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3 # Patterns of modern pollen and plant richness across northern Europe

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29 **Summary**

30 1. Sedimentary pollen offers excellent opportunities to reconstruct vegetation changes over past

31 millennia. Number of different pollen taxa or pollen richness is used to characterise past plant

32 richness. To improve the interpretation of sedimentary pollen richness, it is essential to understand

33 the relationship between pollen and plant richness in contemporary landscapes. This study presents

34 a regional-scale comparison of pollen and plant richness from northern Europe and evaluates the

35 importance of environmental variables on pollen and plant richness.

36 2. We use a pollen dataset of 511 lake-surface pollen samples ranging through temperate, boreal,

37 and tundra biomes. To characterise plant diversity, we use a dataset formulated from the two largest

38 plant atlases available in Europe. We compare pollen and plant richness estimates in different

39 groups of taxa (wind-pollinated vs non-wind-pollinated, trees and shrubs vs herbs and grasses) and

40 test their relationships with climate and landscape variables.

41 3. Pollen richness is significantly positively correlated with plant richness (r=0.53). The pollen–

42 plant richness correlation improves (r=0.63) when high pollen-producers are downweighted prior to

43 estimating richness minimising the influence of pollen-production on the pollen richness estimate.

44 This suggests that methods accommodating pollen-production differences in richness estimates

45 deserve further attention and should become more widely used in Quaternary pollen diversity

46 studies.

47 4. The highest correlations are found between pollen and plant richness of trees and shrubs (r=0.83)

48 and of wind-pollinated taxa (r=0.75) suggesting that these are the best measures of broad-scale plant

49 richness over several thousands of square kilometres.

50 5. Mean annual temperature is the strongest predictor of both pollen and plant richness. Landscape

51 openness is positively associated with pollen richness but not with plant richness. Pollen-richness

52 values from extremely open and/or cold areas where pollen production is low, should be interpreted

53 with caution because low local pollen production increases the proportion of extra-regional pollen.

54 6. *Synthesis*. Our results confirm that pollen data can provide insights into past plant richness

55 changes in northern Europe, and with careful consideration of pollen production differences and

56 spatial scale represented, pollen data make it possible to investigate vegetation diversity trends over

57 long timescales and under changing climatic and habitat conditions.

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59 **Keywords**: climate, diversity, Holocene, landscape, palynological diversity, pollen–plant

60 relationship, Quaternary

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61   Summary in Estonian

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Taimede ja õietolmu liigirikkuse seosed Põhja-Euroopas

64   1. Järvede ja soode settes leiduva õietolmu abil rekonstrueeritakse viimaste kümnete tuhandete

65   aastate taimkatte muutusi. Soontaimede liigirikkust minevikus hinnatakse tihti erinevate

66   õietolmutüüpide arvu alusel. Õietolmu ja taimede liigirikkuse seoste uurimine tänapäeva maastikes

67   aitab sette õietolmuandmeid paremini tõlgendada. Käesolevas uuringus keskendume õietolmu ja

68   taimede liigirikkuse seostele Põhja-Euroopas ja hindame erinevate keskkonnategurite mõju nii

69   taimede ja kui õietolmu liigirikkusele.

70   2. Uuringus kasutatav õietolmu andmestik pärineb 511 järve pinnasettest ja vaadeldav piirkond

71   ulatub parasvöötmest tundrani. Soontaimede liigirikkuse hindamiseks kasutame andmeid kahest

72   Euroopa taimede levikuatlasest. Võrdleme õietolmu ja taimede liigirikkust erinevates

73   taimerühmades (tuultolmlejad vs mitte tuultolmlejad, puud ja põõsad vs rohttaimed) ja testime

74   liigirikkuste seoseid kliimat ja maastiku struktuuri iseloomustavate tunnustega.

75   3. Leidsime, et õietolmu liigirikkus ja soontaimede liigirikkus on positiivselt korreleerunud

76   (r=0.53). Õietolmu ja taimede liigirikkuse korrelatsioon paraneb (r=0.63) kui korrigeerime õietolmu

77   andmestikku, vähendades suurte õietolmutootjate (näiteks kask ja mänd) osatähtsust. Siit järeldub,

78   et kasutades õietolmu liigirikkuse hinnanguid mineviku andmetes, tuleks arvesse võtta

79   liikidevahelised õielmu tootlikkuse erinevused.

80   4. Kõige tugevamad korrelatsioonid taimede ja õietolmu liigirikkuste vahel on puudel ja põõsastel

81   (r=0.83) ja tuultolmlejatel (r=0.75). Meie tulemuste põhjal on just nende taimerühmade õietolmu

82   liigirikkused sobivaimad taimede regionaalse liigirikkuse muutuste tuvastamiseks.

83   5. Nii õitolmu kui taimede liigirikkus on tugevasti seotud aasta keskmise õhutemperatuuriga.

84   Maastiku avatus on positiivselt seotud õietolmu liigirikkusega, aga mitte taimede liigirikkusega.

85   Täiesti avatud maastikes ja/või külma kliimaga aladel, kus kohalik õietolmu tootlikkus on väga

86   madal, mõjutab õietolmu liigirikkuse hinnanguid regiooni välise õietolmu suur osatähsus.

87   6. *Kokkuvõtteks*. Meie tulemused kinnitavad, et õietolmu andmed võimaldavad uurida taimede

88   liigirikkuse muutusi Põhja-Euroopas. Võttes arvesse õietolmu tootlikkuse erinevusi ja ruumilist

89   skaalat, mida andmestik peegeldab, võimaldavad õietolmu andmed uurida taimede liigirikkuse

90   pikaajalisi muutusi ja liigirikkuse seoseid mineviku kliima ja keskkonnatingimustega.

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Introduction

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The regional and global gradients of species diversity – with richness in most taxon groups decreasing from lower to higher latitudes – are well known and the mechanisms behind this pattern are widely discussed (e.g. Gaston, 2000; Hawkins et al., 2003; Ronk, Szava-Kovats, & Pärtel, 2015; Whittaker, Nogués-Bravo, & Araújo, 2007; Worm & Tittensor, 2018). Contemporary climate regulates the availability of water and energy and is strongly associated with broad-scale richness patterns (Hawkins et al., 2003). However, historical factors – both evolutionary history and migration during periods of rapid climate change – have undoubtedly also influenced the patterns of present-day diversity (e.g. Flenley, 2005; Gaston, 2000; Kreft & Jetz, 2007). For example, the contemporary relationships of plant diversity with pH and productivity depend on the environmental conditions in evolutionary centres and the consequent size of regional species pools (Hájek et al., 2007; Harrison & Grace, 2007; Pärtel, 2002). The spread of species and the development of vegetation patterns during the Pleistocene-Holocene transition about 14000 to 11000 years ago offers the closest analogue to the ongoing climate change and helps to improve the projections of biodiversity responses to changing climate (Stivrins et al., 2016). Insights into past long-term changes in vegetation diversity are therefore extremely valuable for evaluating the current and future biodiversity changes.

Palaeoecological material, for example remains of organisms preserved in lake and mire deposits and caves, provides a means to study the historical development of vegetation types and landscapes over the last millennia. In fact, most of our knowledge about regional-scale vegetation history in the late Quaternary comes from sedimentary pollen data (e.g. Smol, Birks, & Last, 2001). Plant macrofossils (e.g. Amon, Veski, & Vassiljev, 2014; H. H. Birks, 2003) and, during the last decade, ancient DNA (e.g. Jørgensen et al., 2012; Parducci et al., 2013) can complement the picture by providing a more local-scale signal. In addition to reconstructing land-cover changes and species-spreading patterns, pollen data can be used to derive information about past vegetation diversity (e.g. H. J. B. Birks, Felde, & Seddon, 2016; Giesecke, Wolters, Jahns, & Brande, 2012; Reitalu et al., 2015; Weng, Hooghiemstra, & Duivenvoorden, 2007). Pollen richness is often used in addition to traditional pollen diagrams to characterise changes in plant richness. To improve the interpretation of the sedimentary pollen diversity, it is essential to understand the relationships between pollen and plant data in contemporary landscapes. There are several studies that have investigated modern pollen–plant diversity relationships (e.g. Felde, Peglar, Bjune, Grytnes, & Birks, 2016; Matthias, Semmler, & Giesecke, 2015; Meltsov, Poska, Odgaard, Sammul, & Kull,

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125 2011; Meltsov, Poska, Reitalu, Sammul, & Kull, 2013) and the results usually show a positive

126 relationship between modern pollen and plant diversity estimates (but see Goring, Lacourse, Pellatt,

127 & Mathewes, 2013; Gosling et al., 2018). Most of these modern-day pollen–plant studies are done

128 at relatively local scales where climate variation is small and the diversity relationships mainly

129 depend on landscape factors (e.g. Matthias et al., 2015; Meltsov et al., 2013) within the relevant

130 source area of pollen (RSAP). RSAP is defined by Sugita (1994) as the area beyond which the

131 strength of the pollen-vegetation relationship does not improve. However, when using pollen

132 richness in stratigraphic studies that cover the entire post-glacial, the climate gradient is relatively

133 large and it is not clear how the pollen–plant diversity relationship behaves along such a gradient

134 and whether climate and/or landscape variables interact with the pollen–plant diversity relationship.

135 In the present study, we test the relationships between pollen and plant richness across northern

136 Europe covering a mean annual temperature range from -6.8 ℃ to 9.2 ℃. We take advantage of

137 existing European-scale modern pollen and plant datasets allowing us to consider both pollen and

138 plant richness estimates.

139   The relationship between pollen and plant richness is influenced by interspecific

140 differences in pollen production and dispersal causing over-representation of some taxa and under-

141 representation or absence of other taxa in pollen assemblages (H. J. B. Birks, Felde, Bjune, et al.,

142 2016; Odgaard, 1999; Weng, Hooghiemstra, & Duivenvoorden, 2006). One proposed solution is to

143 use representation factors that downweight the influence of numerically dominant pollen taxa

144 (Andersen, 1970; Felde et al., 2016) or to look separately at groups of taxa with different pollination

145 types, for example wind-pollination vs. insect-pollination (Weng et al., 2006).

146   When using pollen richness as a proxy for plant richness, it is assumed that the

147 relationship remains constant in different climatic and landscape conditions and that environmental

148 variables influence pollen richness via their influence on plant richness. However, it is unclear how

149 much of the variation in pollen richness is a reflection of plant richness and how much the variation

150 in pollen richness is influenced directly by environmental variables. For example it is well known

151 that plant richness in Europe follows the major temperature gradient (Whittaker et al., 2007) but

152 pollen richness can be influenced by temperature both indirectly through plant richness and directly

153 through the influence of temperature on pollen production. Landscape diversity and openness are

154 known to influence plant diversity (Reitalu et al., 2014; Ronk et al., 2015) but both factors can also

155 directly influence pollen-dispersal patterns (Odgaard, 1999; Sugita, Gaillard, & Broström, 1999).

156 For example, it is known that the pollen-source area is larger in open areas and richness estimates

157 tend to be higher because of a larger "sampling" area (Odgaard, 1999; Sugita et al., 1999). In

158 mountainous areas at high elevations, pollen has been shown to be transported from the lowlands

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159 (Bajpai & Kar, 2018; Bell & Fletcher, 2015) and might thereby influence the pollen–plant richness

160 relationship. Landscape openness in the present-day world is closely associated with human impact

161 with agriculture greatly increasing the extent of open area. Over broad spatial scales, human

162 population size has been shown to correlate positively with species richness in different taxonomic

163 groups (Pautasso, 2007) suggesting that people have preferred to settle in areas of high biodiversity.

164 Moderate human impact increasing landscape diversity and providing habitats for synanthropic

165 species is known to increase both species and pollen richness (Colombaroli et al., 2013; Felde,

166 Grytnes, Bjune, Peglar, & Birks, 2018; Reitalu et al., 2014, 2015) while too intensive human impact

167 can cause local or even total extinction of species (Ceballos et al., 2015).

168 In the present study, we look in detail into the relationships of plant and pollen richness with a range

169 of environmental factors that characterise both climate and landscape structure. Linear mixed

170 effects modelling and variation partitioning are used to examine the differences and similarities

171 between pollen and plant richness in relation to environmental factors.

172   The main aim of this study is to compare patterns of pollen and plant richness across

173 northern Europe in relation to a range of climate and landscape factors. More specifically, we

174 address the following questions:

175 1) Does pollen richness reflect plant richness?

176 2) Are pollen–plant richness relationships different within groups of taxa (wind-pollinated vs not

177 wind-pollinated, trees and shrubs vs herbs and grasses)?

178 3) Are plant and pollen richness influenced by climate and landscape factors?

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180

181 **Material and methods**

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183 **Pollen data**

184 The modern pollen dataset of lake surface samples was compiled from Salonen, Seppä, Luoto,

185 Bjune, & Birks (2012) and Matthias et al. (2015) and comes from small to medium sized lakes

186 (median lake size 9 ha). These samples were collected and prepared in the laboratory using

187 harmonised methodology (Seppä, Birks, Odland, Poska, & Veski, 2004) but counted by a number of

188 different pollen analysts. Geographically, the dataset covers Scandinavia (including Svalbard),

189 Finland, the Baltic countries, the western and northwestern parts of Russia (Salonen et al., 2012)

190 and northern Germany (Matthias et al., 2015) (Figure 1), ranging through temperate, boreal and

191 tundra biomes. In total, the dataset includes 633 pollen lake surface samples. Spores from

192 sporophytes were excluded from the dataset and the richness estimates only include seed plants.

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Aquatic plants are included in the richness estimation. After taxonomic harmonisation, there are 173 pollen types (Appendix S1 in Supporting Information).

The combined dataset includes pollen data from different subregions and different analysts resulting in some variation in the number of pollen grains counted from each pollen sample (the pollen sum) ranging from below 200 in the northernmost sites to over 1000 in the southern sites. For pollen richness, rarefaction analysis where the richness is estimated for a fixed pollen sum is usually recommended (H. J. B. Birks & Line, 1992). In the present study, we use a pollen sum of 500 terrestrial pollen grains. There were 143 samples with a pollen sum below 500. In areas where several sites with low pollen sums are spatially close (less than 50 km), the samples were pooled to achieve the >500 pollen sum. The samples with pollen sums below 500 which could not be grouped together were excluded from the analyses. As a result, we used data from 511 samples: 21 combined samples (from Svalbard, northern Norway and Russia) and 490 samples where the pollen sum was already >500.

Plant data

To characterise plant richness, we merged the two largest plant atlases available in Europe, Atlas Florae Europaeae (Jalas & Suominen, 1972; Jalas, Suominen, & Lampinen, 1996; Jalas, Suominen, Lampinen, & Kurtto, 1999; Kurtto, Lampinen, & Junikka, 2004) and Atlas of North European Vascular Plants (Hultén & Fries, 1986) as described in Kalwij, Robertson, Ronk, Zobel, & Pärtel (2014). The resulting dataset is the most comprehensive broad-scale plant distribution data to date, with distribution information for 5221 European plant taxa (species and subspecies), i.e. approximately half the estimated number of flowering plant taxa in Europe (Mutke, Kreft, Kier, & Barthlott, 2010; Tutin, 1980).

The resolution of the plant dataset is 50×50 km. We first calculated plant richness for the grid cells where the pollen-sample lakes are situated. Second, we calculated the cumulative richness of three grid cells with centroids closest to each of the lakes. A preliminary correlation test indicates that the relationship between pollen and plant data is stronger with plant richness from the larger area (r=0.47 for one 50×50 km quadrat and r=0.53 for three 50×50 km quadrats). The richness data from one grid cell are likely to include a larger random component compared to larger areas. The sampled lakes are not necessarily in the middle of the grid cells and the richness of the larger area therefore gives a more stable result. We thus use the plant richness data from three grid cells in all subsequent analyses and all plant richness estimates were calculated at that scale of $3\times50\times50$ km (=7500 km^2). In case of the 21 pooled pollen samples with pollen data from several lakes, all lakes are situated within the same three plant grid cells and plant richness is calculated

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227 similarly to other samples based on cumulative number of species in the three cells. The plant

228 dataset includes 1982 species in total. In the pollen analysis, only a few plant species are separable

229 to species level. To test the effect of this taxonomic bias, the plant data were translated into pollen

230 types according to Felde, Birks, Peglar, Grytnes and Bjune (2017), which resulted in 388 pollen

231 types or pollen equivalents (H. J. B. Birks, Felde, Bjune, et al., 2016).

232

233 **Richness calculations**

234 To equalise sampling effort in the richness estimations using 500 pollen grains, we randomly

235 resampled 500 pollen grains from each pollen sample without replacement and repeated the

236 randomisation 1000 times – a procedure analogous to rarefaction analysis (Felde et al., 2016; H. J.

237 B. Birks, Felde, Bjune, et al., 2016). All the subsequent calculations of different pollen richness

238 measures are based on each of the 1000 randomization draws and the average of the 1000 is used as

239 the richness estimate.

240 Pollen richness (number of all pollen taxa among 500 grains) and plant richness (number

241 of all plant species) (Figure 1) are used as the main descriptors of pollen and plant diversity and for

242 testing the relationships with environmental variables. To test whether pollen richness is a better

243 predictor of plant richness in some taxon groups, we calculate both pollen and plant richness

244 separately for wind-pollinated taxa and for non-wind-pollinated taxa, for trees and shrubs, and for

245 herbs and grasses. Information about pollination modes was obtained from the plant trait database

246 BiolFlor (Kühn et al. 2004). The pollination mode of pollen taxa is determined based on the

247 prevailing pollination mode of the species within the taxon. The division of pollen taxa into these

248 different taxon groups is given in Appendix S1. To estimate how the differences in taxonomic

249 resolution in the pollen and plant data affect the possibilities of inferring plant diversity from pollen

250 diversity, plant richness is expressed as richness of pollen types and both plant and pollen richness

251 are expressed as richness of families.

252 To test for the effect of pollen-representation bias on pollen diversity estimates, we use

253 Andersen-transformed pollen values (cf. Felde et al., 2016). Pollen counts of common tree and

254 shrub taxa were multiplied by Andersen's (1970) general pollen-representation values and the new

255 minimum pollen sum (149 pollen grains) used for rarefaction analysis with 1000 randomisations.

256 In summary, pollen diversity is characterised as: total pollen richness (R_{po}), Andersen-

257 transformed R_{po}, R_{po} of families, R_{po} of herbs and grasses, R_{po} of trees and shrubs, R_{po} of wind-

258 pollinated taxa, and R_{po} of non-wind-pollinated taxa. Plant diversity is characterised as: total

259 richness (R_{pl}), R_{pl} of pollen types, R_{pl} of families, R_{pl} of herbs and grasses, R_{pl} of trees and shrubs,

260 R_{pl} of wind-pollinated species, and R_{pl} of non-wind-pollinated species.

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Environmental data

263 We use climate data from the WorldClim database (www.worldclim.org) (Hijmans, Cameron, Parra,

264 Jones, & Jarvis, 2005) and the 10-arc-minute "bioclim" dataset which includes 19 bioclimatic

265 variables that are calculated from monthly temperatures and rainfall data for 1961– 1990

266 (O'Donnell & Ignizio, 2012). In addition to these bioclimatic data, we use windspeed data from the

267 ERA-Interim analysis (Dee et al., 2011). Because the bioclimatic variables are highly

268 intercorrelated, we used principal components analysis (PCA) to choose a subset of climate

269 variables. The first six PCA axes explain 98% of the variation in the climate dataset (PC1 explains

270 54% of the variation, PC2 22%, PC3 9%, PC4 6%, PC5 4%, PC6 3% and all the other principal

271 components less than 1%). Six climate variables are chosen for subsequent analyses based on their

272 correlations with the first six PCA axes (Appendix S2 Table S2.1) and intercorrelations with other

273 climate variables (Appendix S2 Table S2.2). For example, the first PCA axis was clearly associated

274 with precipitation – precipitation of driest quarter, precipitation of coldest quarter, precipitation of

275 driest month and annual precipitation have the highest loadings along PC1. Because all four

276 precipitation variables are highly intercorrelated (r>0.98), we choose annual precipitation as the

277 most widely known precipitation variable in our analysis.

278   1) Annual precipitation – total annual precipitation (mm year^{-1});

279   2) Mean annual temperature – mean annual temperature (ºC);

280   3) Precipitation seasonality – coefficient of variation in monthly precipitation totals;

281   4) Temperature seasonality – standard deviation of monthly temperature averages;

282   5) Isothermality – size of day-to-night temperature oscillation in relation to annual oscillations,

283   mean diurnal range divided by the annual temperature range;

284   6) Windspeed – average windspeed (m s^{-1}) for spring and summer (April–August) 10 m above

285   the ground (averaged for 1979–1998).

286

287 Six landscape variables known from previous studies (overview in H. J. B. Birks, Felde, Bjune, et

288 al., 2016) to influence plant and/or pollen richness are used to characterise the landscape:

289   1) Lake area – the surface area of the pollen-sample lake (in ha), estimated from Google Maps

290   (Google, 2016);

291   2) Elevation – elevation of each pollen-sample site (m above sea level), extracted from

292   ETOPO1 1 Arc-Minute Global Relief Model (Amante & Eakins, 2009);

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293   3) Elevation variation – characterises the variation in topography in a 50 km radius around
294   each pollen-sample site, standard deviation of the elevation of ETOPO1 model (Amante &
295   Eakins, 2009);
296   4) Openness – landscape openness calculated from a global forest-cover dataset (Hansen et al.,
297   2013): the original 30-m-resolution dataset was resampled to a 900-m-resolution and
298   average openness in a 50 m radius around the pollen-sample sites is calculated as 100 minus
299   the forest cover;
300   5) Landscape diversity – Simpson diversity estimate for a 50 km radius around each pollen-
301   sample site, based on the land-cover types in the Global Land Cover 2000 database at 1 km
302   resolution (Hartley et al., 2006);
303   6) Human population – human population density (persons km^{-2}), extracted from the Gridded
304   Population of the World (GPW) database (Center for International Earth Science
305   Information Network, 2016). We use the average population density of the 50 km radius
306   area around each pollen-sample site calculated from the 0.5 arc-minute resolution map.
307 In case of the 21 pooled pollen samples with pollen data from several lakes, environmental
308 variables are calculated as averages of the lakes included in the pooling with the exception of lake
309 area that is calculated as the sum of lake areas. The correlations among the landscape variables do
310 not exceed 0.6 and all variables are retained in the subsequent analyses (Appendix S2 Table S2.2.).

311

312 **Statistical analyses**
313 Correlations between the pollen and plant variables and among the environmental variables are
314 quantified by Pearson's product moment correlation coefficients.
315   To identify environmental and climate variables associated with plant and pollen
316 richness, we use linear mixed effects (LME) models (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).
317 To account for the pollen data from different regions being analysed by different scientists and to
318 account for the regional differences in the plant and pollen data, we use "Region" as a random
319 variable in the LME model. Nine regions were used: Estonia, Finland, Germany, Lithuania, Norway
320 (including Svalbard), Sweden1 (analysed in Bergen), Sweden2 (analysed in Helsinki), Russia1
321 (Komi region), and Russia2 (western Russia). Pollen richness (per 500 pollen grains) and plant
322 richness (in three 50×50 km plots) are used as response variables. Six climate variables (annual
323 precipitation, mean annual temperature, precipitation seasonality, temperature seasonality,
324 isothermality, windspeed) and six landscape variables (lake area, elevation, elevation variation,
325 openness, landscape diversity, human population density) are used as explanatory variables.

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326 Quadratic terms of all explanatory variables are tested. Log-transformation is used for annual

327 precipitation, windspeed, lake area, and human population density to ensure a uniform data

328 distribution. Both richness data and explanatory variables are standardised to zero mean and unit

329 variance to enable comparison of model estimates. Backward selection of explanatory variables is

330 used and only significant ($P<0.01$) variables retained in the models. Marginal pseudo-R^2 (reflecting

331 the variation explained by fixed variables) and conditional pseudo-R^2 (reflecting the variation

332 explained by both random and fixed variables) are calculated for the models according to Nakagawa

333 and Schielzeth (2013). In models describing pollen richness, plant richness is also used as an

334 explanatory variable. To test whether the relationship between pollen and plant richness is

335 influenced by climate or landscape configuration, a separate model-selection procedure is used to

336 test for interactions between plant richness and environmental variables in explaining pollen

337 richness.

338 LME models with pollen richness as response, environmental variables as fixed

339 variables, and "Region" as a random variable do not have significant spatial autocorrelation in the

340 errors. However, errors of the LME models with plant data as the response remain spatially

341 autocorrelated. To clarify the proportions of variation explained by purely spatial variation, climate,

342 and landscape variables, we use variation partitioning (Borcard, Legendre, & Drapeau, 1992).

343 Moran's eigenvector map (MEM) approach (Griffith & Peres-Neto, 2006) is used to characterise the

344 spatial structure in the data. In the MEM approach, orthogonal, linearly independent (MEM)

345 eigenvectors are calculated from a spatial weighting matrix. Based on permutation tests, a set of

346 MEM variables significantly ($\alpha < 0.05$) contributing to minimising the global Moran's I is chosen

347 and used as explanatory variables in variation partitioning. In addition to spatial descriptors (the

348 MEM variables), explanatory datasets characterising climate (annual precipitation, mean annual

349 temperature, precipitation and temperature seasonality, isothermality, windspeed) and landscape

350 (elevation, variation in elevation, openness, landscape diversity, human population density) are used

351 in variation partitioning. In the case of pollen richness, plant richness is considered as an additional

352 explanatory variable.

353 The LME analysis and variation partitioning are primarily used to test the effect of

354 climate, landscape, and spatial variables on total pollen and plant richness. However, similar

355 analyses are followed for other richness variables (Andersen-transformed pollen richness, tree and

356 shrub richness in pollen and in plants, herb and grass richness in pollen and in plants, richness of

357 wind-pollinated taxa in pollen and in plants, richness of non-wind-pollinated taxa in pollen and in

358 plants). The results of these analyses are presented in Appendix S3 (LME models) and Appendix S4

359 (variation partitioning).

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360   The statistical software R (R Core Team, 2017) was used for all statistical analyses with

361   packages "nlme" (Pinheiro, Bates, & DebRoy, 2018) for LME models, "vegan" (Oksanen et al.,

362   2017) for variation partitioning, and "spdep" (Bivand & Piras, 2015) for MEM calculations.

363

364   **Results**

365

366   *Pollen richness as a predictor of plant richness*

367   Total pollen richness is relatively weakly associated with plant richness (r=0.53, P<0.001) (Table 1,

368   Figure 2a). The Andersen-transformation improves the pollen–plant richness correlation (r=0.63,

369   P<0.001) (Table 1, Figure 2b). While pollen richness of wind-pollinated taxa is a relatively good

370   predictor of plant richness of wind-pollinated species (r=0.75, P<0.001; Figure 2c), there is no

371   significant correlation between richness estimates of taxa that are not wind-pollinated (r=-0.05, n.s)

372   (Table 1). The highest correlation is found between pollen and plant richness of trees and shrubs

373   (r=0.83, Table 1, Figure 2d). In addition, pollen richness estimates of wind-pollinated taxa and of

374   trees and shrubs appear to be good predictors of all the plant richness estimates included in the

375   study with correlation coefficients above 0.75 (Table 1).

376

377   *Pollen and plant richness in relation to climate and landscape variables*

378   Linear mixed effects models show that while the environmental variables explain most of the

379   variation in plant richness (marginal pseudo-R^2 = 0.92), the relationships between pollen richness

380   and environment are less well determined (marginal pseudo-R^2 = 0.58) (Table 2).

381   Mean annual temperature is the strongest predictor of both pollen and plant richness

382   (Figures 3a–b, Table 2) with more taxa at higher temperatures. The LME models with other richness

383   estimates indicate that mean annual temperature is clearly the strongest predictor of both pollen and

384   plant richness irrespective of the taxon group considered (Appendix S3). Whilst plant richness is

385   significantly associated with all the climate variables tested, the relationships between pollen

386   richness and climate are weaker (Table 2). However, three temperature-related climate variables –

387   mean annual temperature, temperature seasonality and isothermality – have significant interaction

388   terms with plant richness in explaining pollen richness (Table 2, Figure 4). The relationship between

389   pollen and plant richness is less determined at lower mean annual temperature values (Figure 4a)

390   and the pollen–plant richness association is even negative at high latitudes (Figure 4b). When using

391   the Andersen-transformed pollen richness or tree and shrub richness, interactions between plant

392   richness and climate are fewer and are less determined but still statistically significant (Appendix

393   S3 Table S3.1, Figures 4c–d).

12

394   Because all 21 pooled pollen samples (including pollen data from several lakes) are from

395   northern latitudes, we checked whether the pooling of the data might have caused the interaction

396   effects – with pooled pollen samples having higher beta-diversity and thereby higher pollen

397   richness. We calculated the LME interaction model including all original 633 pollen samples and

398   pollen richness rarefied to the lowest pollen sum of 134. The interaction terms with plant richness

399   were significant for annual mean temperature ($p<0.001$) and for temperature seasonality ($p<0.001$),

400   but the interaction between plant richness and isothermality was not significant (Appendix S3 Table

401   S3.6).

402   Of the landscape variables, elevation is similarly associated with both plant and pollen

403   richness with more taxa at higher elevations (Table 2). Other landscape variables have different

404   relationships with pollen and plant richness: openness is only associated with pollen richness

405   (Figures 3c–d) and human population density is only associated with plant richness (Figures 3e–f).

406   While landscape diversity is positively associated with plant richness, the relationship with pollen

407   richness tends to be negative (Table 2). Lake area is not significant in any of the models and is not

408   included in the results tables.

409   When plant richness is included as an explanatory variable in the model together with all

410   the environmental variables, plant richness is significantly associated with pollen richness only after

411   interactions with climate variables are accounted for (Table 2). In the case of Andersen-transformed

412   pollen richness, richness of trees and shrubs and richness of wind-pollinated taxa, the corresponding

413   plant richness is significant also in the models without the interaction terms (Appendix S3).

414   The results of variation partitioning show that the largest proportion of variation in both

415   pollen and plant richness is explained jointly by the climate, landscape, and spatial variables (80%

416   for plant richness, 22% for pollen richness; Figure 5). The share of variation explained by climate

417   and landscape independently of the spatial variables is larger for pollen richness (12.5%) than for

418   plant richness (2.3%) (Figure 5). For pollen richness of herbs and grasses and taxa not wind-

419   pollinated, landscape variables explain relatively large individual shares of variation (7.0% and

420   6.5%, respectively) (Appendix S4; Figures S4.3b and S4.5b). The amount of variation in pollen

421   richness explained only by plant richness is low (<1%) for all richness estimates (Figure 5,

422   Appendix S4). However, the total amount of variation explained by plant richness including the

423   variation explained jointly with other variables varies from 3% (for richness of herbs and grasses

424   and richness of non-wind-pollinated taxa) to >55% (richness of trees and shrubs and richness of

425   wind-pollinated taxa).

426

427   **Discussion**

13

Pollen richness in relation to plant richness

428 The often used rarefaction-based total pollen richness has a relatively low but significant positive

429 correlation with total plant richness ($r=0.53$, $P<0.001$). The most serious critiques against using

430 pollen richness as a proxy of past plant richness relate to the pollen-representation bias *sensu*

431 Odgaard (1999, 2008) where the high pollen producers decrease the probability of finding rare

432 pollen types and thereby influence the estimated richness. Several different methods have been

433 proposed to minimise the pollen-production bias (cf. H. J. B. Birks, Felde, Bjune, et al., 2016).

434 Using pollen-representation values (i.e. Andersen, 1970) or pollen productivity estimates (e.g.

435 Broström et al., 2008) to downweight the high pollen producers prior to rarefaction analysis is one

436 option that has been used by several authors (Felde et al., 2016; Matthias et al., 2015). In our

437 analysis, we test the use of Andersen-transformed pollen richness and although it improves the

438 pollen–plant richness correlation ($r=0.63$, $P<0.001$) it does not completely remove the interaction

439 effects of the richness relationship with climate and latitude. The pollen data are limited by the

440 original pollen counts in the samples and any transformation can only work within the limits of the

441 original counts. To overcome this problem, methods adjusting the maximum pollen count during the

442 counting process have been proposed – allowing pollen counts to be developed relative to the

443 evenness and richness of the specific sample rather than a fixed number (Keen et al., 2014). Our

444 analyses together with earlier studies (Felde et al., 2016; Matthias et al., 2015) suggest that methods

445 accommodating pollen-representation bias in pollen richness-studies warrant further attention and

446 should become as widely used as pollen-production transformations in land-cover reconstruction

447 studies (e.g. Mazier et al., 2015; Mehl & Hjelle, 2015; Roberts et al., 2018).

448 The studies that investigate pollen–plant richness relationships often use the pollen-type

449 based plant richness to reduce the influence of taxonomic bias where some pollen taxa include

450 considerably more species than others (Felde et al., 2016; Goring et al., 2013; Meltsov et al., 2011).

451 For example, the whole family Cyperaceae is included as one pollen type while the main tree

452 species can be separated at the genus or species level. In our dataset, translating the plant data into

453 pollen types or using family-level richness does not improve the correlation between the pollen and

454 plant richness estimates, indicating that taxonomic bias is more-or-less constant across the whole

455 range of the data.

456 In our results, the correlation between plant and pollen richness greatly improves when

457 only trees and shrubs are considered ($r=0.83$). Similarly to our study, Flenley (2005) shows that the

458 palynological richness of woody taxa follows well the latitudinal gradient of tree and shrub species.

459 As with tree and shrub richness, pollen richness of wind-pollinated taxa is a good indicator of

460 corresponding plant species richness ($r=0.75$). Many of the tree and shrub taxa in our study are

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462   wind-pollinated (Appendix S1) and thus the two richness measures largely overlap. Similar to the

463   pollen data in large databases such as the European Pollen Database (Davis et al., 2013; Giesecke et

464   al., 2013) or the Neotoma Paleoecology Database (Williams et al., 2018), our pollen dataset

465   combines the work of multiple analysts and the dataset loses taxonomic precision due to the

466   merging of certain morphologically difficult pollen taxa. The lack of correlation between pollen and

467   plant richness among insect-pollinated taxa or among herbs and grasses may be related to this

468   "analyst effect" but is likely to be additionally influenced by landscape configuration (c.f. Appendix

469   S4, Figs. S4.3 and S4.5) and the spatial scale of the plant data used. Changes in the diversity of

470   insect-pollinated taxa can be detected with good pollen-taxonomic precision, consistent effort in

471   pollen taxonomy, and high pollen sums (>1000 grains) (Meltsov et al., 2011). The relevant source

472   area of pollen (RSAP) for European small lakes is usually estimated to be 1000–2000 m from the

473   lake (Hjelle, & Sugita, 2011; Nielsen, & Sugita, 2005; Poska, Meltsov, Sugita, & Vassiljev, 2011),

474   which is a much finer spatial resolution than the resolution of the plant data in our study. Therefore,

475   to understand better the relationship between plant and pollen richness of both wind-pollinated and

476   non-wind-pollinated taxa, the plant dataset should include several nested spatial scales.

477   Weng et al. (2006) suggest that the wind-pollinated and insect-pollinated pollen taxa

478   should be treated separately in pollen richness studies. Our results strongly support this and we

479   recommend that richness of trees and shrubs or richness of wind-pollinated taxa are good choices

480   when using pollen richness to reflect major changes in past plant richness over broad spatial scales

481   and in studies involving data from different sources. According to our results, pollen richness of

482   trees and shrubs and of wind-pollinated taxa are also good indicators of broad-scale total plant

483   richness (r=0.79 and r=0.81, respectively) because in northern Europe the plant richness of trees

484   and shrubs and the richness of wind-pollinated taxa are, in turn, highly positively correlated with

485   total richness. However, as the relationship between wind-pollinated and non-wind-pollinated taxa

486   is not constant across the globe (Regal, 1982), studies from other regions or global studies of

487   pollen–plant richness are needed to confirm the trends demonstrated here.

488   A series of earlier studies have found similar positive correlations between pollen and

489   plant richness in Europe (H. J. B. Birks, 1973; Felde et al., 2016; Matthias et al., 2015; Meltsov et

490   al., 2011; Odgaard, 2008). However, investigations from the tropics (Gosling et al., 2018; Jantz,

491   Homeier, & Behling, 2014) or from temperate western North America (Goring et al., 2013) have not

492   found such positive correlations. Evaluating pollen–plant diversity relationships not only depends

493   on the nature of pollen data but also on the spatial scale and quality of plant data (H. J. B. Birks,

494   Felde, Bjune, et al., 2016). In the present study we use the best available regional-scale plant

495   database that has a relatively coarse spatial resolution (50×50 km) and both pollen and plant data

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reflect the well-known latitudinal richness gradient relatively well (Figure 4). Goring et al. (2013) showed the relationship between pollen richness and fine-scale (20×20 m) plant richness to be slightly negative. The scale of the plant data is much finer than the estimated relevant source area of pollen for similar-sized lakes (1000 to 2000 m; Hjelle & Sugita, 2011; Nielsen & Sugita, 2005; Poska et al., 2011). This further emphasises the importance of finding relevant spatial scales when interpreting pollen richness in terms of plant richness.

Climate influence on pollen and plant richness

In the plant data, the richness pattern is very strongly spatially autocorrelated and the purely spatial variables are the best descriptors of the richness gradient (Figure 1, Figure 5a). This is related to the relatively coarse spatial resolution of the data (50×50 km) where the influence of local-scale variables (including landscape diversity and structure, microclimate) is smoothed out and the climate and landscape variables explaining the richness patterns covary with the spatial variables. Climate variables explain 91.5% of the variation in plant richness (Figure 5), confirming the importance of water-energy variables for determining richness patterns over broad geographic scales (Hawkins et al., 2003). However, the proportion of variation explained jointly by climate, landscape and spatial variables is extremely high (80.1%) indicating that it is difficult to separate the effects of landscape and climate variables at this spatial resolution. The low vascular plant richness in the northeastern part of the study area (NW Russia) may be an artefact because both Atlas Florae Europaeae (Jalas & Suominen, 1972; Jalas et al., 1996; Jalas et al., 1999; Kurtto et al., 2004) and Atlas of North European Vascular Plants (Hultén & Fries, 1986) concentrate on European species and may lack species with more eastern distributions (Ronk, 2016). However, the west-east richness decrease is also reflected by the pollen data (Figure 1) and the LME models suggest that the gradient is positively related to isothermality both in plants and in pollen (Table 2) indicating that large diurnal temperature oscillations and/or high continentality have a negative influence on plant and pollen richness.

Climate and landscape variables have distinctive independent effects on pollen richness regardless of spatial patterns and plant richness (Figure 5b), indicating that climate and landscape variables influence pollen richness directly and not only through plant richness. Numerous studies of pollen-production estimates across Europe have demonstrated considerable variation in pollen production for the same taxa in different regions (e.g. Broström et al., 2008; Mazier et al., 2012). This is also likely to influence pollen-richness estimates when the detection probability of taxa decreases due to less favourable flowering conditions and reduced pollen production. The significant interactions of the plant–pollen richness relationship with climatic variables and latitude

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530 indicate that pollen richness at conditions corresponding to present-day high latitudes (>70 ºN,

531 mean annual temperature < -3.5 ºC) in sedimentary studies should be treated with caution because

532 the richness values may be heavily influenced by long-distance transport of extra-regional pollen.

533 Pollen data from high latitudes often have low pollen sums because of the scarcity of pollen.

534 Pooling pollen data from several lakes (as we have done in 21 pooled samples) increases the overall

535 pollen source area and might be the reason behind the unproportionally high pollen richness in low

536 temperatures and high latitude (Figure 4). However, the analysis with pollen richness from the

537 original samples (without pooling) indicates that the interaction of pollen–plant richness correlation

538 with temperature is not an artefact of our data handling but is also evident when pollen richness is

539 based on low pollen sums (Appendix S3 Table S3.6). Low temperatures in high latitudes (and

540 elevations) may have a negative influence on local pollen production increasing the proportion of

541 long-distance pollen in the samples (Seppä, 1998; van der Knaap, 1990). The relatively high pollen

542 richness in the late-glacial described in several studies (Berglund, Gaillard, Björkman, & Persson,

543 2008; H. J. B. Birks & Line, 1992; Reitalu et al., 2015) might therefore be influenced by long-

544 distance pollen dispersal from outside the region.

545

546 *Influence of landscape variables on pollen and plant richness*

547 Among the landscape variables, openness and elevation have positive correlations with pollen

548 richness and, as discussed above, earlier studies have also shown that both variables can have a

549 positive effect on pollen richness (but not necessarily through an increase in plant richness) (Felde

550 et al., 2016; Meltsov et al., 2011; Odgaard, 2008). In two modern pollen–plant richness studies from

551 the tropics, where there is no clear link between pollen and plant richness, the gradient of openness

552 is involved: Gosling et al. (2018) describe the diversity from closed evergreen forests to wooded

553 savannah and Jantz et al. (2014) involve elevational gradients. Openness, at high elevations or

554 latitudes, in naturally open dry areas or human-influenced landscapes is known to have a positive

555 effect on pollen richness through the increased pollen-source area in open conditions (Felde et al.,

556 2016; Seppä, 1998; Sugita et al., 1999) and through higher pollen evenness that allows more taxa to

557 be detected (Odgaard, 2008). Our results also demonstrate that openness has a positive effect on

558 pollen richness but not on plant richness (Figure 3) indicating that openness interacts with the

559 pollen–plant richness relationship. These results call for caution in interpreting pollen richness from

560 open areas and for the development of methods that take into account differences in pollen

561 production and source area, for example, calculating pollen diversity from pollen accumulation

562 rates (van der Knaap, 2009), employing varying pollen sums depending on pollen production (Keen

563 et al., 2014), or using expert knowledge to exclude extra-regional pollen (van der Knaap, 1990).

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564   The individual effects of landscape variables are especially high for pollen richness of

565   herbs and grasses and for pollen richness of non-wind-pollinated taxa, further confirming that in our

566   dataset these groups of pollen taxa are influenced by different factors and/or on different spatial

567   scales than the plant species richness used in our study.

568   Late-Holocene pollen-diversity studies from Europe often highlight human impact as

569   having a positive influence on pollen richness where land-clearance for agriculture and

570   anthropogenic disturbance are creating habitats for more taxa that can not grow in forested areas

571   (Berglund et al., 2008; Colombaroli et al., 2018; Felde et al., 2018; Giesecke et al., 2012; Reitalu et

572   al., 2015). It is, therefore, somewhat surprising that there is no association between human

573   population size and pollen richness in the LME models (Figure 4e), while population size is

574   significantly positively correlated with plant richness (Figure 4f). In our dataset the human

575   population size is strongly positively correlated with mean annual temperature (r=0.9, p<0.001,

576   Appendix S2) and the effects of climate and human impact are not clearly separable. We also test

577   the LME model without mean annual temperature, and then human impact is included in the model

578   and it is significantly positively linked with pollen richness. The modern data used in our study are

579   not directly comparable with the situation during the last 4000 years when temperatures were

580   decreasing slightly (Renssen et al., 2009) but the human impact was increasing considerably.

581

582   *Conclusions*

583   Our results offer the first regional-scale comparison of pollen and plant richness from Europe and

584   allow the evaluation of the relative importance of different environmental variables on both pollen

585   and plant richness. Differences in pollen production among taxa influence the pollen-richness

586   estimates and the development of better methods for reducing pollen-production bias should

587   therefore get more attention in further methodological studies. Pollen richness values may be over-

588   estimated in open landscapes, such as arctic tundra, high elevations, and areas of intensive

589   agriculture where the extremely low local pollen production increases the proportion of taxa from

590   outside the region.

591   We suggest that pollen richness of trees and shrubs or of wind-pollinated taxa are good

592   indicators of broad-scale plant richness changes over thousands of square kilometres. The pollen

593   richness of insect-pollinated herbaceous plants is more likely to be influenced by local landscape-

594   scale factors and should be interpreted separately from the wind-pollinated taxa. Our results confirm

595   that pollen data can provide insights into past plant-richness changes, and thus make it possible to

596   investigate vegetation diversity trends over long timescales and under changing climatic and habitat

597   conditions outside the scope of contemporary ecological studies.

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896

897 **Tables**

898

899 **Table 1**. Pearson correlation coefficients between richness calculated from pollen data (columns)
900 and plant data (rows), R_{po} – pollen richnes, R_{pl} – plant richness.

Pollen→ Plants ↓	Richness (R_{po})	R_{po} Andersen-transformed	R_{po} Families	R_{po} herbs and grasses	R_{po} trees and shrubs	R_{po} wind-pollinated	R_{po} non-wind-pollinated
Richness (R_{pl})	0.53	0.63	0.51	0.18	0.79	0.81	-0.07
R_{pl} pollen types	0.52	0.62	0.52	0.16	0.8	0.81	-0.08
R_{pl} families	0.48	0.58	0.51	0.13	0.77	0.76	-0.09
R_{pl} herbs and grasses	0.52	0.62	0.5	0.17	0.78	0.8	-0.07
R_{pl} trees and shrubs	0.59	0.68	0.59	0.24	0.83	0.82	0.02
R_{pl} wind-pollinated	0.47	0.57	0.44	0.12	0.74	0.75	-0.11
R_{pl} non-wind-pollinated	0.54	0.64	0.53	0.19	0.8	0.81	-0.05

901

Table 2. Results of linear mixed effect (LME) models with total pollen richness (per 500 pollen grains) and plant richness as response and "Region" as a random variable. All variables are standardised to zero mean and unit variance to enable comparison of model estimates. The results are post backward selection of variables. Symbol "n" denotes a unimodal quadratic association, "u" denotes u-shaped association, and × denotes interaction with plant richness in pollen richness model. The significance of the variables is indicated as follows: *** $P<0.001$, ** $0.001<P<0.01$, *$0.01<P<0.05$, n.s $P>0.05$. Marginal pseudo-R^2 (reflecting the variation explained by fixed variables) and conditional pseudo-R^2 (reflecting the variation explained by both random and fixed variables) are given for each model.

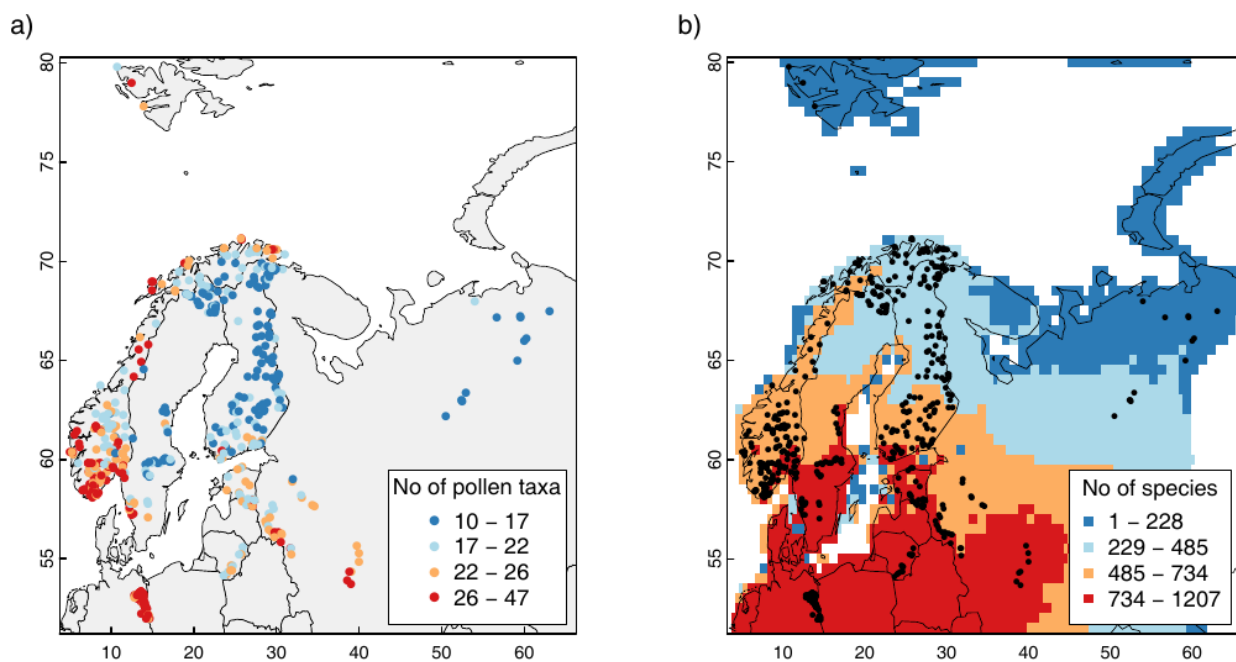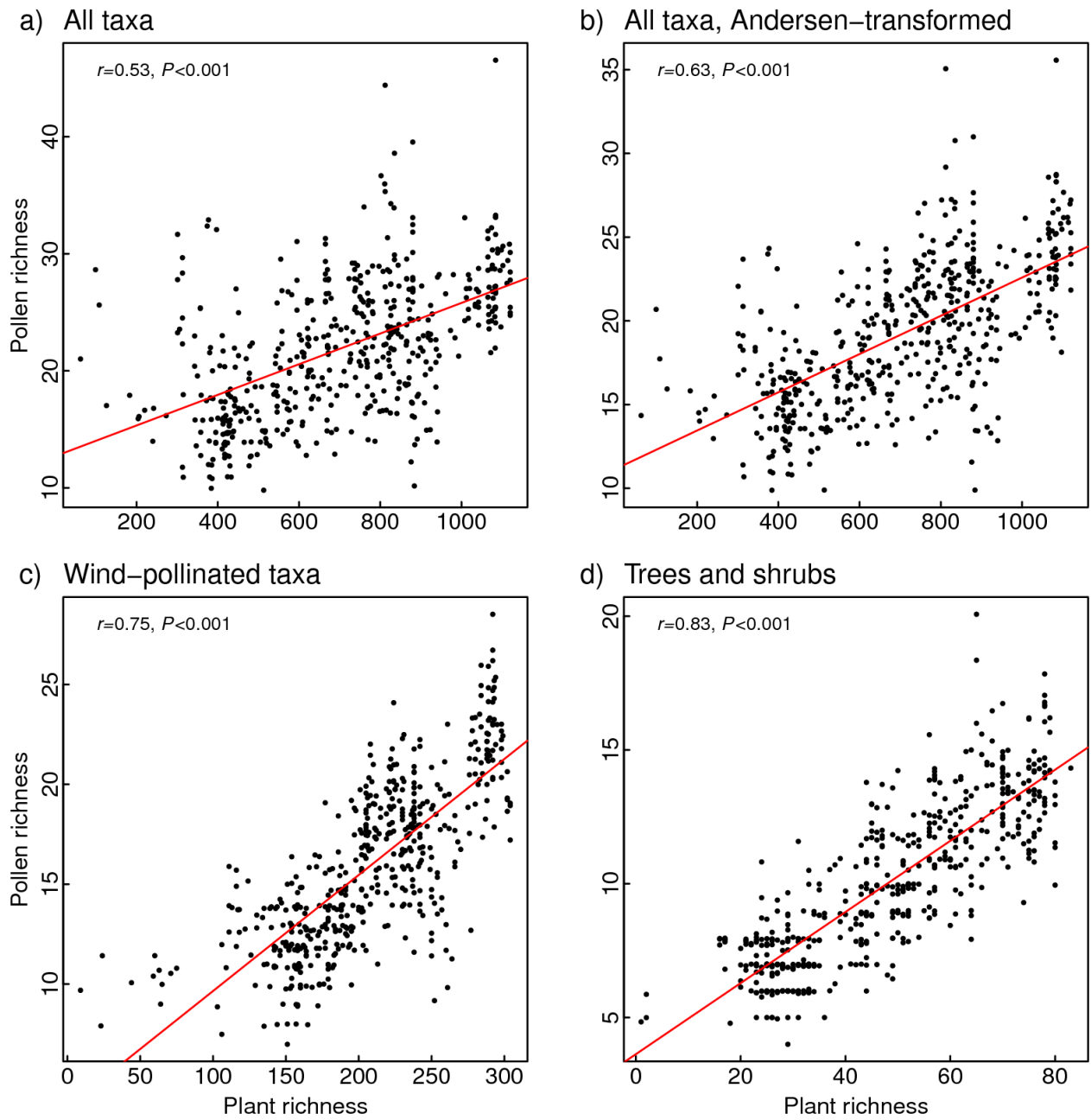|	Variable	Pollen richness		Pollen richness		Plant richness	
		LME with quadratic associations		LME with plant richness interactions		LME with quadratic associations	
		Estimation	t-value	Estimation	t-value	Estimation	t-value
	Plant richness	+ 0.09	1.16 n.s	0.40	6.15 ***	–	–
Climate	Annual precipitation			+ 0.44	7.33 ***	+0.11	3.47 ***
	Mean annual temperature	+0.94 u 0.18	9.70 *** 4.39 ***	+ 0.16 × + 0.36	1.96 * 5.92 ***	+0.79 u 0.21	18.09 *** 11.78 ***
	Precipitation seasonality					–0.05	–3.09 **
	Temperature seasonality			+ 0.11 × + 0.20	1.20 n.s 4.40 ***	+0.10 n 0.15	3.29 ** –7.39 ***
	Isothermality	–0.16	–3.29 **	– 0.06 × – 0.14	-1.28 n.s -2.97 **	–0.02 n 0.1	–1.03 n.s –7.44 ***
	Windspeed					–0.18 ⌣0.04	–8.42 *** 4.64 ***
Landscape	Elevation	+0.23 u 0.09	4.80 *** 4.16 ***			+ 0.2 u 0.05	9.39 *** 5.43 ***
	Elevation variation	+0.25	3.92 ***			–0.02 n 0.08	-0.60 n.s -3.61 ***
	Openness	+0.24 u 0.18	5.74 *** 5.42 ***	+ 0.25	4.88 ***		
	Landscape diversity			–0.11	–3.30 **	+ 0.05 u 0.03	2.62 ** 2.56 *
	Human population					+ 0.31 n 0.04	10.75 *** –2.73 **
		Marginal R^2 = 0.58 Conditional R^2 = 0.68		Marginal R^2 = 0.51 Conditional R^2 = 0.68		Marginal R^2 = 0.92 Conditional R^2 = 0.95	

Figures

918 **FIGURE 1** Map of northern Europe with (a) pollen richness (per 500 pollen grains) in lake-surface
919 samples and (b) locations of surface-sample lakes on the plant richness map.

FIGURE 2 Correlations between pollen richness and plant richness in different taxon groups: (a)
all taxa, (b) all taxa, pollen Andersen-transformed, (c) wind-pollinated taxa, (d) tree and shrubs.
Pearson correlation coefficient and its *P*-value are shown on each figure.

a) All taxa
r=0.53, *P*<0.001

b) All taxa, Andersen–transformed
r=0.63, *P*<0.001

c) Wind–pollinated taxa
r=0.75, *P*<0.001

d) Trees and shrubs
r=0.83, *P*<0.001

923 **FIGURE 3** Relationships between richness and selected environmental variables in pollen (left
924 column) and in plants (right column). Partial regression plots of linear regression analysis are given
925 with all the other significant environmental variables accounted for (see Table 2).
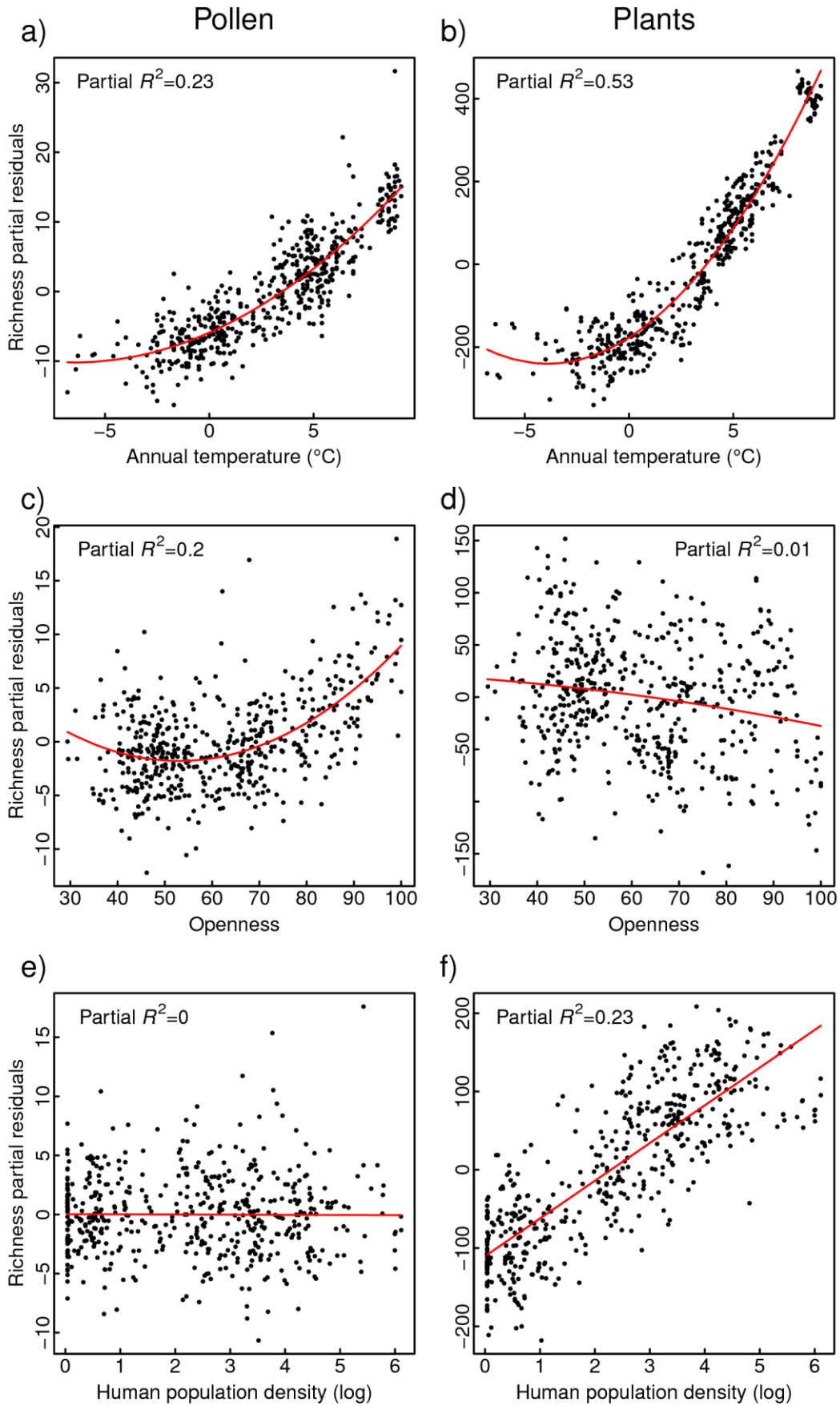
926   **FIGURE 4** Interactions of pollen–plant richness relationships with mean annual temperature (a,c)
927   and with latitude (b,d). The results are given both for pollen richness (a,b) and for Andersen-
928   transformed pollen richness (c,d).
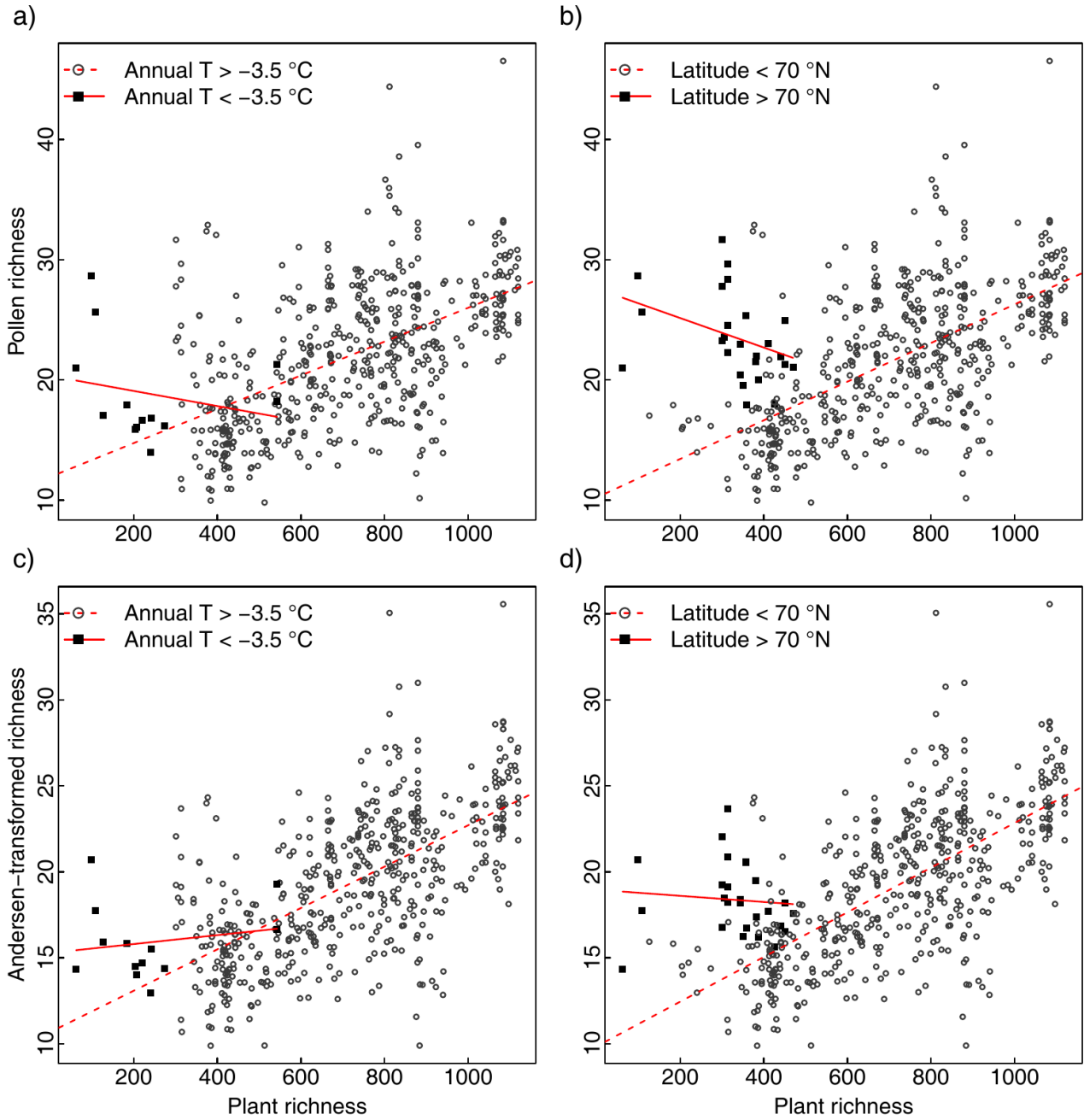
929 **FIGURE 5** Results of variation partitioning for plant richness (a) and pollen richness (b).
930 Explanatory datasets characterise climate (annual precipitation, mean annual temperature,
931 precipitation and temperature seasonality, isothermality, windspeed), landscape (elevation, variation
932 in elevation, openness, landscape diversity, human population density), and spatial autocorrelation
933 (spatial eigenvector [MEM] variables). In the case of pollen richness (b), plant richness is
934 considered as an additional explanatory variable.