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ORIGINAL PAPER

Middle Miocene climatic oscillations controlled by orbital-scale changes triggered environmental and vegetation variability in the Dinarides Lake System (Bugojno Basin, Bosnia and Herzegovina)

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Abstract

The middle Miocene was a key period in Earth's history as climate changed from one of the warmest phases of the Cenozoic Era, the Miocene Climatic Optimum (MCO), to colder conditions with the establishment of permanent ice sheets on Antarctica. This climate change had a profound impact on terrestrial ecosystems affecting vegetation worldwide. However, the scarceness of detailed pollen data at short-scale resolution for this time period precludes us from a deep understanding of environmental and vegetation changes at millennial-scales. Here, we present palynological data from a new sedimentary sequence from the Gračanica open cast mine (Bugojno Basin, Bosnia and Herzegovina), which shows significant changes in the environment and lake sedimentation, probably related with orbital-scale climate dynamics during the middle Miocene. This study also shows that high-amplitude climate variations characterised the middle Miocene climatic optimum (MCO; ~ 16.8–14.7 Ma). Statistical analysis and sedimentary rates suggest that eccentricity- and precession-dominated orbital-scale variability is recorded in the studied core. Warmest conditions are registered at the base of the studied section that could be correlated with an eccentricity maximum at the end of the MCO. A cooling trend is recorded since then and until the top of the sedimentary sequence, with coldest maxima, tentatively correlated with a minimum in eccentricity and insolation. Smaller-scale cyclical climatic events (i.e. warm-dry vs. cold-humid) observed in the vegetation and corresponding with lake-level variations are observed in this study that seems to be related with precession cyclicity. This study suggests that sedimentation in this lake basin lasted for about 200 kyr and was strongly conditioned by climate at the beginning of the middle Miocene climate transition.

Keywords Middle Miocene · Pollen analysis · Flora · Vegetation · Dinarides Lake System · Orbital-scale climatic changes

Introduction

The Dinarides Lake System (DLS) was a widespread and long-lived cluster of lakes that tectonically developed on the Dinaride–Anatolian Island forming a major biogeographic barrier between the Paratethys and the proto-Mediterranean Sea during the early and middle Miocene (Fig. 1). This area, together with other regions of southern Europe, is very interesting from a floristic point of view because it served as a refuge for thermophilous/hygrophilous plants that progressively vanished from Eurasia during the long-term late Miocene and Pliocene cooling/drying trend and the Pleistocene glaciations (Quézel and Médail 2003; Biltekin et al. 2015; Herbert et al. 2016). Therefore, it is necessary to study past environmental and vegetation patterns in relation to climate change to understand present-day plant biogeographic distribution and future dynamics due to climate warming.

This article is a contribution to the special issue "The drowning swamp of Gračanica (Bosnia-Herzegovina) - a diversity hotspot from the middle Miocene in the Bugojno Basin"

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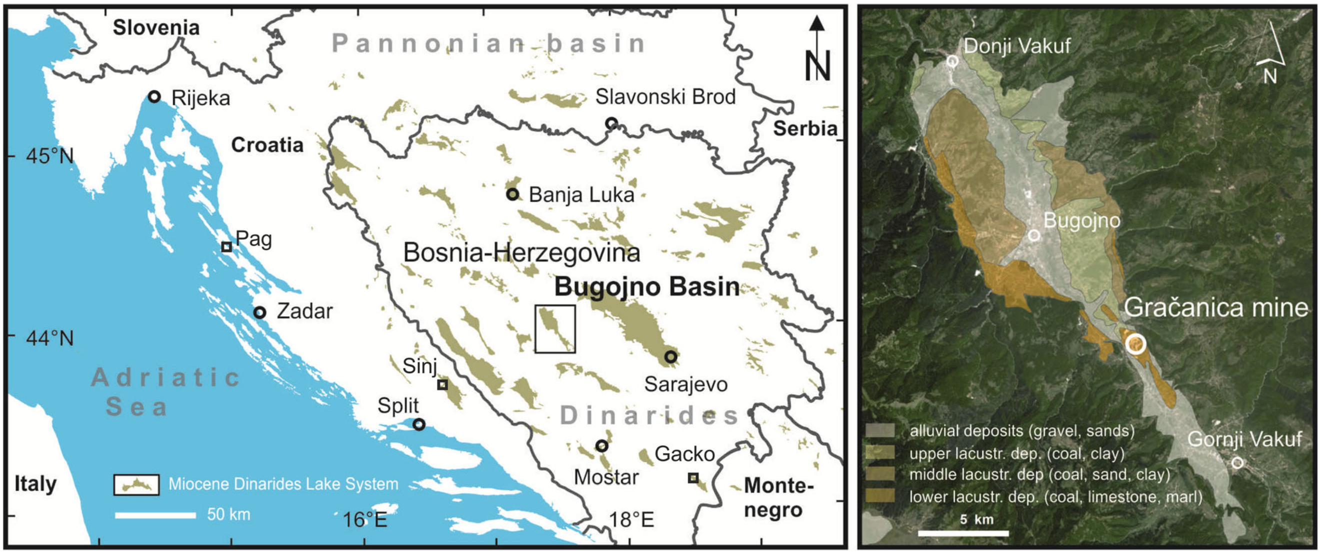

Fig. 1 Location of the Gračanica mine and Bugojno basin within the DLS in Bosnia and Herzegovina. Miocene Dinarides localities mentioned in the present study are indicated by rectangles (modified after Mandic et al. (2012a), Mandic et al. (2016))

A recent effort has been made to understand the influence of orbital-scale climate forcing on past environment and vegetation changes in the central-eastern Mediterranean and Paratethys regions (e.g. Combourieu-Nebout and Vergnaud-Grazzini 1991; Bertini 2001; Popescu 2001; Jiménez-Moreno et al. 2005; Popescu et al. 2006; Kloosterboer-van Hoeve et al. 2006; Biltekin et al. 2015) but such detailed records are still rare in the Dinarides (Jiménez-Moreno et al. 2008, 2009).

The sediments of the DLS are rich in organic layers (i.e. coals) and in plant fossils and thus provide a good opportunity to study palaeovegetation patterns. Several studies have previously described and interpreted the palaeobotanical record of the DLS (Radimsky 1877; Engelhard 1883, 1900, 1901, 1902a, b, 1903, 1904a,b, 1910, 1912, 1913; Katzer 1918, 1921; Vasković 1931; Polić 1935; van Veen 1954; Pantić 1957; Weyland et al. 1958; Muftić and Behlilović 1961; Pantić 1961; Muftić and Luburić 1963; Pantić and Bešlagić 1964; Muftić 1964; Behlilović and Muftić 1966; Pantić et al. 1966; Muftić 1970; Jurišić-Polšak et al. 1993; Krizmanić 1995; Pavelić et al. 2001; Jurišić-Polšak and Bulić 2007). However, in those studies, a general morphological pollen classification devoid of the relationship with the botanical nomenclature was applied and there is a lack of quantitative data, precluding us from obtaining accurate climatic interpretations. Due to this, a detailed vegetation and climate history of the DLS still remains unclear.

The early and middle Miocene was climatically a key period in Earth's history as following the climax of Neogene warmth of the Miocene Climate Optimum (MCO; approximately between 16.8 and 14.7 Ma; Holbourn et al. 2014) during the Burdigalian-Langhian, there was a sharp drop in global temperatures at the end of the Langhian (~ 14.2–13.8 Ma) and the onset of the Serravallian (~ 13.8 Ma; Zachos et al. 2001; Shevenell et al. 2008). These climatic changes during the middle Miocene had profound effects on terrestrial environments that are still not completely understood. In this study, a pollen analysis of the Gračanica sedimentary sequence will add significant palaeobotanical information from the DLS that will help us improve the knowledge of the flora, vegetation and climate dynamics of Southeastern Europe and the Dinarides Lake System during the middle Miocene. These data demonstrate cyclic and paired changes in the environment and vegetation, lake-level fluctuations triggering sedimentary variations that appear to be linked to orbital-scale climate variability.

Geographic setting and stratigraphy

Geography and regional geology

The Gračanica opencast coal mine is located east of Bugojno in central Bosnia and Herzegovina (Fig. 1). A mild temperate climate characterise the area today, with a mean annual precipitation in the Bugojno area of 900 mm (https://en.climate-data.org/europe/bosnia-and-herzegovina/bugojno/bugojno-25620/). The outcropped succession displays the beginning subsidence of the Bugojno basin resulting in the installation of the long-lived perennial lake therein. The lake was part of the Dinarides Lake System (DLS) settling the endorheic intramontane lacustrine basins of the corresponding orogenic belt (Mandic et al. 2011; De Leeuw et al. 2011, 2012). DLS had the maximum extant during the generally humid and warm period of the MCO between 17 and 15 Ma (Sant et al. 2018). The extensional forces in the NE-SE striking asymmetric DLS basins seem to relate with the Pannonian Basin synrift tectonics which were equally active between 18 and 13 Ma (Matenco and Radivojević 2013; Mandic et al. 2012b; Andrić et al. 2017).

Bugojno basin with its 28 km length and the 9 to 1.4 km width is one of the largest DLS basins (Mandic et al. 2016). Its infill comprises about 850 m lacustrine (Neogene) and 100 m alluvial (Quaternary) deposits ending by a planation surface at about 620 m a.s.l. The surrounding mountains, with up to 2000-m-high peaks, display the Palaeozoic core-complex to the northeast and the early Mesozoic sedimentary cover to the southwest dominated by shallow marine carbonates, siliciclastics and volcanoclastic rocks (Hrvatović 2006; Mandic et al. 2016). These units were uplifted and tectonically shaped during the main alpine orogenic phase in the late Cretaceous and Palaeogene due to N-S convergence between Adria and Europe (Schmid et al. 2008; Van Unen et al. 2019).

Gračanica section

Analysis of sedimentary facies and environmental evolution of the Gračanica section was conducted by Mandic et al. (in prep., this issue; Fig. 2). The study section is about 40 m thick and shows a lignite dominated lower and a marl dominated upper part, each about 20 m in length. The lower interval includes four thinning upwards coal seams (5 to 2 m), bounded by ~ 1.5-m-thick marl interlayers. Whereas the lower one is the organic-rich dark marl and clay, the upper two interbeds are represented by a light marly limestone, pointing already to installation of palustrine depositional settings. In contrast, the lowermost ~ 10 m of the succession, showing taxodiacean-type three trunks and the predominantly organic-rich marl intercalations, indicate swamp depositional settings during the initial coal building phase. On top of the uppermost coal seam, about 2-m-thick cross-bedded light marly limestone with masses of melanopsid gastropods develops, representing the initiation of the littoral delta front depositional settings and therefore a flooding event due to a relative lake-level rise. The sedimentary section continues with a general deepening trend, marked initially by deep littoral marls bearing dense congeriinae bivalve pavements, grading upwards into profundal laminated marls barren of fossils. Presence of slump folds in the latter marls indicates palaeoslope depositional conditions. At about 30-m-height, the laminated marls show an upwards increase of the fossil content and therewith a very clear shallowing upwards trend. Starting with leaves and fish remains the latter interval ends about 5 m above by dense shell accumulations made of littoral molluscs. Above, the uppermost 5 m of the study succession shows initially a short-termed reoccurrence of fossil barren laminated marls followed by a rapid increase of the fine sandy component. Installation of a siliciclastic shading from the land is well marked by a peak interval in the magnetic susceptibility and natural gamma radioactivity logs (Fig. 2).

Stratigraphy

Biomagnetostratigraphic dating of the Gračanica section will be presented by Mandic et al. (in prep., this issue). Small mammals found in the study section indicate correlation with the lower to middle Miocene MN4–MN6 mammal zones (Wessels et al. in press, this issue). Large mammal Chalicotheriinae remains, resembling *Anisodon grande* from Sansan and Devinska Nova Ves (both MN6), indicate a Langhian (middle Miocene) age (Coombs and Göhlich in press, this issue). The mollusc record can be correlated with the youngest known endemic DLS assemblages dated at ~ 15 Ma (Harzhauser et al. in press, this issue). The ongoing magnetostratigraphic analyses combining latter biostratigraphic age constrains currently indicate an age range between 15.2 and 14.0 Ma (Mandic et al., in prep., this issue).

Materials and methods

Eighty-one samples (1–3 cm^3) were taken every 0.5 m throughout the studied sedimentary sequence for pollen analysis (Fig. 2). In this study, a selection of 28 samples were analysed. Pollen extraction methods followed a modified Faegri and Iversen (1989) methodology. Sediment was treated with NaOH, HCl and HF and the residue was sieved at 250 μm prior to an acetolysis solution. Counting was performed using a Leica DM-1000 LED transmitted light microscope at 400 magnifications to an average pollen count of ~ 200 terrestrial pollen grains. Fossil pollen was identified using published keys (Beug 2004) and modern reference collections at the University of Granada (Spain). Taxodioideae (subfamily of the Cupressaceae family; i.e. *Taxodium* or *Glyptostrobus*) identification was done based on the presence of papilla (Fig. 1. Supplementary material). Pollen counts were transformed to pollen percentages based on the terrestrial pollen sum. The palynological zonation was executed using cluster analysis using the program CONISS (Grimm 1987) on 12 most abundant pollen taxa—Taxodioideae, *Pinus*, *Cedrus*, *Cathaya*, deciduous and evergreen *Quercus*, *Fagus*, *Carya*, *Engelhardia*, *Ulmus*, *Zelkova* and Poaceae (Figs. 3 and 4). Non-pollen palynomorphs (NPPs) include algal spores. The algae percentages were calculated and represented with respect to the terrestrial pollen sum (Fig. 4). Furthermore, some pollen taxa were grouped, according to present-day ecological bases, into subtropical trees, mid-altitude conifers and Mediterranean trees (Figs. 5 and 6). The subtropical tree group includes Taxodioideae, Rubiaceae, *Mussaenda*-type, Celastraceae, *Microtropis fallax*, *Parthenocissus*, *Cissus*, Sapotaceae, *Distylium*, *Myrica*, *Engelhardia* and *Platycarya*. Mid-high-altitude conifers group is made up of *Pinus*, *Cathaya*, *Cedrus* and *Picea*. The Mediterranean tree taxa are composed of evergreen *Quercus*, *Olea* and *Phillyrea*. A ratio between the

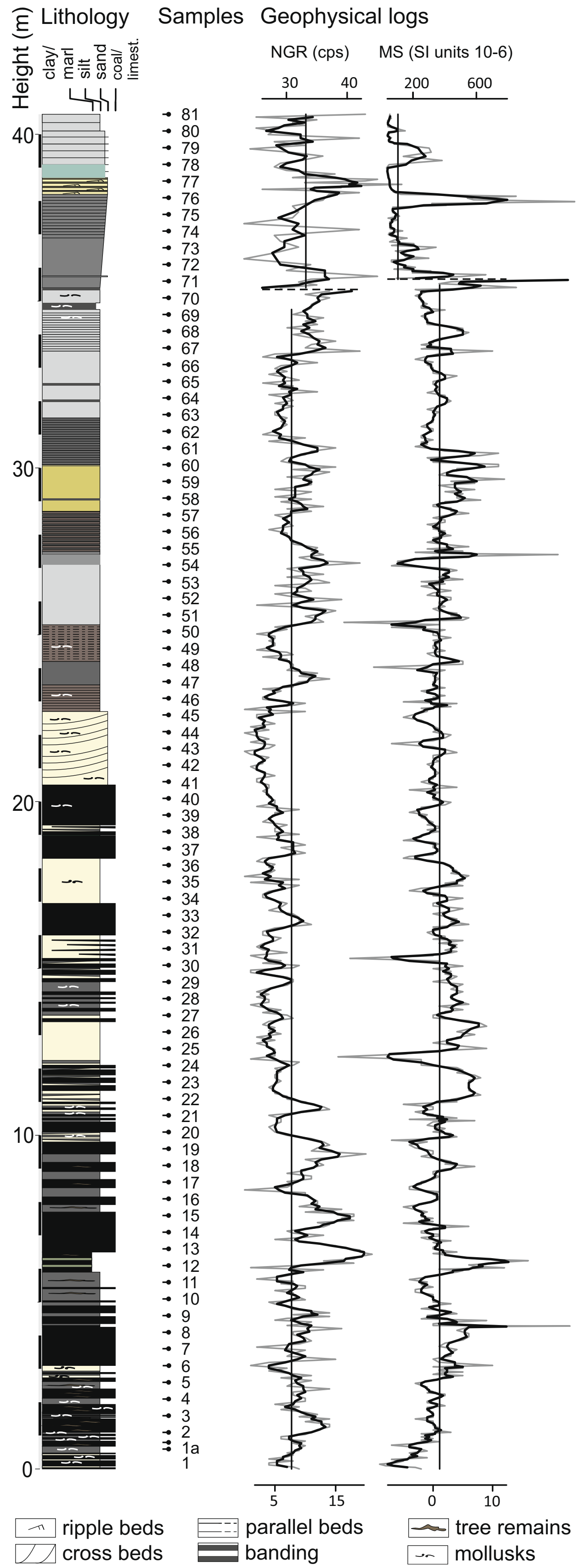

Fig. 2 Lithology, natural gamma radioactivity (NGR) and magnetic susceptibility (MS) from the studied Gračanica sedimentary sequence (after Mandic et al. in prep., this issue). The position of analysed pollen samples is indicated. Note the substantial increase in MS at ~35 m. The colours generalise natural colours of lithological units documented in the log

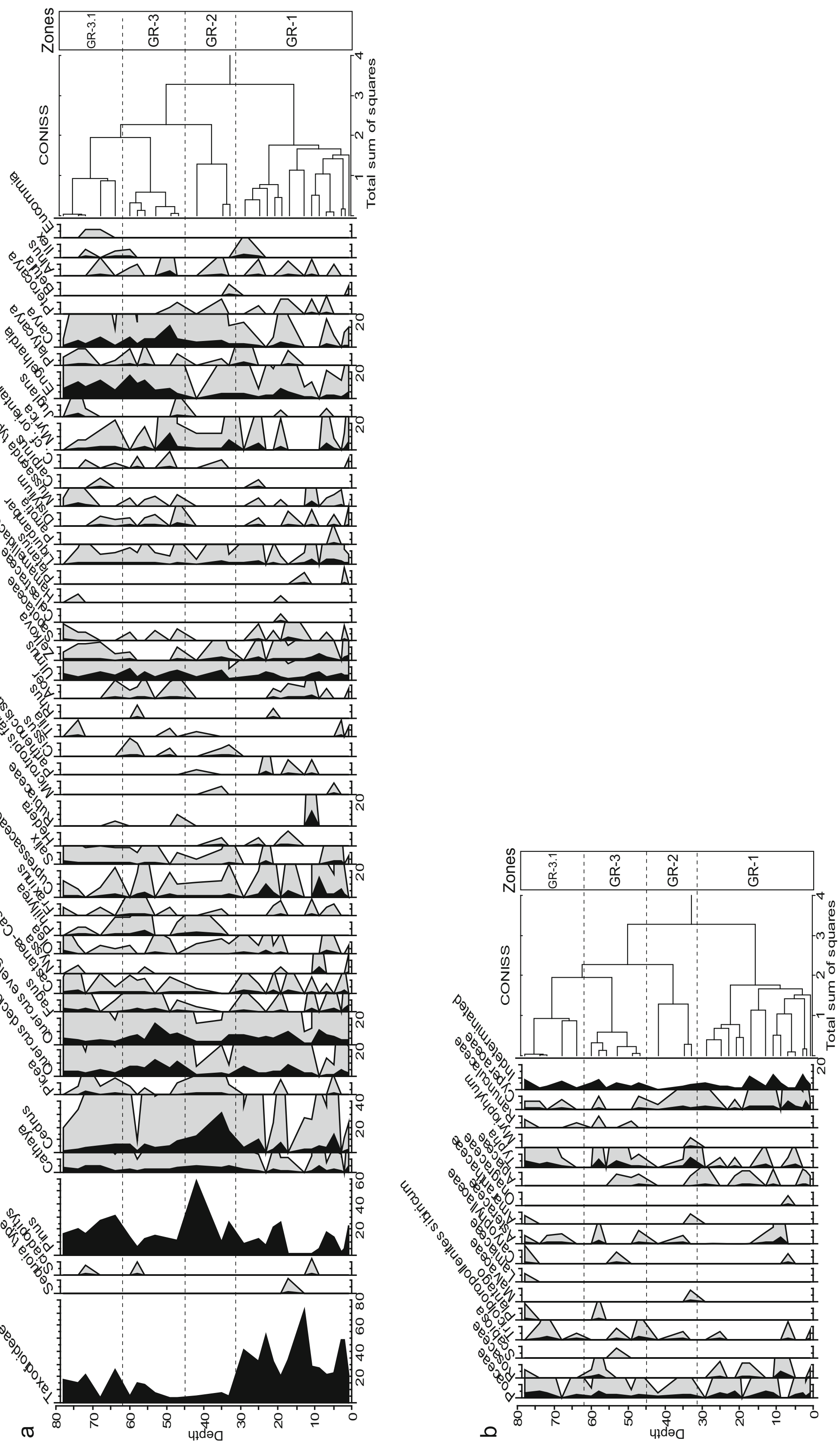

Fig. 3 Detailed pollen diagram from the studied Gračanica sedimentary sequence. Only pollen species more abundant than 1% are shown. Trees are represented in **a** and herbs and grasses and aquatics in **b**. Grey shading in some pollen species is the exaggeration of the abundance × 5. Pollen zonation is shown at the very end of the diagram

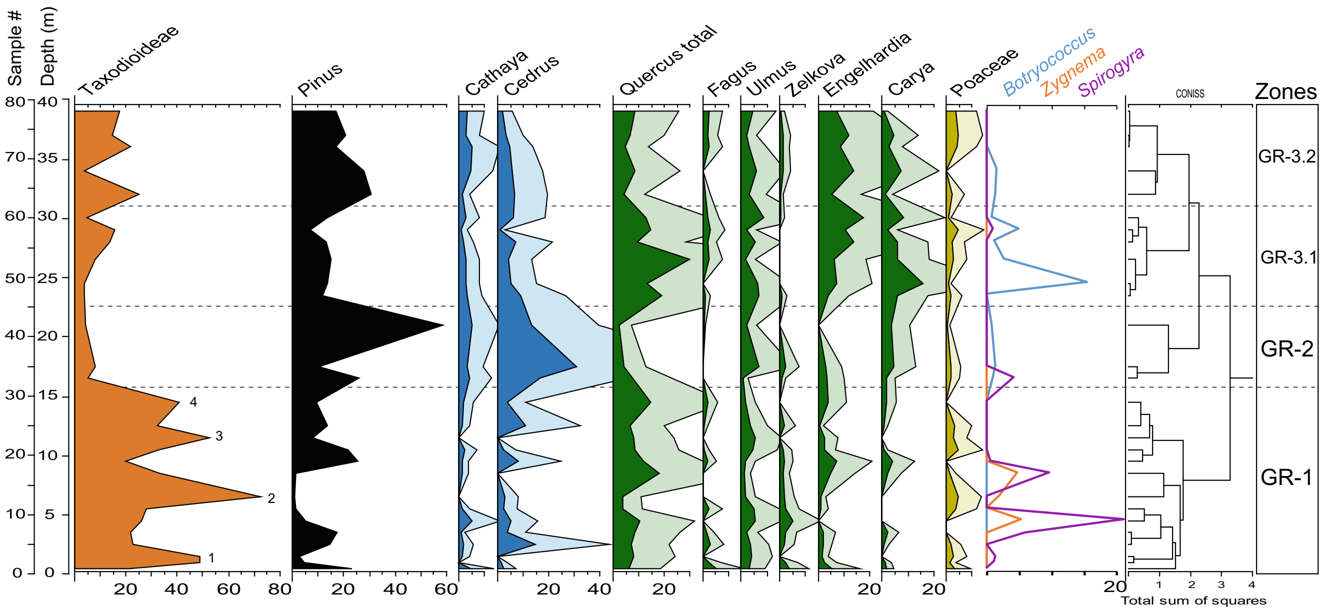

Fig. 4 Synthetic pollen and algae record from Gračanica showing the most abundant pollen/algae species. Shading in some pollen species is the exaggeration of the abundance × 5. Pollen zonation is shown to the right

percentage of thermophilous subtropical plants vs microthermic *Pinus* and other mid-altitude conifers, T/P ratio [(T − P)/(T + P)], was calculated (Fig. 6). Jiménez-Moreno et al. (2008, 2009) showed that the relationship between thermophilous plants and *Pinus* and other conifers can be very useful in identifying important vegetation, eustatic and climate changes. The abundance of arboreal pollen (AP) was also calculated with respect to the total terrestrial pollen sum (Fig. 6).

Principal component analysis (PCA) using PAST (Hammer et al. 2001) was run on the most abundant pollen data (Fig. 5). This was done to find hypothetical variables (components; i.e. environmental or climate parameters) accounting for as much as possible of the variance in the pollen data. A PCA correlation loading and scatter diagrams are shown in Fig. 5. These diagrams show to what degree the different taxa correlate with the different components. A linear Pearson correlation analysis (r, with statistical p significance value) was also run on the most abundant pollen species and is shown in Table 1.

A cyclostratigraphic analysis was performed on the T/P pollen ratio data time series (Fig. 7). We used the software PAST 3.19 software (Hammer et al. 2001) using the REDFIT procedure of Schulz and Mudelsee (2002) under the rectangular window function, and the standard value of 2 for the segments parameter and value of 3 for the oversample

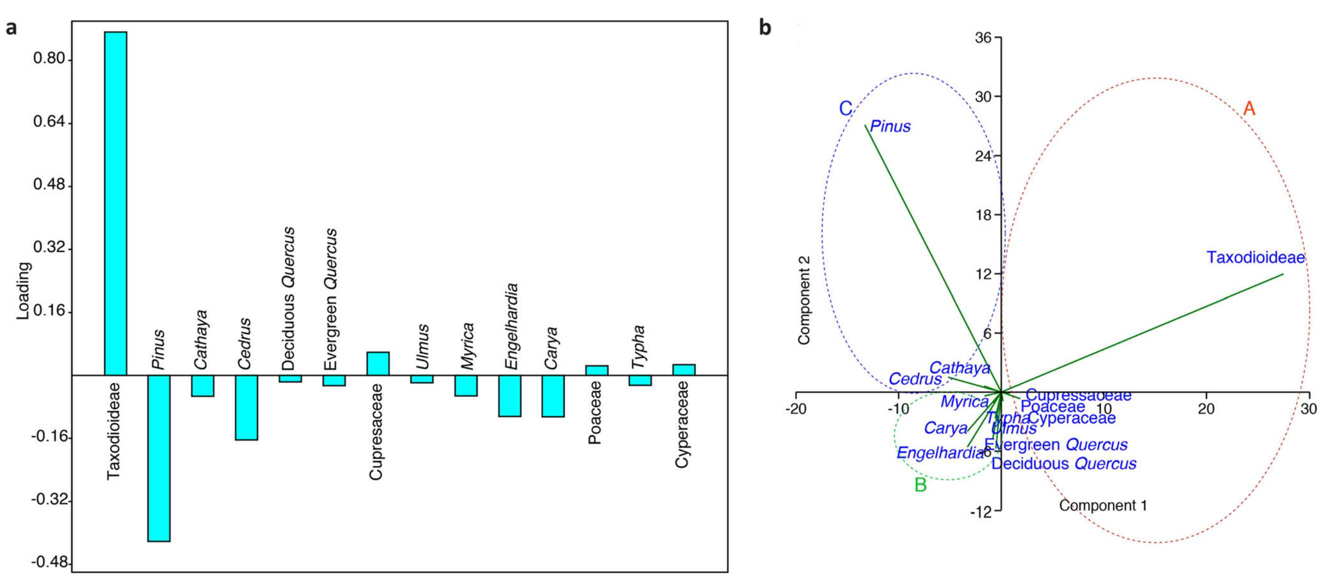

Fig. 5 Principal component analysis (PCA) from the Gračanica pollen data. A PCA correlation loading (to component 1) and scatter diagrams are shown in **a** and **b**, respectively. The analysis was carried out using PAST 3.19 (Hammer et al. 2001). PCA groups are shown

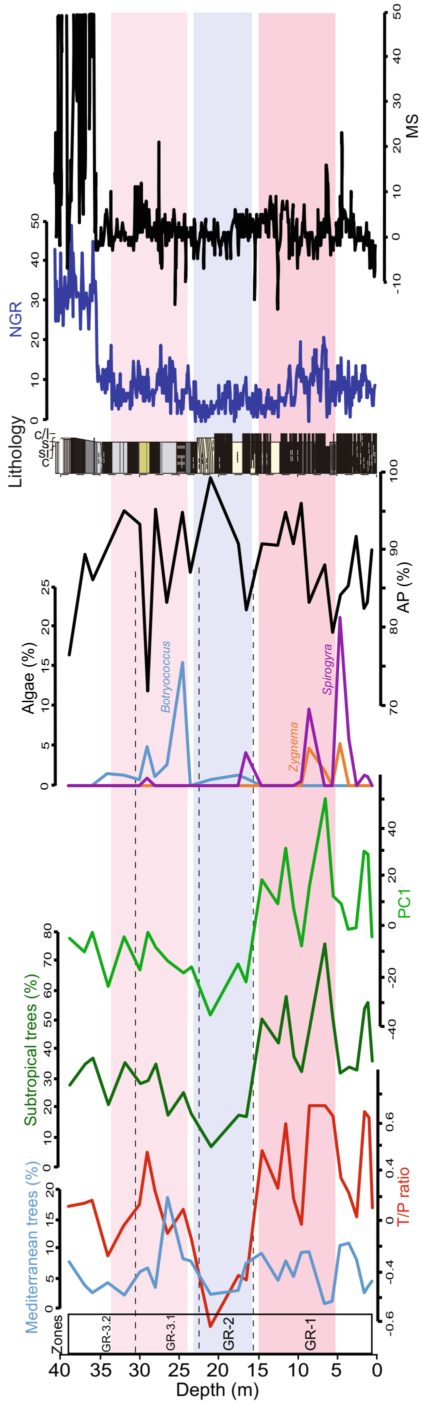

Fig. 6 Comparison of the pollen palaeoclimatic proxies with sedimentation patterns in the Gračanica sequence. From bottom to top: percentages of Mediterranean, T/P ratios, abundance of subtropical taxa, PC1, main algae, arboreal pollen (AP), lithology (for lithology legend, see Fig. 2), natural gamma rays (NGR) and magnetic susceptibility (MS) from the Gračanica pollen record (Mandic et al. in prep., this issue). The pollen zones and climatic inferences (with colour shading, red indicating warm, blue relatively cold) are shown

parameter with the objective of characterising the different periodicities present in the unevenly spaced raw T/P pollen data and estimating their red-noise spectra. The spectral

Table 1 Linear Pearson correlation analysis (*r*, with statistical *p* significance value) run on the most abundant pollen species. The analysis was carried out using PAST 3.19 software (Hammer et al. 2001). In bold and italics are correlations above 0.25, bold and italics for positive and negative correlations, respectively

	Taxodioideae	*Pinus*	*Cathaya*	*Cedrus*	*Quercus deciduous*	*Quercus evergreen*	*Olea*	*Fagus*	Cupressaceae	*Ulmus*	*Myrica*	*Engelhardia*	*Carya*	Poaceae	*Typha*	Cyperaceae
Taxodioideae		0.0052526	0.00051627	0.015777	0.29486	0.21167	0.65947	0.51782	0.14582	0.45622	0.063595	0.0090301	0.0003742	0.16532	0.16336	0.12377
Pinus	*− 0.51293*		0.004657	0.11071	0.15557	0.38654	0.35168	0.97673	0.16699	0.20517	0.29777	0.68089	0.3722	0.24438	0.8348	0.17695
Cathaya	*− 0.61356*	**0.51899**		0.099465	0.36886	0.81064	0.54706	0.73154	0.97843	0.22706	0.50825	0.45899	0.27098	0.39417	0.28866	0.023958
Cedrus	*− 0.45188*	**0.30809**	**0.3177**		0.17578	0.50388	0.768	0.20967	0.37516	0.32327	0.35322	0.50869	0.45616	0.22464	0.77508	0.85305
Quercus deciduous	− 0.2052	*− 0.27571*	− 0.17653	*− 0.26332*		0.0019205	0.6374	0.63372	0.19379	0.40153	0.62818	0.040114	0.014871	0.98101	0.47361	0.33857
Quercus evergreen	− 0.24357	− 0.1702	0.047418	− 0.13177	**0.5605**		0.1794	0.78924	0.27888	0.41833	0.79216	0.91712	0.25592	0.10364	0.14813	0.75674
Olea	− 0.087086	0.18285	− 0.11881	0.05836	− 0.093126	**0.26121**		0.63888	0.81551	0.4781	0.51299	0.67802	0.93529	0.23111	0.49279	0.32835
Fagus	− 0.12753	0.0057759	0.067854	− 0.2446	0.09414	0.052891	0.092718		0.019654	0.86202	0.6902	0.17374	0.56285	0.13086	0.28422	0.68153
Cupressaceae	**0.28211**	*− 0.26858*	0.0053539	− 0.17426	*− 0.25309*	0.21197	− 0.046176	*− 0.43829*		0.17074	0.48361	0.10441	0.13138	0.38303	0.23205	0.66717
Ulmus	− 0.14673	*− 0.24696*	0.2358	0.19373	− 0.16497	− 0.15923	− 0.13977	− 0.034405	**0.26631**		0.97588	0.72007	0.41704	0.44427	0.022295	0.79588
Myrica	*− 0.35523*	0.20399	0.13044	0.18228	− 0.095672	0.052141	0.12899	− 0.078801	− 0.13804	0.0059858		0.98197	0.0017342	0.21283	0.84168	0.98554
Engelhardia	*− 0.4842*	0.081296	0.14584	− 0.1303	**0.39016**	0.020603	− 0.082068	**0.26453**	*− 0.31338*	0.070869	0.0044745		0.0024382	0.94037	0.38245	0.056419
Carya	*− 0.62526*	0.17532	0.2154	0.14675	**0.45545**	0.22213	0.016076	− 0.11419	*− 0.29217*	0.15966	**0.56496**	**0.54982**		0.067483	0.82809	0.13894
Poaceae	**0.2696**	− 0.22747	− 0.16752	− 0.237	− 0.004714	*− 0.31404*	− 0.23382	**0.29255**	− 0.17144	− 0.15061	*− 0.24297*	0.014811	*− 0.35047*		0.020299	0.35128
Typha	*− 0.27081*	0.041277	0.2078	0.056534	0.14118	**0.28056**	0.13519	0.20968	− 0.23336	*− 0.43024*	0.039536	0.17165	− 0.042979	**0.43624**		0.59562
Cyperaceae	**0.29781**	*− 0.26264*	*− 0.42557*	− 0.036666	− 0.1878	− 0.061278	0.19174	0.081126	− 0.084997	− 0.051189	0.0035898	*− 0.36464*	*− 0.28681*	− 0.183	− 0.1048	

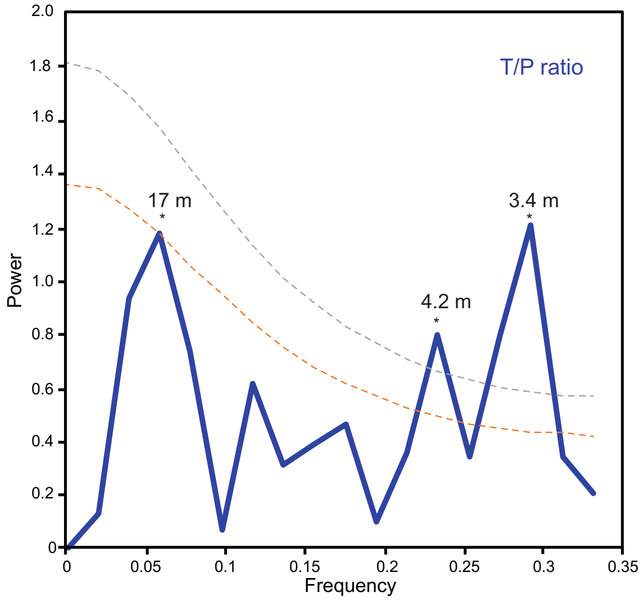

Fig. 7 Spectral analysis of the most significant palaeoclimatic pollen proxy, T/P ratios, from the Gračanica the record. Confidence levels are shown in red (80% confidence level) and grey (90% confidence level). Significant periodicities (above the 80% confidence level) are highlighted with numbers. We used the software PAST 3.19 (Hammer et al. 2001)

analysis assisted in identifying recurrent features or periodicities through spectral peaks registered at differing frequencies throughout the studied sedimentary sequence.

Filtering of the T/P ratios at the most important frequency bands was carried out using Analyseries 2.0.8 (Paillard et al. 1996; Fig. 8). Filtering out certain frequency bands in a time series can be useful to smooth a curve, remove slow variation or emphasise certain periodicities (e.g. orbital-scale cycles).

Results

Pollen analysis

Seventy-two different pollen taxa have been identified in the Gračanica pollen spectra. This record shows a rich and diversified flora, although some of the identified taxa occur in percentages lower than 1% and have not been plotted in Fig. 3. The species that occurred rarely include *Abies*, Arecaceae, Euphorbiaceae, *Symplocos*, Rutaceae, Ericaceae and cf. Restionaceae.

The pollen record from the Gračanica sedimentary sequence is characterised by the abundance of arboreal pollen (AP) throughout the studied sequence and averaging 87% (Fig. 6). The most abundant trees that occurred at Gračanica were Taxodioideae, *Pinus*, *Cedrus*, *Cathaya*, *Quercus* (both evergreen and deciduous), *Engelhardia*, *Carya*, *Fagus* and *Ulmus* (Figs. 3 and 4). Taxodioideae, *Engelhardia* and *Myrica* represent the most frequent thermophilous (subtropical) taxa. Temperate pollen species are dominated by *Quercus* (both evergreen and deciduous) but also *Carya*, *Ulmus* and less abundantly *Fagus*, *Liquidambar*, *Zelkova* and *Fraxinus*. A very interesting feature of this record is the abundance of mid-altitude conifers such as *Cedrus*, *Cathaya*, together with *Pinus* is some intervals. Mediterranean taxa such as *Olea* and *Phillyrea* occur frequently in the pollen spectra. With respect to herbs, Poaceae are the most abundant in the pollen spectra, followed by the aquatics *Typha* and Cyperaceae. Algae also occur in the pollen record, represented by *Botryococcus*, *Spirogyra* and *Zygnema* (Fig. 4).

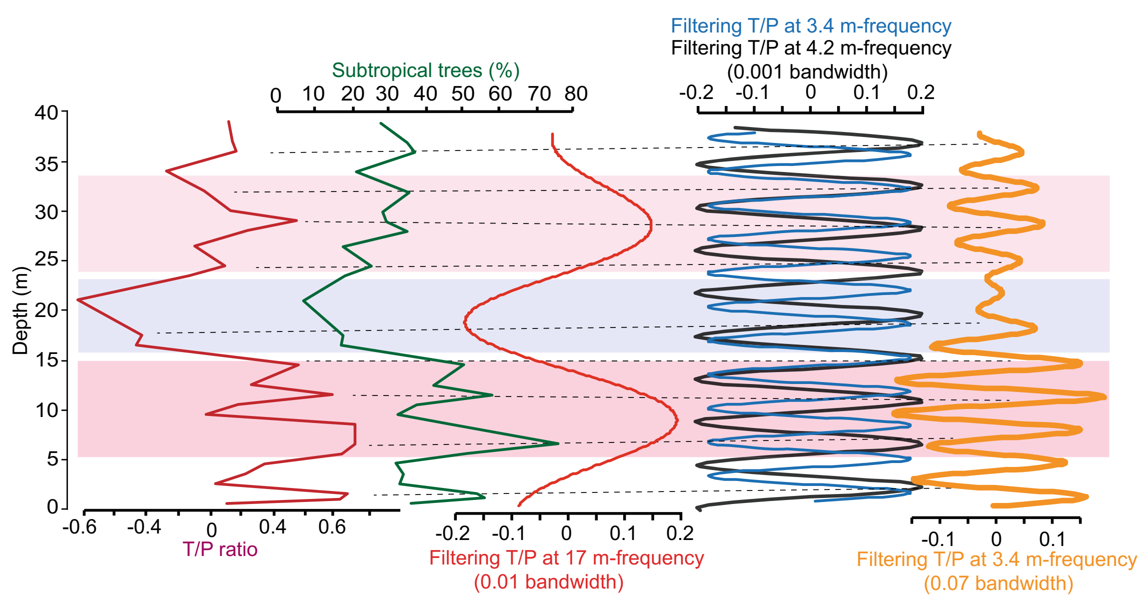

Fig. 8 Comparison and correlations of T/P and subtropical pollen palaeoclimate proxies with 17- and 4.2 and 3.4-m filtered T/P ratios from the Gračanica record. Dashed lines show the possible correlations. Note that the variability observed in the pollen data are explained by two ca. 17-m frequency cycles and nine to eleven 4.2–3.4-m frequency cycles. Palaeoclimatic inferences (with colour shading, red indicating warm, blue relatively cold) are shown

Cluster analysis helped us to objectively subdivide the pollen data, identifying three pollen zones for the Gračanica record (Figs. 3 and 4).

GR-1 zone (from ca. 0–16 m in the Gračanica section) is characterised by highest abundances of Taxodioideae, averaging 40% and peaking between 6.5 and 8.5 m with 72%. Taxodioideae displays varying abundance with four cycles during this zone (numbers on Fig. 4). Poaceae and Cyperaceae exhibit maximum occurrences at this time as well as *Zygnema* and *Spirogyra*. The T/P ratios were also the highest during this zone; peaking at 1.5, 6.5–8.5, 11.5 and 14.5 m.

GR-2 zone (from ca. 16–22.5 m in the Gračanica section) is depicted by the significant decrease in Taxodioideae, reaching minimum values averaging 5%. On the other hand, *Pinus*, *Cathaya* and especially *Cedrus* increased in this zone showing maxima. *Pinus* and *Cathaya* start increasing first, displaying peaks at 16.5 m (26 and 4%, respectively). *Cedrus* increases at the same time but shows the highest abundances of the entire record a little later, at 17.5 m (31%). *Pinus* increases significantly after this maximum in *Cedrus* and depicts a maximum at 21 m (59%). T/P ratios in this zone are the lowest of the entire record, reaching a minimum at 21 m (− 0.84). Algae occur with low abundances during this zone and only a peak in *Spirogyra* of around 5% is observed at 16.5 m.

GR-3 zone (subzone GR-3.1 from ca. 22.5–31 m and subzone GR-3.2 from 31 to 40 m in the Gračanica section) is characterised by the decrease in *Cedrus* and *Pinus*. An increase in temperate taxa such as *Quercus* (both evergreen and deciduous), *Carya* and thermophilous species such as *Engelhardia* occur in this zone. Taxodioideae displays an increase at the end of zone GR-3.1 and into zone GR-3.2 with average values around 15%. *Pinus* recovers later on in subzone GR-3.2 reaching percentages around 31%. T/P ratios show an increase in zone GR-3.1 with two peaks at ca. 24.5 (0.08) and 29 m (0.5). A decrease in this ratio is observed in the beginning of zone GR-3.2, a minimum is reached at 34 m (− 0.28) and a subsequent increase at the end of the sequence is recorded at 37 m (0.13).

PCA and correlation analyses on the pollen data

PCA indicates that principal component 1 (PC1) accounts for much of the variability of the data, explaining the 64.47% of the variance. PC2 explains 16.8% of the variance. PCA shows three main groups of distinctive taxa (Fig. 4). One group, characterised by positive correlation to PC1 (A), is mostly made up of Taxodioideae but also Cupressaceae, Poaceae and Cyperaceae. A second group (B) is characterised by negative values of correlation to PC1 and PC2 and is characterised by *Engelhardia*, *Myrica*, *Carya*, *Quercus* (evergreen and deciduous), *Ulmus* and *Typha*. A third group (C), with negative correlation to PC1 but positive to PC2, is made up of mid-altitude conifers *Pinus*, *Cedrus* and *Cathaya*.

The correlation analysis carried out on the most abundant pollen species confirms the results obtained by the PCA (Table 1). There are significant positive correlations between the species in the A group of the PCA (Taxodioideae, Cupressaceae, Poaceae and Cyperaceae) and Taxodioideae is especially anti-correlated with conifers and thermophilous-temperate forest species of the PCA B group such as *Engelhardia*, *Carya* or *Myrica*. Mid-altitude conifers (*Pinus*, *Cathaya* and *Cedrus*) show good correlations, especially *Pinus* and *Cathaya* ($r = 0.51$), showing close ecological affinity.

Pollen data and cluster analysis agree with the PCA and pollen zone GR-1 is characterised by high relative abundances in the PCA A pollen group (dominated by Taxodioideae), zone GR-2 by higher frequencies in the C pollen group (mid-altitude conifers) and GR-3.1 and 3.2 by higher representation of B group and mixed abundances, respectively.

Cyclicity of the pollen changes

Pollen data show a very clear cyclical pattern in the relative abundance of the most abundant pollen species, in particular in Taxodioideae and mid-altitude conifers (*Pinus*, *Cathaya* and *Cedrus*) and consequently in the subtropical and T/P ratios (Figs. 4 and 6). Cyclical variations are also observed in the lithology and MS, with alternations from darker and organic-rich to lighter organic-depleted layers (Mandic et al. in prep., this issue; Fig. 2). Spectral analysis on the T/P pollen ratios (most abundant pollen species from both PC1+ and PC1−) shows statistically significant results (above the 80 and 90% confidence level) spectral peaks at periodicities between ca. 17 and 4.2–3.4 m (Fig. 7).

Discussion

Middle Miocene flora, vegetation and climate in the DLS

The middle Miocene flora of Gračanica was very diverse, including many extinct thermophilous and hygrophilous species but also temperate taxa and mid- to high-elevation conifers (Figs. 3 and 4). This points to the occurrence of a significant altitudinal gradient in the surroundings to support such a diverse bioclimatic association; from relatively low elevation thermophilous plants to cold-adapted high-elevation conifers. The following plant environments could be distinguished in the pollen data from Gračanica based on present-day vegetation in Southern China (Wang 1961), the closest analogue at present (Jiménez-Moreno et al. 2005):

(1) a swamp and riparian environment with mainly Taxodioideae, *Myrica* and *Nyssa* and *Salix*, *Alnus*,

Carya, *Carpinus* cf. *orientalis*, *Ulmus*, *Zelkova* and *Liquidambar*, respectively;

(2) a broad-leaved evergreen forest, from sea level to around 700 m in altitude (Wang 1961), depicted by Arecaceae, *Myrica*, *Distylium*, *Castanea-Castanopsis*, Sapotaceae, Rutaceae, *Mussaenda*, *Ilex*, *Olea*, Hamamelidaceae and *Engelhardia*;

(3) an evergreen and deciduous mixed forest above 700 m in altitude (Wang 1961), characterised by deciduous *Quercus*, *Engelhardia*, *Platycarya*, *Carya*, *Fagus*, *Liquidambar*, *Carpinus*, *Celtis* and *Acer*;

(4) a mid- and high-altitude (above 1000 m (Wang 1961)) deciduous and coniferous mixed forest with *Betula*, *Fagus*, *Pinus*, *Cathaya*, *Cedrus* and *Picea*.

Pollen results from Gračanica agree with previous studies from this area bearing taxa characteristic of all of the above-mentioned different vegetal environments (Jiménez-Moreno et al. 2008 and 2009). However, the forest composition seems to be different in Gračanica, with higher occurrence of mid-altitude conifers such as *Cedrus* and *Cathaya* and less occurrence of thermophilous trees such as *Engelhardia* or Sapotaceae than in the other previously studied sites. This could be due to the fact that Gračanica (today at ca. 650 m.a.s.l.) was located towards the more mountainous eastern area at higher elevation than those two other sites, which are located at lower elevation at present (Sinj at ca. 300 m and Pag near sea level; Fig. 1).

The Gračanica pollen record shows that during the middle Miocene, this area of the DLS was characterised by a dense forest, pointing to high water availability for supporting such a large amount of trees in the local environment. High regional forest landscape is also observed in previous studies from the DLS area such as in Sinj and Pag basins (Jiménez-Moreno et al. 2008 and 2009). Also, the presence of many hygrophilous plants (i.e. *Engelhardia*: 800–2000 mm; *Platycarya*: 1000–2400 mm; Taxodioideae: 1100–2400 mm; Fauquette et al. 1998), living in SE China under high precipitation regimes, indicates mean annual precipitations higher than Present (mean annual precipitation is 900 mm). The occurrence of hygrophilous species also indicates that, at that time, seasonality (in particular summer drought) was probably less marked than today (Jiménez-Moreno et al. 2009). However, typical Mediterranean drought-adapted taxa such as evergreen *Quercus*, *Olea* and *Phillyrea* do occur in Gračanica (pollen percentages up to 18%) during the middle Miocene (Fig. 6). This pollen abundance of Mediterranean sclerophyllous taxa could suggest that this area was then affected by a certain seasonal Mediterranean climate.

The occurrence of many thermophilous species (such as Taxodioideae, Sapotaceae, *Mussaenda*, *Engelhardia* or *Myrica*) points to a subtropical climate. However, there are significant vegetation variations through time in the Gračanica record and cooler indicators such as *Cedrus* are abundant at certain times (Fig. 4). *Cedrus* is a conifer tree living today at mid elevations (usually above 1500 m.a.s.l.) on mountains around the Mediterranean in northern Africa (Rif, Atlas) and the Middle East (Turkey, Syria, Lebanon) (Quézel and Médail 2003). This taxon is well adapted from cool to cold climatic conditions and it is best represented under humid to subhumid climates (Quézel and Médail 2003). *Cedrus*, as well as other hygrophilous and thermophilous plant species, disappeared from this area due to the drying and cooling trend that occurred globally throughout the Neogene and Quaternary (Zachos et al. 2001).

Vegetation changes and palaeoecological-palaeoclimatic implications

Significant changes in the vegetation that parallel sedimentary variations are observed through time in the Gračanica section. The beginning of the section (pollen zone GR-1) shows peaks and maxima in subtropical (mostly Taxodioideae), PC1 and T/P ratios showing the warmest and driest climatic phases (Fig. 6). A relatively shallow swamp environment is interpreted for such high Taxodioideae occurrence, which is also supported by the sedimentary facies characterised by lignites containing tree trunks probably belonging to Taxodioideae. Algae, mostly *Spirogyra* and *Zygnema*, are also relatively abundant at this time (Fig. 6). Algal blooms of these algae occur in shallow and ephemeral lakes (Jiménez-Moreno et al. 2013), supporting our environmental interpretations.

A significant cooling is observed after warming maxima, coinciding with pollen zone GR-2 between 16 and 22 m. This is interpreted by the strong decrease in subtropical and T/P ratios, reaching coldest conditions between ca. 17 (maxima in *Cedrus*) and 21 m (maxima in *Pinus* and *Cathaya*). Regional cooling would have driven mid-elevation conifers to descend towards lower elevations and *Cedrus* probably occurred around the lake during that period. This is deduced by similar pollen percentages of *Cedrus* higher than 20% in the Holocene records from the Atlas Mountains, where they occur at Present (Cheddadi et al. 2017). Maximum in forest development (AP) and minima in herbs would also indicate that maximum in humid conditions occurred at ca. 21 m in the Gračanica sedimentary sequence. This is supported by the sedimentary change pointing to a deepening in the lake environment, from a swamp lignite towards profundal open-lake marls. The fact that high-elevation subalpine conifers present very low occurrences (*Picea*, with 2.5%) or are even absent (i.e. *Abies)* during this cold period indicates that either the mountains around the lake were not high enough then to support such a floristic association or that the cooling was not sufficiently strong to generate the displacement of these conifers towards the lake elevation.

Warming is observed in the Gračanica pollen record (pollen zone GR-3) after the coldest maxima, between 22 and the top of the section. This is indicated by the increase in subtropical forest and consequently, PC1 and T/P ratios (Fig. 6). However, temperatures would have been relatively lower than earlier on during warmest maxima. The high occurrence of *Botryococcus* shows that lake level would have stayed relatively high at that time. The Chlorophyceae alga *Botryococcus* sp. has been used as an indicator of freshwater environments in relatively productive water bodies (Guy-Ohlson 1992). Maxima in *Botryococcus* at this time could also support relatively warm temperatures as it has been related to reflect temperature variations in lake productivity increasing with warmer water temperatures (Ramos-Román et al. 2018).

The Gračanica pollen record seems to show a long-term cooling trend throughout the studied sedimentary sequence. This is indicated by a progressive reduction in all the palaeoclimatic subtropical, T/P and PC1 proxies (Fig. 6).

A vegetation succession is observed in the tree taxa during the climate changes described above. A very clear succession occurred during warming after the coldest maxima represented with *Cedrus*, which gives turn to *Pinus*, then temperate *Quercus* and *Carya* and subsequently to subtropical, *Myrica*, *Engelhardia* and then to Taxodioideae representing maxima in temperature (Fig. 4).

Cyclostratigraphic analysis and age implications

Short-scale cyclical vegetation changes represented by the alternation between lowland Taxodioideae swamp and subtropical forest and upland mid-elevation conifer forest are observed in the Gračanica pollen record, most-likely representing warm/arid-cold/humid climatic cycles, respectively (see explanation above).

Different scale cyclicities can be observed visually within the different pollen zones (Figs. 6 and 8) and statistically through spectral analysis of the T/P pollen ratios (Fig. 7). Two main vegetation and climate cycles can be observed with periodicities around 17 m, characterising the main climate and environmental trends described above (see filtered data in Fig. 8), and a shorter-scale cyclicity with a frequency around 4.2–3.4 m (Fig. 7). As the Gračanica section lacks of an accurate age control, we cannot directly associate these periodicities to a certain time frequency (i.e. orbital-scale cyclicity). However, their time duration could be roughly estimated making a few suppositions supported by the available age control for the sequence and knowing the main external forcings of vegetation changes in the study area. The most statistically significant cyclicities in the T/P pollen palaeoclimatic proxy have a periodicity of ca. 4.2 and 3.4 m (Fig. 7) and so T/P data were filtered at these frequencies (0.233 and 0.292 frequencies; 0.001 and 0.07 bandwidths) and the resulting data seem to explain the smaller-scale variability observed, especially the 3.4-m frequency (Fig. 8). If the 3.4-m cycle could be considered forced by precession (ca. 21 kyr), one of the main forcings of vegetation changes at mid-altitudes (Kloosterboer-van Hoeve et al. 2006; Tzedakis 2007; Sánchez Goñi et al. 2008; Jiménez-Moreno et al. 2013), the 17 m would exactly correspond to the ca. 100 kyr eccentricity cycle (17 m × 21 kyr/3.4 m = 105 kyr), producing a perfect orbital-scale fit (5:1) for the observed spectral peaks. This sedimentary sequence would then be characterised by two entire eccentricity cycles (ca. 200 kyr; Fig. 8) and a sedimentary rate of ~ 0.2 mm/year, which agrees with average sedimentary rates in other nearby lake environments (for example 0.1 mm/year calculated for the middle Miocene Gacko Basin: Mandic et al. (2011); 0.3 mm/year from the Miocene sediments from Lake Sinj (de Leeuw et al. 2010) or 0.19 mm/year in Camp dels Ninots maar, Spain, Jiménez-Moreno et al. 2013). Filtering of the T/P data at 4.2 and 3.4 m periodicities shows that smaller-scale variability would have been forced by between nine and eleven precession-scale cycles (Fig. 8).

Highest temperatures, recorded by the highest subtropical taxa and T/P ratios between 6.5–8.5 m, could be then related to an eccentricity and insolation maxima (Fig. 8) that probably occurred during the Langhian or middle Badenian in the Central Paratethys stratigraphic terminology (Piller et al. 2007). The Gračanica record shows a minimum in temperature (T/P ratios) and maximum in humidity (AP percentages) at around 20 m depth that could have been triggered by a subsequent eccentricity and insolation minima (Fig. 8). This cooling could be related to an early stage of the middle Miocene ice expansion (~ 14.7 Ma), as recorded in the Southern Ocean δ^{18}O palaeoclimate record from IODP Holes 1171C and U1338, confirming previous observations that Antarctic ice growth began since 15.5 Ma (Shevenell et al. 2008; Holbourn et al. 2014). Interestingly, the end of the sedimentation in this basin estimated here at around 14.55 Ma could coincide closely with the end of the MCO (around 15–14.7 Ma) and the beginning of the Middle Miocene Climate Transition (MMCT, ~ 15 to 13.8 Ma) (Woodruff and Savin 1991; Miller et al. 1991; Flower and Kennett 1994). There are multiple palaeoclimatic evidences of a significant cold event at ca. 14.55 Ma on marine δ^{18}O and δ^{13}C records (Holbourn et al. 2014) with a significant carbon maxima event, the CM5a [(after Woodruff and Savin (1991) and Diester-Haass et al. (2013)], implying enhanced marine productivity response by enhancing ocean circulation during significant cold periods (Diester-Haass et al. 2013). Perhaps this climatic transition (i.e. a long-term increasing trend in aridity) produced significant environmental and palaeogeographical and changes in this basin triggering the desiccation of the lake and sedimentation in the Bugojno basin. Holbourn et al. (2007) and Diester-Haass et al. (2013) also related this ca. 14.55 Ma cold event with the long-term component of eccentricity (~ 400 kyr), highlighting the importance of this orbital forcing conditioning global climate at this time.

Interestingly, the 100-kyr-long eccentricity cycles characterising the MCO pollen record from Gračanica differ remarkably from the typical saw-tooth morphology of the also eccentricity-driven late Pleistocene glacial-interglacial cycles. The MCO cycles are more symmetrical, with sharp decreases and increases, implying that different climate dynamics with a more transitional warming during glacial terminations drove these events (Fig. 8). This was previously noticed by Holbourn et al. (2014) through a high-resolution $\delta^{18}O$ analysis of a deep marine core from the Equatorial Pacific.

Conclusions

The pollen analysis of the Gračanica sedimentary sequence permitted the reconstruction of the vegetation and climate history during the middle Miocene in the Dinarides Lake System area. We obtained the following main conclusions through comparing this study with orbital parameters, insolation and other palaeoclimate records:

(1) Pollen data indicate that during the middle Miocene, a very diverse flora organised in altitudinal vegetation belts existed in this area including subtropical, temperate and mid-altitude conifers.
(2) Vegetation indicates that overall climate around the lake was a relatively humid subtropical climate subjected to significant variability.
(3) Warmest conditions occurred at the beginning of the studied section deduced by the highest abundance of subtropical taxa and the occurrence of a Taxodioideae swamp environment. A cooling is noticed afterwards with a coldest maximum represented by a maximum in mid-altitude conifers that probably reached the lake area due to a displacement of forest species towards lower elevations. Enhanced humidity also occurred and the lake level increased at this time triggering an environmental change towards deeper lake conditions. A relative warming occurred at the top of the studied sedimentary sequence before the studied interval ended.
(4) A clear smaller-scale cyclicity is observed in the vegetation and sedimentation in the Gračanica record. Climate variability was probably forced by eccentricity (main vegetation trends) and precession (smaller-scale variability).
(5) Correlation of the observed pollen palaeoclimate proxy with orbital parameters and insolation suggests that the studied sedimentary sequence was deposited in ca. 200 kyr, perhaps between ca. 14.80 and 14.55 Ma, right at the end of the MCO.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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