Novel insights into post-glacial vegetation change: functional and phylogenetic diversity in pollen records

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Keywords
Biodiversity; Late quaternary; Long-term; Millennial time-scale; Palynological diversity; Plant diversity; Pollen data

Abbreviations
Cal. yr BP = Calibrated years Before Present (present=1950); CWM = Community-weighted mean; GAM = Generalized additive model; LG = Late glacial; NGRIP = North Greenland ice core project; SESMPD = Standardized effect size of the mean pair-wise distance; SLA = Specific leaf area.

Nomenclature
Krall et al. (2010)

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Abstract

Question: How do pollen-based functional and phylogenetic diversity help to explain post-glacial vegetation change in relation to climate and human influence?

Location: Estonia and Latvia, NE Europe.

Methods: We used a data set of 1062 pollen samples from 20 sites covering the last 14 500 yrs to estimate plant richness, evenness, functional and phylogenetic diversity (community-weighted mean and mean pair-wise distance). We adjusted existing functional and phylogenetic diversity measures for the pollen data and tested the methods with a simulation study. The simulations showed that species-based and pollen-based diversity estimates were all significantly positively correlated.

Results: The Late Glacial (14 500–11 650 cal. yr BP) and the mid-Holocene (8000–4000 cal. yr BP) periods showed contrasting values for most of the diversity components, and several diversity estimates were strongly associated with climate. The cold climate during the Late Glacial led to high phylogenetic diversity, and relatively low functional diversity. Climate warming during the transition from the Late Glacial to the Holocene was followed by a decrease in phylogenetic diversity but an increase in functional diversity based on plant height and seed weight. Increasing human impact in the late Holocene was associated with an increase in plant richness and decreases in functional diversity based on plant height and seed weight and in phylogenetic diversity of herbs.

Conclusions: Pollen-based functional and phylogenetic diversity provide novel insights into post-glacial vegetation change and its drivers. Both functional and phylogenetic diversity were closely related to climatic conditions, suggesting that trait differences play an important role in long-term community response to climate change. Our results indicate that human impact during the last two millennia has influenced functional and phylogenetic diversity negatively by suppressing plants with certain traits (functional convergence) and giving advantage to plants from certain phylogenetic lineages. We see great potential in the further development of functional and phylogenetic diversity methods for pollen data.

Introduction

Sedimentary pollen data are a valuable information source for millennial-scale vegetation change; palynological records have also been used to reveal past landscape-scale plant diversity (Lindbladh 1999; Odgaard 1999; Fredh et al. 2012; Giesecke et al. 2012). In glaciated areas, most of (if not all) the vegetation diversity was eradicated and reformed when the ice retreated. As such, observing diversity patterns during the entire post-glacial period provides insights into the mechanisms underlying the formation of contemporary diversity, for example, to estimate the importance of migration lags for post-glacial diversity changes (Giesecke et al. 2012), to study the
relative importance of climatic and human impact (Reitalu et al. 2013), and to elucidate the role of competition in long-term turnover of species (Seppä et al. 2009). In the face of climate change and widespread anthropogenic impact, understanding the roles of past climate changes and human impact on biodiversity is crucial to being able to make predictions based on possible future scenarios.

Traditionally, palynological studies use pollen-type richness as the estimate of diversity. In Northern and Central Europe, pollen richness has been shown to be relatively high during the Late Glacial (LG) period (from the onset of ice retreat until 11 650 cal. yr BP (calibrated years before 1950)), to decrease considerably during the first millennia of the Holocene and to increase during the Holocene, with the maximum values close to the present day (Birks & Line 1992; Berglund et al. 2008). High palynological richness during the Late Holocene has often been found to be related to human impact (Lindbladh 1999; Berglund et al. 2008; Colombaroli et al. 2013). Pollen sample evenness has been proposed as an additional measure to reflect vegetation diversity (Odgaard 1999) and has been used in several palynological studies (Fredh et al. 2012; Giesecke et al. 2012; Colombaroli et al. 2013).

Richness and evenness are essential diversity measures also in studies of contemporary plant communities. However, functional diversity (accounting for functional and phenotypic differences between species) and phylogenetic diversity (considering the differences in the evolutionary history of species) have recently been used as additional measures of community diversity (e.g. Gerhold et al. 2013; Purschke et al. 2013). Functional diversity is estimated from the traits of co-existing species and high functional diversity is often interpreted as an indication of interspecific competition, such as limiting similarity, under which species that are functionally too similar cannot co-exist (Purschke et al. 2013). Low functional diversity can be the result of environmental filtering, through which co-existing species need to have particular traits to cope with their environment. Low functional diversity can also be the result of competitive exclusion (Mayfield & Levine 2010), which favours species with similar trait values (e.g. plant height in competition for light). Phylogenetic diversity reflects the accumulated evolutionary history of co-existing species. The relationship between functional and phylogenetic diversity has been subject to debate. On the one hand, phylogenetic diversity could be used as a proxy for functional diversity of phylogenetically conserved traits in order to infer community assembly (Webb et al. 2002), while on the other hand, trait variation within phylogenetic lineages could be even greater than the variation between lineages (Prinzing et al. 2008). Functional and phylogenetic diversity have so far not been assessed in palaeoecological vegetation studies. Studies of temporal changes in functional and phylogenetic diversity enable both evaluation of the importance of random vs deterministic processes in long-term community assembly (Purschke et al. 2013; Correa-Metrio et al. 2014) and identification of plant traits related to extinction or success following environmental changes (Bhagwat & Willis 2008; Lacourse 2009; Jeffers et al. 2011). Functional aspects of diversity have also been shown to be closely related to climate (Díaz et al. 1998; Lacourse 2009), thus long-term studies of the interactions between climate, human impact, functional and phylogenetic diversity are fundamental to predict ecosystem response to future climate change (Reitalu et al. 2014a).

In the present study, we use sedimentary pollen data to characterize plant diversity expressed as richness, evenness, functional and phylogenetic diversity in NE Europe (Estonia and Latvia) throughout the post-glacial period (14 500 yrs). We adjust existing methods from vegetation science to calculate pollen-based functional and phylogenetic diversity (community-weighted mean and mean pair-wise distance) and test the methods with the help of a simulation study that compares species-based and pollen-based estimates of functional and phylogenetic diversity. Specifically, we hypothesize that:

1. Diversity components (richness, evenness, functional and phylogenetic diversity) all convey independent additional information and show varying trends through the 14 500-yr period;
2. The Late Glacial (LG) and the Holocene have contrasting values in diversity owing to climatic differences;
3. Diversity components are influenced differently by climate and human impact.

**Methods**

**Study area**

The study area (56°–60° N, 22°–28° E) is situated in the boreo-nemoral forest zone and covers Estonia and Latvia. The contemporary vegetation consists of a mixture of boreal tree species with less frequent nemoral species. Approximately half of the study area is forested, with the remainder covered by agricultural fields, semi-natural and intensively managed pastures and hay meadows. During the LG period (from 14 500 to 11 650 cal. yr BP), the area was covered with treeless tundra vegetation, intermixed with mixed pine–birch–aspen forests (Amon et al. 2014). The thermophilous taxa (e.g. *Tilia, Quercus, Ulmus* and *Corylus*) became abundant during the Holocene thermal maximum (8000–4000 cal. yr BP). Around 4000 cal. yr BP, the thermophilous forests declined in favour of *Betula, Pinus* and *Picea* as a result of climate cooling and increasing human impact after the introduction of agriculture (Poska & Saarse 2002).
Pollen data

Estonia and Latvia are well represented by pollen records from the Holocene (e.g. Poska & Saarse 1999, 2002; Veski et al. 2005, 2012; Niinemets & Saarse 2006, 2007a,b), with some sites covering the LG period (e.g. Veski et al. 2012; Amon et al. 2014). In order to use only pollen samples with higher counting effort, we selected samples in which the sum of terrestrial pollen counts exceeded 1000 for the samples younger than 10 500 cal. yr BP, and 450 for the samples from earlier than 10 500 BP. Pollen samples from the LG and the first millennium of the Holocene are sparse, and counting more than 500 pollen grains is difficult and time consuming. Tree pollen considered exotic for the LG and counting more than 500 pollen grains is difficult and time consuming. Tree pollen considered exotic for the LG period because there is no evidence for pollen taxa in the LG samples did not exceed 1% except for Alnus (max 7%) and Corylus (max 3%). Despite the relatively high proportions of the Alnus pollen, we decided to exclude it from the LG period because there is no evidence from macro-remains that Alnus occurred in the study area before 11 650 cal. yr BP (Amon et al. 2014).

Radiocarbon dates were combined with lithological data to re-calculate the chronologies of the selected pollen sequences using the same methodology as in Reitalu et al. (2013). Only the samples for which the SD of the age estimate did not exceed 100 yrs were kept in the analysis. Our selection criteria (for pollen sum and dating accuracy) resulted in 1062 samples with 140 pollen taxa from 20 sites throughout Estonia and Latvia (Appendix S1). Because the focus of this study was on the overall temporal trends in palynological diversity, the 1062 pollen samples were pooled into one data set by unifying the taxonomy of the 20 pollen data sets and retaining the assigned ages of the samples. Because the data came from a small number of investigators following the same pollen taxonomical school, it was relatively straightforward to combine the data sets.

Background vegetation and environmental data

To provide information on the overall vegetation change, we reconstructed the vegetation cover with the help of REVEALS vegetation reconstruction model (Sugita 2007). Cover percentages were estimated for the 23 dominant pollen taxa for which we had the pollen production and fall speed estimates (Alnus, Artemisia, Betula, Calluna, Carpinus, Cerealia, Corylus, Fagus, Filipendula, Fraxinus, Juniperus, Picea, Pinus, Plantago lanceolata, Plantago major/media, Poaceae, Quercus, Rumex acetosa/acetosella, Salix, Secale, Tilia, Ulmus, Urtica; Appendix S2). These 23 taxa constituted, on average, 97% of the total pollen. To illustrate the vegetation change, we used the REVEALS-estimated cover percentages of four major tree taxa (Betula, Picea, Pinus, Ulmus), sum of herbaceous taxa (excluding cereal taxa) and sum of cereal taxa. The cover percentage of herbaceous taxa gave an indication of landscape openness and cover percentage of cereal taxa were used as a proxy of agricultural activity (Colombaroli et al. 2013).

We used Ellenberg N and R values (Ellenberg et al. 1991) to characterize changes in soil nutrient availability and soil reaction, respectively. Specifically, we used the Ellenberg indicator values of the 21 taxa for which we had the REVEALS estimates (all taxa listed above, except Cerealia and Secale). For taxa that included more than one species, we used an average of species growing in the study region today. For each sample, we then calculated taxon-weighted average Ellenberg N and R values using the REVEALS-estimated vegetation proportions as weights.

To characterize the overall climatic change, we used North Greenland Ice Core Project δ18O values (NGRIP δ18O; Rasmussen et al. 2006) as a climate proxy. Lower values of δ18O indicate cooler and/or moister climatic conditions; higher values indicate warmer and/or drier conditions.

Richness and evenness

To account for the effect of differences in sampling effort, we calculated richness both as the total number of taxa and number of taxa rarefied to the minimum pollen sum (Birks & Line 1992), which in our case was 411. Both diversity measures were highly correlated ($r = 0.88$, $P < 0.001$) and only the rarefied richness is shown in the subsequent analyses (referred to as ‘richness’).

Evenness calculations based on pollen percentages may be biased because pollen percentages depend not only on vegetation composition but also on taxon-specific differences in pollen production (Odgaard 1999). Therefore, in addition to the pollen percentage-based evenness measure, we used the REVEALS estimates of the 21 most common pollen taxa to calculate REVEALS-based evenness measure (Fredh et al. 2012). Simpson’s evenness was calculated as:

$$E_{1/D} = \frac{1}{S} \sum p_i^2$$

where $S$ is the number of pollen taxa and $p_i$ is the proportion of $i$-th taxon. REVEALS-based evenness ($Even_{REVEALS}$) and pollen percentage-based evenness ($Even_{PERC}$) were significantly but weakly correlated ($r = 0.17$, $P < 0.001$) and both evenness measures were included in subsequent analyses.
Functional diversity

We used four traits to characterize functional diversity: plant height, specific leaf area (ratio of leaf area to dry weight, SLA), seed weight and clonality. These traits are known to have the following properties (Cornelissen et al. 2003):

1. plant height is related to competitive vigour and is often negatively associated with stress tolerance;
2. SLA is considered a good proxy of potential relative growth rate;
3. seed weight is related to reproductive strategies, with small seeds likely to disperse better, while storage resources in large seeds help young plants to establish under stressful environmental conditions;
4. clonality is related to the ability to expand by producing new above-ground shoots; it is effective behaviour for short-distance dispersal when seed dispersal is inhibited.

Trait values were obtained from literature and existing databases: plant height and SLA from LEDA traitbase (Kleyer et al. 2008), seed weight from BioFlor database (Kühn et al. 2004) and Kew Botanic Gardens seed information database (Liu et al. 2008). Clonality was derived from a trait ‘type of reproduction’ in BioFlor database (Kühn et al. 2004) with the original qualitative trait coded as follows: ‘mostly vegetatively, rarely by seed’ = 0.9, ‘by seed and vegetatively’ = 0.5, ‘mostly by seed, rarely vegetatively’ = 0.1, ‘by seed’ = 0.

The calculation of functional diversity was based on the trait values and presence/absence of all identified pollen taxa excluding cultivated taxa (132 taxa in total). Assigning trait values to pollen taxa was straightforward when pollen taxon only included one species (e.g. *Picea abies*). For pollen taxa including several species, we used an average trait value of the species currently present in the study region or with known presence in post-glacial history. For taxa with up to ten species in the current flora (e.g. *Polygala* including *P. amarella*, *P. comosa* and *P. vulgaris*), all species were used to calculate the average. For taxa with more than 10 species (e.g. Poaceae), we used a random subset of species so that the number was approximately proportional to the total number of species in Estonian flora belonging to the taxon. Pollen taxon average trait values are given in Appendix S3.

Functional diversity was characterized according to each of the four traits by the community-weighted mean (CWM) trait value and the mean pair-wise distance (MPD) in the trait space using the Gower distance (Gower 1971). We used standardized effect size (SES) of MPD because it has been shown to be independent of richness (Pavoine & Bonsall 2011). To calculate SES, the observed MPD values were compared with the MPD values from 999 random communities (drawing the same number of species as in each sample randomly from the set of all species). SES_MPD was then calculated as \((MPD_{\text{obs}} - MPD_{\text{rand, mean}})/MPD_{\text{rand, sd}}\) where \(MPD_{\text{rand, mean}}\) and \(MPD_{\text{rand, sd}}\) are the mean and SD, respectively, of the MPD values in the randomized communities. Negative SES_MPD indicates functional clustering (functional convergence) and positive SES_MPD indicates functional over-dispersion (functional divergence); values ≤ −2 and ≥ 2 indicate significant \((P < 0.05)\) clustering and over-dispersion, respectively (Gotelli & Graves 1996).

Phylogenetic diversity

Phylogenetic diversity was calculated for the same 132 taxa as functional diversity. For pollen taxa with more than one species, we randomly chose one representative species from the list of species in Estonian flora, e.g. Primulaceae was represented by *Primula veris*. A phylogenetic tree was then constructed based on the 132 representative species and dated phylogeny of higher plants for Central Europe (Durka & Michalski 2012; Appendix S4). Phylogenetic distance was measured as the branch length between pair-wise combinations of species on the phylogenetic tree. The phylogenetic distance between the families/genera does not depend on the identity of the representative species. Phylogenetic diversity was calculated as the standardized effect size of the mean pair-wise distance between the representative species (SES_MPD). We calculated three different phylogenetic diversity measures – one for all taxa together, one for angiosperms and one for herbs (angiosperms excluding trees and shrubs). The three phylogenetic trees that were the basis of the calculations are given in Appendix S4.

We used R environment (R Foundation for Statistical Computing, Vienna, AT) and the package ‘picante’ (Kembel et al. 2010) to calculate both functional and phylogenetic diversity.

Simulation study

In order to check the validity of our pollen-based diversity measures, we used a simulation to compare functional and phylogenetic diversity based on floristic data and pollen types. We constructed a set of 110 random communities with species richness ranging between 100 and 200 using a list of taxa from a landscape-scale vegetation survey (Meltsov et al. 2011, 2013). The species list was transformed into pollen types following the procedure from Meltsov et al. (2011). Functional and phylogenetic diversity was then calculated based on both floristic data and according to our methods based on pollen taxon average trait values (for functional diversity) and representative species (for phylogenetic diversity).
The pollen-based and species-based diversity estimates of plant height and seed weight were relatively highly correlated in case of functional diversity: Pearson’s correlation coefficients 0.74 and 0.75, respectively, for CWM, and 0.86 and 0.77 for SESMPD (Appendix S5a, b). For SLA, the correlations were 0.59 and 0.58, for CWM and SESMPD, respectively (Appendix S5a, b). For clonality, the correlations were 0.51 and 0.49 for CWM and SESMPD, respectively (Appendix S5a, b). All correlations were highly significant. The SESMPD values based on species data and on pollen data were significantly positively correlated in case of phylogenetic diversity (Pearson’s $r = 0.63, P < 0.001$; Appendix S5c).

In summary, the correlations between pollen-based and simulated vegetation diversity ranged between 0.49 and 0.86, and show that the variation is too large to use pollen-based functional and phylogenetic diversity to estimate the true values of species-based diversity, but should be suitable to reflect general trends in historical functional and phylogenetic plant diversity.

Statistical analysis

We used generalized additive models (GAMs) to fit the relationship of each diversity variable with time to test for significant trends in time. For each of the diversity–time associations, we reported the estimated degrees of freedom (edf), $P$-value of the smoothed function and the adjusted $R^2$. We used Pearson’s product-moment correlations ($r$) to investigate the associations among the diversity variables and between the diversity variables and environmental variables.

Results

The cover estimate of herbaceous taxa was the largest during the LG and increased again during the last 4000 yrs (Fig. 1a). The proportion of cereal taxa began to increase about 2000 cal. yr BP but a stable occurrence of cereal pollen was present already since 4000 cal. yr BP (Fig. 1a). Ellenberg reaction (R) attained its maximum in the LG, decreased gradually until ca. 1500 cal. yr BP and then increased quite rapidly until the present (Fig. 1b). Ellenberg nutrient availability (N) peaked in the mid-Holocene (8000–6000 cal. yr BP) and increased again during the last 1500 yrs (Fig. 1b). The climate proxy – NGRIP $\delta^{18}$O (Rasmussen et al. 2006) – which is positively associated with warmer and/or drier conditions, attained its minimum during our study period around 12 000 cal. yr BP, increased sharply at the beginning of the Holocene and was relatively stable during the rest of the Holocene, with only a slight decrease during the last four millennia.

Pollen richness exhibited relatively high values during the LG period, decreased slightly at the beginning of the Holocene and increased steadily through the Holocene, attaining its maximum close to the present (Fig. 2a). Evenness, on the other hand, had two maxima – one in the LG and one in the mid-Holocene (Fig. 2b,c). The REVALS-based evenness exhibited a trend similar to the pollen percentage-based evenness, although the trend was less well defined ($R^2 = 0.12$ for EvenREV and $R^2 = 0.55$ for Even%). Richness was negatively correlated with both evenness estimates ($r = -0.43$ for Even, $r = -0.24$ for EvenREV: Appendix S6).

Community-weighted mean (CWM) values of plant height and seed weight showed similar trends in time, with minimum values in the LG and the highest values around 8000–4000 cal. yr BP (Fig. 3a,g). The CWM of the SLA showed a slightly increasing trend throughout the study period, with the maximum values close to the present (Fig. 3c). The CWM of clonality, on the other hand, showed the opposite trend, with maximum values in the LG (Fig. 3e). The SESMPD of plant height attained its maximum values during the last 4000 cal. yr BP (Fig. 3b). The SESMPD values of SLA and clonality were relatively weakly associated with time ($R^2$-values 0.06 and 0.13, respectively). The SESMPD of seed weight, on the other hand, showed a well-determined trend in time ($R^2 = 0.78$) and had its maximum values during a relatively long period between 8000 and 1000 cal. yr BP (Fig. 3h). Plant height and seed weight showed indications of significant functional over-dispersion (SESMPD > 2) – the taxa were significantly less similar in terms of plant height and seed weight than expected by chance during the second half of the Holocene (Fig. 3b, h).

The three measures of phylogenetic diversity (based on all taxa, angiosperms and herbs) were positively correlated to each other (Appendix S6) and showed roughly similar trends in time, with their maxima in the LG (Fig. 4). Whereas phylogenetic diversity estimates including trees decreased already at the beginning of the Holocene (Fig. 4a, b), phylogenetic diversity based on herbs began to decrease at the end of the study period, during the last 2000 yrs (Fig. 4c). Phylogenetic diversity based on all taxa showed significant over-dispersion (SESMPD > 2), indicating that taxa in one sample were phylogenetically more dispersed than expected by chance (Fig. 4a). However, phylogenetic diversity based on all taxa was clearly dependent on the presence/absence of individual gymnosperms, whereas phylogenetic diversity based on angiosperms (Fig. 3b) showed no significant over-dispersion.

The correlations between diversity estimates and environmental variables showed that functional diversity based on plant height and seed weight was positively correlated with NGRIP $\delta^{18}$O, but functional diversity based on
clonality and phylogenetic diversity was negatively correlated with NGRIP $\delta^{18}$O (Table 1). The diversity variables most strongly associated with the cover of cereals (indicating agriculture) were richness ($r = 0.62$), SESMPD SLA ($r = 0.41$) and phylodiversity based on herbs ($r = -0.41$; Table 1).

**Discussion**

Our study shows, for the first time, trends of four different palynological diversity components – richness, evenness, functional and phylogenetic diversity – through the entire post-glacial period (14 500 yrs) in NE Europe. The results of our simulation exercise suggest that pollen data can reflect general trends in long-term changes of plant functional and phylogenetic diversity. Functional diversity reflecting the trait differences between the co-existing taxa and phylogenetic diversity reflecting the evolutionary distances between the co-existing taxa provide novel insights into post-glacial vegetation change and its drivers.

Richness and evenness

Palynological richness is by far the most commonly used measure of palaeo plant diversity (e.g. Lindbladh 1999; Berglund et al. 2008; Giesecke et al. 2012), and the trend of palynological richness gradually increasing throughout the Holocene is well known. Recent modern analogue studies show strong positive relationships among palynological richness, plant richness and the extent of human-induced openness in the temperate forest zone of Northern Europe (Meltsov et al. 2011, 2013). In our study, the relatively fast increase in palynological richness during the last 2000 yrs most likely reflects human intervention: the creation of additional habitats (open areas, arable fields, pastures), increased grazing pressure, improved dispersal possibilities, and the direct or indirect introductions of new plant taxa.

Pollen sample evenness has been shown to be positively correlated with palynological richness and to increase with enhanced human impact (Peros & Gajewski 2008; van der Knaap 2009; Colombaroli et al. 2013). However, these studies use the probability of interspecific counter (PIE; Hurlbert 1971) as the index of evenness. PIE is not strictly an evenness measure, but a diversity measure that incorporates both species richness and evenness. PIE is, therefore, intrinsically dependent on the number of species/taxa in the sample. In our study, the REVEALS-based Simpson’s evenness estimate $\text{Even}_{\text{REV}}$ (Fredh et al. 2012) varied little in time because it uses only a subset of pollen taxa – the most abundant taxa found in the majority of the samples. In its present form, the REVEALS-based evenness is more a measure of land-cover equitability than vegetation evenness, and we would recommend the use of pollen percentage-based evenness as long as the REVEALS reconstructions do not enable the inclusion of rare taxa that play an important role in the evenness estimate.

Like studies of long-term succession (Morrison & Yarranton 1973; Clebsch & Busing 1989), our results showed that evenness and richness clearly exhibit different trends.
in time. The two evenness minima – one at the transition between the LG and the Holocene and the other at the late Holocene – coincide with large environmental changes. During the transitional period between the LG and the Holocene, the climate changed relatively fast (Fig. 1) and there was an increase in anthropogenic disturbances in the late Holocene. During these environmental changes, habitat specialists of the previous environmental conditions and newly arriving species can be expected to be rare, and communities are dominated by relatively few habitat generalist species (cf. Clebsch & Busing 1989). The evenness maximum in the mid-Holocene coincides with the warmest period of the Holocene, around 6000 cal. yr. BP, when Picea abundances were increasing and abundances of broad-leaved trees were decreasing – a period when none of the major tree taxa were dominant.

Functional diversity

A simplified functional division of pollen data into arboreal and non-arboreal pollen has been used in palaeoecology for almost a century (Firbas & Preuss 1934). Several palaeoecological studies have used plant functional types to classify pollen samples into biomes with which to characterize principal changes in vegetation over large (continental) spatial scales, and to use as training data sets for climate models (Prentice et al. 1996; Fyfe et al. 2010). However, our study shows that palaeoecological information has potential for finer resolution reconstructions of functional diversity in terms of both spatial scale and biological information. Pollen-based functional diversity showed clear association with past climate changes, and studies predicting future changes in plant abundances and functional traits (e.g. Thuiller et al. 2006) could benefit from more detailed knowledge of palaeo-functional diversity.

Our results showed that the largest changes in functional diversity occurred during the transition from the LG to the Holocene associated with major climatic changes. These results agree with earlier studies that show close associations between climate and functional aspects of diversity (Díaz et al. 1998; Lacourse 2009). CWM values show that the taxa dominating in the LG can be characterized by low plant height, small seeds, good ability for vegetative reproduction and relatively low SLA (Fig. 3). These traits have been shown to be characteristic of species that had relatively widespread distributions during the last glacial period (Bhagwat & Willis 2008).

Climate warming during the transition from the LG to the Holocene allowed for the expansion of taller plants with larger seeds and led to lower proportions of vegetative regeneration in the vegetation. In addition to the changes in mean trait values, the inter-taxon differences in seed weight and plant height (SES_{HDP}) were higher in the Holocene than in the LG. Both seed weight and plant height also showed indication of functional over-dispersion or functional divergence in the Holocene but not in the LG, indicating that the Holocene taxa were more different in their height and seed weight than expected by chance. The low temperatures in the LG can be viewed as a strong environmental filter, preventing tall and large-seeded plants from establishing and keeping the variation of plant height and seed weight low. During the Holocene, on the other hand, the environmental constraints were weaker and our results suggest niche complementarity in plant height and seed weight.

In contrast to the transitional period between the LG and the Holocene, the climate changed little during the second half of the Holocene, yet there were changes in functional diversity. The decrease in average plant height and seed weight and increase in clonality during the last 4000 yrs were clearly associated with increased proportions of herbaceous taxa. The SES_{HDP} values of plant height and seed weight showed a decreasing trend during the last 1500 yrs (Fig. 3b,h), suggesting that human
Pollen-based functional and phylogenetic diversity

impact has influenced overall functional diversity negatively by suppressing the tall-growing, large-seeded taxa. Our results add to the evidence that land-use intensification has had a negative impact on trait diversity (Flynn et al. 2009; Laliberté et al. 2010) and indicate that land-use intensification has influenced functional diversity of plants over the last 1500 yrs.

Several of the diversity estimates showed similar tendencies in the LG and in the late Holocene (relatively high richness, low functional diversity based on plant height and seed weight). These two periods can both be characterized by high landscape openness (climate-induced in the LG and human-induced in the late Holocene) and the effects on some diversity aspects are similar.

Phylogenetic diversity

Phylogenetic diversity based on all pollen taxa was clearly influenced by gymnosperms (Fig. 4a, Appendix S4 a). The presence of gymnosperms (Juniperus, Pinus and Picea) led to significant over-dispersion of the phylogenetic diversity, indicating that the phylogenetic distances were larger than
expected by chance (Fig. 4a). We conclude that a few phylogenetically distinct taxa had a strong influence on the palaeo-phylogenetic diversity measure. However, phylogenetic diversity estimates with and without gymnosperms both attained their maximum values in the LG period. Earlier studies have also shown that phylogenetic diversity is higher under stressful conditions (Tallents et al. 2005; Reitalu et al. 2014b). We can, therefore, conclude that the traits that are related to survival under harsh environmental conditions (low height, small seeds, ability for vegetative reproduction; Fig. 3) have evolved separately in different plant lineages.

In addition to the climate effects on phylogenetic diversity, our results indicate an association between phylogenetic diversity and human impact. While human impact has had a positive effect on palynological richness, its effect on phylogenetic diversity of herbs has been negative. Winter et al. (2009) showed that introductions of new species since AD 1500 have increased species richness but decreased phylogenetic diversity in 23 European regions (including our study area). They explain that the introduced species were often closely related to the already existing species, while species going extinct in the same regions were phylogenetically unique (Winter et al. 2009). Our results follow the same pattern – taxa that appear in the pollen samples of the late Holocene tend to be phylogenetically clustered. For example, taxa from families such as Plantaginaceae, Lamiaceae and Scrophulariaceae that are phylogenetically relatively close became abundant during the second half of the Holocene and are likely related to increased human impact. These families have high proportions of alien species also in today’s European flora (Lambdon et al. 2008), and probably

Table 1. Correlations of the diversity variables with the REVEALS-based cover estimates of major taxa and with environmental variables, Pearson’s product moment correlations.

<table>
<thead>
<tr>
<th>Richness</th>
<th>Betula Cover %</th>
<th>Picea Cover %</th>
<th>Pinus Cover %</th>
<th>Ulmus Cover %</th>
<th>Herbaceous Taxa Cover %</th>
<th>Cereals Cover %</th>
<th>Ellenberg R</th>
<th>Ellenberg N</th>
<th>NGRI 818O</th>
</tr>
</thead>
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<tr>
<td>Even_b</td>
<td>-0.12***</td>
<td>NS</td>
<td>NS</td>
<td>-0.35***</td>
<td>0.16***</td>
<td>0.62***</td>
<td>NS</td>
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The significances of the correlation coefficients are given as: ***P < 0.001; **P < 0.01; *P < 0.05; NS P > 0.05.
possess traits that facilitate invasion. Extensive spread of agriculture and livestock grazing in semi-natural pastures enlarged the open areas and created new habitats for herbaceous taxa. We can hypothesize that the traits that enable the survival in human-influenced habitats and provide tolerance to human-induced disturbances (livestock grazing, trampling, mowing, etc.) are phylogenetically clustered and humans have, therefore, indirectly ‘selected’ for phylogenetically more similar taxa. Phylogenetic diversity has also been associated with the evolutionary age of the communities, with younger communities being phylogenetically clustered (Procheş et al. 2006; Yan et al. 2013). In Europe, ruderal communities are the youngest habitats (Zohary 1996) and the decline in phylogenetic diversity in the late Holocene may have been caused by human impact via facilitating the dispersal of ruderal communities and species with invasive characteristics (from families such as Dipsacaceae, Lamiaceae, Plantaginaceae, Polygonaceae, Scrophulariaceae).

Conclusions

The present study demonstrates that pollen-based estimates of functional and phylogenetic diversity add new insights into the processes behind millennial-scale vegetation change. We show that both functional and phylogenetic diversity are closely related to climatic conditions, suggesting that trait differences play an important role in long-term plant community response to climate change. Our results suggest that human impact has influenced plant functional diversity negatively by suppressing the tall-growing, large-seeded taxa, leading to functional convergence. Human impact has facilitated plant lineages with high proportion of ruderal species (e.g. Dipsacaceae, Lamiaceae, Plantaginaceae, Polygonaceae, Scrophulariaceae), which is leading to an increase in overall plant richness but a decrease in phylogenetic diversity. Based on our results, we see great potential in continuing development of functional and phylogenetic diversity methods for pollen data with the help of simulations and analogue studies in contemporary plant communities.

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References


**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

- **Appendix S1.** Details of pollen data sets.
- **Appendix S2.** Details of REVEALS model.
- **Appendix S3.** Pollen taxon trait values.
- **Appendix S4.** Pollen taxon-based phylogenetic trees.
- **Appendix S5.** Results of the simulation study.
- **Appendix S6.** Correlations among the diversity variables.