

SPECIAL ISSUE ARTICLE

Oligocene vegetation of Europe and western Asia—Diversity change and continental patterns reflected by plant functional types

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Spatial vegetation patterns potentially reflect coeval continental climate variations which are also impacted by palaeogeographical settings. Plant functional types (PFTs) and their distribution, frequently applied in ecological studies and biome modelling, serve as a tool for reconstructing palaeovegetation units and ultimately tracing palaeoecological/climate gradients. Earlier quantitative studies focusing on distribution patterns of PFTs and designed to put forward data-model comparisons were carried out on well-dated Middle and Late Miocene floras. Moreover, the PFT approach has been successfully applied to reconstruct Eocene vegetation patterns in several time slices at a global scale as well as in regional vegetation reconstructions throughout the Cenozoic. In the current study, a PFT approach with 41 different classes is applied on Rupelian and Chattian fossil floras of Europe and western Asia to infer spatial vegetation differences across the study area. A comprehensive palaeobotanical record including ~163 macro- (leaves, fruits and seeds) and microfloras was compiled. The floristic components of these palaeofloras are translated to PFTs including herbaceous to arboreal classes. The PFTs are defined using traits and climatic thresholds of key taxa, and comprise species assigned by morphological and phenological features with respect to the related ecosystem. Diversity values of each PFT are calculated for the fossil floras and spatial gradients over western Eurasia are investigated for the Rupelian and Chattian. PFT diversity maps and transects for both time slices reveal basic patterns of the vegetational structure at the continental scale. It is shown that in both time slices studied tropical and broadleaved evergreen PFTs were more diverse in the West and at lower latitudes. Consistently with the global climate evolution as known from marine archives and regional continental records their level was higher in the Rupelian

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compared to the Chattian. All over low diversities of xeric PFTs coincide with the previously assumed dominance of humid climate conditions in western Eurasia throughout the Oligocene, however, the reconstructed spatial gradients suggest somewhat drier conditions to the southwest and southeast of the study area.

KEYWORDS

Eurasia, Oligocene, plant diversity, plant functional types, vegetation

1 | INTRODUCTION

The Oligocene represents a crucial time-span of the transformation of terrestrial phytocoenoses from primarily evergreen vegetation existing throughout most of the Palaeocene and Eocene, under distinct greenhouse conditions with high atmospheric CO₂ (Beerling & Royer, 2011; Collinson & Hooker, 2003) and very flat temperature gradients (Fricke & Wing, 2004; Popova et al., 2017) to mixed mesophytic forests (MMFs) existing in the mid- and higher latitudes under the conditions of a long-term unipolar Oligocene glaciation and phases of potentially lower CO₂ (Mai, 1995; Zachos, Pagani, Sloan, Thomas, & Billups, 2001). The cooling trend already set on in the Eocene as expressed by a substantial decrease of deep-sea temperatures since the Early Eocene Climatic Optimum (Zachos et al., 2001). First evidence for the onset of Antarctic glaciation comes from Late Eocene ice-rafted debris (IRD) records from the Weddell Sea (Carter, Riley, Hillenbrand, & Rittner, 2017). This evolution culminated in the Oi-1 glaciation event at ca. 34 Ma associated with intensified growth of Antarctic ice sheets (Zachos et al., 2001). As indicated by marine data, Rupelian global mean temperatures increased again after the Oi-1 event, but thereafter declined towards the earlier part of the Chattian. For the later part of the Chattian, the global benthic isotope record shows a distinct trend to lower $\delta^{18}\text{O}$ values (Late Oligocene warming, cf. Mudelsee, Bickert, Lear, & Lohmann, 2014; Zachos et al., 2001; Zachos, Dickens, & Zeebe, 2008) that can be either referred to a decline of Antarctic glaciation or more probably to the expansion of Northern Hemisphere warmer deep-water masses, due to changes in the Southern Ocean Circulation system (Pekar & Christie-Blick, 2008; Pekar, DeConto, & Harwood, 2006), under the persistence of an ice sheet near or even larger than modern size covering much of the Antarctic continental shelf (Hauptvogel, Pekar, & Pincay, 2017).

Continental archives of western Eurasia reveal a similar pattern. Early Oligocene continental temperatures reconstructed from the palaeobotanical record tended to be lower compared to the Late Eocene (Bozukov, Utescher, & Ivanov, 2008; Mosbrugger, Utescher, & Dilcher, 2005; Roth-Nebelsick, Utescher, Mosbrugger, Diester-Haass, & Walther, 2004; Utescher, Bondarenko, & Mosbrugger, 2015). The temperature decline across the Eocene–Oligocene Transition (EOT) was quantified in the southern North Sea realm and amounted to $\sim 2.5^\circ\text{C}$ (mean annual temperature, MAT), combined with a distinct increase in seasonality of temperature in the order of 5°C (e.g., Weisselster Basin, cf. Utescher et al., 2015). For the Oligocene, temperatures compiled from western Eurasian palaeofloras (Li et al., 2018) indicate a minor

cooling in Europe and warming in western Siberia, and thus revealed no uniform pattern for this time-span with a potentially high variability of climate (Liu et al., 2018; Pekar et al., 2006; Zachos et al., 2008). The general pattern of a relatively warm Rupelian and a cooler Chattian in the European part of the study area (cf. Li et al., 2018) is partly supported by other continental, macroflora-based records based on various different methods (Coexistence Approach [CA], Leaf Margin Analysis, CLAMP; cf. Bozukov et al., 2008; Moraweck, 2017; Roth-Nebelsick et al., 2004). Other studies revealed no clear-cut trends, dependent on the method employed in each case (Teodoridis & Kvaček, 2015; Uhl et al., 2007). For western Germany pollen-based data and $\delta^{18}\text{O}$ values of fossil bivalve shells and shark teeth first indicate a decline of terrestrial and sea surface temperatures (SSTs) by $\sim 4^\circ\text{C}$ throughout the Chattian and a subsequent warming towards the Oligocene–Miocene transition (Schäfer & Utescher, 2014; Walliser, Lohmann, Niezgodzki, Tütken, & Schöne, 2016).

In this context, it is noteworthy that the majority of temperatures inferred from Oligocene palaeobotanical proxies are warmer compared to data from various modelling approaches available for that time-span (cf. Li et al., 2018). This holds especially for the sites located at higher latitudes, and is part of the known polar amplification problem (Pithan & Mauritsen, 2014).

Oligocene precipitation data available for western Eurasia mainly represent plant-based estimates, all indicating humid climate conditions. From various European records there is evidence for a decrease of mean annual precipitation and precipitation of the warmest month (MPwet) from the Rupelian to Chattian (Bozukov et al., 2008; Mosbrugger et al., 2005; Utescher et al., 2015). Data from the eastern part of the study area (western Siberia) indicate somewhat drier conditions getting slightly wetter throughout the Oligocene (Li et al., 2018). With MPwet being mostly in the order of 100–250 mm and mean precipitation of the driest month (MPdry) at 20–50 mm, a distinct seasonal rainfall signal is reported in the aforementioned studies. All in all, the plant-based precipitation reconstructions point to more humid conditions compared to present and to rainfall rates obtained in Oligocene model scenarios (cf. Li et al., 2018).

The role of CO₂ as a major driver of Oligocene climate change is still a matter of debate. Atmospheric pCO₂ levels have been inferred from a variety of proxies such as biomarkers, boron isotopes and stomata (e.g., Pagani, Zachos, Freeman, Tipler, & Bohaty, 2005; Pearson, Foster, & Wade, 2009; Roth-Nebelsick, Grein, Utescher, & Konrad, 2012; Zhang, Pagani, Liu, Bohaty, & DeConto, 2013) yielding pCO₂ levels from ~ 300 ppm to over 1,000 ppm for this time-span.

For the Rupelian, Erdei et al. (2012) report a relatively high $p\text{CO}_2$ with overlapping intervals of 503–839 ppm during NP23. However, these $p\text{CO}_2$ proxies all have considerable uncertainties (Beerling & Royer, 2011). On the whole, data suggest a general declining trend in atmospheric CO_2 throughout the Oligocene. This coincides with the temperature decline observed in various archives (see above) but might be incompatible with a potential warm global phase in the later Chattian.

Vegetation evolution in western Eurasia during the Oligocene is usually characterized by a gradual replacement of thermophilous (para/subtropical), primarily evergreen forest types persisting in the study area since the Early Paleogene by a more temperate, mainly deciduous vegetation. Having already started in the Late Eocene, this replacement process was most significant in the later Oligocene (Walther, 1994). However, the timing and scale of this floral transition was not uniform in various regions of central and southeastern Europe (Kvaček & Walther, 2001) and was partly related to large-scale palaeogeographical changes in the study area (Erdei et al., 2012).

Spatial vegetation pattern in the study area, based on qualitative interpretations of the floral record, are provided in a study by Collinson and Hooker (2003) integrating over the entire Oligocene. The described vegetation units (VUs) include broadleaved mixed deciduous and evergreen forest types with a varying proportion of sclerophyllous elements, revealing both, latitudinal and longitudinal vegetation patterns over Eurasia. According to this reconstruction sclerophyllous evergreen forest vegetation, probably existing under winter-dry conditions, occurred in a belt stretching from the western Mediterranean and the Tethyan Archipelago including the Balkan area to Kazakhstan in the East (cf. Collinson and Hooker, 2003 for a summary, and see also Axelrod, 1975). A somewhat different picture is obtained in a reconstruction based on vegetational interpretations of pollen spectra across the EOT (Priabonian and Rupelian; cf. Pound & Salzmann, 2017) showing a more restricted occurrence of xerophytic biomes (sites in southern Spain) in the study area. Moreover, the study shows that at most of the sites regarded vegetation had undergone gradual change already in the Late Eocene or persisted across the EOT, without any notable changes reported.

In the western part of the study area, broadleaved evergreen vegetation persisted in the warm phase of the earlier Rupelian, mainly in the more southerly parts such as the Eastern Paratethys (Bulgarian Early Oligocene sites; cf. Palamarev, Kitanov, & Bozukov, 1999), or the floras of the Paleogene Basin (Hungary, Slovenia; cf. Erdei et al., 2012). However, also more northerly sites such as the Early Oligocene Rauenberg flora from the Upper Rhine Graben represent broadleaved evergreen forest (Kovar-Eder, 2016), while the majority of sites of the Bohemian Massif and Upper Lausitz Basin have a considerable admixture of deciduous taxa and thus are considered to represent broadleaved MMFs (e.g., Walther, 2005). As regards increased immigration of temperate, deciduous elements in the zonal vegetation during the climatically more variable Chattian and the timing of this process, clear trends are hard to identify and details remain yet unsolved. Many Late Oligocene floras of mid-latitudinal Europe represent mesophytic forest types with a higher proportion of deciduous

versus evergreen elements. This has been substantiated by analysing sites in upland settings (so-called “volcanic” floras) best reflecting zonal vegetation such as the Central European Kleinsaubernitz (Walther, 2005) and Enspel (Koepler & Uhl, 2014) macrofloras. According to a study based on the IPR approach high proportions of broadleaved evergreen elements in the vegetation occurred again in sites of the Bohemian Massif during warm phases of the Chattian (Teodoridis & Kvaček, 2015).

The Eocene–Oligocene vegetation evolution in Central Eurasia was characterized by the replacement of Early Paleogene evergreen vegetation by MMFs and the establishment of the primarily deciduous Turgai type vegetation in the Rupelian (Akhmetiev & Beniamovski, 2009). In western Siberia the significant decline in evergreen elements predated the EOT and the Early Oligocene floras represent the typical Turgai type (Popova et al., 2013). Mixed conifer-broadleaved deciduous forest assemblages with a minor diversity proportion of broadleaved evergreen elements persisted in western Siberia and large parts of Kazakhstan throughout the Oligocene and earliest Miocene (Popova, Utescher, Gromyko, Mosbrugger, & François, 2019; Zhilin, 2001). A considerable increase in taxonomic diversity in the Late Oligocene of western Siberia involving the appearance of various typical Miocene taxa, for example, from the mainly deciduous Betulaceae and Rosaceae families, and a variety of zonal mesic and intrazonal herbaceous species, was probably triggered by increasing humidity (Popova et al., 2019).

In the present study we present for the first time a comprehensive, quantitative vegetational data set for the Oligocene of western Eurasia generated based on the interpretation of the palaeobotanical record at the level of plant functional types (PFTs) and integrating over micro- and macroflora. Although Oligocene vegetation is not interpreted in terms of autecology and modern reference phyto-coenoses the PFT-based reconstruction provides insight into spatio-temporal diversity patterns. Moreover, the ecospectra obtained for the single palaeofloras can be translated into major vegetation types as a basis for biomes that can be mapped in the palaeogeographical context. The comparison of internally consistent vegetation patterns of an Early and a Late Oligocene time slice allows for a discussion and validation in the context of previous vegetation reconstructions, continental climate data recently published for the same region and partly based on the same floristic record, and Oligocene climate change as evident from marine archives.

2 | STUDY AREA

The study area selected for the analysis of Oligocene vegetational patterns comprises western Eurasia including Greenland and Spitsbergen. In the East, our area of interest extends to $\sim 85^\circ$ longitude and includes the rich palaeobotanical record of western Siberia and Kazakhstan. For a better representation of zonal vegetation patterns we also included North African sites as far as available.

In the later Paleogene significant tectonic activities occurred in Eurasia which were linked to the collision of the Indian and Eurasian plates in the East of the study area and in the West the compression

between Africa and Europe formed an active Alpine mountain belt along the southern border of the Eurasian continent. The earlier Paleogene Tethyan Archipelago evolved to a proto-Mediterranean Sea and intercontinental Paratethys to the North, at times connected by seaways (Rögl, 1998; Schulz, Bechtel, & Sachsenhofer, 2005). Especially during the global sea-level highstand in the early Rupelian epicontinental seaways covered large parts of Europe, and temporarily a marine connection of Paratethys and Cenozoic North Sea was established (Rögl, 1999). In Central Eurasia, however, the Proto-Paratethys system already had retreated from both the Tarim area and the Siberian Basin (former Turgai Strait) by the end of the Late Eocene (Bosboom et al., 2017), thus promoting plant migration in Eurasia on the one hand, but potentially leading to a more continental type of climate in the inland, on the other.

3 | MATERIALS AND METHODS

3.1 | The palaeobotanical record

The selection of palaeobotanical sites we use in this study primarily includes floras compiled in the frame of previous studies, mainly on Cenozoic climate, carried out in the frame of the NECLIME (Neogene Climate Evolution of Eurasia) network (Erdei et al., 2012; Mosbrugger et al., 2005; Popova et al., 2013; Roth-Nebelsick et al., 2004). This NECLIME data set was recently used in a study on climate signals and forcings in Eurasia including a comprehensive data-model inter-comparison (Li et al., 2018). About 30 floras were newly added in the frame of this study to complement records based on microflora, and to include information on vegetation of the Tethyan south coast.

The present western Eurasian dataset comprises a total of 161 published macro- (woods, carpoflora, leaves) and microfloras having sufficient stratigraphical information to allow allocation to either an Early (Rupelian) or Late Oligocene (Chattian) time slice. Newly compiled flora lists include 22 microfloras and four xylofloras from the Tethyan realm including North Africa. Position and flora type are shown in the palaeogeographical context in Figure 1. Details on the floras including diversity, dating, and references are provided in Supporting Information 1. The 36 microfloras in the records have a mean diversity of 45.9 taxa (SD 23.4), carpofloras attain a diversity of 55 taxa (SD 39.6), while the 78 leaf floras, most frequent type in our record have a relatively low diversity (26.3 taxa; SD 15.2). With only 15.4 taxa on average (SD 6.2) xylofloras are the least diverse in our record.

3.2 | The plant functional type approach

The PFT approach has been successfully applied to reconstruct past vegetation patterns throughout the Cenozoic (e.g., Popova et al., 2013; Utescher, Erdei, Hably, & Mosbrugger, 2017; Utescher & Mosbrugger, 2007) and was used in various model-data inter-comparisons in biome model reconstructions of Neogene vegetation (Forrest et al., 2015; François et al., 2011; Henrot et al., 2017). A PFT

is defined using traits and climatic thresholds of key taxa, and comprises species assigned by morphological and phenological features with respect to the related ecosystem (François et al., 2011). The PFT approach is mainly based on the assumed autecology of the fossil taxa based on their nearest living relatives (NLRs). The method employs all taxa recorded in a given palaeoflora while the abundance of fossil taxa is not considered, thus minimizing taphonomic bias and making the method applicable on various organ types of fossil plants (Utescher et al., 2017).

The basic set of PFT categories comprising 13 arboreal and two herbaceous types, serving as a basis of the presently employed concept, as detailed in Utescher and Mosbrugger (2007) exemplifying an application on Eocene floras. The current classification (Table 1) has been obtained by adding categories corresponding to shrub forms (PFTs 5–16; 18), herbs (PFTs 1–4), tuft plants and mangrove elements (PFTs 34–35), lianas and climbers (PFT 36), epiphytes and parasitic plants (PFT 37) and halophytes (PFT 38). Temperate PFT groups are split into cold/cool and warm temperate groups. The warm temperate broadleaved/needleleaved and evergreen/deciduous categories are split into groups according to their drought tolerance (PFTs 7; 11–12; 15–16; 21–22; 25; 28–31). The new classification also accommodates potential non-zonal wetland elements (PFTs 39–41) to approximate the azonal or intrazonal imprint on an individual assemblage. It should be noted that fossil plant assemblages, especially the fruit/seed and also leaf floras, inherently provide a significant sample of the intrazonal/azonal vegetation. Due to frequent uncertainties in separating zonal and non-zonal elements, the present study considers all plant taxa identified in a given assemblage with an approximation of the potential non-zonal imprint in the vegetation. The extended PFT classification system (40 PFTs) was first applied on a set of palaeofloras from the Pannonian of the Pannonian Basin (Utescher et al., 2017). The presently used system with 41 PFTs (PFT 26, broadleaved deciduous cold temperate trees, was added) is also employed in a study on Miocene peat-forming vegetation (Utescher, Ashraf, Kern, & Mosbrugger, 2020).

The PFTs are identified based on the NLRs of the fossil record. More details on the classification procedure are provided in François et al. (2011) and Utescher, Erdei, François, and Mosbrugger (2007). Taxa representing various PFTs proportionally contribute to several model classes (sum of proportions per taxon is 1). Various palynomorph taxa referable to dicot plant families with a very broad ecological range remain unclassified. A complete list over fossil taxa, NLRs, and corresponding PFTs is given in Supporting Information 2. If a PFT concept established for a taxon allows for several different solutions, improbable PFTs are excluded using a coexistence table between tree PFTs modified from Henrot et al. (2017). The coexistence table is provided in Supporting Information 3.

3.3 | Statistical analysis and mapping of the results

To interpret PFT spectra in terms of vegetation herbaceous PFTs (1–4) are excluded from the analysis in order to ensure comparability of carpo- and palynofloras on the one hand, and leaves and xylofloras

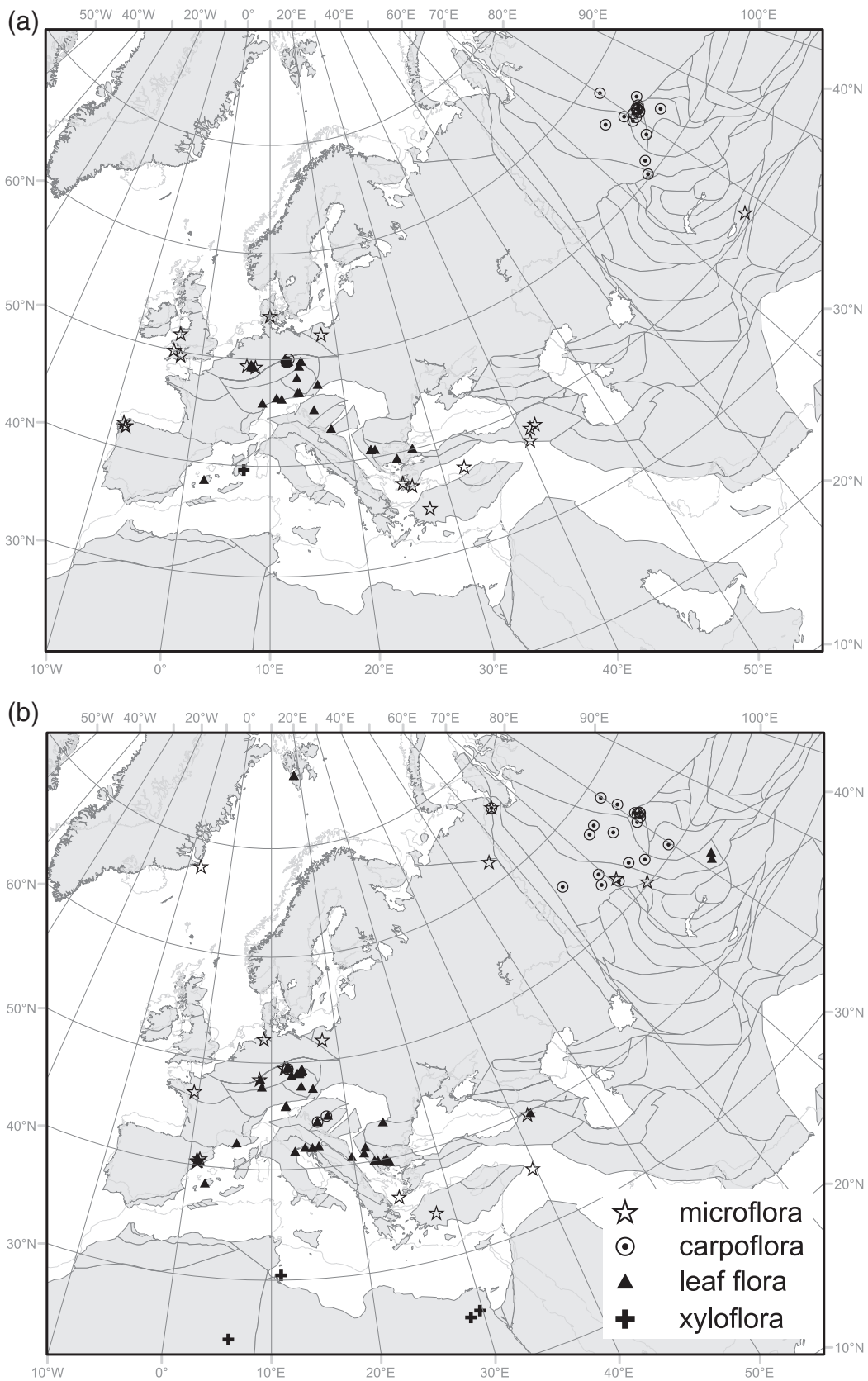


FIGURE 1 Plate reconstructions (GPlates 2.2, hotspot reference frame; Müller et al., 2018) and rotated positions of the palaeobotanical sites addressed in this study. (a) Late Oligocene; (b) Early Oligocene

TABLE 1 Plant functional types

Plant functional types	
1	C3 aquatic herbs
2	C3 mesic herbs
3	C3 xeric herbs
4	C4 herbs
5	Needleleaved evergreen cold temperate shrubs
6	Needleleaved evergreen cool temperate shrubs
7	Needleleaved evergreen warm temperate drought-tolerant shrubs
8	Broadleaved deciduous arctic shrubs
9	Broadleaved deciduous cold temperate shrubs
10	Broadleaved deciduous cool temperate shrubs
11	Broadleaved deciduous warm temperate drought-intolerant shrubs
12	Broadleaved deciduous warm temperate drought-tolerant shrubs
13	Broadleaved evergreen cold temperate shrubs
14	Broadleaved evergreen cool temperate shrubs
15	Broadleaved evergreen warm temperate drought-intolerant shrubs
16	Broadleaved evergreen warm temperate drought-tolerant shrubs
17	Succulents
18	Tropical evergreen shrubs
19	Needleleaved evergreen cold temperate trees
20	Needleleaved evergreen cool temperate trees
21	Needleleaved evergreen warm temperate drought-intolerant trees
22	Needleleaved evergreen warm temperate drought-tolerant trees
23	Needleleaved deciduous cold temperate trees
24	Needleleaved deciduous cool temperate trees
25	Needleleaved deciduous warm temperate drought-intolerant trees
26	Broadleaved deciduous cold temperate trees
27	Broadleaved deciduous cool temperate trees
28	Broadleaved deciduous warm temperate drought-intolerant trees
29	Broadleaved deciduous warm temperate drought-tolerant trees
30	Broadleaved evergreen warm temperate drought-intolerant trees
31	Broadleaved evergreen warm temperate drought-tolerant trees
32	Broadleaved raingreen tropical trees
33	Broadleaved evergreen tropical trees
34	Tuft trees/shrubs
35	Mangrove
36	Lianas and climbers
37	Epiphytes and parasitic plants
38	Halophytes
39	Broadleaved wetland trees

TABLE 1 (Continued)

Plant functional types	
40	Broadleaved wetland shrubs
41	Needleleaved wetland trees

on the other. The latter commonly have a strong underrepresentation of herbaceous components for taphonomic reasons (e.g., Popova et al., 2017). Further taphonomic aspects in our data set are discussed in Section 5.3. As a tool for multivariate classification we employ principal component analysis (Past 3.0 software).

The results are visualized in the palaeogeographical contexts using plate tectonic reconstructions for 25 Ma for the Late Oligocene and 30 Ma for the Early Oligocene, respectively. Our maps show major plate boundaries, not the particular position of the coast line, but sites are represented in their correct palaeo-position. For the plate configuration and rotation of coordinates we use GPLates 2.2 and the hotspot reference frame (Müller et al., 2018).

4 | RESULTS

4.1 | Representation and diversity of PFTs

4.1.1 | Herbaceous PFTs

Herbaceous PFTs are underrepresented in leaf and xylofloras for taphonomic reasons. This has to be considered when interpreting their diversity (Figure 2). In both time slices regarded, the intrazonal PFT 1 (aquatic herbs) has a clear core area in the western Siberian floras where diversity proportion attains 36% (SD 14) of total diversity, with a clear focus on Early Oligocene sites (42.7%; SD 14.6). In the European carpofloras diversity percentages of PFT 1 attain 9.1% (SD 8.5) on average only. As regards microfloras, values all stay below 5% (mean 3.7%; SD 2.9), which may be attributed to taphonomic constraints.

When considering carpofloras, mesic C3 herbs (PFT 2) show the same longitudinal gradient, attaining 17.3% (SD 9.6) in the western Siberian carpofloras while staying below 10% (mean 5.8; SD 3.8) in the European carpo-record. In the microfloras, PFT 2 has highly variable proportions ranging from 5 to 50%. According to our data PFT 2 shows no clear spatial trend in the study area but tends to be more diverse in Late Oligocene microfloras (mean 22.1%; SD 13.2) compared to the Early Oligocene (17.9%; SD 11.5). The PFT 3 (xeric herbs)/PFT 2 (mesic herbs) ratio may indicate dry conditions. As regards carpoflora highest values are obtained for the Trubach H3048, Shchurchya River, and Pavlograd H4036 floras, all of Early Oligocene age, and located in western Siberia. Among the microfloras, very high values are obtained for Tekesk flora (Late Oligocene, northern Tien Shan), Karasor Lake with an overall low diversity, and Orros in Spain, also having a moderate diversity only. All in all, microfloras-based PFT 3/2 ratios show a latitudinal gradient although not all

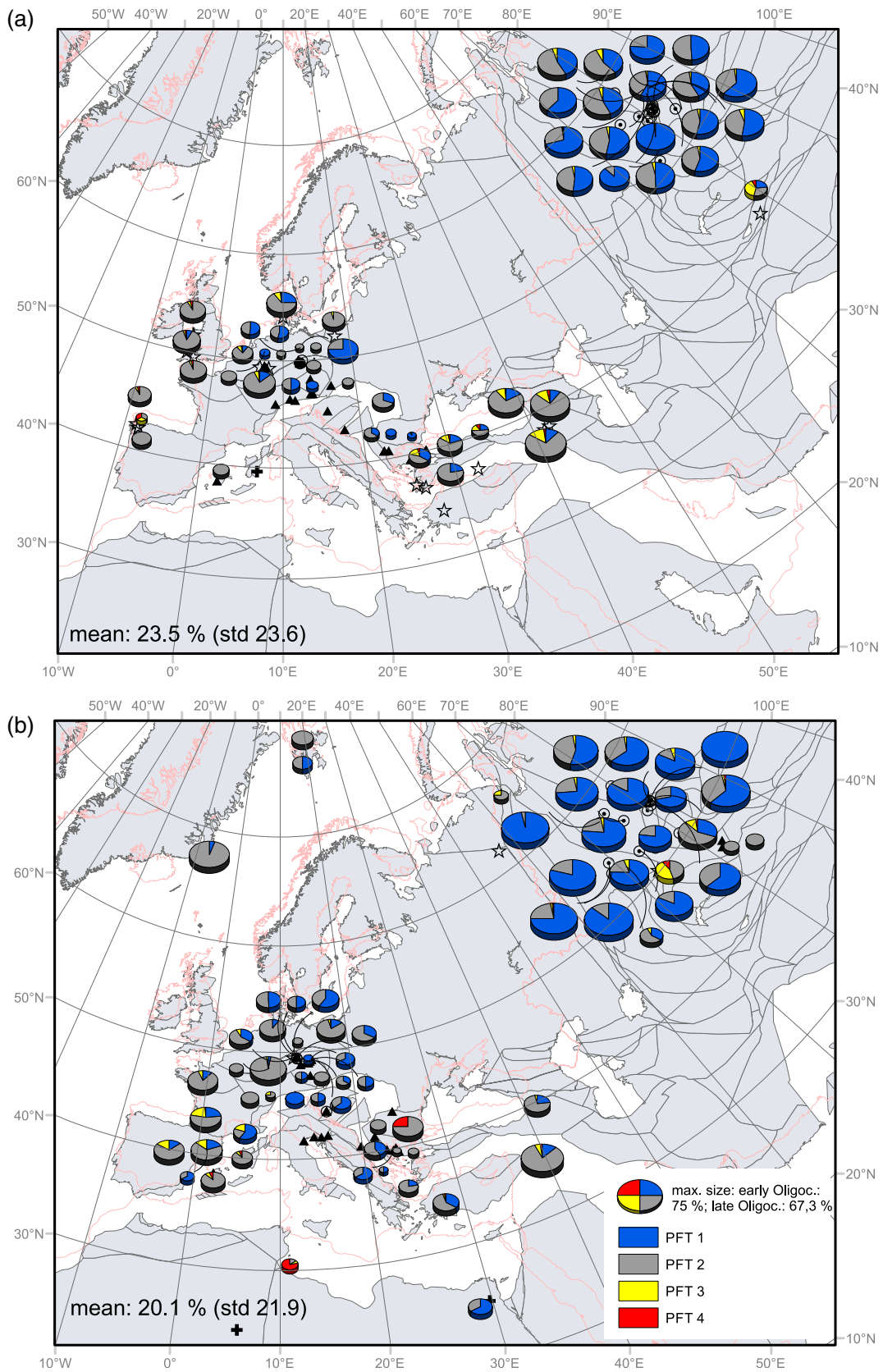


FIGURE 2 Diversity of herbaceous PFTs (1–4). For palaeogeographical reconstructions, cf. Figure 1. (a) Late Oligocene; (b) Early Oligocene. Sizes of the pie charts relate to the ratio of total PFT diversity [Colour figure can be viewed at wileyonlinelibrary.com]

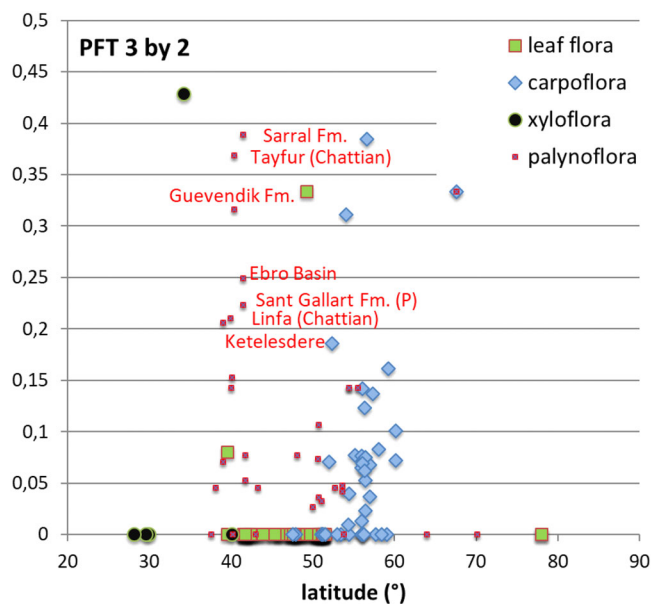


FIGURE 3 Proportion of dry by wet herbs in relation to the organ type of the fossil floras. Microfloras with an exceptionally high proportion of dry herbs (labelled) are located in the southwest and southeast of the study area [Colour figure can be viewed at wileyonlinelibrary.com]

southerly sites necessarily have raised values (Figure 3). The Spanish sites Sarral Fm. (P), Ebro Basin, and Sant Gallart Fm. (P), as well as Tayfur Chattian (P), Guevendik Fm. Chattian (P), Keleresdere Chattian (P), Linfa Chattian (P) located in Turkey all have exceptionally high ratios >0.2 thus pointing to drier conditions in the SW and SE of the study area. For the southeast of the study area there is evidence for a higher proportion of PFT 3 in the Late Oligocene compared to the Early Oligocene (Figure 2). For the southwest our Late Oligocene data coverage does not allow for relevant conclusions. Components potentially representing C4 herbs (PFT 4) sporadically occur in our Oligocene record (Figure 2).

4.1.2 | Woody PFTs

Diversities of woody PFTs are overall comparable among all organ types of floras. Shrubs are represented by PFTs 8–18 (Table 1) in our floral record. Needleleaved shrub PFTs (5–7) are absent from the floras. The diversity proportion of shrub PFTs varies between ~5 and 35%, and in the western part of the study area it does not show any distinct spatial gradient. Most of the western Siberian carpofloras, however, show distinctly raised diversity proportions of deciduous shrubs.

The composition of arboreal diversity provides interesting insight into the main composition of biomes. Conifer trees are represented by PFTs 19–25. Our data indicate that conifers are slightly better represented by microfloras compared to leaf and fruit and seed floras, partly referable to their high pollen production. The ratio of needleleaved versus broadleaved trees is highly variable and does not

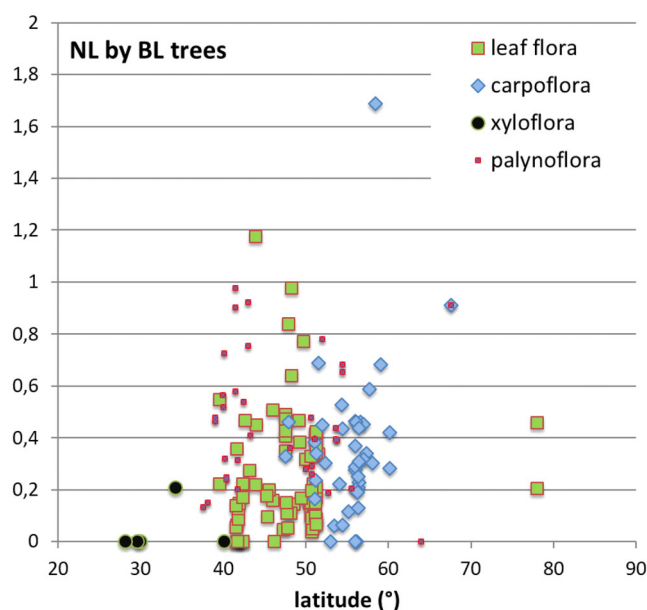


FIGURE 4 Proportion of needleleaved by broadleaved trees in relation to the organ type of the fossil floras [Colour figure can be viewed at wileyonlinelibrary.com]

display a distinct latitudinal gradient (Figure 4). The composition of the conifer tree fraction is likewise variable (Figure 5). Needleleaved cold temperate and cool temperate trees (PFTs 19–20) tend to be more diverse in the northerly floras while in the middle and lower latitudes of Europe warm temperate conifers (PFTs 21–22) were more diverse. It is noteworthy that the taxa about evenly scored for the drought-tolerant (PFT 22) and -intolerant PFT (PFT 21). This is due to the fact that the majority of taxa provided by the NLR concept may exist in both, permanently wet and seasonally dry conditions. Taxa referred to modern *Tetraclinis*, today restricted to dry conditions were not used as an indicator for dry conditions, but were allocated to both PFTs in this reconstruction because in most of the cases climatic requirements of *Tetraclinis* were inconsistent with the majority of taxa. Needleleaved deciduous warm temperate drought-intolerant trees (PFT 25) may occur throughout the study area in both time slices. In some floras PFT 25 may represent the entire conifer fraction. In more southerly sites, PFT 25 tends to be less diverse or even is absent (Figure 5). The needleleaved deciduous cold/cool temperate tree PFTs (23–24) are represented by *Larix*, recorded at a single Early Oligocene site (Krabbedalen Fm., southern Greenland).

Broadleaved deciduous PFTs attain up to ~49% (mean 21.1%; SD 13.1) of total diversity in the Early Oligocene and ~66% (mean 22.3%; SD 14.3) in the Late Oligocene (Figure 6). Cold and cool deciduous types (PFTs 26–27) are in many cases excluded from the spectra when applying the coexistence procedure. This concerns not only floras located in the lower latitudes, but also northerly sites such as the Early Oligocene Aspelintoppen, Renardodden (Spitsbergen), and Sediya River (western Siberia) localities. As in the conifer PFTs, drought-tolerant (PFT 29) and intolerant (PFT 28) types occur mostly in about equal proportions, except for the Early Oligocene Cervera

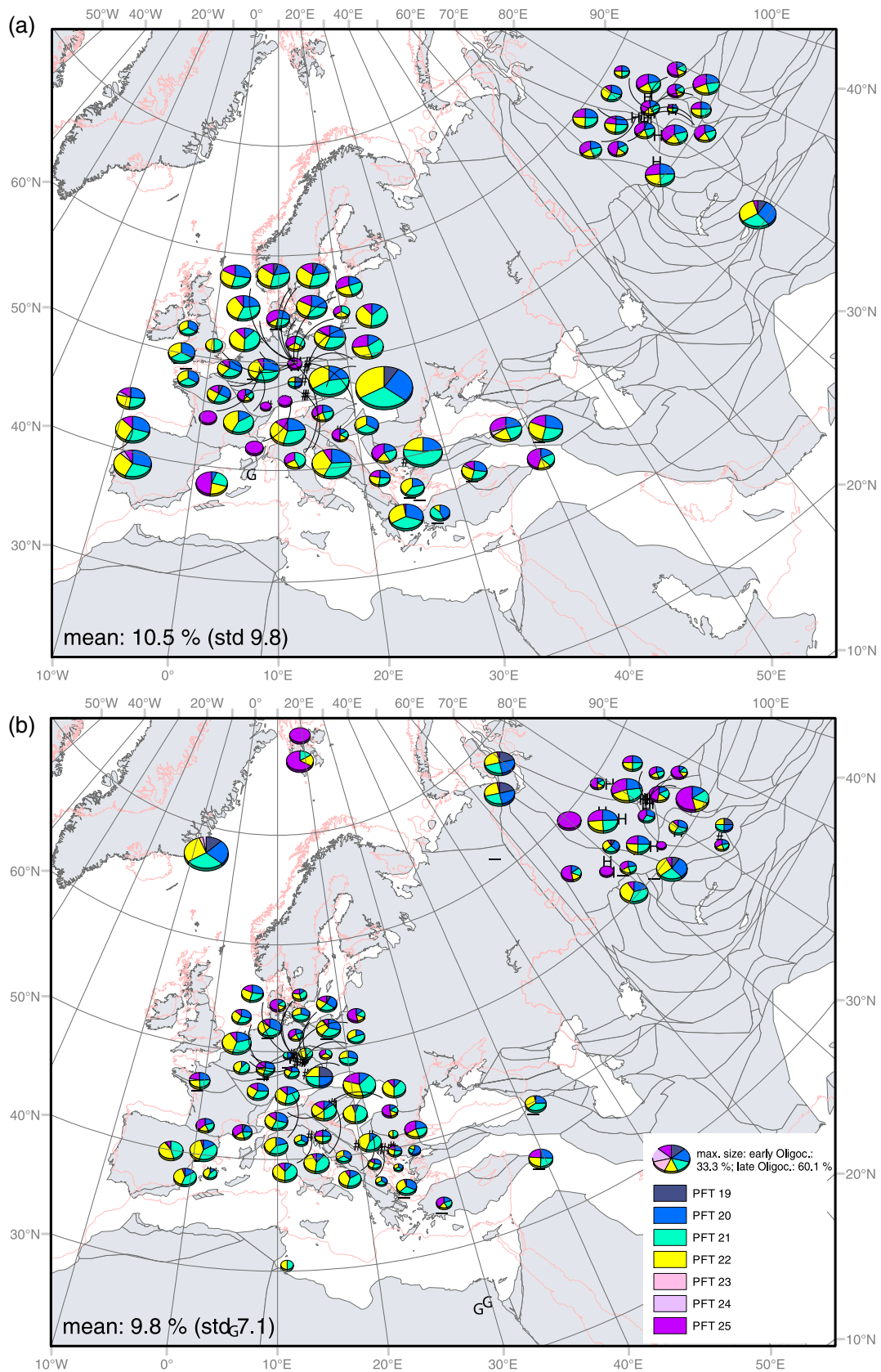


FIGURE 5 Composition of the needleleaved arboreal component (PFTs 19–25) and diversities. For palaeogeographical reconstructions, cf. Figure 1. (a) Late Oligocene; (b) Early Oligocene. Sizes of the pie charts relate to the ratio of total PFT diversity [Colour figure can be viewed at wileyonlinelibrary.com]

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leaf flora (Spain) where no drought-intolerant types are reported. The broadleaved evergreen component attains somewhat higher proportions for the Early Oligocene sites (max. value 44.8%; mean 15.3%, SD 11.3) compared to the Late Oligocene (max. value 41.2%; mean 12.9%, SD 10.3) (Figure 7). The patterns obtained for both time slices indicate overall higher proportions at lower latitudes and lower values in western Siberia in general, in particular for the Late Oligocene. When regarding the composition of the broadleaved evergreen fraction it is shown that the tropical PFT 33 is mainly confined to low latitudes and is more diverse in Early Oligocene floras. For the vast majority of mid- and higher latitude floras, possible scores for PFT 33 were in contradiction to unequivocally present temperate PFTs and excluded in the coexistence considerations. For the presence of PFT 33 in the western Siberian floras Nizhnya-Tav, Katyl'g, and Vasyug cf. discussion in Section 5.2. Also for the broadleaved evergreen component it is shown that proportions of drought-tolerant and -intolerant types are again rather balanced in most of the floras.

The broadleaved evergreen versus broadleaved deciduous ratio, depicted for Early and Late Oligocene sites in Figure 8, shows a clear zonal gradient, with higher values observed for floras located at lower latitude. For the European mid-latitude sites, ratios exceeded 0.5 in many floras while significantly lower values are obtained for most western Siberian floras at a comparable palaeolatitude. Differing high values resulting for three Early Oligocene western Siberian carpofloras (Nizhnya-Tav, Katyl'g and Vasyug) are discussed in Section 5.2. Ratios resulting for the North African floras are among the highest.

In the Rupelian, tuft trees (PFT 34; Figure 9) are reported from a single site in western Siberia (Neverovka pollen flora) while they are common at the majority of European localities, also at higher mid-latitudes such as the southern North Sea Basin (Wursterheide and Komorza pollen floras). Very high diversity proportions (>15%) are obtained for the North African sites. In the Chattian, tuft trees had completely disappeared from the eastern part of the study area but also from many sites of the mid-latitude Europe. Raised proportions recorded from microfloras recovered in the Bristol Channel and southern Irish Sea are discussed in Section 5.2.

Mangrove components (PFT 35) are recorded in three Rupelian sites in the southern part of the study area (<2.2%; Peguera [Spain], Kuzu Harbour [Turkey], Jebel Qatrani [Egypt]), but are absent from the Chattian dataset. Lianas and climbers (PFT 36) are most diverse in the mid-latitude sites, are recorded at ~50% of the studied sites (mean values: Early Oligocene, 2.0%; Late Oligocene, 1.3%). For single sites higher proportions are obtained (up to 14%). Epiphytes (PFT 37) occur sporadically and with low diversities.

Broadleaved wetland trees and shrubs (PFTs 39–40) are present throughout the study area, except for the North African sites and various localities in the northern part of western Siberia. Proportions may attain ~8% of total diversity (mean: ~5% in both time slices). The same holds for the needleleaved wetland tree PFT 41 which may attain up to 7% (mean: ~2% in both time slices). Raised proportions of PFTs 39–41 indicate an intrazonal signature in the studied plant community.

4.2 | Vegetational interpretation at the level of PFTs

Principle component analysis of PFT diversity proportions of the studied floras excluding herbaceous PFTs yielded a total of eight interpretable VUs (Figure 10; Supporting Information 4). VU 1 includes mainly western Siberian carpofloras and is characterized by high PC 1 loadings, correlated to a high proportion of broadleaved deciduous shrubs, a moderate proportion of deciduous trees and a minor contribution of conifers and broadleaved evergreen PFTs. For most of the sites cool temperate PFTs are not excluded while the very minor tropical PFT proportions refer to the presence of shrubs. The sites all have an affinity to wetland PFTs (39–41). VU 2 including 27 sites and various types of floras represents the broadleaved deciduous forest with moderately diverse shrub layer (broadleaved deciduous and evergreen), conifer trees and a broadleaved evergreen arboreal component. Tropical evergreens are excluded or rarely present in the shrub layer only. Proportions of azonal wetland PFTs are lower compared to VU 1. VU 3 includes 31 sites and all types of floras. It has a moderately diverse shrub layer including deciduous and evergreen broadleaved types. The arboreal spectra of these sites include needleleaved, deciduous broadleaved, and evergreen types and can be characterized as MMF. Needleleaved PFTs (cf. PC 3, Supporting Information 4) significantly contribute to the arboreal diversity of VU 3 thus pointing to a conifer-rich version of the MMF. Cool temperate conifers are included for most of the sites while cool temperate broadleaved trees are sporadically present. Tropical PFTs are absent, excluded, or only present as shrubs. VU 4 combines 39 sites and represents MMF vegetation with an about equal distribution of all discerned shrub and arboreal PFTs, except for the arboreal tropical component that, in rarer cases, may attain high percentages. Therefore, all the sites grouped to VU 4 obtained no specific factor loadings and are located close to the origin in the PCA scatter plots (Supporting Information 4). VU 4 has a thermophilous aspect because cool temperate types are absent or have been excluded according to the coexistence table (Supporting Information 3). High PC 4 loadings characterized by high loading of non-tropical broadleaved evergreen trees and shrubs specify a dominantly evergreen, non-tropical vegetation type. Thermophilous broadleaved deciduous PFTs are present at minor to moderate diversities while conifers attain minor proportions only. High negative loadings of PC 3 (Supporting Information 4) characterize the tropical forest (VU 6) where PFTs 32, 33, 11 attain diversity proportions >75%. The five tropical sites are all located on the African Plate. Finally, high loading of PC 5 are indicative for arboreal wetland vegetation (Figure 10). The small group including three sites represents azonal (intrazonal) vegetation and is not established here as vegetation unit.

When mapping the VUs for both time slices considered here it is shown that vegetational interpretation at the level of PFTs reveals distinct spatio-temporal patterns over the study area (Figure 11). The mainly deciduous VU 1 with diverse shrubs and azonal imprint is confined to Early and Late Oligocene sites of western Siberia south of 60°N (palaeolatitude). VU 2, also characterized as temperate, mainly

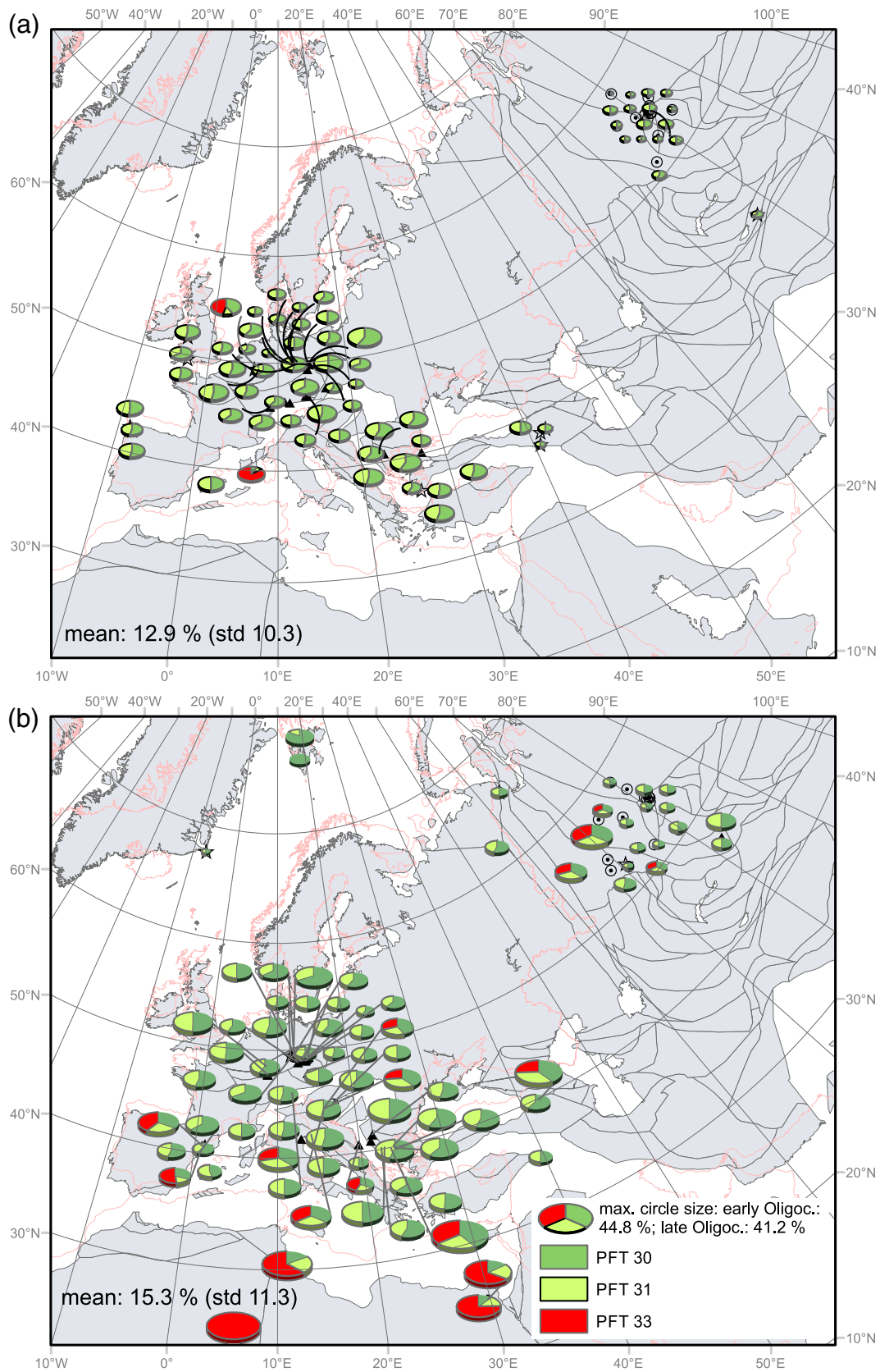


FIGURE 7 Composition of the broadleaved evergreen arboreal component and diversities (PFTs 30, 31, 33). For palaeogeographical reconstructions, cf. Figure 1. (a) Late Oligocene; (b) Early Oligocene. Sizes of the pie charts relate to the ratio of total PFT diversity [Colour figure can be viewed at wileyonlinelibrary.com]

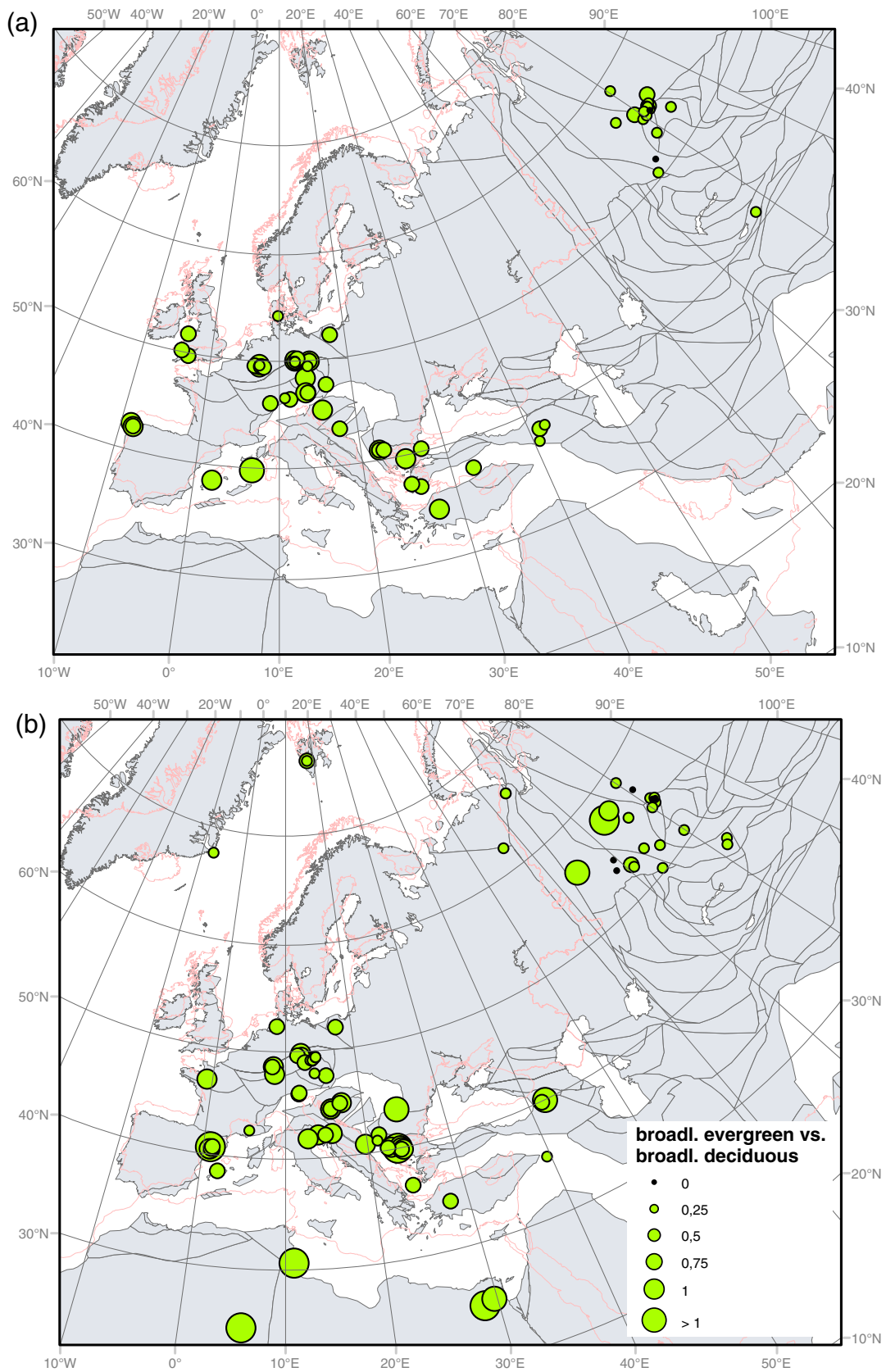


FIGURE 8 Proportion of broadleaved evergreen by deciduous PFTs. For palaeogeographical reconstructions, cf. Figure 1. (a) Late Oligocene; (b) Early Oligocene [Colour figure can be viewed at wileyonlinelibrary.com]

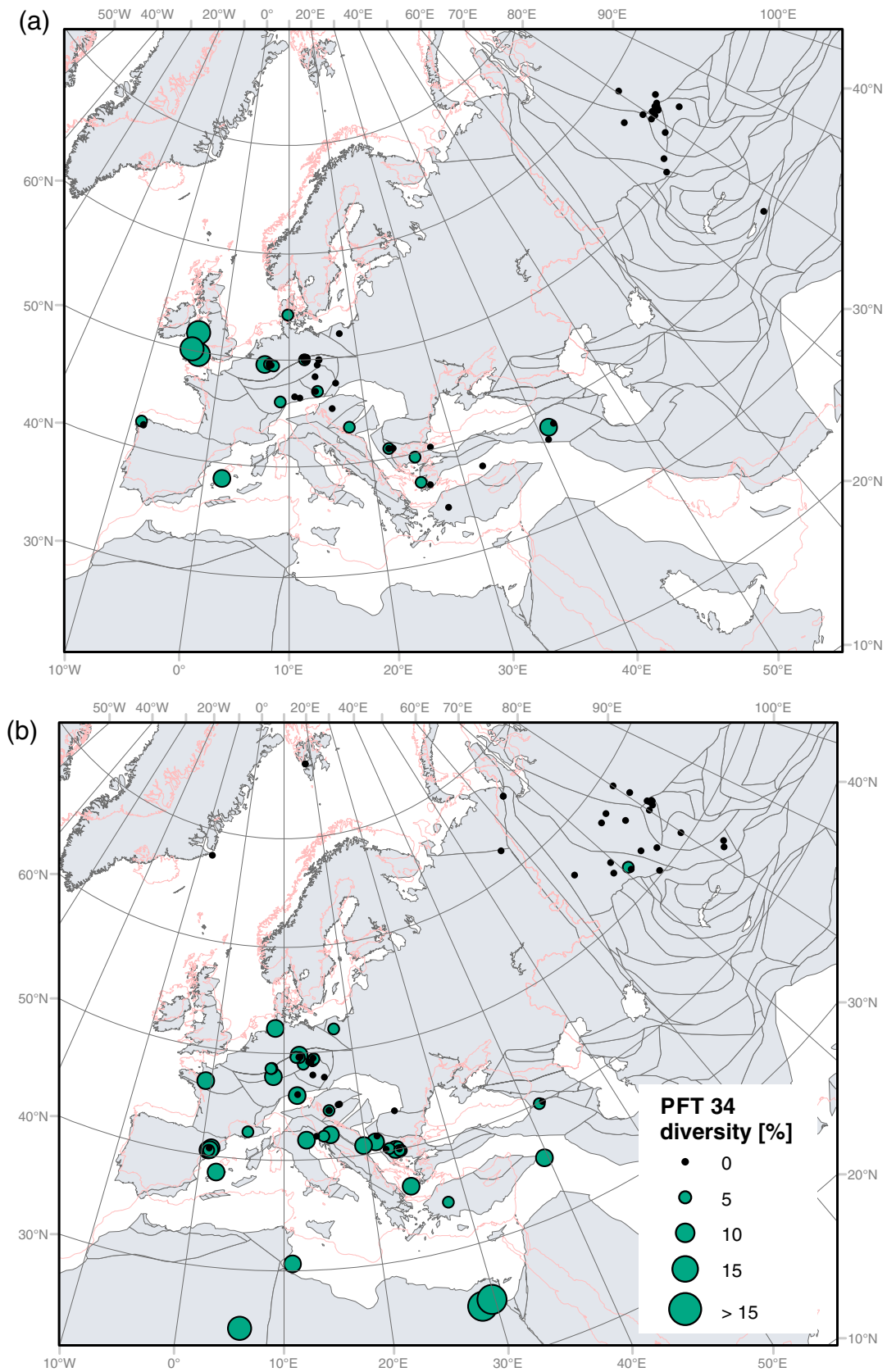


FIGURE 9 Diversity of tuft trees (PFT 34). For palaeogeographical reconstructions, cf. Figure 1. (a) Late Oligocene; (b) Early Oligocene [Colour figure can be viewed at wileyonlinelibrary.com]

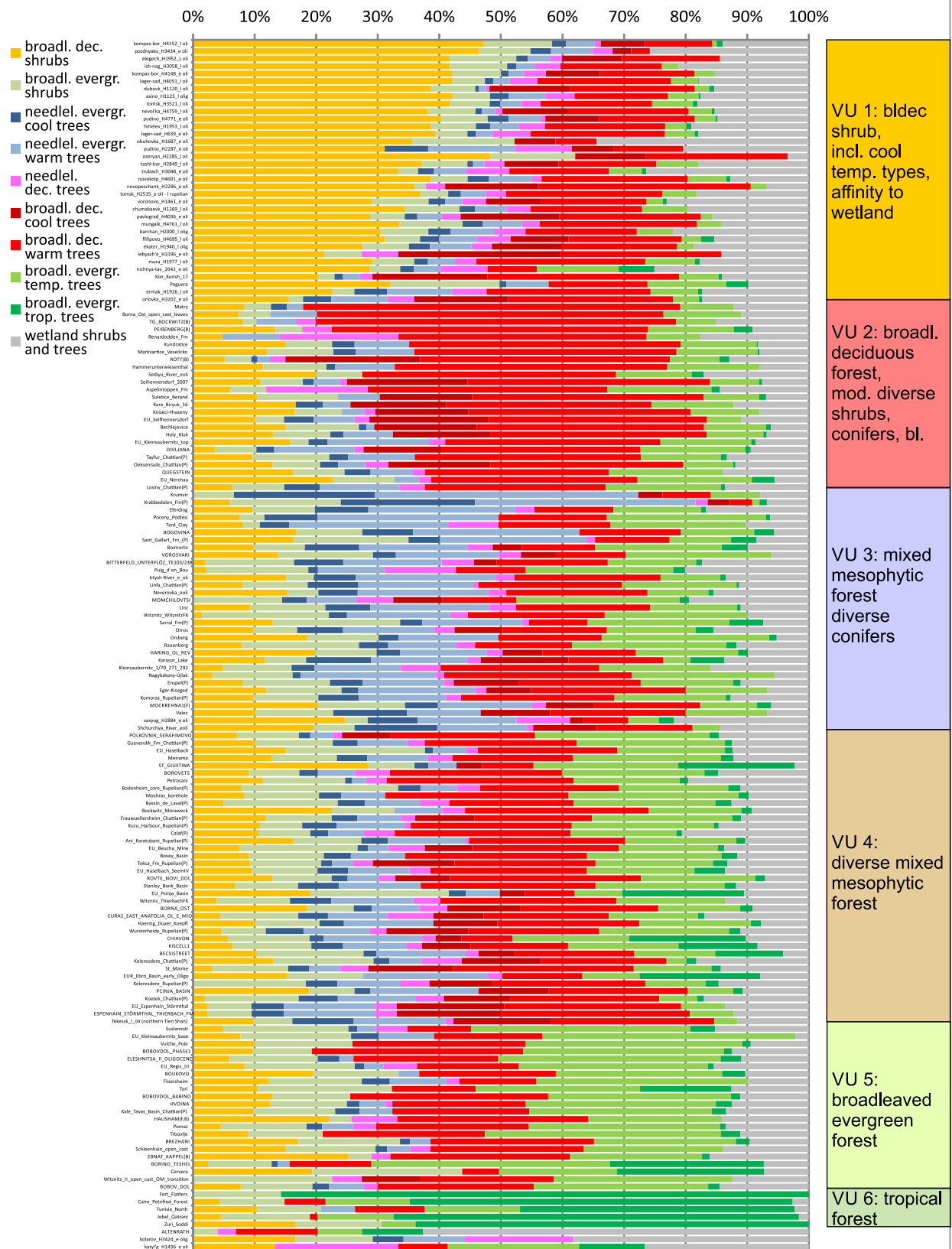


FIGURE 10 Ecospectra for the fossil floras showing major groups of woody PFTs. Vegetation units as obtained from principal component analysis [Colour figure can be viewed at wileyonlinelibrary.com]

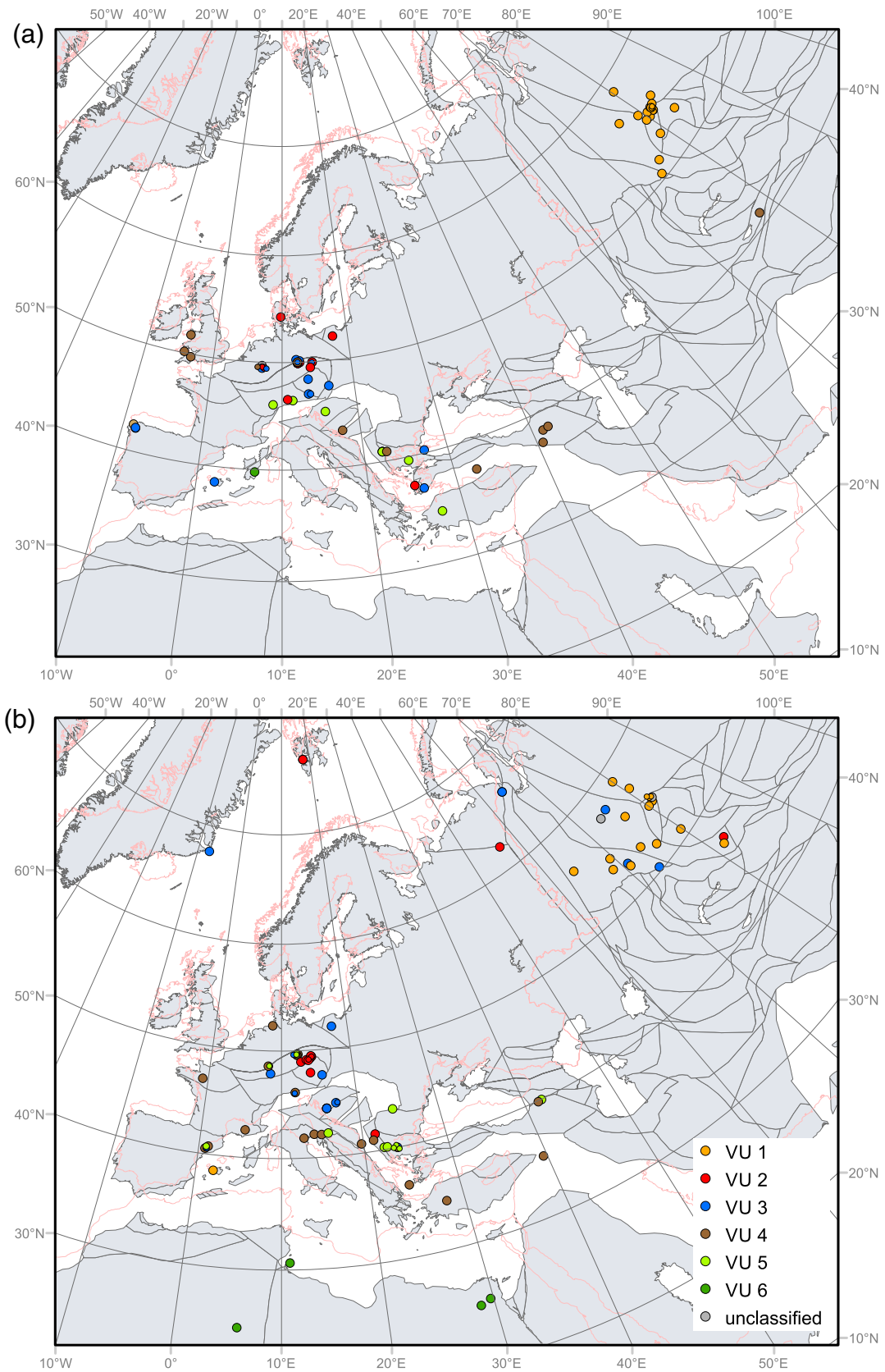


FIGURE 11 Spatial distribution of vegetation units obtained from principal component analysis. For palaeogeographical reconstructions, cf. Figure 1. (a) Late Oligocene; (b) Early Oligocene [Colour figure can be viewed at wileyonlinelibrary.com]

broadleaved deciduous vegetation type, is recorded at higher latitude (Sediyu River, Siberia; Aspelintoppen Fm., Spitsbergen), and at the mid-latitudes of Central Europe, between ~45 and 55°N (palaeolatitude). Two floras allocated to VU 2 have a more southerly position, namely the rather poor Rupelian Divlyana flora (Serbia) and the Chattian Tayfur microflora (western Turkey). VU 3, the MMF with diverse conifers, occupied a zone between 45°N and 70°N (palaeolatitude) in the Early Oligocene, in the Late Oligocene VU 3 extended to lower latitudes (e.g., Linfa microflora, western Turkey, at ~37°N [palaeolatitude]). VU 4 had its main distribution in the western part of the study area at lower latitudes (~34–42°N [palaeolatitude]) in both time slices studied, in NW Europe however, it reached at least 53°N (palaeolatitude). The more thermophilous VU 5 MMF type was also typical for floras of the Tethyan Archipelago and the Proto-Paratethys. In the Early Oligocene, VU 5 also played an important role in coastal areas of the southern North Sea realm (Kleinsaubernitz base level, Regis 3, Schleenhain, Witznitz II open cast, OM transition, Flörshem). As was stated earlier, VU 6 sites with tropical spectra are confined to the African Plate while Chattian sites from that region are not at disposal in the present selection. However, tropical VU 6 vegetation results from the Sardinian Zuri Soddi xyloflora.

5 | DISCUSSION

5.1 | PFT patterns and palaeoclimate evolution

5.1.1 | Temperatures

The observed dominance of warm temperate PFTs in the spectra, combined with the overall equal importance of evergreen and deciduous PFTs of the broadleaved component are in broad agreement with the still relatively high global temperature level under moderately raised atmospheric CO₂ of the Oligocene unipolar icehouse (Zachos et al., 2008). Moreover, the composition of the ecospectra and their vegetational interpretation confirm the CA-based climate reconstruction revealing warm temperate Cfa/Cwa climates with distinct seasonality for most of the Eurasian sites considered here (Li et al., 2018). Even though integrating over longer time-spans with considerable variability of climate both Early and Late Oligocene PFT diversity data support the basic pattern of a cooler western Siberia (MAT and CMT) with respect to the West of the study area at comparable latitude as suggested by Li et al. (2018). Most western Siberian sites from both time slices represent the VU 1 vegetation unit, characterized by the lowest proportions of thermophilous PFTs and highest proportions of deciduous elements among all other VUs. However, since almost all western Siberian data are based on carpofloras, a taphonomic signal cannot be excluded (cf. Section 5.3). For the higher latitude floras located north of 60°N palaeolatitude, that is, the Early Oligocene Sediyu River, Shchurchya River, and Krabbedalen microfloras and the Aspelintoppen leaf flora of Spitsbergen, the presence of warm temperate broadleaved and needleleaved PFTs in the ecospectra points to frost-free conditions in regions presently bearing boreal conifer

forest and Arctic tundra, and thus to a considerable polar amplification, at least during the Rupelian. This coincides with the persistence of relatively high SSTs in the North Atlantic across the EOT and the thermal decoupling of the Arctic realm from the glaciated southern high latitudes (Liu et al., 2018).

The comparison of Early and Late Oligocene ecospectra with respect to inherent temperature signals is complicated by the considerable thickness of the time slices regarded and the known variability of climate (e.g., Zachos et al., 2008). For Europe, the trend to a cooler Chattian suggested by various studies (Bozukov et al., 2008; Li et al., 2018; Moraweck, 2017; Roth-Nebelsick et al., 2004; Walliser et al., 2016) is confirmed by a decline of the diversity of broadleaved evergreen PFTs, the disappearance of the tropical PFT 33 from most of the Tethyan / Proto-Paratethyan ecospectra, and, most clearly, by the overall diversity decline / disappearance of tuft trees (PFT 34). Ecospectra from Chattian floras of the S North Sea Basin realm allocated to the more thermophilous VU 4 biome type such as the Bockwitz, Witznitz (Thierbach), Borna Ost, and Espenhain macrofloras (Weisselster Basin) and the Frauwüllersheim microflora (Lower Rhine Basin) may be related to warm phases in the later Chattian reflected in both marine and continental records (Mudelsee et al., 2014; Schäfer & Utescher, 2014; Zachos et al., 2001, 2008). Apart from a few exceptional cases, the ecospectra obtained for Early and Late Oligocene floras of western Siberia are comparatively close to each other regarding their climatic inference. This is in line with earlier studies suggesting the persistence of relatively warm and mostly frost-free conditions throughout the Oligocene to Early Miocene, with MAT in the order of 12–15°C and CMT at 0–7°C (Popova et al., 2019).

5.1.2 | Precipitation

Drought-tolerant (7, 12, 16, 22, 29, 31) and xeric PFTs (3, 17) play a key role for assessing precipitation regimes in which the fossil floras existed. Unfortunately, no clear signal is obtained from the presence of drought-tolerant woody PFTs because almost all taxa scoring for these types in the present analysis may exist as well under humid conditions. *Tetraclinis*, today restricted to dry climates, was excluded from the analysis because in many floras it was in conflict with the majority of taxa (cf. Section 4.1.2). The somewhat higher proportions of drought-intolerant PFTs in all arboreal functional fractions that is observed in most of the floras from both time slices is in line with the mainly CA-based precipitation reconstructions all indicating more humid conditions for western Eurasia compared to present (Bozukov et al., 2008; Erdei et al., 2012; Li et al., 2018; Mosbrugger et al., 2005; Utescher et al., 2015). However it is important to note, that the presence of woody drought-tolerant PFTs in most of the ecospectra, also after excluding incompatible types (cf. Supporting Information 3), points to a clearly seasonal pattern of rainfall as has been suggested by various proxy-based studies (e.g., Erdei et al., 2012). In some regions of Eurasia seasonally dry conditions must have existed during the Oligocene, but not in the warm season (cf. Bozukov et al., 2008; Erdei et al., 2012; Kayseri-Özer, 2017). This may explain the missing

evidence for substantial drought in the studied records, and overall confirms the statement by Collinson and Hooker (2003) that Oligocene phytocoenoses existed under an overall humid, warm temperate climate with only slightly drier winters.

Further clues for possible drought are obtained from the herbaceous PFT fraction. As regards the West of the study area higher proportions of xeric herbs result for Rupelian sites in Spain (Sarral Fm., Ebro Basin, Sant Gallart Fm. microfloras) and southern France (St. Maime macroflora). For the Early Oligocene Ebro Basin playa lake sediments provide additional evidence for seasonally dry conditions (Anadón, Cabrera, Colldeforns, & Saez, 1989). Sites further to the South and East of the Tethyan Archipelago have herbaceous spectra with mainly mesic herbs. For the Chattian time slice herbaceous records from the SW Mediterranean are scarce while raised proportions of xeric herbs are recorded for various sites of the Eastern Tethyan and Proto-Paratethyan realm (Tayfur, Linfa, Güvendic, Kötek, Keteresdere microfloras). The coexistence of diverse palynomorphs belonging to mesic woody taxa with xeric, mainly herbaceous components is observed in various Late Oligocene records of this region and is possibly explained by a relatively strongly structured relief and rain shadow effects in this tectonically very active region (Kayseri-Özer et al., 2017) while the main drying pulses occurred in the Miocene (Kayseri-Özer, 2017; Meijers et al., 2016).

In the western Siberian floras, xeric herbs are sporadically present at minor proportion in both time slices regarded and thus there is no evidence for substantial drying in this part of the study area at that time (Popova et al., 2013). However, indication for dryer conditions comes from the Late Oligocene Tekesk microflora (Northern Tian Shan), possibly in spatial relation to the stepwise aridification reported for NW China (Xining Basin, cf. Bosboom et al., 2017).

5.2 | Oligocene PFT patterns in view of previous vegetation reconstructions

The interpretation of fossil floras at the level of PFTs primarily yields information on the vegetation types represented in each case, apart from the presence or absence of a specific PFT at a given site (e.g., François et al., 2011; Utescher & Mosbrugger, 2007). The fact that the PFT approach does not take into account the richness of vegetational components may reduce its ecological resolution. As an advantage, the PFT approach potentially is more robust to taphonomic effects thus making floras of different organ type inter-comparable. Nonetheless it has to be stressed that the reconstructed VUs are based on taphocoenoses and hence represent a composite assemblage that may represent various vegetation types.

The PFT-based vegetation reconstruction points to the existence of largely zonally arranged patterns, with the more temperate broadleaved deciduous and mixed needleleaved–broadleaved deciduous VUs 1–3 forming a vegetation belt in the higher latitudes of the study area, and thermophilous MMFs and evergreen broadleaved forests (VUs 4, 5) at the more southerly mid-latitudes. A comparable

subdivision in a more temperate vegetation zone with broadleaved mixed deciduous forests in the higher mid-latitudes and a more evergreen “sclerophyllous” vegetation belt in the Tethyan-Proto-Paratethyan Archipelago was reported by Collinson and Hooker (2003) based on qualitative interpretation of macrofloras and integrating over the entire Oligocene. From the present study there is evidence for a tropical vegetation belt, (VU 6) extending to ~30°N palaeolatitude in the Rupelian, or even further to the North (Chattian, Zuri Soddi xyloflora, Sardinia, at ~40°N).

When comparing patterns of both Oligocene time slices of our reconstruction it is shown that Central Europe experienced the local replacement of the thermophilous VUs 4–5 by more temperate, mainly deciduous VUs 2–3. Deciduous woody components first appearing in the Oligocene of Europe and western Siberia contribute to PFTs 9–12 and 26–29 in this reconstruction and mainly belong to the Betulaceae, Cercidiphyllaceae, Fagaceae, Hamamelidaceae, Malvaceae, Rosaceae, Sapindaceae and Ulmaceae families. This largely confirms earlier interpretations of the floristic changes throughout the Oligocene (Collinson & Hooker, 2003; Erdei et al., 2012; Kvaček & Walther, 2001; Popova et al., 2019; Walther, 1994). The warm temperate broadleaved evergreen fraction (PFTs 15–16, 30–31) characterizing VUs 4–5 and comprising typical “palaeotropical” elements is mainly represented by taxa of the Cornaceae, Elaeocarpaceae, Fagaceae, Lauraceae, Myricaceae, Symplocaceae, and Theaceae families. In view of the palaeoclimate evolution (cf. Section 5.1) their declining diversity/disappearance from the record was probably related to (winter) cooling and increasing seasonality as suggested by palaeoclimate records available for various parts of the study area (Bozukov et al., 2008; Moraweck, 2017; Mosbrugger et al., 2005; Popova et al., 2019; Utescher et al., 2015). The same holds for the significant diversity decline in tuft trees evident from our records (Figure 9).

Early Oligocene sites located in North Africa point to the presence of a tropical vegetation belt. The xylofloras include a variety of taxa from mainly tropical families such as Bombacaceae (*Bombax*), Combretaceae (*Terminalia*, *Anogeissus*), Ebenaceae, Euphorbiaceae (*Anthostema*), Fabaceae (*Azalia*, *Dalbergia*, *Copaifera*, *Detarium*, *Sindora*, *Cynometra*, *Calpocalyx*, *Tetrapleura*), Meliaceae (*Entandrophragma*, *Lovoa*), Moraceae (*Ficus*), and various palms (cf. Jacobs, Pan, & Scotese, 2010). Even when considering the more southerly position of the sites due to plate tectonics by up to ~7° palaeolatitude the indication of tropical forest vegetation in presently dry settings is noteworthy. Especially members of the Fabaceae family may point to more seasonal rainfall conditions and the presence of Savannah woodlands. However, it remains unclear whether the xylofloras include remains of the tropical forest biome covering larger areas or represent gallery forests sustained by high groundwater level of coastal swamps and river systems in an otherwise drier landscape (for a discussion cf. Jacobs et al., 2010).

The presence of sclerophyllous elements in Oligocene floras and their climatic significance were discussed in numerous studies (cf. Collinson and Hooker, 2003 for a summary). Partly, the occurrence of distinct taxa with small, coriaceous leaves in the fossil record may

point to subhumid conditions, partly, mesic taxa may display xeromorphic features, as an adaptations to the prevailing environmental conditions (Collinson & Hooker, 2003). Since the present approach is based on PFTs represented by the NLRs of the plant fossil record evidence coming directly from a fossil leaf specimen is not considered. Except for *Tetraclinis*, presently restricted to seasonally dry conditions, all NLR taxa of the presently studied fossil record and allocated to drought-tolerant PFTs (12, 16, 22, 29, 31) may also occur under humid conditions and therefore are as well classified to the drought-intolerant counterparts of those PFTs (15, 21, 25, 28, 30). This is expressed in Figures 5–7 where drought-tolerant and -intolerant PFTs in almost each case attain about equal diversity proportions. Hence, the present analysis does not provide any clear evidence for the existence or absence of xerophytic vegetation, but may explain the considerable variety of interpretations provided in the literature (cf. Collinson & Hooker, 2003; Kovar-Eder, 2016 for a discussion). While almost all taxa in our record allocated to the drought-tolerant PFT 31 may also represent the perhumid PFT 30, various taxa are confined to PFT 30 (species of *Castanopsis*, *Quercus*, *Reveesia*, *Symplocos*, *Trochodendron*, various Lauraceae genera). Thus, a drought-intolerant/-tolerant ratio >1 may serve as an indicator for humid conditions throughout the year. This condition is true for 99 sites out of 163 distributed over the study area. For 64 sites the ratio equals 1, only for one site, namely the Early Oligocene Peguera macroflora (Mallorca) a ratio of <1 is obtained (presence of *Myrica faya*; possible PFTs: 16, 18, 31, 33). As regards *Tetraclinis*, it was classified to both, drought-tolerant and -intolerant PFTs (21, 22) to avoid inconsistencies with taxa occurring in the same flora and restricted to permanently humid conditions. Although no final conclusions can be drawn our results largely confirm the statement by Collinson and Hooker (2003) that the Oligocene vegetation existed in an “overall humid, warm temperate climate with only a slightly drier season.”

Although the reconstructed VUs display well-defined distribution zones PFT diversity interpretation yielded conspicuous aberrations. The high proportion of the broadleaved evergreen component (PFT 33) in the western Siberian Nizhny-Tav, Katyl'g and Vasyug carpofloras is attributable to the presence of Moraceae and Rutaceae with *Tetradium* (originally recorded as *Euodia*), in associations otherwise dominated by herbs and shrubs. While Moraceae also score for summergreen PFTs, the record of the thermophilous *Tetradium* might be a case for revision. Chattian microfloras recovered in the Bristol Channel and southern Irish Sea (cf. Boulter & Craig, 1979), Stanley Bank Basin, Mochras Borehole, Bovey Basin) suggesting a probable high proportion of tuft trees (*Arecipites*, *Cycadopites*, *Dicolpopollis*, *Monocolpopollenites*) might belong to the Rupelian (King, Gale, & Barry, 2016), or even be of Eocene age which would explain their thermophilous aspect.

5.3 | Taphonomic effects and azonal imprints

As has been shown in various previous studies using integrative approaches such as the IPR (integrated plant record) and PFT

technique (e.g., Kovar-Eder, Jechorek, Kvaček, & Parashiv, 2008; Popova et al., 2017) taphonomy may affect the results obtained in vegetation reconstruction even though both methods use diversity instead of richness of components. To quantify taphonomic effects flora lists for various organ types would be required from the same site, in the best case originating from the same stratigraphic level in order to rule out climatic signals, unmet premises in the present record. For all that, scatter diagrams showing the array of the studied sites with respect to taxa number and PFT diversity and considering the organ type of the flora shed more light on the structure of the data (Figure 12).

It is shown that diversity of herbaceous PFTs (1–4) (Figure 12a) is clearly underrepresented or not recorded in leaf floras while palyno- and carpofloras well reflect the diversity of herbs. As regards diversity of woody plants, scatter fields of leaves, pollen, and fruits and seeds show a considerable degree of overlapping, as in the diagrams for conifer (Figure 12b) and shrub diversity (Figure 12d). The diversity of the evergreen broadleaved arboreal component (Figure 12c) shows overlapping scatters for pollen, leaf floras and those carpofloras originating from the climatically warmer Central European realm (cf. labelled sites in Figure 12c) while the cluster of carpofloras with a very low proportion of evergreen broadleaved trees mainly consists of sites from the cooler western Siberian part thus primarily expressing a climatic gradient and not a taphonomic signal. The same holds for the few xylofloras having a high diversity of evergreens, all originating from the subtropical/tropical part of the study area.

Thus, the exclusion of herbaceous components is advantageous when studying integrative fossil records consisting of leaf and wood floras and micro-/carpofloras, respectively, prior to the application of statistical ordination methods. This step in the analysis does not completely remove taphonomic signals such as the high affinity of the shrubby VU 1 to carpoflora (Figure 10), but it enables a general comparability of spectra obtained from different organ types of palaeoflora. Certainly, the diversity of herbaceous components is important to assess openness of landscape. While high proportions in PFTs 1–4 in our carpo-record primarily refer to azonal (intraazonal), riverine vegetation microfloras with diverse herbs more likely point to more open zonal habitats. Diversities of herbaceous components $>50\%$ of the total diversity are recorded for both Early and Late Oligocene microfloras of Turkey (Keleresdere Chattian (P), Koetek Chattian (P) Keleresdere Rupelian (P)).

The 41 PFT systems include three wetland types and thus allows for an assessment of the azonal imprint in any ecospectra. It is shown that apart from the xylofloras almost all records include taxa that score for wetland PFTs in variable proportions (mean 7.3%, SD 2.8). Hence, the vast majority of floras include taxa that may exist in intra-zonal communities. On the other hand, it should be stressed that diversities of non-zonal PFTs do not exceed 14.1% in the studied floras and hence do not provide any evidence for exclusively non-zonal records.

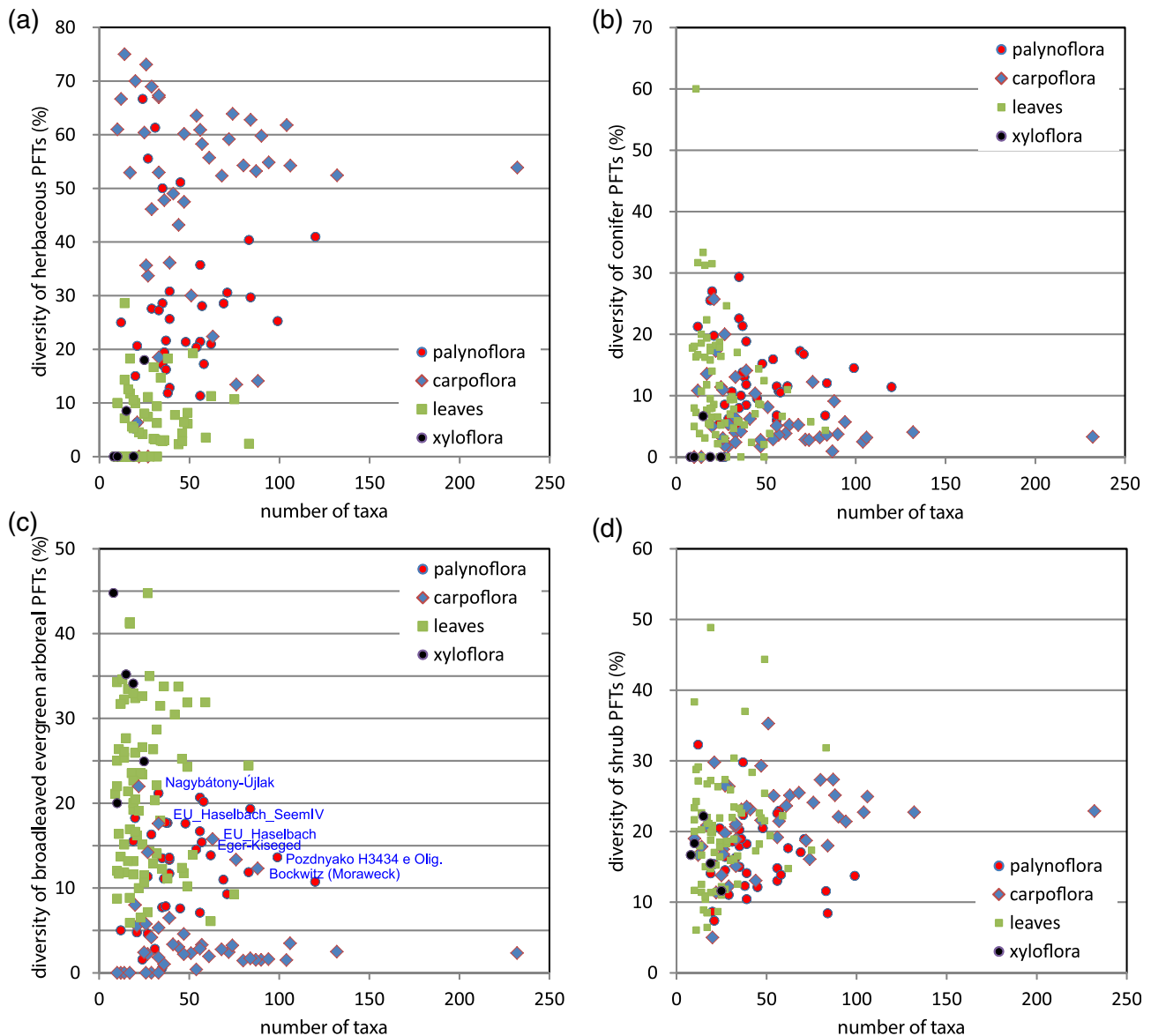


FIGURE 12 Taphonomic effects: PFT diversity in relation to plant organ type and number of taxa in the plant fossil record. (a) Herbaceous PFTs; (b) conifer PFTs; (c) broadleaved evergreen arboreal PFTs; (d) shrub PFTs. Carpofloras (c) with >10% broadleaved evergreen arboreal PFTs are labelled and almost all originate from the warmer Central European realm (except for Pozdnyako H3434) while all unlabelled records represent sites from the cooler western Siberian part [Colour figure can be viewed at wileyonlinelibrary.com]

6 | CONCLUSIONS

- The PFT technique provides quantitative, internally consistent diversity data that can be interpreted in terms of vegetation and that can be used for the validation of reconstructions obtained from palaeoclimate and biome modelling.
- The 41 PFT systems employed here for the first time allows for classifying the entire fossil record of different organ types preserved in each case. Azonal PFT classes facilitate the identification of “facies signals” and zonal character of past phytocoenoses.
- The present dataset including 89 Early and 73 Late Oligocene sites yields the first comprehensive, quantitative vegetational

reconstruction for western Eurasia of that time-span. When considering the differing representativeness of herbs and facies components an integrative approach (palyno-/macroflora) seems possible.

- The results obtained are well interpretable in the context of the global climate evolution and previously reconstructed regional patterns. The PFT-based vegetation reconstruction points to the existence of largely zonally arranged patterns, with the more temperate broadleaved deciduous and mixed needleleaved-broadleaved deciduous vegetation units forming a belt in the higher latitudes of the study area, thermophilous MMFs and evergreen broadleaved forests at the more southerly mid-latitudes, and tropical vegetation south of $\sim 30^{\circ}\text{N}$.

- Mid- and higher latitude vegetation of the Rupelian was overall more thermophilous compared to the Chattian where our data indicate a declining diversity of broadleaved evergreen components and tuft trees.
- Proportions of drought-tolerant/-intolerant PFTs point to overall humid conditions for western Eurasia during the Oligocene. For some sites of the Western Tethys and Eastern Tethyan and Proto-Paratethyan realm raised diversities and proportions of xeric herbs indicate more open vegetation and seasonally dry climate.

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