1):134-143. doi:10.1111/j.1466-8238.2009.00490.x
316   Bennett KD, Tzedakis PC, Willis KJ (1991) Quaternary refugia of north European trees. Journal of
317   Biogeography 18 (1):103-115
318   Birks HJB (1986) Late Quaternary biotic changes in terrestrial and limnic environments, with
319   particular reference to north west Europe. In: Berglund BE (ed) Handbook of Holocene
320   Palaeoecology and Palaeohydrology J Wiley & Sons, Chichester, pp 3-65
321   Birks HJB (2007) Estimating the amount of compositional change in late-Quaternary pollen-
322   stratigraphical data. Vegetation History and Archaeobotany 16:197-202. doi:10.1007/s00334-
323   006-0079-1
324   Birks HJB, Birks HH (2004) The rise and fall of forests. Science 305 (5683):484-485
325   Brauer A, Allen JRM, Mingram J, Dulski P, Wulf S, Huntley B (2007) Evidence for last interglacial
326   chronology and environmental change from southern Europe. Proceedings of the National
327   Academy of Sciences USA 104:450-455
328   Buckley LB, Jetz W (2008) Linking global turnover of species and environments. Proceedings of the
329   National Academy of Sciences USA 105 (46):17836-17841. doi:10.1073/pnas.0803524105

330   Descombes P, Vittoz P, Guisan A, Pellissier L (2017) Uneven rate of plant turnover along elevation
331   in grasslands. Alpine Botany 127 (1):53-63. doi:10.1007/s00035-016-0173-7
332   Dutton A, Carlson AE, Long AJ, Milne GA, Clark PU, DeConto R, Horton BP, Rahmstorf S, Raymo ME
333   (2015) Sea-level rise due to polar ice-sheet mass loss during past warm periods. Science 349
334   (6244):aaa4019. doi:10.1126/science.aaa4019
335   Fischer H, Meissner KJ, Mix AC, Abram NJ, Austermann J, Brovkin V, Capron E, Colombaroli D,
336   Daniau A-L, Dyez KA, Felis T, Finkelstein SA, Jaccard SL, McClymont EL, Rovere A, Sutter J,
337   Wolff EW, Affolter S, Bakker P, Ballesteros-Cánovas JA, Barbante C, Caley T, Carlson AE,
338   Churakova O, Cortese G, Cumming BF, Davis BAS, de Vernal A, Emile-Geay J, Fritz SC, Gierz P,
339   Gottschalk J, Holloway MD, Joos F, Kucera M, Loutre M-F, Lunt DJ, Marcisz K, Marlon JR,
340   Martinez P, Masson-Delmotte V, Nehrbass-Ahles C, Otto-Bliesner BL, Raible CC,
341   Risebrobakken B, Sánchez Goñi MF, Arrigo JS, Sarnthein M, Sjolte J, Stocker TF, Velasquez
342   Alvárez PA, Tinner W, Valdes PJ, Vogel H, Wanner H, Yan Q, Yu Z, Ziegler M, Zhou L (2018)
343   Palaeoclimate constraints on the impact of 2 °C anthropogenic warming and beyond. Nature
344   Geoscience 11 (7):474-485. doi:10.1038/s41561-018-0146-0
345   Harting P (1874) De bodem van het Eemdal. Verslagen en Mededelingen van de Koninklijke
346   Academie van Wetenschappen, Afdeling Naturkunde II 8:282-290
347   Helmens KF (2014) The Last Interglacial-Glacial cycle (MIS 5-2) re-examined based on long proxy
348   records from central and northern Europe. Quaternary Science Reviews 86:115-143.
349   doi:10.1016/j.quascirev.2013.12.012
350   Iversen J (1960) Problems of the early post-glacial forest development in Denmark. Danmarks
351   Geologiske Undersøgelse IV 4 (3):1-32
352   Jackson ST, Blois JL (2015) Community ecology in a changing environment: Perspectives from the
353   Quaternary. Proceedings of the National Academy of Sciences USA 112 (16):4915-1921.
354   doi:10.1073/pnas.1403664111
355   Jarzyna MA, Finley AO, Porter WF, Maurer BA, Beier CM, Zuckerberg B (2014) Accounting for the
356   space-varying nature of the relationships between temporal community turnover and the
357   environment. Ecography 37 (11):1073-1083. doi:10.1111/ecog.00747
358   Jessen K, Milthers V (1928) Stratigraphical and paleontological studies of interglacial fresh-water
359   deposits in Jutland and northwest Germany. Danmarks Geologiske Undersøgelse II 48:1-379
360   Kühl N (2003) Der Bestimmung botanisch-klimatolgischer Transferfunktion und die
361   Rekonstruktion der hodennahen Klimazustandes in Europa wähend der Eem-Warmzeit.
362   Dissertationes Botanicæ 375:1-149
363   Kukla GJ, Bender ML, de Beaulieu J-L, Bond G, Broecker WS, Cleveringa P, Gavin JE, Herbert TD,
364   Imbrie J, Jouzel J, Keigwin LD, Knudsen K-L, McManus JF, Merkt J, Muhs DR, Müller H, Poore
365   RZ, Porter SC, Seret G, Shackleton NJ, Turner C, Tzedakis PC, Winograd IJ (2002) Last
366   Interglacial Climates. Quaternary Research 58 (1):2-13. doi:10.1006/qres.2001.2316
367   Kupryjanowicz M, Nalepka D, Pidek IA, Walanus A, Balwierz Z, Bińka K, Fiłoc M, Granoszewski W,
368   Kołaczek P, Majecka A, Malkiewicz M, Nita M, Noryśkiewicz B, Winter H (2018a) The east-
369   west migration of trees during the Eemian Interglacial registered on isopollen maps of
370   Poland. Quaternary International 467:178-191. doi:10.1016/j.quaint.2017.08.034
371   Milner AM, Müller UC, Roucoux KH, Collier REL, Pross J, Kalaitzidis S, Christanis K, Tzedakis PC
372   (2013) Environmental variability during the Last Interglacial: a new high-resolution pollen
373   record from Tenaghi Philippon, Greece. Journal of Quaternary Science 28 (2):113-117.
374   doi:10.1002/jqs.2617
375   Müller H (1974) Pollenanalytische Untersuchungen und Jahresschichtenzählungen an der
376   holsteinzeitlichen Kieselgur von Munster-Breloh. Geologisches Jahrbuch A21:107-140
377   Salonen JS, Helmens KF, Brendryen J, Kuosmanen N, Väliranta M, Goring S, Korpela M, Kylander
378   M, Philip A, Plikk A, Renssen H, Luoto M (2018) Abrupt high-latitude climate events and
379   decoupled seasonal trends during the Eemian. Nature Communications 9 (1):#2851.
380   doi:10.1038/s41467-018-05314-1

381 Sánchez Goñi MF, Bakker P, Desprat S, Carlson AE, van Meerbeeck CJ, Peyron O, Naughton F,
382   Fletcher WJ, Eynaud F, Rossignol L, Renssen H (2012) European climate optimum and
383   enhanced Greenland melt during the Last Interglacial. Geology 40 (7):627-630.
384   doi:10.1130/G32908.1
385 Shackleton NJ, Sánchez Goñi MF, Pailler D, Lancelot Y (2003) Marine Isotope Substage 5e and the
386   Eemian interglacial. Global and Planetary Change 36 (3):151-155. doi:10.1016/S0921-
387   8181(02)00181-9
388 Simpson GL, Birks HJB (2012) Statistical learning in palaeolimnology. In: Birks HJB, Lotter AF,
389   Juggins S, Smol JP (eds) Tracking Environmental Change Using Lake Sediments Volume 5:
390   Data Handling and Numerical Techniques. Springer, Dordrecht, pp 249-327. doi:10.1007/978-
391   94-007-2745-8_9
392 ter Braak CJF, Šmilauer P (2012) Canoco Reference Manual and User's Guide: software for
393   ordination (version 5.0). Microcomputer Power, Ithaca, New York
394 ter Braak CJF, Verdonschot PFM (1995) Canonical correspondence analysis and related
395   multivariate methods in aquatic ecology. Aquatic Sciences 57:255-289
396 Tuomisto H (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 2.
397   Quantifying beta diversity and related phenomena. Ecography 33:23-45. doi:10.1111/j.1600-
398   0587.2009.06148.x
399 Tzedakis PC (2007a) Pollen records, last interglacial of Europe. In: Elias SA (ed) Encyclopedia of
400   Quaternary Science, vol 3. Elsevier, Amsterdam, pp 2597-2605
401 Tzedakis PC (2007b) Seven ambiguities in the Mediterranean palaeoenvironmental narrative.
402   Quaternary Science Reviews 26 (17-18):2042-2066. doi:10.1016/j.quascirev.2007.03.014
403 Tzedakis PC, Andrieu V, de Beaulieu JL, Birks HJB, Crowhurst S, Follieri M, Hooghiemstra H, Magri
404   D, Reille M, Sadori L, Shackleton NJ, Wijmstra TA (2001) Establishing a terrestrial
405   chronological framework as a basis for biostratigraphical comparisons. Quaternary Science
406   Reviews 20 (16-17):1583-1592
407 Tzedakis PC, Channell JET, Hodell DA, Kleiven HF, Skinner LC (2012) Determining the natural length
408   of the current interglacial. Nature Geoscience 5 (2):138-141. doi:10.1038/ngeo1358
409 Tzedakis PC, Drysdale RN, Margari V, Skinner LC, Menviel L, Rhodes RH, Taschetto AS, Hodell DA,
410   Crowhurst SJ, Hellstrom JC, Fallick AE, Grimalt JO, McManus JF, Martrat B, Mokeddem Z,
411   Parrenin F, Regattieri E, Roe K, Zanchetta G (2018) Enhanced climate instability in the North
412   Atlantic and southern Europe during the Last Interglacial. Nature Communications 9 (1):4235.
413   doi:10.1038/s41467-018-06683-3
414 Tzedakis PC, Emerson BC, Hewitt GM (2013) Cryptic or mystic? Glacial tree refugia in northern
415   Europe. Trends in Ecology & Evolution 28 (12):696-704. doi:10.1016/j.tree.2013.09.001
416 Williams JW, Blois JL, Shuman BN (2011a) Extrinsic and intrinsic forcing of abrupt ecological
417   change: case studies from the late Quaternary. Journal of Ecology 99:664-677.
418   doi:10.1111/j.1365-2745.2011.01810.x
419 Zagwijn WH (1996) An analysis of Eemian climate in western and central Europe. Quaternary
420   Science Reviews 15:451-469

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Figure captions
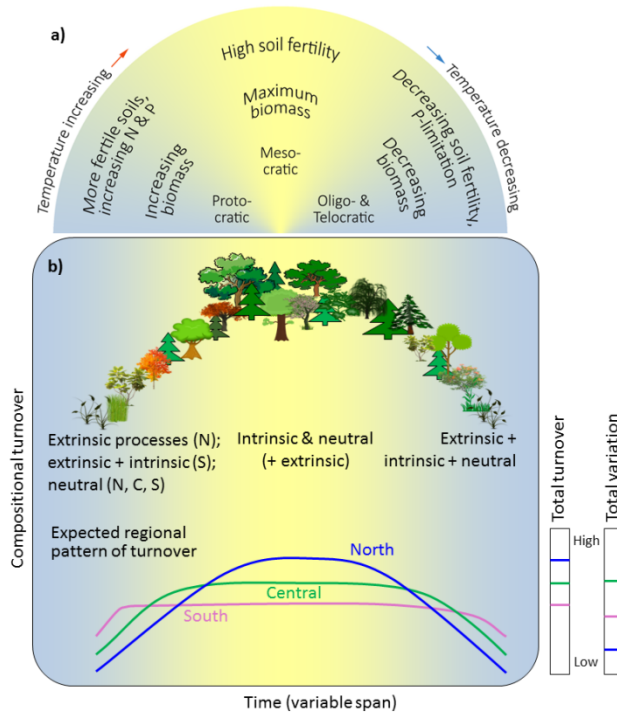
Fig. 1 Hypothetical responses of an ecosystem in the last interglacial (Eemian) in terms of biomass and fertility (modified from Birks & Birks, 2004). **a** The three phases of Eemian vegetation history, namely protocratic, mesocratic, and oligocratic plus telocratic, in response to changing temperature (outer circle). **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.
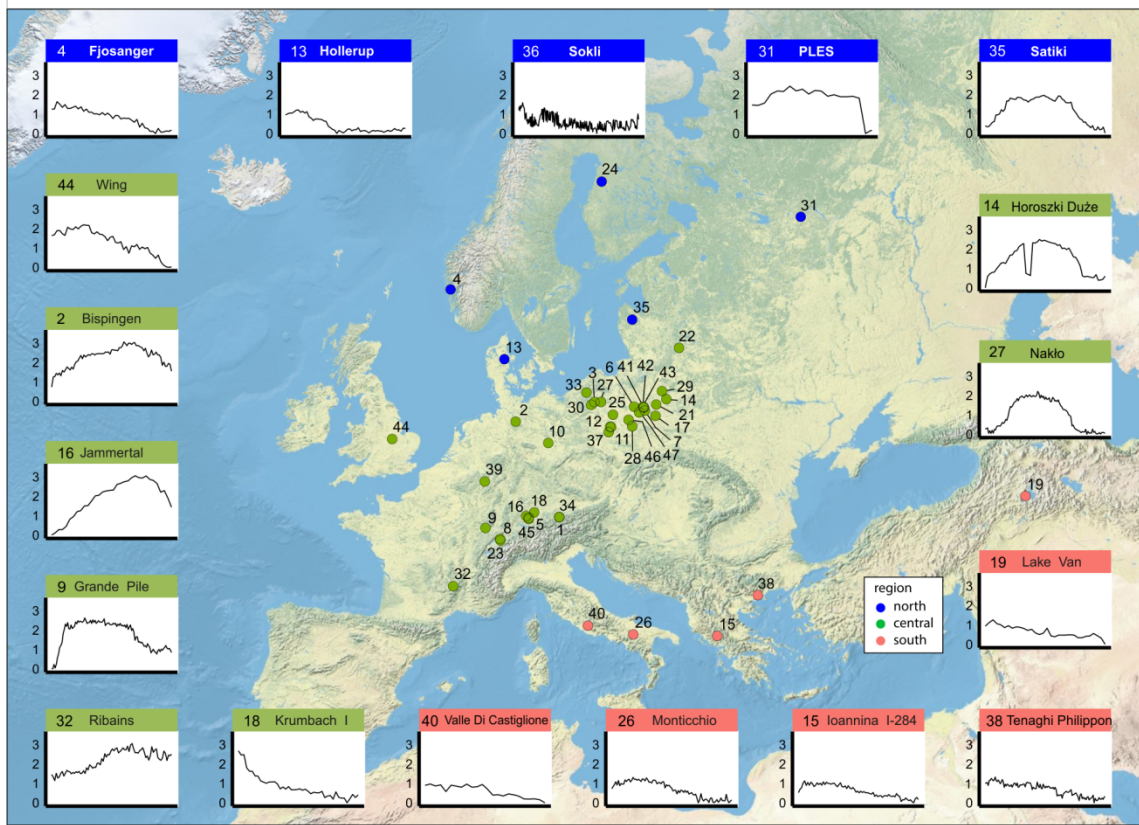
Fig. 2 Map of the 47 analysed Eemian pollen sequences and individual sample scores (standard deviation units) of selected detrended canonical correspondence analysis (DCCA) axis 1 plots for 18 sequences (the remaining 29 sequences are in ESM 8). Colours of locations indicate assigned region (blue = north; 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).

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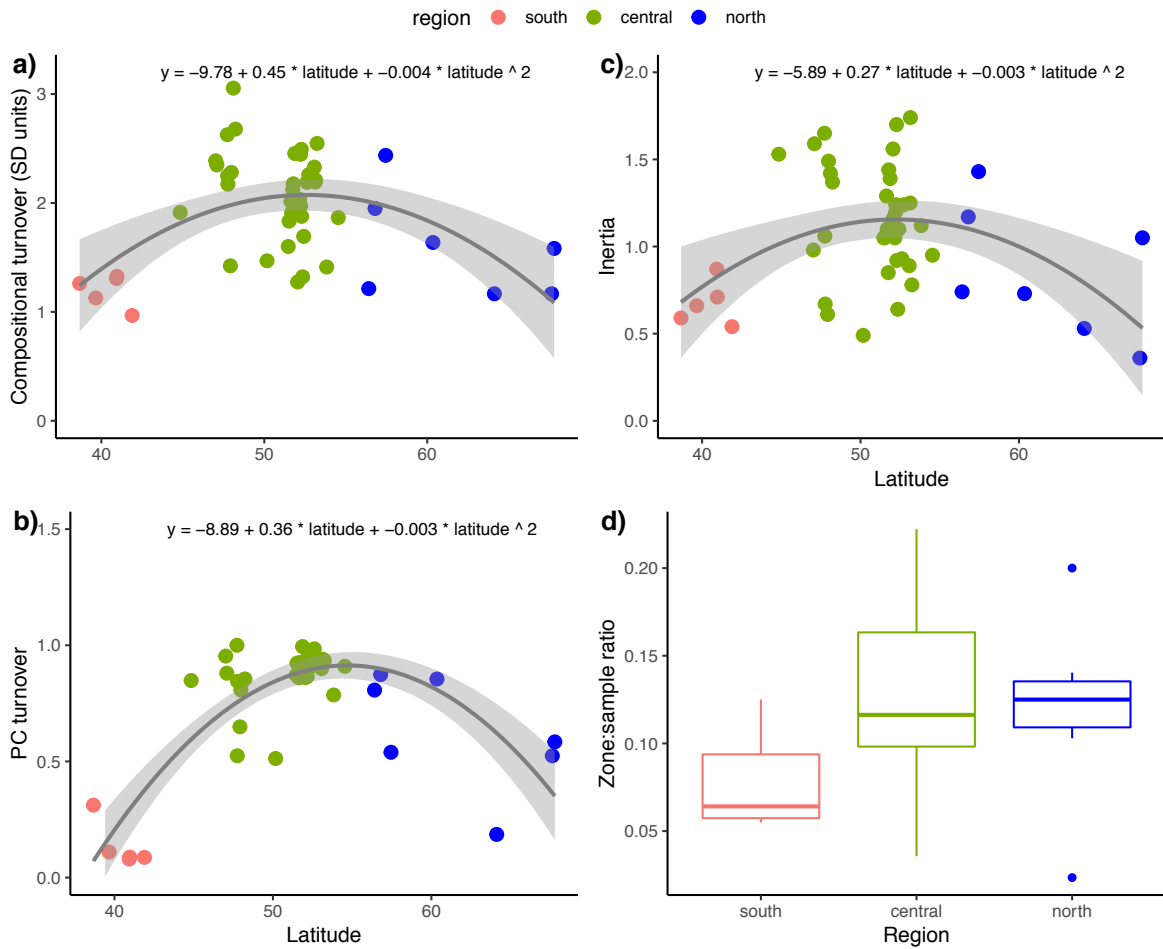
Fig. 3 Total compositional turnover in each sequence plotted against latitude estimated by **a** detrended canonical correspondence analysis (DCCA; in standard deviation units) and **b** principal curves (PC; proportional distance); **c** total inertia or variation for each sequence estimated by DCCA; 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.