

1 **Compositional turnover and variation in Eemian pollen**

2 **sequences in Europe**

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64

65 **Abstract**

66 The Eemian interglacial represents a natural experiment on how past vegetation with negligible human
67 impact responded to amplified temperature changes compared to the Holocene. Here, we assemble 47
68 carefully selected Eemian pollen sequences from Europe to explore geographical patterns of i) total
69 compositional turnover and total variation for each sequence and ii) stratigraphical turnover between
70 samples within each sequence using detrended canonical correspondence analysis, multivariate
71 regression trees, and principal curves. Our synthesis shows that turnover and variation are highest in
72 central Europe (47–55°N), low in southern Europe (south of 45°N), and lowest in the north (above
73 60°N). These results provide a basis for developing hypotheses about causes of vegetation change
74 during the Eemian and their possible drivers.

75

76 **Keywords:** Detrended canonical correspondence analysis, Extrinsic processes, Inertia, Intrinsic
77 processes, Last interglacial dataset, Multivariate regression trees, Neutral processes, Principal curves

78 **Introduction**

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

84 The duration of the last interglacial represents the interval of reduced ice volume, demarcated at
85 its onset by deglaciation and at its close by glacial inception (Tzedakis et al. 2012) and is broadly
86 equivalent to Marine Isotope sub-Stage 5e (~ 132 –116 ka) and the Eemian interglacial of north-west
87 Europe (Kukla et al. 2002). The term Eemian was introduced by Harting (1874) to describe a subsoil
88 characterised by warm marine molluscs in the Eem valley near Amersfoort in The Netherlands
89 (Tzedakis 2007a). Integrated palaeoceanographic and pollen analyses from the Portuguese Margin
90 show that the marine isotopic and terrestrial stage boundaries are not synchronous, with the interval of
91 temperate forest conditions extending from ~ 129 to ~ 111 ka (Shackleton et al. 2003; Tzedakis et al.
92 2018). Here we use the term ‘Eemian’ informally to refer to the forested interval (protocratic,
93 mesocratic, and oligocratic/telocratic phases – see Fig. 1a) in last interglacial pollen sequences across
94 Europe. While the long duration ($\sim 18,000$ years) of the forest interval in southern Europe is supported
95 by independent chronologies (Brauer et al. 2007), a shorter duration ($\sim 11,000$ years) has generally been
96 applied to north-central European pollen sequences on the basis of a partially annually laminated
97 record at Bispingen, Germany at 53 $^{\circ}\text{N}$ (Müller 1974). However, recent joint palaeoceanographic pollen
98 analyses from the Bay of Biscay (Sánchez Goñi et al. 2012) and comparisons with pollen sequences in
99 southern France and southern Germany indicate a long Eemian duration ($\sim 18,000$ years) at least as far
100 north as 48 $^{\circ}\text{N}$. It is possible that the unlaminated upper part of the Bispingen sequence represents a
101 longer time interval than presently assumed and that the duration of the forested interval in northern
102 Germany was approximately as long as farther south. In the absence of any independent chronology
103 and duration estimates, the length of the Eemian in Fennoscandia remains unclear.

104 Ever since the pioneering studies in Denmark and Germany by Jessen and Milthers (1928), many
105 Eemian pollen sequences have been analysed, focussing mainly on sedimentary settings, stratigraphies,
106 pollen assemblages, vegetation histories, dating, and climate (e.g. Zagwijn 1996; Kühl 2003; Tzedakis
107 2007a). Eemian pollen records present a valuable opportunity to study vegetation patterns across
108 broad spatial and temporal scales without extensive human impact (Kühl 2003; Tzedakis 2007a; Milner
109 et al. 2013). Ecological questions abound about the Eemian. For example, are Eemian inferred
110 vegetation patterns similar to Holocene patterns prior to human influence? How similar are Eemian
111 pollen stratigraphies across Europe? Are there consistent temporal patterns in the appearance,
112 expansion, and decline of major arboreal taxa across Europe? What are the spatial variations in pollen
113 compositional change (“turnover”) and total variation across Europe?

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

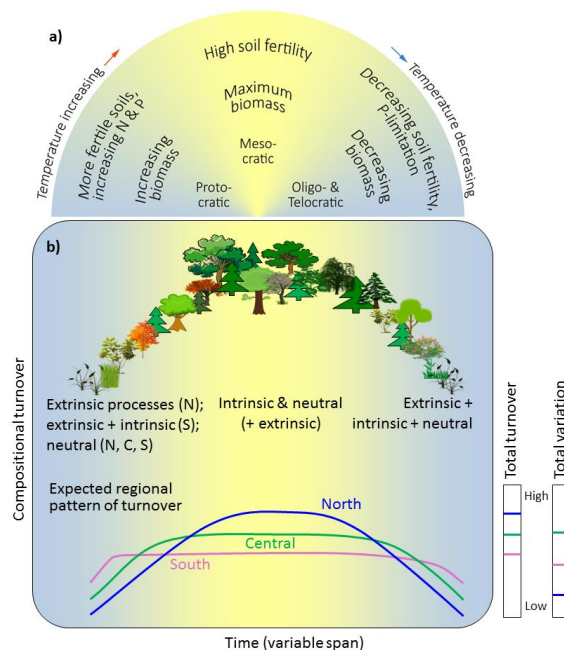
122 As the concept of turnover is rarely used in pollen analysis (see Birks 2007), we summarise what
123 this concept is. In community ecology, turnover is used to describe and possibly to quantify the
124 replacement of one species by another in an assemblage in space or time or both. In pollen analysis,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

135 Variation in pollen-stratigraphical data is simply the total amount of variation in a sequence. In
136 the case of linear-based methods of data-analysis (ter Braak and Prentice 1988), it is estimated by the
137 classical variance statistic. In non-linear unimodal-based methods (ter Braak and Prentice 1988), as
138 here, it is estimated as total inertia (Šmilauer and Lepš 2014). There are many causes of variation in a
139 pollen sequence, for example stratigraphical changes, inherent statistical variation in pollen counts, and
140 differential pollen preservation in different sediment types within a sequences (see Maher et al. 2012).

141 Based on previous studies of vegetation development during interglacials spanning part of one
142 precession cycle (e.g. Andersen 1994; Birks and Birks 2004; Tzedakis 2007b; Helmens 2014), we expect
143 all sequences to show a generally unimodal pattern of compositional change or turnover within the
144 Eemian reflecting the protocratic, mesocratic, and oligocratic plus telocratic phases (Q1; Fig. 1a).
145 Additionally, we predict the total amount of turnover to have been highest in northern Europe,
146 intermediate in central, and lowest in southern Europe, whereas total variation may have been highest
147 in central Europe and lowest in the north (Q2; Fig. 1b). These hypotheses are based on the assumption
148 that a different mix of extrinsic, intrinsic, and neutral processes play out in the different regions. At the
149 beginning of the Eemian, most taxa would have already been present in the south and compositional
150 change was likely driven primarily by extrinsic and/or intrinsic processes (*sensu* Williams et al. 2011a),

151 such as climatic shifts, competition, and facilitation, along with neutral processes such as historical
 152 legacies and location of glacial-stage refugia (Jackson and Blois 2015). In the north, turnover may
 153 reflect species spread as driven by extrinsic and neutral processes. In the mesocratic phase, changes in
 154 all regions may have been a result primarily of intrinsic and neutral processes (e.g. Iversen 1960; Birks
 155 1986) with some extrinsic processes, whereas changes in the oligocratic/telocratic phase may have
 156 been driven by an interaction of extrinsic, intrinsic, and neutral processes (e.g. Wardle et al. 2008).

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.



157

158 Dataset and methods

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

165 Compiling a European Eemian pollen dataset

166 We implemented four criteria to select Eemian pollen sequences from different sources, including
 167 Pangaea, the European Pollen Database, and the Polish Pleistocene Pollen Database (Kupryjanowicz
 168 et al. 2018a) (see ESM 2 for details). These criteria are (1) they must cover the entire Eemian and
 169 display signals of protocratic, mesocratic, and oligocratic/telocratic phases of an interglacial, allowing
 170 for differences in how these phases are reflected in different parts of Europe (Birks 1986); (2) the
 171 sequences must have at least 15 analysed samples; (3) there must be no clear evidence for any major

172 hiatuses; and (4) the sequences should have consistent pollen identifications of reasonable analytical
173 standard. For sequences in geographically critical areas with few complete Eemian sequences and the
174 primary data no longer available, published Eemian diagrams were digitised. Pollen values are
175 expressed as percentages of total pollen excluding pollen of aquatics and all spores.

176 Because samples in sequences are in stratigraphical order, numerical analysis should, when
177 appropriate, take account of this data-property and be constrained by sample order. Ideally, this
178 constraint should be sample age but age estimates are not available for almost all Eemian sequences. In
179 the absence of age estimates, we have used depth which reflects sample order within a sequence. Birks
180 (2007) discusses using either age or depth as external constraints in the ordination of Holocene
181 sequences and obtains almost identical results irrespective of the type of constraint imposed.

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

185 (1) all the sequences are Eemian, are complete with no discernible hiatuses, and have roughly
186 constant or at least monotonic sediment accumulation rates

187 (2) a minimum number of 15 samples in a sequence is adequate to assess variability and
188 turnover (our numbers of samples range from 16–213; mean = 60; median = 52)

189 (3) pollen taxonomy is of a comparable and consistent standard for all sequences, with all
190 major non-arboreal taxa identified and recorded for each sequence (our taxa range from 13–
191 99; mean = 48; median = 47)

192 (5) in the absence of independent chronologies from northern Europe, we assume that the
193 duration of the forested interval across Europe was approximately similar.

194 The numerical assumptions are

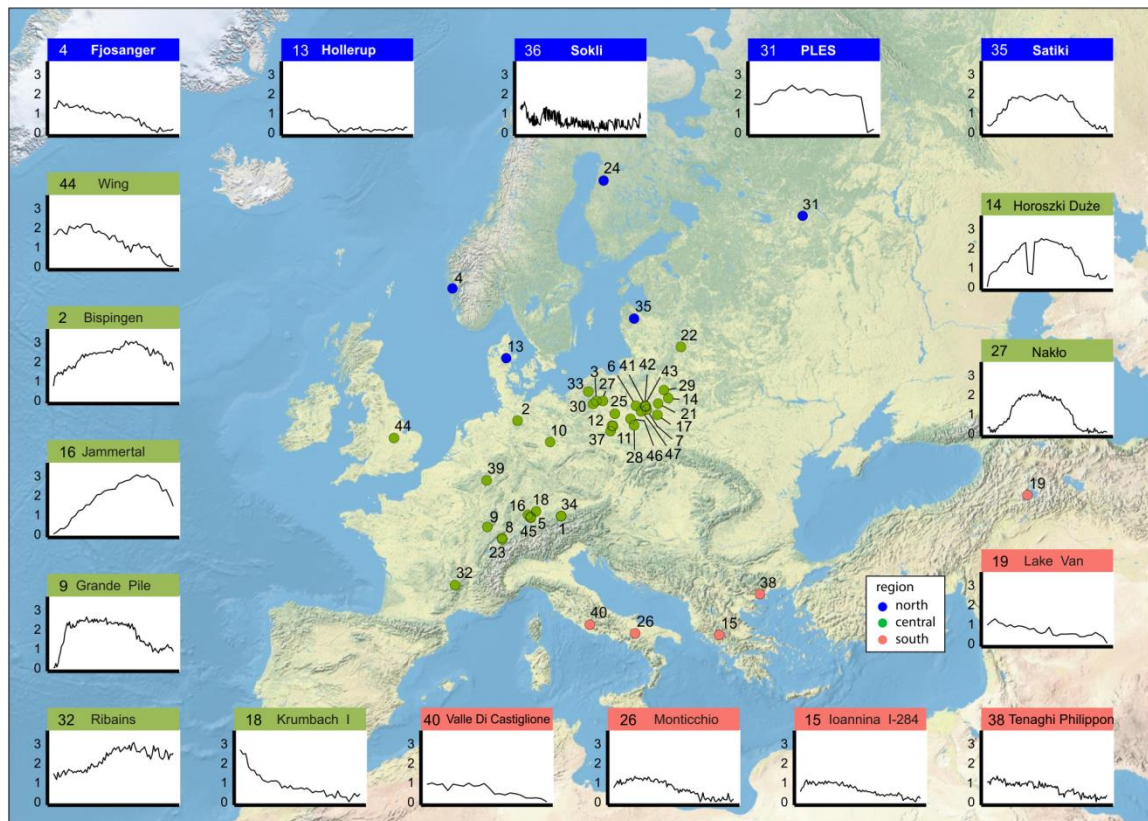
195 (1) detrended canonical correspondence analysis (DCCA) provides robust estimates of
196 turnover and variation (see also ESM 1)

197 (2) multivariate regression trees (MRT) and associated cross-validation are robust in
198 identifying the optimal partition tree, even with small numbers of samples (Simpson and Birks
199 2012) and hence in accessing the amount of palynological variation in a sequence (see ESM 1)

200 (3) the numerical results are not overly affected by pollen-count size and hence number of taxa

201 (4) the numerical results are not overly affected by the number of samples in a sequence.

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



203

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

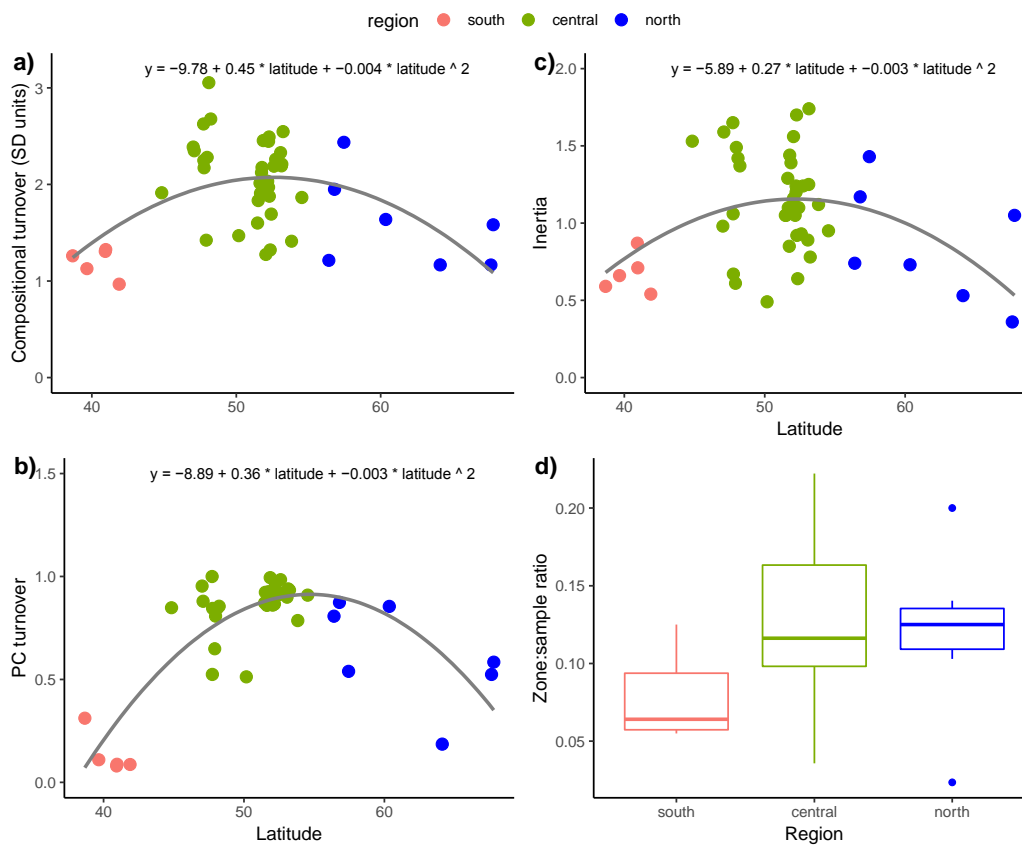
211 **Estimating compositional turnover within each sequence and total turnover for**
 212 **each pollen sequence**

213 Compositional turnover is estimated using DCCA constrained by depth (or order) plus depth² (Birks
 214 2007; ter Braak and Šmilauer 2012) and principal curves (PCs) (Simpson and Birks 2012). DCCA
 215 directly scales variables' (in our case pollen taxa) ordination scores such that their average within-
 216 sample standard deviation is unity along the ordination axes which are here constrained by sample
 217 depth or order. The change in weighted average (WA) sample scores (*CaseR sensu* ter Braak and
 218 Šmilauer 2012) reflects compositional change or turnover in standard deviation (SD) units. PCs are
 219 more “neutral” than DCCA in that they make fewer assumptions of the data than DCCA does. In the
 220 PC approach, a PC is fitted to the entire Eemian dataset of 2840 samples. Sample locations along the
 221 final PC are determined and scaled to 0–1. Maximum difference of sample scores within a sequence is
 222 a relative turnover measure (Simpson and Birks 2012). For each sequence, total compositional
 223 turnover is estimated and within each sequence we explore patterns of turnover. Emphasis here is

224 placed on the DCCA results for both total turnover and changes within a sequence because they are
 225 expressed in ecologically interpretable units of standard deviation (SD) of taxon turnover (Figs. 2–3;
 226 ESM 8). The PC results for total turnover are summarised in Fig. 3b.

227 **Estimating total variation for a sequence**

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



236

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

245 **Results**

246 We assemble 47 suitable sequences from 14 countries grouped into three regions (above 60°N, 45–
247 60°N, below 45°N; Fig. 2; ESM 2). The sequences range from 16–213 samples and 13–99 pollen taxa
248 after basic taxonomic harmonisation (ESM 4). The dataset is chosen to cover as much of Europe as
249 possible and to contain representative (but not all) Eemian sequences from Europe. Some areas,
250 however, have many more Eemian sequences than others (e.g. N Germany and Poland compared with
251 Scandinavia).

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

260 The greatest Eemian turnover and variation are in central Europe, whereas the southern and
261 northern regions show less change (Fig. 3; ESM 9). Total compositional turnover (DCCA, Fig. 3a; PC,
262 Fig 3b) and inertia (weighted variance) (Fig. 3c) have peaks between 47 and 55°N. Lowest values are
263 above 60°N and are low south of 45°N. In contrast, the proportion of optimal partitions has highest
264 values in central and north Europe (Fig. 3d). The null hypothesis that the mean change in optimal
265 partitions does not differ between regions is not rejected. An analysis of variance indicates a probability
266 >0.05 that the null hypothesis is true ($F = 2.575, p = 0.088$). Full analytical results are given in ESM 4–
267 7.

268 **Discussion**

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

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

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

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

294 An alternative and more convincing hypothesis to explain differences between the predicted (Fig.
295 1b) and observed (Figs 2 and 3; ESM 8, ESM 9) patterns is that in southern Europe many taxa were
296 already present at the onset of the Eemian (Bennett et al. 1991; Tzedakis et al. 2013). The observed
297 pollen-stratigraphical changes there may be mostly a result of intrinsic processes such as facilitation
298 and competition between species and of neutral processes leading to a gradual shift from a landscape
299 dominated by evergreen sclerophyll and deciduous-*Quercus* and *Ulmus* to a vegetation with later
300 expansion of *Carpinus*, *Ostrya*, and *Abies* into locally favourable habitats. Such changes may be recorded
301 palynologically as relatively low turnover (Fig. 3).

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

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

320 An alternative, more general and simpler hypothesis (and hence more attractive) for the observed
321 patterns in turnover is ‘silent palynological turnover’. North of the Alps today there are only two native
322 *Quercus* species, one native *Pinus* species, one native *Abies* species, and one native *Juniperus* species. In
323 contrast, in southern Europe all of these genera comprise several, if not many (e.g. *Quercus*), species.
324 The pollen, however, of the various species within these genera cannot generally be distinguished. This
325 pollen species-morphological limitation may result in compositional turnover at the species level not
326 being detected palynologically. In central and northern Europe with only one or two species in these
327 genera, turnover is at or near the species level and is thus more visible palynologically. Such silent
328 turnover could thus contribute, at least in part, to the observed patterns within Europe as a whole (Fig.
329 3; ESM 8, ESM 9). It also suggests that the apparent persistence of some genera in southern European
330 sequences may result in a potentially misleading record of the amount of ecological turnover that
331 actually took place during the Eemian.

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

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

340 **Conclusions**

341 We have compiled a dataset of 47 representative Eemian pollen sequences from across Europe. We
342 have consistently analysed the sequences using multivariate numerical methods to estimate total pollen
343 compositional change (turnover) and total variation for each sequence and to explore how
344 composition turnover changes within each sequence and between sequences. The turnover and
345 variation estimates show coherent but unexpected geographical and temporal patterns. They provide a
346 basis for developing hypotheses about palynological changes during the Eemian and their possible
347 causes. This demonstration that numerical analysis of our Eemian dataset produces robust and

348 ecologically interpretable patterns gives confidence in our dataset. Further questions about Eemian
349 vegetation dynamics and history will be explored using this dataset in subsequent studies.

350

351 **Data sources** See ESM 2.

352 **Author contributions** Ideas – VAF, HJBB, BB; data compilation, digitising – SGAF, CRJ; data
353 management, harmonisation, screening – VAF, BB, HJBB, SGAF; computing – VAF, BB; discussion
354 and/or detailed comments –J-LdB, WG, BH, PK, DM, BR, CJFtB; writing and editing – HJBB, VAF,
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