Received: 4 October 2018 | Accepted: 7 January 2019

DOI: 10.1111/1365-2745.13134

RESEARCH ARTICLE

Journal of Ecology
BRITISH ECOLOGICAL SOCIETY

Patterns of modern pollen and plant richness across northern Europe

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Funding information
Estonian Research Council, Grant/Award Number: PUT1173, IUT1-8, PRG323, IUT21-1 and IUT20-29; Norges Forskningsråd, Grant/Award Number: 249894; H2020 European Research Council, Grant/Award Number: 741413; European Regional Development Fund

Handling Editor: Guillaume de Lafontaine

Abstract

1. Sedimentary pollen offers excellent opportunities to reconstruct vegetation changes over past millennia. Number of different pollen taxa or pollen richness is used to characterise past plant richness. To improve the interpretation of sedimentary pollen richness, it is essential to understand the relationship between pollen and plant richness in contemporary landscapes. This study presents a regional-scale comparison of pollen and plant richness from northern Europe and evaluates the importance of environmental variables on pollen and plant richness.
2. We use a pollen dataset of 511 lake-surface pollen samples ranging through temperate, boreal and tundra biomes. To characterise plant diversity, we use a dataset formulated from the two largest plant atlases available in Europe. We compare pollen and plant richness estimates in different groups of taxa (wind-pollinated vs. non-wind-pollinated, trees and shrubs vs. herbs and grasses) and test their relationships with climate and landscape variables.
3. Pollen richness is significantly positively correlated with plant richness ($r = 0.53$). The pollen plant richness correlation improves ($r = 0.63$) when high pollen producers are downweighted prior to estimating richness minimising the influence of pollen production on the pollen richness estimate. This suggests that methods accommodating pollen-production differences in richness estimates deserve further attention and should become more widely used in Quaternary pollen diversity studies.
4. The highest correlations are found between pollen and plant richness of trees and shrubs ($r = 0.83$) and of wind-pollinated taxa ($r = 0.75$) suggesting that these are the best measures of broad-scale plant richness over several thousands of square kilometres.

5. Mean annual temperature is the strongest predictor of both pollen and plant richness. Landscape openness is positively associated with pollen richness but not with plant richness. Pollen richness values from extremely open and/or cold areas where pollen production is low should be interpreted with caution because low local pollen production increases the proportion of extra-regional pollen.
6. *Synthesis*. Our results confirm that pollen data can provide insights into past plant richness changes in northern Europe, and with careful consideration of pollen-production differences and spatial scale represented, pollen data make it possible to investigate vegetation diversity trends over long time-scales and under changing climatic and habitat conditions.

KEYWORDS
climate, diversity, Holocene, landscape, palynological diversity, pollen–plant relationship, Quaternary

1 | INTRODUCTION

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 14,000–11,000 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; 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. 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, 2011; Meltsov, Poska, Reitalu, Sammul, & Kull, 2013) and the results usually show a positive relationship between modern pollen and plant diversity estimates (but see Goring, Lacourse, Pellatt, & Mathewes, 2013; Gosling et al., 2018). Most of these modern-day pollen–plant studies are done at relatively local scales where climate variation is small and the diversity relationships mainly depend on landscape factors (e.g. Matthias et al., 2015; Meltsov et al., 2013) within the relevant source area of pollen (RSAP). RSAP is defined by Sugita (1994) as the area beyond which the strength of the pollen–vegetation relationship does not improve. However, when using pollen richness in stratigraphic studies that cover the entire postglacial, the climate gradient is relatively large and it is not clear how the pollen–plant diversity relationship behaves along such a gradient and whether climate and/or landscape variables interact with the pollen–plant diversity relationship. In the present study, we test the relationships between pollen and plant richness across northern Europe covering a mean annual temperature range from −6.8°C to 9.2°C. We take advantage of existing European-scale modern pollen and plant datasets allowing us to consider both pollen and plant richness estimates.

The relationship between pollen and plant richness is influenced by interspecific differences in pollen production and dispersal causing over-representation of some taxa and under-representation or absence of other taxa in pollen assemblages (Birks, Felde, Bjune et al., 2016; Odgaard, 1999; Weng, Hooghiemstra, & Duivenvoorden, 2006). One proposed solution is to use representation factors that downweight the influence of numerically dominant pollen taxa (Andersen, 1970; Felde et al., 2016) or to look separately at groups of taxa with different pollination types, for example wind-pollination versus insect-pollination (Weng et al., 2006).

When using pollen richness as a proxy for plant richness, it is assumed that the relationship remains constant in different climatic and landscape conditions and that environmental variables influence pollen richness via their influence on plant richness. However, it is unclear how much of the variation in pollen richness is a reflection of plant richness and how much the variation in pollen richness is influenced directly by environmental variables. For example, it is well known that plant richness in Europe follows the major temperature gradient (Whittaker et al., 2007) but pollen richness can be influenced by temperature both indirectly through plant richness and directly through the influence of temperature on pollen production. Landscape diversity and openness are known to influence plant diversity (Reitalu et al., 2014; Ronk et al., 2015) but both factors can also directly influence pollen dispersal patterns (Odgaard, 1999; Sugita, Gaillard, & Broström, 1999). For example, it is known that the pollen-source area is larger in open areas and richness estimates tend to be higher because of a larger "sampling" area (Odgaard, 1999; Sugita et al., 1999). In mountainous areas at high elevations, pollen has been shown to be transported from the lowlands (Bajpai & Kar, 2018; Bell & Fletcher, 2016) and might thereby influence the pollen–plant richness relationship. Landscape openness in the present-day world is closely associated with human impact with agriculture greatly increasing the extent of open area. Over broad spatial scales, human population size has been shown to correlate positively with species richness in different taxonomic groups (Pautasso, 2007) suggesting that people have preferred to settle in areas of high biodiversity. Moderate human impact increasing landscape diversity and providing habitats for synanthropic species is known to increase both species and pollen richness (Colombaroli, Beckmann, Knaap, Curdy, & Tinner, 2013; Felde, Grytnes, Bjune, Peglar, & Birks, 2018; Reitalu et al., 2015, 2014), while too intensive human impact can cause local or even total extinction of species (Ceballos et al., 2015).

In the present study, we look in detail into the relationships of plant and pollen richness with a range of environmental factors that characterise both climate and landscape structure. Linear mixed effects (LME) modelling and variation partitioning are used to examine the differences and similarities between pollen and plant richness in relation to environmental factors.

The main aim of this study was to compare patterns of pollen and plant richness across northern Europe in relation to a range of climate and landscape factors. More specifically, we address the following questions:

1. Does pollen richness reflect plant richness?
2. Are pollen–plant richness relationships different within groups of taxa (wind-pollinated vs. not wind-pollinated, trees and shrubs vs. herbs and grasses)?
3. Are plant and pollen richness influenced by climate and landscape factors?

2 | MATERIALS AND METHODS

2.1 | Pollen data

The modern pollen dataset of lake-surface samples was compiled from Salonen, Seppä, Luoto, Bjune, and Birks (2012) and Matthias et al. (2015) and comes from small- to medium-sized lakes (median lake size 9 ha). These samples were collected and prepared in the laboratory using harmonised methodology (Seppä, Birks, Odland, Poska, & Veski, 2004) but counted by a number of different pollen analysts. Geographically, the dataset covers Scandinavia (including Svalbard), Finland, the Baltic countries, the western and northwestern parts of Russia (Salonen et al., 2012) and northern Germany (Matthias et al., 2015) (Figure 1), ranging through temperate, boreal and tundra biomes. In total, the dataset includes 633 pollen lake-surface samples. Spores from sporophytes were excluded from the dataset and the richness estimates only include seed plants. Aquatic plants are included in the richness estimation. After taxonomic harmonisation, there are 173 pollen types (Appendix S1).

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 1,000 in the southern sites. For pollen richness, rarefaction analysis where the richness is estimated for a fixed pollen sum is usually recommended (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.

2.2 | 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, and Pärtel (2014). The resulting dataset is the most comprehensive broad-scale plant distribution data to date, with distribution information for 5,221 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).

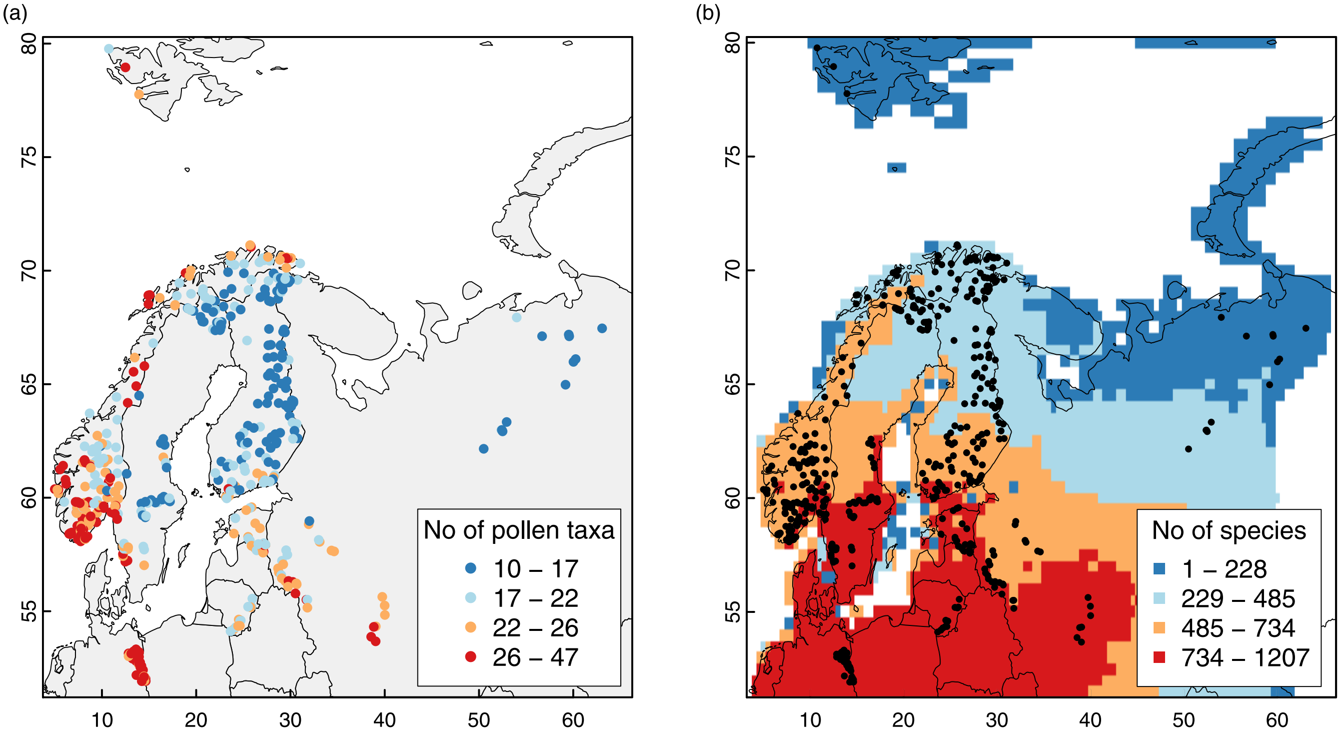

FIGURE 1 Map of northern Europe with (a) pollen richness (per 500 pollen grains) in lake-surface samples and (b) locations of surface-sample lakes on the plant richness map

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 × 50 × 50 km (=7,500 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 similarly to other samples based on cumulative number of species in the three cells. The plant dataset includes 1982 species in total. In the pollen analysis, only a few plant species are separable to species level. To test the effect of this taxonomic bias, the plant data were translated into pollen types according to Felde, Birks, Peglar, Grytnes, and Bjune (2017), which resulted in 388 pollen types or pollen equivalents (Birks, Felde, Bjune et al., 2016).

2.3 | Richness calculations

To equalise sampling effort in the richness estimations using 500 pollen grains, we randomly resampled 500 pollen grains from each pollen sample without replacement and repeated the randomisation 1,000 times—a procedure analogous to rarefaction analysis (Birks, Felde, Bjune et al., 2016; Felde et al., 2016). All the subsequent calculations of different pollen richness measures are based on each of the 1,000 randomisation draws and the average of the 1,000 is used as the richness estimate.

Pollen richness (number of all pollen taxa among 500 grains) and plant richness (number of all plant species) (Figure 1) are used as the main descriptors of pollen and plant diversity and for testing the relationships with environmental variables. To test whether pollen richness is a better predictor of plant richness in some taxon groups, we calculate both pollen and plant richness separately for wind-pollinated taxa and for non-wind-pollinated taxa, for trees and shrubs, and for herbs and grasses. Information about pollination modes was obtained from the plant trait database BiolFlor (Kühn, Durka, & Klotz, 2004). The pollination mode of pollen taxa is determined based on the prevailing pollination mode of the species within the taxon. The division of pollen taxa into these different taxon groups is given in Appendix S1. To estimate how the differences in taxonomic resolution in the pollen and plant data affect the possibilities of inferring plant diversity from pollen diversity, plant richness is expressed as richness of pollen types and both plant and pollen richness are expressed as richness of families.

To test for the effect of pollen-representation bias on pollen diversity estimates, we use Andersen-transformed pollen values (cf. Felde et al., 2016). Pollen counts of common tree and shrub taxa were multiplied by Andersen's (1970) general pollen-representation values and the new minimum pollen sum (149 pollen grains) used for rarefaction analysis with 1,000 randomisations.

In summary, pollen diversity is characterised as: total pollen richness (R_{po}), Andersen-transformed R_{po}, R_{po} of families, R_{po} of herbs and grasses, R_{po} of trees and shrubs, R_{po} of wind-pollinated taxa and R_{po} of non-wind-pollinated taxa. Plant diversity is characterised as: total richness (R_{pl}), R_{pl} of pollen types, R_{pl} of families, R_{pl} of herbs and grasses, R_{pl} of trees and shrubs, R_{pl} of wind-pollinated species and R_{pl} of non-wind-pollinated species.

2.4 | Environmental data

We use climate data from the WorldClim database (www.worldclim.org) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and the 10-arc-minute “bioclim” dataset which includes 19 bioclimatic variables that are calculated from monthly temperatures and rainfall data for 1961–1990 (O'Donnell & Ignizio, 2012). In addition to these bioclimatic data, we use windspeed data from the ERA-Interim analysis (Dee et al., 2011). Because the bioclimatic variables are highly intercorrelated, we used principal components analysis (PCA) to choose a subset of climate variables. The first six PCA axes explain 98% of the variation in the climate dataset (PC1 explains 54% of the variation, PC2 22%, PC3 9%, PC4 6%, PC5 4%, PC6 3% and all the other principal components less than 1%). Six climate variables are chosen for subsequent analyses based on their correlations with the first six PCA axes (Appendix S2 Table S2.1) and intercorrelations with other climate variables (Appendix S2 Table S2.2). For example, the first PCA axis was clearly associated with precipitation—precipitation of driest quarter, precipitation of coldest quarter, precipitation of driest month and annual precipitation have the highest loadings along PC1. Because all four precipitation variables are highly intercorrelated ($r > 0.98$), we choose annual precipitation as the most widely known precipitation variable in our analysis.

1. Annual precipitation—total annual precipitation (mm/year);
2. Mean annual temperature—mean annual temperature (°C);
3. Precipitation seasonality—coefficient of variation in monthly precipitation totals;
4. Temperature seasonality—standard deviation of monthly temperature averages;
5. Isothermality—size of day-to-night temperature oscillation in relation to annual oscillations, mean diurnal range divided by the annual temperature range;
6. Windspeed—average windspeed (m/s) for spring and summer (April–August) 10 m above the ground (averaged for 1979–1998).

Six landscape variables known from previous studies (overview in Birks, Felde, Bjune et al., 2016) to influence plant and/or pollen richness are used to characterise the landscape:

1. Lake area—the surface area of the pollen-sample lake (in ha), estimated from Google Maps (Google, 2016);
2. Elevation—elevation of each pollen-sample site (m above sea level), extracted from ETOPO1 1 Arc-Minute Global Relief Model (Amante & Eakins, 2009);
3. Elevation variation—characterises the variation in topography in a 50 km radius around each pollen-sample site, standard deviation of the elevation of ETOPO1 model (Amante & Eakins, 2009);
4. Openness—landscape openness calculated from a global forest-cover dataset (Hansen et al., 2013): the original 30-m-resolution dataset was resampled to a 900-m-resolution and average openness in a 50-m radius around the pollen-sample sites is calculated as 100 minus the forest cover;
5. Landscape diversity—Simpson diversity estimate for a 50 km radius around each pollen-sample site, based on the land-cover types in the Global Land Cover 2000 database at 1 km resolution (Hartley et al., 2006);
6. Human population—human population density (persons/km^2), extracted from the Gridded Population of the World (GPW) database (Center for International Earth Science Information Network, 2016). We use the average population density of the 50 km radius area around each pollen-sample site calculated from the 0.5 arc-minute resolution map.

In case of the 21 pooled pollen samples with pollen data from several lakes, environmental variables are calculated as averages of the lakes included in the pooling with the exception of lake area that is calculated as the sum of lake areas. The correlations among the landscape variables do not exceed 0.6 and all variables are retained in the subsequent analyses (Appendix S2 Table S2.2).

2.5 | Statistical analyses

Correlations between the pollen and plant variables and among the environmental variables are quantified by Pearson's product moment correlation coefficients.

To identify environmental and climate variables associated with plant and pollen richness, we use LME models (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). To account for the pollen data from different regions being analysed by different scientists and to account for the regional differences in the plant and pollen data, we use “Region” as a random variable in the LME model. Nine regions were used: Estonia, Finland, Germany, Lithuania, Norway (including Svalbard), Sweden1 (analysed in Bergen), Sweden2 (analysed in Helsinki), Russia1 (Komi region) and Russia2 (western Russia). Pollen richness (per 500 pollen grains) and plant richness (in three 50 × 50 km plots) are used as response variables. Six climate variables (annual precipitation, mean annual temperature, precipitation seasonality, temperature seasonality, isothermality, windspeed) and six landscape variables (lake area, elevation, elevation variation, openness, landscape diversity, human population density) are used as explanatory variables. Quadratic terms of all explanatory variables are tested. Log-transformation is used for annual precipitation, windspeed, lake area and human population density to ensure a uniform data distribution. Both richness data and explanatory variables are standardised to zero mean and unit variance to enable comparison of model estimates. Backward selection of explanatory variables is used and only significant ($p < 0.01$) variables retained in the models. 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 calculated for the models according to Nakagawa and Schielzeth (2013). In models describing pollen richness, plant richness is also used as an explanatory variable. To test whether the relationship between pollen and plant richness is influenced by climate or landscape configuration, a separate model-selection procedure is used to test for interactions between plant richness and environmental variables in explaining pollen richness.

Linear mixed effect models with pollen richness as response, environmental variables as fixed variables, and "Region" as a random variable do not have significant spatial autocorrelation in the errors. However, errors of the LME models with plant data as the response remain spatially autocorrelated. To clarify the proportions of variation explained by purely spatial variation, climate, and landscape variables, we use variation partitioning (Borcard, Legendre, & Drapeau, 1992). Moran's eigenvector map (MEM) approach (Griffith & Peres-Neto, 2006) is used to characterise the spatial structure in the data. In the MEM approach, orthogonal, linearly independent (MEM) eigenvectors are calculated from a spatial weighting matrix. Based on permutation tests, a set of MEM variables significantly ($\alpha < 0.05$) contributing to minimising the global Moran's I is chosen and used as explanatory variables in variation partitioning. In addition to spatial descriptors (the MEM variables), explanatory datasets characterising climate (annual precipitation, mean annual temperature, precipitation and temperature seasonality, isothermality, windspeed) and landscape (elevation, variation in elevation, openness, landscape diversity, human population density) are used in variation partitioning. In the case of pollen richness, plant richness is considered as an additional explanatory variable.

The LME analysis and variation partitioning are primarily used to test the effect of climate, landscape and spatial variables on total pollen and plant richness. However, similar analyses are followed up for other richness variables (Andersen-transformed pollen richness, tree and shrub richness in pollen and in plants, herb and grass richness in pollen and in plants, richness of wind-pollinated taxa in pollen and in plants, richness of non-wind-pollinated taxa in pollen and in plants). The results of these analyses are presented in Appendix S3 (LME models) and Appendix S4 (variation partitioning).

The statistical software R (R Core Team, 2017) was used for all statistical analyses with packages "nlme" (Pinheiro, Bates, & DebRoy, 2018) for LME models, "vegan" (Oksanen et al., 2017) for variation partitioning, and "spdep" (Bivand & Piras, 2015) for MEM calculations.

3 | RESULTS

3.1 | Pollen richness as a predictor of plant richness

Total pollen richness is relatively weakly associated with plant richness ($r = 0.53$, $p < 0.001$) (Table 1, Figure 2a). The Andersen transformation improves the pollen–plant richness correlation

TABLE 1 Pearson correlation coefficients between richness calculated from pollen data (columns) and plant data (rows), R_{po} – pollen richness, 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

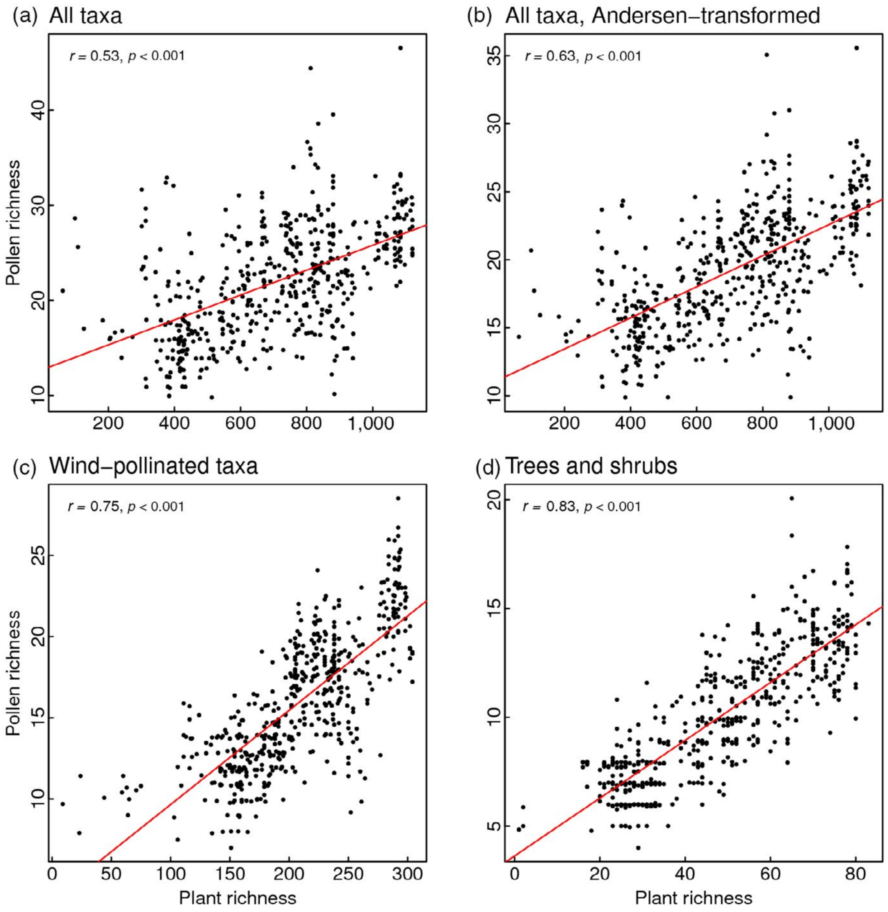

FIGURE 2 Correlations between pollen richness and plant richness in different taxon groups: (a) all taxa, (b) all taxa, pollen Andersen-transformed, (c) wind-pollinated taxa, (d) tree and shrubs. Pearson correlation coefficient and its *P*-value are shown on each figure [Colour figure can be viewed at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

($r = 0.63$, $p < 0.001$) (Table 1, Figure 2b). While pollen richness of wind-pollinated taxa is a relatively good predictor of plant richness of wind-pollinated species ($r = 0.75$, $p < 0.001$; Figure 2c), there is no significant correlation between richness estimates of taxa that are not wind-pollinated ($r = -0.05$, n.s) (Table 1). The highest correlation is found between pollen and plant richness of trees and shrubs ($r = 0.83$, Table 1, Figure 2d). In addition, pollen richness estimates of wind-pollinated taxa and of trees and shrubs appear to be good predictors of all the plant richness estimates included in the study with correlation coefficients above 0.75 (Table 1).

3.2 | Pollen and plant richness in relation to climate and landscape variables

Linear mixed effects models show that while the environmental variables explain most of the variation in plant richness (marginal pseudo-$R^2 = 0.92$), the relationships between pollen richness and environment are less well determined (marginal pseudo-$R^2 = 0.58$) (Table 2).

Mean annual temperature is the strongest predictor of both pollen and plant richness (Figure 3a,b, Table 2) with more taxa at higher temperatures. The LME models with other richness estimates indicate that mean annual temperature is clearly the strongest predictor of both pollen and plant richness irrespective of the taxon group considered (Appendix S3). While plant richness is significantly associated with all the climate variables tested, the relationships between pollen richness and climate are weaker (Table 2). However, three temperature-related climate variables—mean annual temperature, temperature seasonality and isothermality—have significant interaction terms with plant richness in explaining pollen richness (Table 2, Figure 4). The relationship between pollen and plant richness is less determined at lower mean annual temperature values (Figure 4a) and the pollen–plant richness association is even negative at high latitudes (Figure 4b). When using the Andersen-transformed pollen richness or tree and shrub richness, interactions between plant richness and climate are fewer and are less determined but still statistically significant (Appendix S3 Table S3.1, Figure 4c,d).

Because all 21 pooled pollen samples (including pollen data from several lakes) are from northern latitudes, we checked whether the pooling of the data might have caused the interaction effects—with pooled pollen samples having higher beta-diversity and thereby higher pollen richness. We calculated the LME interaction model including all original 633 pollen samples and pollen richness rarefied to the lowest pollen sum of 134. The interaction terms with plant richness were significant for annual mean temperature ($p < 0.001$) and for temperature seasonality ($p < 0.001$), but the interaction between plant richness and isothermality was not significant (Appendix S3 Table S3.6).

Of the landscape variables, elevation is similarly associated with both plant and pollen richness with more taxa at higher

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

	Pollen richness				**Plant richness**	
	LME with quadratic associations		**LME with plant richness interactions**		**LME with quadratic associations**	
Variable	**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	

elevations (Table 2). Other landscape variables have different relationships with pollen and plant richness: openness is only associated with pollen richness (Figure 3c,d) and human population density is only associated with plant richness (Figure 3e,f). While landscape diversity is positively associated with plant richness, the relationship with pollen richness tends to be negative (Table 2). Lake area is not significant in any of the models and is not included in the results tables.

When plant richness is included as an explanatory variable in the model together with all the environmental variables, plant richness is significantly associated with pollen richness only after interactions with climate variables are accounted for (Table 2). In the case of Andersen-transformed pollen richness, richness of trees and shrubs and richness of wind-pollinated taxa, the corresponding plant richness is significant also in the models without the interaction terms (Appendix S3).

The results of variation partitioning show that the largest proportion of variation in both pollen and plant richness is explained jointly by the climate, landscape and spatial variables (80% for plant richness, 22% for pollen richness; Figure 5). The share of variation explained by climate and landscape independently of the spatial variables is larger for pollen richness (12.5%) than for plant richness (2.3%) (Figure 5). For pollen richness of herbs and grasses and taxa not wind-pollinated, landscape variables explain relatively large individual shares of variation (7.0% and 6.5% respectively) (Appendix S4; Figures S4.3b and S4.5b). The amount of variation in pollen richness explained only by plant richness is low (<1%) for all richness estimates (Figure 5, Appendix S4). However, the total amount of variation explained by plant richness including the variation explained jointly with other variables varies from 3% (for richness of herbs and grasses and richness of non-wind-pollinated taxa) to >55% (richness of trees and shrubs and richness of wind-pollinated taxa).

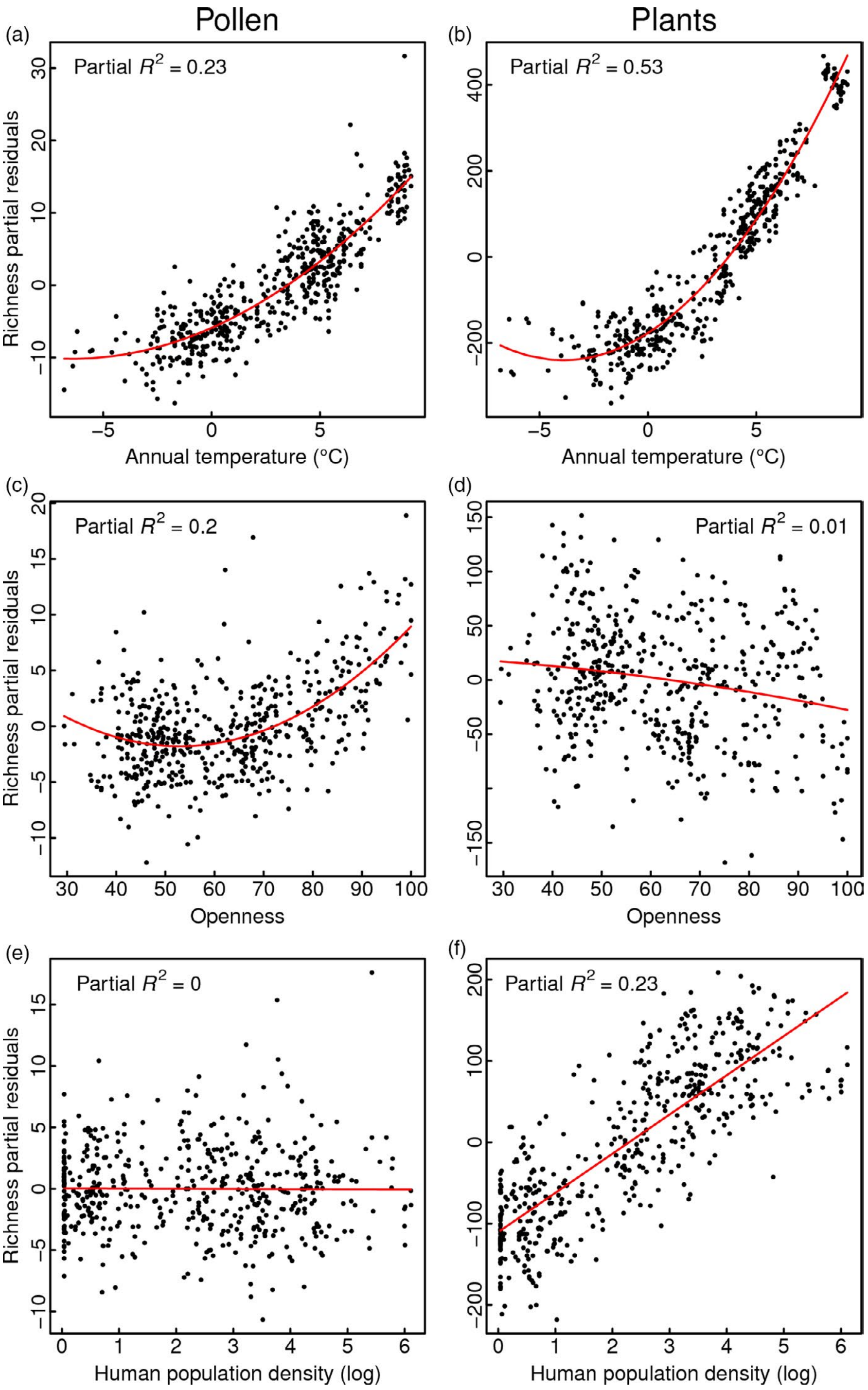

FIGURE 3 Relationships between richness and selected environmental variables in pollen (left column) and in plants (right column): annual mean temperature (a, b), openness (c, d), human population density (e, f). Partial regression plots of linear regression analysis are given with all the other significant environmental variables accounted for (see Table 2) [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | Pollen richness in relation to plant richness

The often used rarefaction-based total pollen richness has a relatively low but significant positive correlation with total plant richness (*r* = 0.53, *p* < 0.001). The most serious critiques against using pollen richness as a proxy of past plant richness relate to the pollen-representation bias sensu Odgaard (1999, 2008) where the high pollen producers decrease the probability of finding rare pollen types and thereby influence the estimated richness. Several different methods have been proposed to minimise the pollen-production bias (cf. Birks, Felde, Bjune et al., 2016). Using pollen-representation values (i.e. Andersen, 1970) or pollen productivity estimates (e.g. Broström et al., 2008) to downweight the high pollen producers prior to rarefaction analysis is one option that has been used by several authors (Felde et al., 2016; Matthias et al., 2015). In our analysis, we test the use of Andersen-transformed pollen richness and although it improves the pollen–plant richness correlation (*r* = 0.63, *p* < 0.001) it

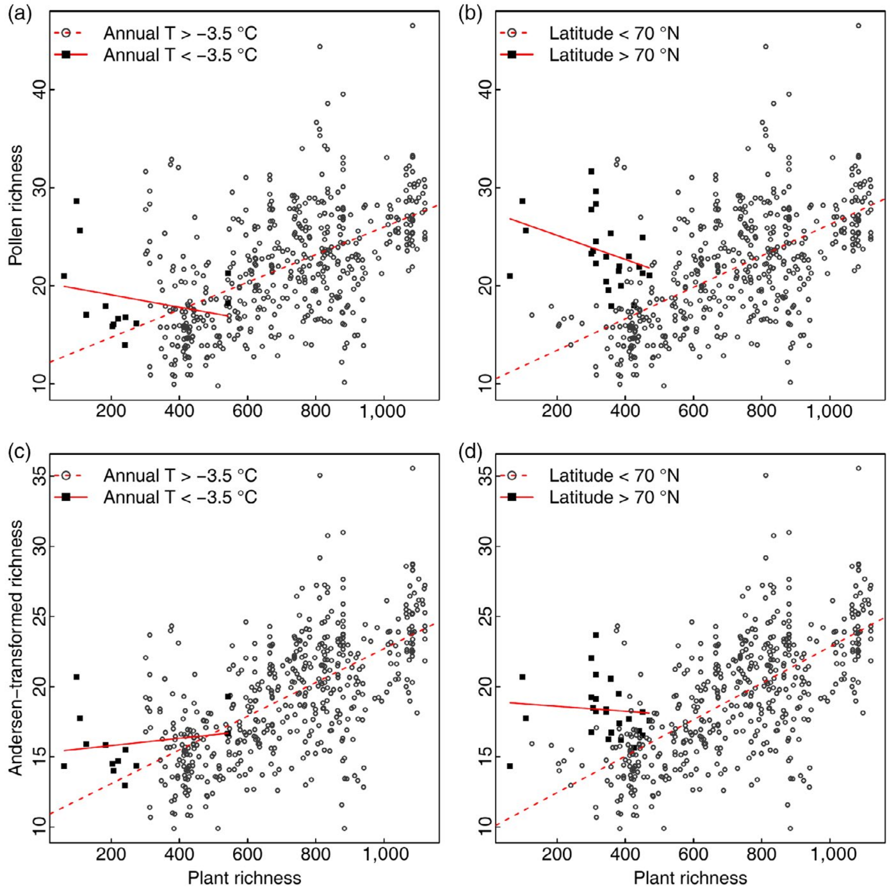

FIGURE 4 Interactions of pollen–plant richness relationships with mean annual temperature (a, c) and with latitude (b, d). The results are given both for pollen richness (a, b) and for Andersen-transformed pollen richness (c, d) [Colour figure can be viewed at wileyonlinelibrary.com]

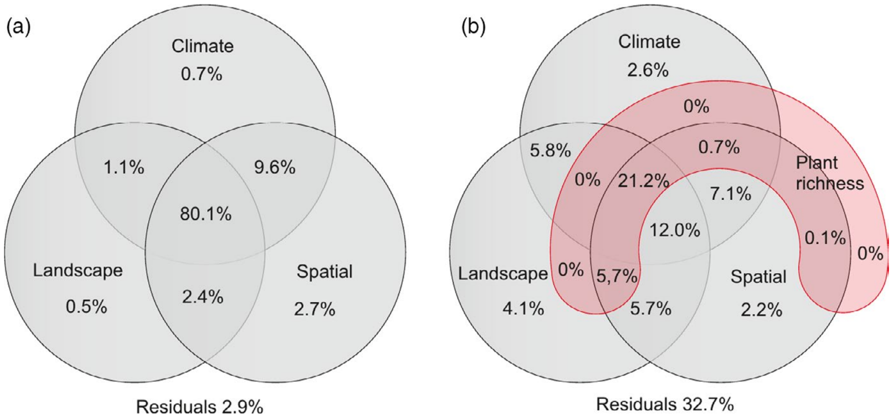

FIGURE 5 Results of variation partitioning for plant richness (a) and pollen richness (b). Explanatory datasets characterise climate (annual precipitation, mean annual temperature, precipitation and temperature seasonality, isothermality, windspeed), landscape (elevation, variation in elevation, openness, landscape diversity, human population density) and spatial autocorrelation (spatial eigenvector [MEM] variables). In the case of pollen richness (b), plant richness is considered as an additional explanatory variable [Colour figure can be viewed at wileyonlinelibrary.com]

does not completely remove the interaction effects of the richness relationship with climate and latitude. The pollen data are limited by the original pollen counts in the samples and any transformation can only work within the limits of the original counts. To overcome this problem, methods adjusting the maximum pollen count during the counting process have been proposed—allowing pollen counts to be developed relative to the evenness and richness of the specific sample rather than a fixed number (Keen et al., 2014). Our analyses together with earlier studies (Felde et al., 2016; Matthias et al., 2015) suggest that methods accommodating pollen-representation bias in pollen richness studies warrant further attention and should become as widely used as pollen-production transformations in land-cover reconstruction studies (e.g. Mazier et al., 2015; Mehl & Hjelle, 2015; Roberts et al., 2018).

The studies that investigate pollen–plant richness relationships often use the pollen type–based plant richness to reduce the influence of taxonomic bias where some pollen taxa include considerably more species than others (Felde et al., 2016; Goring et al., 2013; Meltsov et al., 2011). For example, the whole family Cyperaceae is included as one pollen type, while the main tree species can be separated at the genus or species level. In our dataset, translating the plant data into pollen types or using family-level richness does not improve the correlation between the pollen and plant richness estimates, indicating that taxonomic bias is more-or-less constant across the whole range of the data.

In our results, the correlation between plant and pollen richness greatly improves when only trees and shrubs are considered ($r = 0.83$). Similar to our study, Flenley (2005) showed that the palynological richness of woody taxa follows well the latitudinal gradient of tree and shrub species. As with tree and shrub richness, pollen richness of wind-pollinated taxa is a good indicator of corresponding plant species richness ($r = 0.75$). Many of the tree and shrub taxa in our study are wind-pollinated (Appendix S1) and thus the two richness measures largely overlap. Similar to the pollen data in large databases such as the European Pollen Database (Davis et al., 2013; Giesecke et al., 2013) or the Neotoma Paleoecology Database (Williams et al., 2018), our pollen dataset combines the work of multiple analysts and the dataset loses taxonomic precision due to the merging of certain morphologically difficult pollen taxa. The lack of correlation between pollen and plant richness among insect-pollinated taxa or among herbs and grasses may be related to this "analyst effect" but is likely to be additionally influenced by landscape configuration (c.f. Appendix S4, Figures S4.3 and S4.5) and the spatial scale of the plant data used. Changes in the diversity of insect-pollinated taxa can be detected with good pollen-taxonomic precision, consistent effort in pollen taxonomy, and high pollen sums (>1,000 grains) (Meltsov et al., 2011). The RSAP for European small lakes is usually estimated to be 1,000–2000 m from the lake (Hjelle & Sugita, 2011; Nielsen & Sugita, 2005; Poska, Meltsov, Sugita, & Vassiljev, 2011), which is a much finer spatial resolution than the resolution of the plant data in our study. Therefore, to understand better the relationship between plant and pollen richness of both wind-pollinated and non-wind-pollinated taxa, the plant dataset should include several nested spatial scales.

Weng et al. (2006) suggest that the wind-pollinated and insect-pollinated pollen taxa should be treated separately in pollen richness studies. Our results strongly support this and we recommend that richness of trees and shrubs or richness of wind-pollinated taxa are good choices when using pollen richness to reflect major changes in past plant richness over broad spatial scales and in studies involving data from different sources. According to our results, pollen richness of trees and shrubs and of wind-pollinated taxa are also good indicators of broad-scale total plant richness ($r = 0.79$ and $r = 0.81$ respectively) because in northern Europe the plant richness of trees and shrubs and the richness of wind-pollinated taxa are, in turn, highly positively correlated with total richness. However, as the relationship between wind-pollinated and non-wind-pollinated taxa is not constant across the globe (Regal, 1982), studies from other regions or global studies of pollen–plant richness are needed to confirm the trends demonstrated here.

A series of earlier studies have found similar positive correlations between pollen and plant richness in Europe (Birks, 1973; Felde et al., 2016; Matthias et al., 2015; Meltsov et al., 2011; Odgaard, 2008). However, investigations from the tropics (Gosling et al., 2018; Jantz, Homeier, & Behling, 2014) or from temperate western North America (Goring et al., 2013) have not found such positive correlations. Evaluating pollen–plant diversity relationships not only depends on the nature of pollen data but also on the spatial scale and quality of plant data (Birks, Felde, Bjune et al., 2016). In the present study, we use the best available regional-scale plant database that has a relatively coarse spatial resolution (50 × 50 km) and both pollen and plant data 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 (1,000–2,000 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.

4.2 | 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 (Figures 1 and 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, 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 indicate that pollen richness at conditions corresponding to present-day high latitudes (>70°N, mean annual temperature <−3.5°C) in sedimentary studies should be treated with caution because the richness values may be heavily influenced by long-distance transport of extra-regional pollen. Pollen data from high latitudes often have low pollen sums because of the scarcity of pollen. Pooling pollen data from several lakes (as we have done in 21 pooled samples) increase the overall pollen-source area and might be the reason behind the unproportionally high pollen richness in low temperatures and high latitude (Figure 4). However, the analysis with pollen richness from the original samples (without pooling) indicates that the interaction of pollen–plant richness correlation with temperature is not an artefact of our data handling but is also evident when pollen richness is based on low pollen sums (Appendix S3 Table S3.6). Low temperatures in high latitudes (and elevations) may have a negative influence on local pollen production increasing the proportion of long-distance pollen in the samples (van der Knaap, 1990; Seppä, 1998). The relatively high pollen richness in the late-glacial described in several studies (Berglund, Gaillard, Björkman, & Persson, 2008; Birks & Line, 1992; Reitalu et al., 2015) might therefore be influenced by long-distance pollen dispersal from outside the region.

4.3 | Influence of landscape variables on pollen and plant richness

Among the landscape variables, openness and elevation have positive correlations with pollen richness and, as discussed above, earlier studies have also shown that both variables can have a positive effect on pollen richness (but not necessarily through an increase in plant richness) (Felde et al., 2016; Meltsov et al., 2011; Odgaard, 2008). In two modern pollen–plant richness studies from the tropics, where there is no clear link between pollen and plant richness, the gradient of openness is involved: Gosling et al. (2018) described the diversity from closed evergreen forests to wooded savanna and Jantz et al. (2014) involved elevational gradients. Openness, at high elevations or latitudes, in naturally open dry areas or human-influenced landscapes is known to have a positive effect on pollen richness through the increased pollen-source area in open conditions (Felde et al., 2016; Seppä, 1998; Sugita et al., 1999) and through higher pollen evenness that allows more taxa to be detected (Odgaard, 2008). Our results also demonstrate that openness has a positive effect on pollen richness but not on plant richness (Figure 3) indicating that openness interacts with the pollen–plant richness relationship. These results call for caution in interpreting pollen richness from open areas and for the development of methods that take into account differences in pollen production and source area, for example calculating pollen diversity from pollen accumulation rates (van der Knaap, 2009), employing varying pollen sums depending on pollen production (Keen et al., 2014), or using expert knowledge to exclude extra-regional pollen (van der Knaap, 1990).

The individual effects of landscape variables are especially high for pollen richness of herbs and grasses and for pollen richness of non-wind-pollinated taxa, further confirming that in our dataset these groups of pollen taxa are influenced by different factors and/or on different spatial scales than the plant species richness used in our study.

Late-Holocene pollen diversity studies from Europe often highlight human impact as having a positive influence on pollen richness where land-clearance for agriculture and anthropogenic disturbance are creating habitats for more taxa that cannot grow in forested areas (Berglund et al., 2008; Colombaroli et al., 2013; Felde et al., 2018; Giesecke et al., 2012; Reitalu et al., 2015). It is, therefore, somewhat surprising that there is no association between human population size and pollen richness in the LME models (Figure 4e), while population size is significantly positively correlated with plant richness (Figure 4f). In our dataset, the human population size is strongly positively correlated with mean annual temperature ($r = 0.9$, $p < 0.001$, Appendix S2) and the effects of climate and human impact are not clearly separable. We also test the LME model without mean annual temperature, and then human impact is included in the model and it is significantly positively linked with pollen richness. The modern data used in our study are not directly comparable with the situation during the last 4,000 years when temperatures were decreasing slightly (Renssen et al., 2009) but the human impact was increasing considerably.

5 | CONCLUSIONS

Our results offer the first regional-scale comparison of pollen and plant richness from Europe and allow the evaluation of the relative importance of different environmental variables on both pollen and plant richness. Differences in pollen production among taxa influence the pollen richness estimates and the development of better methods for reducing pollen-production bias should therefore get more attention in further methodological studies. Pollen richness values may be overestimated in open landscapes, such as arctic tundra, high elevations and areas of intensive agriculture where the extremely low local pollen production increases the proportion of taxa from outside the region.

We suggest that pollen richness of trees and shrubs or of wind-pollinated taxa are good indicators of broad-scale plant richness changes over thousands of square kilometres. The pollen richness of insect-pollinated herbaceous plants is more likely to be influenced by local landscape-scale factors and should be interpreted separately from the wind-pollinated taxa. Our results confirm that pollen data can provide insights into past plant richness changes, and thus make it possible to investigate vegetation diversity trends over long time-scales and under changing climatic and habitat conditions outside the scope of contemporary ecological studies.

ACKNOWLEDGEMENTS

We thank Anneli Poska for valuable comments on the earlier version of the manuscript. We are grateful to Cathy Jenks for help with editing the manuscript and to Will Gosling and an anonymous reviewer for helpful comments. The study was supported by the Estonian Research Council grants PUT1173, IUT1-8 and PRG323 to T.R. and A.B., IUT21-1 to V.V. and IUT20-29 to A.H. A.H. was supported by the European Union through the European Regional Development Fund (Centre of Excellence EcolChange). T.R., A.H. and V.V. thank the Estonian Government for continuously keeping up our hopes about raising research funding to 1% of GDP. H.J.B.B. is supported by the NRF (project 249894, IGNEX) and the ERC Horizon 2020 programme (project 741413, HOPE).

AUTHORS' CONTRIBUTIONS

T.R. designed the study and wrote the paper with the input from H.J.B.B., H.S. and all other co-authors; H.J.B.B., A.E.B., T.G., I.M., S.M.P., J.S.S. and H.S. provided the pollen-analytical data; A.H. prepared the gridded plant distribution dataset; V.V. and T.R. harmonised the pollen taxonomy and divided the plant data into pollen types; A.E.B. and T.R. prepared the climate and environmental datasets; T.R. and A.E.B. did the statistical analyses with suggestions from H.J.B.B.

DATA ACCESSIBILITY

The original pollen counts are available from the European Modern Pollen Database http://wp.unil.ch/davisgroup/research (Davis et al., 2013). Coordinates of pollen-sample lakes, the dataset of plant species associated with each of the 511 pollen samples and pollen and plant richness calculations are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.m4s45t4 (Reitalu et al., 2019).

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SUPPORTING INFORMATION

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How to cite this article: Reitalu T, Bjune AE, Blaus A, et al. Patterns of modern pollen and plant richness across northern Europe. *J Ecol*. 2019;107:1662–1677. https://doi.org/10.1111/1365-2745.13134