Modern pollen – vegetation – plant diversity relationships across large environmental gradients in northern Greece

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Abstract
Past vegetation and biodiversity dynamics, reconstructed using palaeoecological methods, can contribute to assessing the magnitude of the current biodiversity crisis and anticipating future risks and challenges. Among the different palaeoecological techniques, pollen analysis is probably the most widely used to reconstruct vegetation and plant diversity changes through time. Such reconstructions demand robust and comprehensive calibration studies addressing the pollen representation of extant vegetation to be sound. However, calibration studies are rare in the Mediterranean biodiversity hotspot, particularly regarding plant diversity. Here, we contribute to filling this gap by investigating the modern pollen signature of Mediterranean vegetation across a large environmental gradient in northern Greece. At each sampling site (n = 61), we quantitatively compared the composition and diversity of plant (vegetation surveys) and pollen assemblages (moss/topsoil samples) using numerical techniques. Further, we compared these terrestrial pollen assemblages with those from lake sediment surface samples of the same region. We found an overall good match between plant and pollen assemblages, with maquis and mixed deciduous forest displaying particularly distinct pollen signatures. In contrast, the high regional importance of pines and oaks and their large pollen production blurred the pollen representation of other forested vegetation types and of shrublands and grasslands. Plant and pollen richness and their evenness showed similar declining trends with increasing altitude, but plant and pollen evenness bore a better match than richness. A more detailed vegetation-specific view on the data suggests that pine pollen seriously affected pollen richness and evenness in most of the pine-dominated stands. Lastly, our results suggest a rather straightforward application of vegetation-pollen relationships from moss/topsoil samples to interpret pollen assemblages from lakes in Mediterranean settings.

Keywords
evenness, indicator species, Mediterranean region, multivariate classification tree, palaeoecology, palynological richness, pollen analysis, surface samples

Introduction
The ongoing global climate change crisis is posing serious challenges to biodiversity conservation and management (Dawson et al., 2011; Urban et al., 2016). In this context, global biodiversity hotspots such as the Mediterranean Basin (c. 25,000 plant species, almost half of them endemic) are of particular importance (Blondel et al., 2010; IPBES, 2018; Myers et al., 2000). Located in the northeastern Mediterranean sub-region, Greece hosts one of the richest floras in the Mediterranean Basin (c. 5800 plant species), with a high proportion of narrow endemic species (15.6%; Georghiou and Delipetrou, 2010). Because in Greece all major vegetation types of the Mediterranean are represented, it offers a unique setting to investigate southern European plant and vegetation diversity. The notably large number of plant species mainly results from the following factors: (i) located in Europe, Greece’s proximity to two other continents (Asia and Africa) makes it a biogeographical crossroad; (ii) Greece shows a high topographic diversity; (iii) most of Greece remained ice-free during the cold periods of the Quaternary (glaciations) and was therefore a refugium for many European plant species; and (iv) Greece has a very long (>8000 years) history of human impact (e.g. Gas snen et al., 2020; Glais et al., 2016a). Past natural environmental variability and human impacts have thus played a central role in defining today’s species diversity and distribution, as well as vegetation composition and structure (Birks, 2012; Bottma, 1974; Georghiou and Delipetrou, 2010; Jahns, 2005; Tzedakis, 1993). Therefore, a deeper knowledge of past vegetation and plant diversity, including natural biodiversity conditions prior to the establishment of land use, is needed to better understand and manage present and future dynamics (Willis et al., 2010).

Palaeoecology may provide such long-term perspectives on the dynamics of vegetation and plant diversity, enabling us to reconstruct changes in the past distribution of species and communities (e.g. Giesecke et al., 2017; Herring et al., 2018; Morales-Molino et al., 2020a). Moreover, palaeoecology allows assessing the roles of the different drivers of vegetation change, such as climate change or human activities (e.g. Henne et al., 2013; Morales-Molino et al., 2020a). In this context, a question that might be addressed by...
Material and methods

Sampling, vegetation surveys and pollen analyses

Our 61 sampling sites are spread across northern Greece, spanning an elevational gradient from 0 to 2449 m a.s.l, and covering most of the regional vegetation zones of Greece (Figure 1, Supplemental Table S1, available online). We grouped the sites into eight different vegetation types defined according to the composition and structure of the extant local and extra-local vegetation (e.g. coastal mesomediterranean maquis, temperate and subalpine forests, alpine treeless vegetation). We denominated the forest vegetation types following the European forest types (Barbati et al., 2007) and the 'Map of the Natural Vegetation of Europe' (Bohn and Neuhäuslová, 2000/2003) (summarised in Supplemental Figure S1, available online).

At each site, we recorded vegetation composition within a plot of c. 10 × 10 m with a focus on woody species (trees and shrubs), in April (lowlands) and July 2019 (uplands). Specifically, we recorded plant species (presence/absence) and canopy cover (presence/absence) every metre along two orthogonal 10-m long transects (2 × 10 points). We later transformed the records of both variables into a semi-quantitative scale as follows: presence in 0, 1, 2 . . . , 20 out of 20 points equals to a ground cover of 0, 5, 10, . . . , 100%. For herbs and ferns, we only recorded the presence or absence in the plots.

We identified plant species using regional floras (Dimopoulou et al., 2016; Lefranchis and Silfakas, 2009; Pigatti, 1982; Strid, 1980). Due to the phenological status, we could identify some plant taxa only to genus or even family level (e.g. Rosa, Lactuca, Poaceae, Cyperaceae), but we numbered different taxa within a family or genus to keep track of diversity (e.g. Apioaceae 1, Apioaceae 2). The sampling season and its associated phenological status also hampered detection and identification of some plant species: for instance, late-season and early-season herbs went undetected in April and July respectively and distinguishing Ostrya carpinifolia from Carpinus orientalis was challenging in early spring.

In the same plots, we collected terrestrial surface samples (mainly moss polsters, but also O and A soil horizons) in several spots distributed all over the plot. Once in the laboratory, we homogenised the sample and treated 1 cm² for pollen analysis following a slightly modified protocol with respect to Moore et al. (1991): we skipped the first HCI step and applied HF only to samples containing mineral soil. We identified and counted pollen and spore types at 400×, 630× and 1000× magnifications aided by the reference collection at the Institute of Plant Sciences of the University of Bern, dichotomous keys and photo atlases (Beug, 2004; Moore et al., 1991; Punt, 1976–2009; Reille, 1992). A minimum sum of 500 pollen grains was generally achieved, although bad pollen preservation prevented us from reaching this number in some samples (minimum 437). We harmonised pollen type taxonomy according to the European Pollen Database (EPD, Giesecke et al., 2019). We split Quercus pollen into three groups according to morphological features (Beug, 2004): (1) Quercus pubescens type, which includes all the Quercus section Quercus species of the region (e.g. Quercus frainetto, Q. petraea, Q. pubescens, Q. robur), (2) Quercus ilex type, which includes the Quercus section Ilex species, that is, Quercus ilex and Quercus cocifera and (3) Quercus cerris type, which includes the Quercus section Cerris species (e.g. Quercus cerris and Quercus troiana; Denk et al., 2017). Ostrya type includes also pollen of Carpinus orientalis and Juniperus type might include pollen from other Cupressaceae (Beug, 2004). Finally, Pinus sylvestris t. is used here as a synonym of Pinus subgenus Pinus. We plotted pollen diagrams using Tilia (Version 2.6.1; Grimm, 1992–2019).

To assess the relationship between the pollen assemblages from terrestrial and lake surface samples we retrieved short cores from the following twelve lakes (Figure 1; Supplemental Table S2, available online) using UWITEC or Jakaj gravity corers: Limni Kastoria (KAS), Limni Petres (PET), Limni Vegoritis
(VEG), Limni Zazari (ZAZ) – cored in 2016 –, Limni Amvrakia (AMV), Limni Doirani (DOJ), Limni Ioannina (IOA), Limni Koroneia (KOR), Limni Megali Prespa (PRE), Drakolimni Smolika (SMO), Limni Strofilia (STRO) and Limni Volfi (VOL) – cored in 2020 – (Supplemental Dataset 7, available online). We treated 1–2 cm$^3$ of the uppermost sediment following the standard procedure in Moore et al. (1991), and the pollen was analysed as described above for terrestrial samples. We re-counted the surface sample from Limni Zazari (Gassner et al., 2020) to avoid biases in the pollen diversity related to differences in the taxonomic precision achieved by different analysts.

**Pollen and plant data processing and environmental variables**

For the numerical analyses we considered two data sets: (1) terrestrial plant species abundances (estimated ground cover, %); and (2) pollen relative abundances (%). Pollen percentages were
calculated with respect to the terrestrial pollen sum excluding pollen of aquatic and wetland plants and spores in lake surface samples. In contrast, all pollen taxa found in the terrestrial samples were considered non-aquatic as they come from terrestrial sites. The percentage data were Hellinger-transformed because it is recommended for species abundance data with many zero presences (as in our case) and to preserve Euclidean distance for the analysis in Cartesian space (Legendre and Birsks, 2012b). For further diversity analyses, we compiled available information about the growing form (tree, shrub, herb, fern) and pollination mode (wind-pollinated vs not wind-pollinated) of the plant species and pollen types (Landolt et al., 2010; Pignatti, 1982).

We tested the relationships between the pollen and plant data-sets with the environmental variables elevation, canopy cover and distance to the sea. These three variables were selected because of their relevance from an ecological and pollen dispersal perspective (elevation is related to temperature and precipitation; distance to the sea is a proxy for continentality; canopy cover may have an influence on pollen transport) and to avoid collinearity with other environmental variables (e.g. distance to the sea was correlated with latitude). The environmental data for each sampling site were obtained as follows: elevation (Knapp and Verdin, 1998; processed in ArcGIS), canopy cover (fieldwork; see above) and distance to the sea (‘natural earth’ – South, 2017 – and ‘rgdal’ – Bivand et al., 2019 – packages running in R version 3.6.5 – R Core Team, 2020).

**Correspondence between plant and pollen assemblages**

We used Detrended Correspondence Analysis (DCA) to estimate species turnover in standard deviation (SD) units. Considering the length of the DCA axis 1 of the plant dataset (9.66 SD), we decided to use the DCA as it is a unimodal-based ordination method (Birks et al., 2012). We conducted DCA on the plant and pollen assemblage data sets and added the environmental variables passively to the ordinations because this prevents them from affecting the results directly. We used Procrustes analysis to compare the plant and pollen DCA axes scores and thereby quantify the similarities between paired assemblages from the same site, whereby the rotation was non-symmetric on the favour of the plant data sets. Procrustes sum-of-squares m^2 ranges between 0 and 1, with a 0 indicating that the ordinations are identical (Felde et al., 2014b; Goodall, 1991; Gower, 1975; Jackson, 1995; Peres-Neto and Jackson, 2001). Further, lake surface samples were added as supplementary data to the pollen DCA ordination plot to evaluate the comparability between the pollen composition from the terrestrial and lake surface samples.

Multivariate classification trees (MCT) were used to investigate how well the plant and pollen assemblages can distinguish our eight vegetation types (De'ath, 2002; Ouellette and Legendre, 2013; Simpson and Birsks, 2012; Therneau et al., 2014). Tree size was based on the 1-SE rule of Breiman et al. (1984). We also identified the discriminant species (i.e. those taxa contributing most to the splitting into two branches) and indicator species (i.e. those taxa best defining a vegetation type) using an Indicator most to the splitting into two branches) and indicator species (i.e. those taxa contributing was based on the 1-SE rule of Breiman et al. (1984). We also tested the relationships between the pollen and plant data-sets with the environmental variables elevation, canopy cover and distance to the sea. These three variables were selected because of their relevance from an ecological and pollen dispersal perspective (elevation is related to temperature and precipitation; distance to the sea is a proxy for continentality; canopy cover may have an influence on pollen transport) and to avoid collinearity with other environmental variables (e.g. distance to the sea was correlated with latitude). The environmental data for each sampling site were obtained as follows: elevation (Knapp and Verdin, 1998; processed in ArcGIS), canopy cover (fieldwork; see above) and distance to the sea (‘natural earth’ – South, 2017 – and ‘rgdal’ – Bivand et al., 2019 – packages running in R version 3.6.5 – R Core Team, 2020).

**Diversity analyses**

We conducted diversity analyses on the entire plant and pollen assemblage datasets, on the subset of trees and shrubs, and the subset of wind-pollinated trees and shrubs. We focussed on woody species because their presence/absence was recorded consistently (see section 2.1). This procedure also intends to minimise the dominance of wind-pollinated taxa. We removed site number 54 from the two subsets because the absence of woody species in the plot resulted in unsolvable diversity indices. We calculated diversity indices on the percentage data of plant species and on the rarefied pollen counts to reduce the effect of different counting effort (Birks and Line, 1992; Chao et al., 2014). We used Hill numbers (N0, N1, N2; pollen’s N0 is equal to pollen richness (PRI) and associated evenness ratios (E0, mod E0, E1, modE1, E3; see Felde et al., 2016), as well as the Probability of Interspecific Encounter (PIE; Hurlbert, 1971) as a rough proxy for evenness.

Minimum pollen sums for the entire dataset, its subset of trees and shrubs and the subset of pollenination mode were 437, 164 and 130, respectively. For the rarefaction, the function rarefy() of the R package ‘vegan’ was used (Oksanen et al., 2019). We did not rarely the plant datasets, as proposed by Connor et al. (2021), because of their semi-quantitative structure. In a second step, palynological richness (PRI) was detrended (DE-PRI) with PIE to reduce the influence of high pollen producers and dispersers (Colombaroli and Tinner, 2013) and to investigate if PRI is affected by evenness distortions.

Pearson’s correlation matrices were calculated for the contrast between the different indices of plant and pollen of the entire data, and the two subsets (Harrell, 2020). Finally, N0, PRI, DE-PRI and PIE were plotted against their sampling sites clustered in vegetation groups, which are ordered along their median elevation, to visually assess patterns (Wickham, 2016).

**Results and interpretation**

**Pollen data**

We found 341 plant species and 133 pollen types (after taxonomic harmonisation). Pollen assemblages from mixed deciduous forests are mainly dominated by pollen of deciduous trees (Tilia, Castanea sativa, Alnus glutinosa t. (t. = type), Platanus, Fraxinus ornus), Hedera helix and Solanum dulcamara, which only occurs here. Occasionally evergreen broadleaved Quercus ilex t. dominates (site 35) (Figure 2). Quercus pubescens t. pollen dominates in samples from mixed oak woodlands, mostly admixed with pollen of temperate deciduous trees and Juniperus t. Non-arboreal pollen (NAP) is slightly more abundant. Beech-dominated stands show a dominance of Pinus sylvestris t. pollen accompanied by Fagus and some Q. pubescens t. Pinus sylvestris t. is also dominant in pine-dominated stands and mixed fir forests, whereas in the latter, Abies and Q. ilex t. are more abundant. The exceptionally high percentages of Juniperus t. pollen (49%) found in site 58 (pine-dominated stand) are remarkable. Compared to the following three vegetation types, all these samples show high percentages of arboreal pollen (AP).

Pollen of evergreen mediterranean shrubs and trees (e.g. Erica, Phillyrea, Pistacia, Cistus, Q. ilex t.) dominate the maquis pollen assemblages (Figure 2). Shrublands have more Juniperus t., Q. pubescens t. and Ostrya t. with higher percentages of NAP (Figure 2). Grasslands have the highest percentages of NAP, mainly Poaeeae and Artemisia (Figure 3). Overall, pollen assemblages from mixed deciduous forests, mixed oak woodlands, maquis, shrublands and grasslands are distinct and agree reasonably well with their vegetation types (as described in Supplemental Figure S1, available online). On the contrary, the high abundance of P. sylvestris t. pollen makes pollen assemblages from the temperate forests notably resemble each other. The exceptional site number 58, however, records likely the many juniper shrubs found in the understory.
Correspondence and dissimilarities between plant and pollen assemblages

DCA axis 1 for plant assemblages is notably longer than that of the pollen dataset (9.657 SD vs 2.109 SD respectively; Supplemental Figure S2, available online). The large turnover observed in plant assemblages reflects large differences in the plant communities sampled, which is in turn related to the high number of plant species identified. This diversity results from the large environmental gradients covered by our sampling sites (c. 2500 m difference in altitude; 1–110 km distance to the sea). The turnover in the pollen assemblages (Supplemental Figure S2d–f, available online) is still relatively high (see Felde et al., 2014a; Giesecke et al., 2019), certainly because of the same reason. However, the shorter length of axis 1 indicates that pollen assemblages are more similar overall.

For the plant assemblages, DCA axes 1 and 2 explain 34.04% and 26.77% of the total variance respectively. Results for pollen assemblages are comparable, as DCA axes 1 and 2 explain 32.16% and 30.66% of the total variance. Fitting environmental variables to the ordination plots reveals that elevation (primarily related to climate) is correlated with axis 1 for both datasets (plant assemblages: $r^2 = 0.8562$, Supplemental Figure S2a, available online; pollen assemblages: $r^2 = 0.5149$, Supplemental Figure S2d, available online). Canopy cover and distance to the sea are both aligned with axis 2. Canopy cover is more linearly correlated with pollen ($r^2 = 0.5209$, Supplemental Figure S2e, available online) than with the plant assemblages ($r^2 = 0.4131$, Supplemental Figure S2h, available online). Moreover, isolines of canopy cover for the plant assemblages (Supplemental Figure S2b, available online) suggest a quadratic response, with the highest canopy cover at intermediate elevations. Distance to the sea shows a considerably stronger correlation with the pollen assemblages ($r^2 = 0.6446$, Supplemental Figure S2f, available online) than with the plant assemblages ($r^2 = 0.304$, Supplemental Figure S2c, available online), suggesting that the distance to the sea, in principle a proxy for continentality, affects pollen dispersal stronger than plant distribution. All the above mentioned $r^2$ are significant at $p < 0.001$.

Comparing the DCA for the plant and pollen assemblages using Procrustes analysis (Figure 4a) reveals that the ordinations significantly match (Procrustes sum-of-squares $m^2 = 0.6393$; $p = 0.001$) but there are also some discrepancies. The residuals of the analysis (Figure 4b) display the dissimilarities between all pairs of plant and pollen assemblages. Exceptionally high dissimilarities (above the 75th percentile) occur mostly in open vegetation sites at high elevation and/or surrounded by pine- and oak-dominated stands (site numbers 8–10, 38–41, 43–44, 50, 55, 57–60), probably due to greater deposition of long-distance transported pollen (Figure 4b; Supplemental Table S3, available online). Specifically, pollen composition differs more from the plant assemblage when local and extra-local vegetation are different, and particularly when the extra-local vegetation is dominated by high pollen producers such as pines (9–10, 38–41, 43, 50, 55, 57–59), oaks (50) or junipers (58). Most similar sampling sites with the lowest Procrustes residuals (below 25th percentile) are those from maquis and mixed deciduous forests, where the surrounding vegetation is quite homogeneous.

Lake surface samples in the DCA (Figure 5) cluster together with grasslands (PET), grasslands/mixed oak woodlands (KAS), mixed oak woodland (DOJ, IOA, STR, ZAZ), mixed oak...
woodland/other shrublands (KOR, PRE, VEG), maquis (VOL) and grasslands/beech dominated stands (SMO). The sample of AMV is outside of any hull, located between mixed oak woodland and maquis. The pollen composition of PET (Petres) and KAS (Kastoria) show a dominance of Poaceae, Juniperus t. but also higher abundances of Quercus pubescens t., Pinus sylvestris t. and Ostrya t. (Figure 6). The latter differs from PET with higher percentages of shrubs and less herbs (Figure 6). ZAZ (Zazari) has a lower proportion of tree pollen and Juniperus t. but more deciduous Quercus and grassland pollen (Figure 6). Based on the DCA plot, this pollen assemblage points towards an open anthropogenic landscape with mixed oak woodlands (Figures 2, 3 and 5; Deza-Araujo et al., 2020). KOR (Koroneia), PRE (Prespa) and VEG (Vegoritis) surface pollen assemblages are co-dominated by P. sylvestris t., Juniperus t., Quercus pubescens t., Ostrya t., Fagus sylvatica t. and Poaceae (Figure 6). DOJ (Doirani), IOA (Ioannina) and STR (Strofilia) are characterised, besides Olea europaea, by Poaceae, P. sylvestris t., Quercus ilex t. and Juniperus t. In comparison to IOA and STR, DOJ records fewer Q. ilex t. and P. sylvestris t., but some more deciduous Quercus and NAP (Figure 6).

The pollen assemblage of VOL (Volvi) is dominated by Quercus ilex t., P. sylvestris t., Platanus, Olea europaea and Ostrya t. pollen. The abundance of Poaceae is lower compared to other lakes (Figure 6). The pollen assemblage of SMO (Smolika) records a very high abundance of P. sylvestris t. but also some Juniperus t. and lowland trees like evergreen and deciduous Quercus, Ostrya t. or Olea europaea. Finally, AMV (Amvrakia) has an outstanding proportion of Olea europaea pollen (Figure 6), and this probably explains why it is not inside any hull. Overall, pollen assemblages of lake surface samples closely reflect the vegetation cover around the lakes, as indicated by their composition and the DCA (Figures 5 and 6). Likewise, pollen assemblages of lake surface samples generally match the pollen composition of the terrestrial surface samples (Figure 5). The relatively poor correspondence between pollen and vegetation composition found at Drakolimni Smolika probably results from the low pollen production of the high-elevation open vegetation around the lake, combined with the high pollen influx from the extensive pinewoods that dominate at slightly lower elevation.

Distinction, prediction and indicator species

The MCT for pollen has a considerably higher adjusted $R^2$ (41.59%) than for plants (17.73%, Figure 7a and b). Prediction
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accuracy is also higher for the pollen MCT (26.4%) than for the plant MCT (12.1%). In both the plant and pollen MCTs (Figure 7a and b), the mixed deciduous forest and maquis vegetation types can be clearly separated. *Q. coccifera* is the plant species that contributes most to differentiating maquis from the other vegetation types (Figure 7a), whereas *Q. ilex* t. (which also includes *Q. coccifera*) is the pollen counterpart (Figure 7b). Both *Quercus coccifera* and *Q. ilex* are common components of evergreen forests and scrub communities across most of the Mediterranean region (San-Miguel-Ayanz et al., 2016). *Fraxinus ornus*, a rather widespread deciduous tree frequent in submediterranean forests (San-Miguel-Ayanz et al., 2016), is the discriminant species separating mixed deciduous forest from grassland, shrubland and mixed oak woodland pollen assemblages (Figure 7b). Grassland, shrubland and mixed oak woodland cannot be distinguished based on their pollen assemblages (Figure 7b). In the plant dataset, *Q. frainetto*, usually found in pure stands or together with *Fraxinus ornus, Ostrya carpinifolia* and other *Quercus* species in mixed deciduous submediterranean forests, is the main species leading to the distinction between mixed oak woodlands on the one hand and grasslands and shrublands on the other hand (Figure 7a). *Fagus sylvatica* and *Abies borisii-regis* are the discriminant species for the vegetation types they dominate (Figure 7a).

Maquis and mixed deciduous forest are the vegetation types that share the highest number of indicator species in the plant and pollen MCTs: (i) maquis: *Phillyrea, Pistacia, Cistus* and *Q. coccifera* (*Q. ilex* t. in the pollen dataset); and (ii) mixed deciduous forest: *Castanea sativa, Tilia, Fraxinus ornus, Ostrya* and *Corylus avellana* (Supplemental Table S4, available online). Those taxa are all listed among the characteristic species of the maquis and deciduous forests, respectively, in classic vegetation maps (Bohn and Neuhäuslová, 2000/2003). Grassland, shrubland and mixed oak woodland vegetation types share *Q. frainetto* (*Q. pubescens* t. in the pollen dataset) but differ in their other indicator taxa. Poaceae were very important in the grassland and shrubland plots, but, somehow unexpectedly, this taxon was not indicator of these vegetation types in the plant MCT (Supplemental Table S4, available online).
Fagus sylvatica and Abies borisii-regis are indicator species of their homonymous vegetation types in the plant dataset, but not in the pollen MCT. In the plant MCT, Pinus spp. is neither present as discriminant nor as indicator species, probably because it comprises several pine species with different ecological behaviour (P. heldreichii, P. nigra and P. sylvestris).
Diversity trends and relationships

Since trends in the various richness and evenness indices were similar (Supplemental Table S5, available online), we focus on the trends in the evenness-related index PIE, the richness indices $N_0$ or PRI, and the PIE-detrended richness DE-PRI. Examining richness and evenness per vegetation type along an elevation gradient (Figure 8, Supplemental Figures S3–S5, available online) suggests a decreasing trend in pollen (PRI, corresponding to $N_0$) and plant richness ($N_0$) towards higher elevation vegetation types. Pollen and plant evenness (PIE) are comparable: higher at the lowland sites, and becoming lower for the temperate forests. Detrended richness (DE-PRI; Figure 8b, Supplemental Figure S3b, S4b, available online), as a function of PRI and PIE, shows much fewer oscillations than PRI, especially for temperate forests. Results are similar for the full dataset and their subsets. A closer comparison between pollen and plant diversity can be made for the subset of trees and shrubs (Figure 8). It reveals that local trends in pollen and vegetation PIE are inverted for the pine-dominated stands. Local pollen and plant data suggest that the divergence between the two PIEs is caused by the overrepresentation of pine pollen, which likely lowered pollen richness (PRI) if compared to vegetation richness ($N_0$; Figure 8). Such local pollen evenness distortion effects can also be found at the sites where pine trees were present in the local to regional surrounding (e.g. 9–10, 38, 43, 49–51, 55, 57, 38, temperate forests except sampling sites 8 and 60 with a dense beech canopy cover; Supplemental Table S1, available online). As a consequence of uneven conditions due to excessive pine pollen abundances (if compared to vegetation), DE-PRI (which accounts for uneven conditions) is higher than PRI (Figure 8). The comparison of PRI and DE-PRI with plant species richness suggests that in such cases DE-PRI is able to partly correct for palynological distortions of evenness (artificially low PRI is corrected to higher DE-PRI values; Figure 8a and b; Supplemental Figures S3, S4, available online).

Figure 7. Multivariate Classification Tree (MCT) of (a) the plant and (b) the pollen assemblage data with the eight vegetation types as response variables. The tree individually splits the sampling sites based on their different plant and pollen assemblages, respectively. Each split includes the split number, its coefficient of determination ($r^2$) and the discriminant species/taxa if available. Number of sampling sites within a leaf (n) and leaf number noted below the leaves. Adjusted $R^2$, $R^2$, error, cross-validated error (CV Error) and standard error (SE) for the entire model are depicted below the tree. Prediction accuracy of the model is 1–CV Error, that is, 0.121 in (a) and 0.261 in (b). Indicator species for each leaf (leaves 1–7 for plants, leaves 1–4 for pollen) are listed together with its indicator value in Supplemental Table S4, available online.
be a combination of scaling (pollen catchment is far larger than the plots surveyed for plant diversity) and data quality (herbaceous species were recorded only semi-quantitatively) issues. However, if divided by pollen dispersal strategy, a significant relationship between plant and pollen diversity indices appears for wind-pollinated trees and shrubs (Supplemental Table S5, available online).

**Discussion**

**Vegetation types and pollen**

Following a numerical approach similar to the previous study of Felde et al. (2014b) in Norway, we show here that it is possible to distinguish most of the main vegetation types of northern Greece using plant and pollen assemblages. Maquis showed particularly
distinct plant and pollen composition, making it readily distinguishable from other Mediterranean vegetation types, in agreement with previous studies (Fall, 2012; Glas et al., 2016b). These results are in line with previous research showing that pollen assemblages accurately reflected the main vegetation types in Norway (Folde et al., 2014b), the Tibetan Plateau (Zhang et al., 2018) and Crete (López-Sáez et al., 2019). However, our data from northern Greece show a poorer performance of pollen assemblages to represent open vegetation as the correspondence between plant and pollen assemblages declined further at the highest altitudes where vegetation was more open (Figure 4b). Folde et al. (2014b) found similar issues in Norway with an only slightly closer match between plant and pollen assemblages ($m^2_{\text{Sen}} = 0.64$ vs $m^2_{\text{Folde}} = 0.57$). This may be due to high pollen producers like pines overshadowing the pollen signature of other taxa, which in turn makes it also difficult to differentiate among temperate (conifer) forests (Figures 2 and 7). In the study area (as elsewhere in the Mediterranean) pine species and pinewoods are key features in the regional vegetation, thus *Pinus sylvestris* type cannot be simply excluded from the calibration analyses. Indeed, pine forests were widespread around many of the beech-dominated stands and mixed fir forests sites. Some of the temperate forests also had pine trees in their composition, and mixed fir stands were mostly small. Several recent studies have reported high shares of tree pollen, especially *Pinus*, in pollen assemblages from grassland vegetation (e.g. Li et al., 2019; Liu et al., 2020; Zhang et al., 2020). However, all these studies analysed moss polsters, which are prone to trapping too high amounts of bisaccate pollen grains (Pardoe et al., 2010). Our results highlight the need of collecting information about the extra-local and regional vegetation when conducting calibration studies.

Reduced taxonomic resolution of pollen types compared to plant species may also have affected pollen-inferred reconstructions of vegetation dynamics. This problem arises especially in regions where different tree species with different ecological requirements and habitats are represented by the same pollen type. For example, we found three different pine species (i.e. *P. heldreichii*, *P. nigra* and *P. sylvestris*) in different habitats, but they were merged into a single vegetation type because the species composition of their stands was very similar, so that merging was indicated to avoid an excessive number of vegetation types. Although previous research has provided promising results on the identification of pine pollen even to species level in Iberia (Desprat et al., 2015), no similar study has been accomplished in the north-eastern Mediterranean yet. This, alongside the rather different ecological requirements of Mediterranean pines (Quézel and Médail, 2003), may explain why *P. sylvestris* t. is not listed as indicator species in the MCT analysis. These issues are more relevant in southern Europe because the diversity of tree species is higher compared to northern Europe, and future research should clearly aim at refining the taxonomic resolution of pollen identification for key taxa like pines and oaks, following recent efforts in the Iberian Peninsula (Desprat et al., 2015; Mutrech et al., 2020). Furthermore, (ancient) DNA studies may provide higher resolution pollen composition (Birks and Birks, 2016; Parducci et al., 2017).

The role of environmental variables

Previous research has shown that elevation and landscape openness (comparable to our canopy cover) are relevant in driving the composition of plant and pollen assemblages (Glas et al., 2016b; López-Sáez et al., 2018; Matthias et al., 2015; Meltsov et al., 2013). Our results from northern Greece (Supplemental Figure S2a, b, d, e, available online) suggest that elevation, as surrogate for climate, is of greater importance than any other environmental variable (see Supplemental Figure S2, available online). Nevertheless, the elevational gradient influences pollen assemblages less than expected, probably because the upward transport of pollen ‘averages’ the composition of pollen assemblages at different elevations (e.g. pollen of *P. sylvestris* t. and *Quercus* in high-elevation assemblages; Supplemental Figure S2, available online; Akabane et al., 2020; Cañellas-Bolta et al., 2009; Markgraf, 1980; Zhang et al., 2017). The effect of upward and long-distance transported pollen deposition is even increased by reduced local pollen production of open vegetation (Supplemental Figure S2e, available online). Concerning canopy cover, the hump-shaped curve of plant assemblage data show increasingly open vegetation at high elevation and close to the seashore (Supplemental Figure S2b, available online), with densest vegetation at mid-elevations. Indeed, closed forests establish best at intermediate elevations where moisture availability and temperature are most suitable for tree growth and human disturbance is usually low because the usually steep terrain is not particularly attractive for agriculture. In contrast, at coastal and lowland areas open vegetation is primarily a result from long-lasting human impact (Hadjibibros, 2013) as well as reduced summer moisture availability, while at high altitudes reduced temperatures affect tree performance (Yang et al., 2006).

Previously published research showed that isothermality, a proxy for continentality like distance to the sea, might also drive pollen composition (López-Sáez et al., 2018; Reitalu et al., 2019). Our results also show that changes in plant and particularly pollen composition are associated with the distance to the sea (Supplemental Figure S2c, f, available online). In our study region, the distance to the sea is probably not only related to continentality but also implies decreasing human impact. Human disturbance leads to decreased vegetation cover which in turn results in reduced local to extra-regional pollen deposition. Based on the studied environmental variables, our results therefore may suggest that climate together with human impact drives vegetation and pollen compositional changes.

Comparison of terrestrial and lake sediment surface samples

Comparing terrestrial and lake samples is essential to assess the utility of pollen–vegetation comparisons for reconstructions from natural archives (e.g. Lisitsyna et al., 2012; Qin et al., 2015; Wilmshurst and McGlone, 2005). Here, we assess for the first time the relationships between terrestrial and lake surface samples in the Mediterranean region and can show a close analogy between them (Figure 5). In addition, the lake surface samples seem to reflect the gradients in elevation and distance to the sea, although to a lesser extent. Further, the residuals of the Procrustes analysis (Figure 4) strongly suggest that pollen assemblages from terrestrial surface samples also record extra-local to regional vegetation, as it was found in the lake surface samples. This is more pronounced in open vegetation settings such as the tree line ecotone and grasslands. Nonetheless, our findings and previous studies (Folde et al., 2014a, 2016; Hagemans et al., 2019) hint that this association might be weaker at high elevation or when surrounding vegetation is open (see SMO in Figure 5). Thus, terrestrial surface sample pollen assemblages may also assist the interpretation of fossil lake pollen sequences to reconstruct past vegetation. Despite the amount of lakes sampled is not too high (12), these conclusions are robust enough because they comprise a wide range of environmental conditions from the mesomediterranean to the subalpine belt.

Diversity

Pollen richness (PRI) was argued to be a measure of plant species richness but with a component of evenness (Odgaard, 2013), thus making it a good proxy for plant diversity. Comparable trends in
plant and pollen richness were found across latitudinal, altitudinal and continental transects (Connor et al., 2021; Felde et al., 2016; Jantz et al., 2014; Reitalu et al., 2019; van der Sande et al., 2021). Discrepancies between pollen and plant diversity were also found at higher latitudes and altitudes presumably due to higher influence of long-distance transport (Felde et al., 2016; Jantz et al., 2014; van der Sande et al., 2021). The data from northern Greece point to the occurrence of decreasing trends in pollen and plant evenness (PIE) across the large elevation gradient studied, suggesting that pollen evenness is generally a good proxy for plant evenness. Common declining trends with increasing altitude also link plant and pollen richness. In any case, they seem less pronounced than those between plant and pollen evenness (Figure 8; Supplemental Figure S1, available online). We assume that pollen richness was affected by long-distance upward transport from the valley bottoms to the mountain tops, an effect which is very well-known from other studies (e.g. Connor et al., 2021; Felde et al., 2016; van der Sande et al., 2021). This effect, in combination with the bias introduced by high pollen producers, may contribute to palynological distortions if compared with species richness in vegetation relevées. Taken together, a striking finding of our study is that pollen PIE and PRI are markedly distorted at sites with pine occurrence, likely due to the high pollen production and dispersal ability of pine species (Odgaard, 2001, 2013; Figure 8, Supplemental Table S1, available online).

To counterbalance the over- and underrepresentation of certain pollen types, correction factors are used (e.g. Davis, 1963; Prentice, 1985). However, many of them apply to northern and central European vegetation. Alternatively, the exclusion of tree pollen may lead to good results in Europe, since most trees are wind-pollinated and their pollen is transported over long distances (Connor et al., 2021). This procedure certainly needs sufficiently large pollen counts. It is noteworthy to use a method which is appropriate to the scale and to the research question. For example, Jantz et al. (2014) reported a better representation of pollen richness after combining smaller study plots from the same vegetation belt. Within the summed-up areas, the pollen evenness was higher. Connor et al. (2021) studied the diversity within smaller vegetation plots (1 m × 1 m vs 10 × 10 m in this study). The exclusion of trees thus may seem reasonable to detect diversity trend. However, lake sediment samples might capture wider areas than terrestrial surface samples and an exclusion might be misleading. Furthermore, trees are key features at our sampling sites and in the regional vegetation and makes an exclusion of tree pollen unjustifiable. Alternatively, evenness-detrended palynological richness (DE-PRI) might be applied to reduce the effect of palynological evenness distortions (Colombaroli and Tinner, 2013). Specifically, DE-PRI might locally correct biases, for instance increasing richness in samples with overrepresentation of pine pollen. Indeed, DE-PRI reflects N0 better than PRI within the pine-dominated stands (Figure 8). However, our vegetation records suggest that the discrepancies between DE-PRI and PRI might either arise from underrepresented plant evenness or under-represented plant richness (Figure 8). The unknown distortion effects between DE-PRI and PRI highlight that DE-PRI should be seen as a check for PRI, with a good agreement between PRI and DE-PRI suggesting that the reconstructed richness estimates are robust and unaffected by evenness effects (see discussion in Colombaroli and Tinner, 2013).

Conclusion

This study evaluated the correspondence between vegetation type, plant diversity and pollen and the use of pollen analysis as proxy for past vegetation dynamics and diversity in northern Greece, a hotspot of plant diversity and endemism. We showed that it is possible to discern the main vegetation types based on pollen assemblages. Further, the observed linkages of terrestrial surface samples with lake surface samples are essential to generalise the application of our results to lake sediments. Increasing discrepancies between vegetation and pollen assemblages are detected with rising pollen catchment size (higher altitudes, open vegetation) but also due to high pollen producers (e.g. pines). To weaken such discrepancies, *P. sylvestris* t. pollen might be excluded from the pollen sum, but given its relevance in the Mediterranean vegetation we rather suggest checking the presence of rare accompanying taxa or applying complementary approaches such as aDNA (Birks and Birks, 2016; Gosling et al., 2018; Morales-Molino et al., 2020b; Parducci et al., 2017). With enhanced taxonomic resolution it will be possible to refine the reconstruction of diversity patterns along environmental gradients or through time. We propose that plant and pollen diversity, as captured by richness and evenness measures, show a rather close relationship over wide spatial scales. Our Greek case study may thus contribute to refine reconstructions of past Mediterranean vegetation dynamics. Future studies may investigate the role of pollen productivity and dispersal in creating marked discrepancies and biases between plant and pollen diversity measures (evenness, richness), as observed for pines in this study. Similar distortions might be caused by other strong pollen producers (e.g. Corylus, Betula, Alnus), potentially affecting pollen-based diversity reconstructions. This hypothesis would need to be verified in temperate or boreal vegetation types, in which such woody plants are important.

Acknowledgements

We sincerely thank John Birks for his comments and advice on statistical analyses, and the Ecological and Environmental Change Research Group at the University of Bergen for hosting CS. Cordial thanks go to Christoph Schwörer for his help with R and GIS, and Shauna-Kay Rainford for her help with ArcGIS, Giorgia Beffa and Lieveke van Vugt for their help with pollen identification, and all members from the Palaeoecology Group in Bern for their support. We thank all participants in the 2016 and 2020 coring campaigns in Greece, namely Sandra Brügger, Sebastian Eggenberger, Tryfon Giagkoulis, Andy Lotter, Willi Tanner, Kathrin Ganz, Elmar Gasteli, Markus Glimmer, Luc Hächler, Peter Ruprecht, Antoine Thévenaz and Lieveke van Vugt. We would also like to thank Jamie Giannaka (Olympus National Park Management Agency) for her help with the organisation of our fieldwork expeditions at the Olympus National Park. We also thank the Ministry for Environment and Energy, Directorate General for the Protection and Development of Forests and the Rural Environment, Directorate of Forest Management for the permits to work at the Olympus National Park (Reference Number 181711/1361) and the North Pindos and Koroneia Lakes National Parks (Reference Number 83049/3963 and 83048/3962), as well as the Hellenic Survey of Geology and Mineral Exploration (HSGME; Reference number 1825 A and B) for the coring permits. We would also like to thank two anonymous reviewers for their constructive comments on a previous version of the paper.

Declaration of conflicting interests

The authors declare that there is no conflict of interest.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This study was part of the EXPLO-Project (ERC Synergy Grant ID 810586) funded by the European Research Council. CS received a personal Excellence Scholarship of the Swiss Study Foundation in collaboration with the Bärbel and Paul Geissbühler Foundation, which enabled her visit to the University of Bergen.
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