ENSO- and solar-driven sub-Milankovitch cyclicity in the Palaeogene greenhouse world; high-resolution pollen records from Eocene Lake Messel, Germany

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Abstract: The annually laminated oil shale from the Eocene maar lake at Messel (Germany) provides unique palaeoenvironmental and palaeoclimatological information for the Palaeogene greenhouse phase. Two palynological analyses of 6.3 and 70 kyr long records with a temporal resolution of 70 and 700 years respectively confirm vegetation and climate variability in the sub-Milankovitch range. This variability clearly corresponds to cyclic climate fluctuations indicating the influence of solar activity and a millennial-scale variability of the El Niño–Southern Oscillation also seen during the Quaternary icehouse system. This provides strong evidence of cyclic fluctuations in the sub-Milankovitch frequency band that represent a pervasive and persistent system not only of the Quaternary icehouse, but also throughout the entire Neogene and the Palaeogene greenhouse. This is proof for the long-term stability of the driving forces of natural climate change on Earth. Fluctuations in the frequency of palynomorphs indicate cyclic short-term quantitative changes in the composition of the vegetation. These changes were related to precipitation and corresponding fluctuations of the lake level as well as to changes in pollen production, transport and deposition.

Supplementary material: A complete list of variables and palynomorphs used for pollen diagrams and statistical analyses, as well as additional time series analyses, are available at https://doi.org/10.6084/m9.figshare.c.3458778

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As modern society is currently coping with very severe environmental consequences of global climate change, climate research is focused on understanding the driving factors and mechanisms. The central issue has thereby shifted from merely detecting the role of anthropogenic change to estimating its possible current and future impact (Waple et al. 2002). Accordingly, it is important to analyse the long-term evolution of the climate system to understand the forcing and feedback of processes and responses of the biosphere. Therefore, Quaternary archives were studied preferentially during recent decades as it was realized that reliable predictions of future global climate change and its environmental impact require understanding of processes operating on timescales both those covered by the instrumental record of the last few centuries (see PAGES research programme, Alverson & Kull 2009). Such archives are important in unravelling the relative contributions of natural variability forced by, for example, orbital parameters or changes in solar irradiance and the human influence in the observed modern climate change (Waple et al. 2002).

It is commonly accepted that the Palaeogene greenhouse may represent a past analogue for future warmer climate on Earth. For example, the Intergovernmental Panel on Climate Change (IPCC 2007) predicts CO2 levels for the year 2100 that will be comparable with those of the Eocene (Parrish & Soreghan 2013). This illustrates the need to consider deep time records older than 2 Ma, to confidently model and predict future climate (Parrish & Soreghan 2013).

Apart from the commonly used oxygen and carbon isotope data from ocean or lake sediments, pollen and spores are important terrestrial climate proxies as plants are sensitive indicators of continental palaeoenvironments and palaeoclimate (Traverse 2007).

The annually laminated oil shale from the Early to Middle Eocene maar lake of Messel (Germany) provides a unique palaeoenvironmental and palaeoclimatological archive for a time interval of more than 640 kyr within the Palaeogene greenhouse phase. Because physiological conditions and sedimentation rate within Lake Messel remained stable during that interval, changes in the surrounding vegetation as documented by the palynological record (e.g. Thiele-Pfeiffer 1988; Lenz et al. 2011) can be considered to be climate controlled. In a recent study (Lenz et al. 2011) it could be demonstrated that a paratropical angiosperm-dominated climax vegetation responded to Milankovitch cyclicity even within the Palaeogene greenhouse system.

Here we present two highly resolved pollen records from the Eocene oil shale of Messel spanning time series of about 70 kyr in c. 700 year increments and of about 6.3 kyr with a temporal resolution of c. 70 years, which confirm variability of vegetation and climate in the sub-Milankovitch range. Almost all time series analyses in palaeoclimate studies use a single dataset (e.g. oxygen isotope data), representing only a single feedback to climate variation. We are now able to achieve a more detailed and complex picture by analysing the cyclic behaviour of 26 independent palynological taxa or groups of taxa to ascertain whether different plants responded differently to climate change.

Geological setting

The Messel site is one of half a dozen deposits of Palaeogene age scattered across the Sprendlinger Horst, the northern extension of the Palaeozoic Odenwald Basement in SW Germany flanking the
Upper Rhine Graben to the NE (Fig. 1). Sedimentation in these structures probably started during the Eocene owing to initial crustal weakness in advance of rifting and graben formation (e.g. Felder et al. 2001; Hottenrott 2002; Schumacher 2002; Derer et al. 2005; Hinsken et al. 2007). Geophysical studies and scientific drilling have proved that most of these Palaeogene deposits, such as those at Messel, Offenthal and Groß-Zimmern (Fig. 1), are fillings of maar craters within Permian and Lower Triassic host rocks (e.g. Harms et al. 1999; Jacoby et al. 2000; Felder et al. 2001; Felder & Harms 2004). Among these, Messel is renowned worldwide because of the exceptional preservation and diversity of fossils and has been included in the UNESCO World Heritage List in 1995.

A research core drilled at the centre of the Messel structure in 2001 proved that it was formed by one or more phreatomagmatic explosions (Lorenz 2000; Schulz et al. 2002; Harms et al. 2003; Felder & Harms 2004). According to revised 40Ar/39Ar dating of a basaltic clast from immediately below the lacustrine succession, maar lake formation began in the Early Eocene between 48.5 and 47.9 Ma (Lenz et al. 2015).

The lower part of the lacustrine maar filling is composed of clastic sediments of the Lower Messel Formation, which were deposited during the holomictic stage of the lake (Fig. 2). In the upper part of the Lower Messel Formation intermittent deposition of laminated bituminous claystones heralds the transition to meromictic conditions in the lake. The succeeding Middle Messel Formation is characterized by the finely laminated classical fossiliferous oil shale (Fig. 2). The varve-like stratification of the oil shale formed under permanently meromictic conditions and was caused by annual algal blooms of the coccol green alga Tetraedron minimum (Irion 1977; Goth 1990; Lenz et al. 2010). Countings of oil shale varves by Goth (1990) resulted in a sedimentation rate of 0.15 mm a⁻¹, whereas El Bay et al. (2001) calculated a sedimentation rate of 0.146 ± 0.052 mm a⁻¹ for an older well and Schulz et al. (2002) a rate of 0.14 mm a⁻¹ for the Messel 2001 core both by using gamma-ray log and magnetic susceptibility data. Lenz et al. (2010) counted oil shale varves at different depths between 90 and 4 m in the Messel 2001 core. The sedimentation rates derived from these counts vary between 0.10 and 0.15 mm a⁻¹, corresponding to an average sedimentation rate of 0.14 mm a⁻¹ for the entire oil shale of the Middle Messel Formation. These short-term fluctuations in varve thickness can be attributed to an ‘Eocene ENSO (El Niño–Southern Oscillation)’ (Lenz et al. 2010), but there is no sedimentary evidence that the sedimentation rate changed sustainably for a longer time. This allowed establishment of a detailed age model for the deposition of the Middle Messel Formation on the basis of an average sedimentation rate of 0.14 mm a⁻¹ (El Bay et al. 2001; Schulz et al. 2002; Lenz et al. 2010), which resulted in a time of deposition of the Middle Messel Formation of 640 kyr. Cyclicities in the pollen rain were used for an astronomical bracketing of the Middle Messel Formation and indicate an age-range between 47.41 and 48.05 Ma or between 47.61 and 48.25 Ma (Lenz et al. 2015). Taking the new 40Ar/39Ar age for the initial phreatomagmatic explosion(s) into account a total time of deposition between 700 and 900 kyr can be estimated for both the Lower Messel Formation and the Middle Messel Formation (Lenz et al. 2015). This is a minimum calculation as an unknown thickness of the Middle Messel Formation and the Upper Messel Formation has been removed by mining. Little is known about the Upper Messel Formation, but Matthess (1956) reported that it consists of clays and intermittent lignites probably representing the silting-up phase of the lake.

Previous work

The lamination of the oil shale (Fig. 2) is composed of a light spring–summer algal layer formed by blooms of Tetraedron minimum, and a dark winter layer mainly composed of terrigenous background sediment with little algal material (Goth 1990). Previous time series analyses revealed significant fluctuations of varve and laminae thickness in the biennial (2.1–2.5 years) and low-frequency band (2.8–3.5 years, 4.9–5.6 years). They were attributed to ENSO effects (Lenz et al. 2010) because these periodicities closely correspond to modern ENSO signals.
(Rasmussen et al. 1990) as well as to Eocene El Niño rhythms as calculated by applying a climate model (Huber & Caballero 2003). This confirmed that sedimentation was controlled by the effects of a robust Eocene ENSO (Lenz et al. 2010).

Varve thickness also showed significant peaks within a quasi-decadal (10 – 11 years), interdecadal (17 – 26 years) and multi-decadal band (c. 52 years, c. 82 years) (Lenz et al. 2010), which resulted either from the influence of cyclic instabilities of the ocean–atmosphere system such as the modern Pacific Decadal Oscillation (PDO; see Schlesinger & Ramankutty 1994; Mann et al. 1995; Mantua & Hare 2002) or from variations in solar intensity.

A first high-resolution palynological analysis of the lake sediments from the Middle Messel Formation with samples at 20 cm intervals provided insight into the dynamics of a climax vegetation during the Eocene greenhouse climate (Lenz et al. 2010).

Time series analyses of pollen assemblages showed that variations in the Milankovitch range of short eccentricity, obliquity and precession indicate orbital forcing as the main controlling factor of vegetation changes in the vicinity of Lake Messel (Lenz et al. 2011). However, these changes remained transient and were completely restricted to the quantitative composition of the vegetation.

In particular, precession-paced changes in the vegetation with fluctuations between 20 and 24 kyr could be recognized as well as a short eccentricity signal of 100 kyr, which modulates the amplitude of the precession signal (Lenz et al. 2015). It has been reported that changes in the orbital precession today influence the seasonal distribution of insolation and, as a consequence, the distribution and amount of seasonal precipitation (Merlis et al. 2013). Therefore, in a monsoonal climate as suggested for the Eocene of Messel by Mai (1995) and Grein et al. (2011) orbitally controlled latitudinal shifts of continental climate belts may have caused changes in the intensity of precipitation responsible for quantitative changes in the vegetation around Lake Messel (Lenz et al. 2011, 2015).

Some millennial-scale fluctuations of the pollen rain have already been recognized by Lenz et al. (2011); however, the sampling interval for that study was insufficient to truly resolve sub-Milankovitch cyclicity.

**Methods**

**Sample site and sampling procedure**

For the present study the sampling intervals have been significantly reduced in selected parts of the Middle Messel Formation to resolve the frequency range between fluctuations within the biennial to decadal ENSO scale band and the Milankovitch frequency band. Time series analyses are based on the palynological analysis of two more highly resolved sample sets. In a first set, 102 samples were
taken from the Messel 2001 research core as 1 cm thick slices at 10 cm intervals between 26.97 and 16.68 m depth (Fig. 2). In this way the number of analysed samples from that core segment has been doubled from 51 for the study of Lenz et al. (2011) to 102 for the present study. Applying the calculated average sedimentation rate of 0.14 mm a\(^{-1}\) (Lenz et al. 2010) the 10 cm sample interval covers a time interval of about 700 years and the total time series between 26.97 and 16.68 m thus corresponds to about 70.7 kyr.

This segment was chosen because it represents the stable paratropical climax vegetation, which flourished in the vicinity of the maar lake during deposition of the Middle Messel Formation (Lenz et al. 2011) and is regarded as typical for inland areas during the Eocene of Central Europe (Mai 1981, 1995; Schaarschmidt 1988). Furthermore, this part of the section is characterized by undisturbed laminations without any indication of redeposition or turbidities, or of significant changes of the sedimentation rate. For a second set of samples a c. 1 m thick oil shale block (OSB), roughly correlated to a depth of c. 24 to c. 23 m in the Messel 2001 research core by marker horizon \(\alpha\) (Fig. 2), was taken directly from the excavation site (Felder & Harms 2004). It was transferred to the laboratory and split into 1 cm slices, resulting in a total of 91 samples for palynological study. Based on the sedimentation rate, the OSB in total represents a time series of c. 6300 years with the 1 cm splits each representing c. 70 years.

**Sample preparation**

Following standard procedures as described by Kaiser & Ashraf (1974) all samples were successively treated with HCl, HF and KOH. The residue was sieved with a mesh size of 10 µm and slightly oxidized with diluted HNO\(_3\) to remove flocculating organic matter and to improve the transparency of the palynomorphs.

**Quantitative palynological analysis**

The identification of pollen and spores for the present study is primarily based on the systematic–taxonomic study of Thielemann & Pfeiffer (1988). For quantitative analysis a minimum of 300 individual sporomorphs per sample was counted at 400 times magnification. Altogether, 101 taxa of pollen and spores were identified. Remains of algae such as Botryococcus or cysts of freshwater dinoflagellates (Messelodinium thielepfeifferae) and Zygnemataceae (Oovidites) were counted as additional percentages of the total sum of pollen and spores. All of the 193 samples studied contained sufficient palynomorphs, but preservation of the single grains is only moderate throughout the oil shale. Thus, 10–20% of the total assemblage could not be determined and was recorded as ‘Varia’.

Because of the great diversity of the palynomorph assemblage as well as the frequent occurrence of transitional forms, some of the palynomorph taxa (families, genera or single species) were lumped for the core segment and to 48 ‘variables’ for the OSB. The results of the quantitative analysis are presented in two pollen diagrams (Figs 3a and 4a).

To detect significant quantitative changes within the palynomorph spectra, the percentage values of individual taxa or ‘variables’ were assigned to frequency classes to minimize the effect of minor fluctuations (Figs 3b and 4b). These are probably due to regular variation in pollen precipitation and therefore do not reflect true changes in the frequency of the mother plants within the vegetation. Nevertheless, at the same time significant changes in the palynomorph spectra are preserved or even emphasized. Following Gauch (1982), nine cut levels (0, <0.5, <1, <2, <4, <8, <16, <32 and <64%) were defined for the palynomorph percentages.

**Statistical analysis**

**Principal component analysis**

To reveal the underlying pattern as well as ecological gradients, principal component analysis (PCA) was implemented for numerical treatment of the palynological data using the software PAST (Hammer et al. 2001). This ordination method was chosen as the appropriate multivariate model, because a gradient lengths analysis estimated with a detrended correspondence analysis (DCA, Hill & Gauch 1980) using the software DECORANA (Hill 1994) determined a length of 1.2 SD (units of average standard deviation of species turnover) for the samples from the core segment and 1.1 SD for the OSB. Following Ter Braak & Smilauer (2002) a maximum gradient length of less than 2 SD indicates an approximately linear trend in species composition. Therefore, the linear response model of the PCA should be used rather than a unimodal response model of a (detrended) correspondence analysis (DCA/CA; Ter Braak & Smilauer 2002). For PCA we used the frequency class values to avoid the influence of insignificant fluctuations in the pollen rain on the ordination result and the covariance matrix of the frequency classes as a weighting variable where higher frequency fluctuations were encountered (Townend 2002).

PCA was also used to select palynomorphs or groups of palynomorphs for the succeeding time series analysis. Species that plot near the origin of the principal component axes (as indicated by short vectors in the biplot) are characterized by a more balanced distribution without significant frequency fluctuations through the analysed sections. On the other hand, taxa with long vectors (which therefore plot at some distance from the origin) show significant frequency fluctuations owing to the underlying ecological gradient(s). They are therefore especially suited for time series analyses.

**Time series analysis**

For the recognition of persistent cyclic patterns in pollen precipitation, we employed with the REDFIT procedure and the wavelet transform two independent techniques of spectral analysis using software PAST (Hammer et al. 2001). For time series analysis frequency class values were also used.

The REDFIT procedure of Schulz & Mudelsee (2002) allows us to test if dominant frequencies in the spectrum of a time series are significant against a red-noise background from a first-order autoregressive (AR1) process. For calculation of REDFIT periodograms the Welch-type spectral window was applied. Different numbers of overlapping (50%) segments as well as oversampling rates were used to achieve clear peaks in the periodograms of each dataset (see Auer et al. 2015). For detection of significant peaks a Monte Carlo simulation was performed using 1000 random realizations of an AR(1) process (Hammer et al. 2001, software PAST 3.10).

However, pollen precipitation is not a typical stationary signal because vegetation responds to diverse factors some of which are independent of climate variability, such as facies changes owing to the generation of new habitats by landslides following tectonic activity; for example, at the base of the Middle Messel Formation (see Lenz et al. 2007, 2011). Therefore, many of the analysed taxa show significant cyclicities only in those parts of the times series when the parent plants had a wider distribution within the vegetation. For this reason we applied the Morlet wavelet (Morlet 1983; Torrence & Compo 1998), a continuous wavelet transform, which has the advantage that it can be used for time series that are non-stationary and contain a variety of frequencies (Daubechies...
Fig. 3. Pollen diagrams of core Messel 2001 (Forschungbohrung Messel 2001, FB2001) between 26.97 and 16.68 m core depth. (a) Diagram with percentage values. (b) Diagram with assignment to frequency classes (0: 0%; 1: >0 to <0.5%; 2: 0.5 to <1%; 3: 1 to <2%; 4: 2 to <4%; 5: 4 to <8%; 6: 8 to <16%; 7: 16 to <32%; 8: >32%).
A wavelet transform visualizes a time series in a time–frequency space, which allows us to identify the dominant frequency signals and to follow their variation with time (Torrence & Compo 1998). For the calculation of significance levels in the wavelet transform an appropriate background spectrum that is either white noise or red noise has to be chosen (Torrence & Compo 1998). The respective MA(1) autocorrelation coefficient that specifies the lag-value and therefore a white-noise model (lag =

**Fig. 4.** Pollen diagrams of the oil shale block (OSB) from a section between 4.5 and 3.5 m above the marker horizon α. (a) Diagram with percentage values. (b) Diagram with assignment to frequency classes (0: <0%; 1: >0 to <0.5%; 2: 0.5 to <1%; 3: 1 to <2%; 4: 2 to <4%; 5: 4 to <8%; 6: 8 to <16%; 7: 16 to <32%; 8: >32%).
0) or red-noise model (0 < lag < 1) was calculated using the method described by Hammer (2015, software PAST 3.10).

**Results**

**Quantitative palynological results**

The pollen diagram (Fig. 3a) of the samples from the core between 26.97 and 16.66 m depth shows a comparatively uniform pollen record. No major turnover of the vegetation is indicated and qualitative changes such as the appearance or disappearance of taxa do not occur. Changes within the pollen spectrum are restricted to quantitative fluctuations, a clear sign of a stable climax vegetation as typical for the Middle Messel Formation (Lenz et al. 2011).

The pollen diagram from the oil shale block (OSB) is also characterized by a regular distribution of the palynomorphs (Fig. 4a). The OSB covers c. 6300 years, which is only a hundredth of the time represented by the whole Middle Messel Formation in the Messel 2001 core. Because of the shorter time span covered, qualitative changes in the pollen spectrum are much less pronounced (see Lenz et al. 2011). Because the OSB can be correlated to the core at about 24–23 m the quantitative palynological results are very similar to those from the studied core segment between 26.97 and 16.66 m depth.

The pollen spectra in both cores are dominated by *Plicapollis plicatus* (Juglandaceae, walnut family, Krutzsch 1962) with abundances between 25 and >40% in the Messel core and between 30 and 45% in the OSB. Because of a relatively large number of grains that cannot be unequivocally assigned to one of both ‘species’, *Tricolpopollenites liblarensis* and *Tricolporo pollenites cir culum* have been treated as a single unit in the present study, together representing another dominant element of the pollen spectra with frequencies between 20 and 40% in the core and between 25 and 35% in the OSB. Both ‘species’ certainly include pollen of more than one natural taxon. Whereas *T. cingulum* is mainly attributed to the Fagaceae (beech family, Kedves 1978; Nickel 1996), *T. liblarensis* has affinities to pollen of different families such as the Fagaceae, Fabaceae (bean family), Combretaceae (Myrttales) or Verbenaceae (Verbena family) (Stuchlik 1994). Because macroscopic remains of Fagaceae have not been found at Messel (Wilde 1989, 2004) it can be assumed that members of the family did not live in the catchment area of the lake and the pollen therefore more probably represents the true zonal vegetation. Nevertheless, both Fagaceae and Juglandaceae were major elements of the paratropical rainforest.

Both *P. plicatus* and *T. liblarensis* + *T. cingulum* clearly show long-term trends. Whereas *P. plicatus* is represented with higher values in the lower part of the studied segment of the Messel 2001 core, there is a decrease in frequency by about 10% in the upper part (Fig. 3a). In contrast, the proportion of *T. liblarensis* + *T. cingulum* increases from the lower to the upper part by 10% from c. 30% to 40%. These significant shifts in the quantity of dominant elements indicate a slight change in the composition of the paratropical rainforest. The Juglandaceae dominate up to a depth of about 22.5 m, followed by a transition in which both elements are equally represented, and the dominance of Fagaceae starts at a depth of about 19 m. This change from a Fagaceae- to a Juglandaceae-dominated forest is regularly observed in the Middle Messel Formation and can be interpreted as a response of the vegetation to eccentricity-driven climate changes (Lenz et al. 2011). The dominance of *P. plicatus* over *T. liblarensis* + *T. cingulum* in the OSB (Fig. 4a) corresponds to the position of the OSB in relation to the studied core segment.

With *Plicapollis pseudoexcelsus*, *Momipites* spp., *Plotycaryopollenites* spp., *Pterocaryopollenites stellatus* and *Subtrirhopollenites* spp. several other pollen taxa of juglandaceous origin (Thomson & Pflug 1953; Thiem-Pfeiffer 1980, 1988; Friis 1983) occur in the samples and support a remarkable diversity of the walnut family in the paratropical rainforest at Messel. Especially frequent are *P. pseudoexcelsus* and *Plotycaryopollenites* spp. in the core and in the OSB with values between 5 and 10%. However, they are characterized by regular fluctuations in frequency, which may also be interpreted as a response to cyclic climate variations. Other palynomorphs with values up to 10% are *Pityosporites labdacus* (Pinaceae, pine family, Thomson & Pflug 1953), *Tricolporo pollenites microreticulatus* (Oleaceae, Thiem-Pfeiffer 1980), *Tetracolporo pollenites* spp. (Sapotaceae, Thiem-Pfeiffer 1980, 1988; Nickel 1996) and *Labropollis laabraferus* (unknown botanical affinity). All other sporomorphs are relatively evenly distributed and only occasionally reach frequencies above 2% (Figs 3a and 4a).

The studied part of the Messel 2001 core is characterized by distinct changes in frequency of the coccal green alga *Botryococcus*. Whereas it occurs in huge numbers between 26.5 and 24.75 m, around 23 m and between 21.0 and 19.5 m, it is completely absent between these depths (Fig. 3). Compared with the distribution of *Botryococcus* throughout the whole Middle Messel Formation, the distribution in the studied segment of the core fits to the transition from a lack of *Botryococcus* between 94 and 26 m in the whole core to a permanent mass occurrence of *Botryococcus* in its uppermost 15 m (Lenz et al. 2011). The almost complete lack of *Botryococcus* in the OSB samples (Fig. 4) fits to the fact that the OSB correlates to a *Botryococcus*-free part of the Middle Messel Formation in the Messel 2001 core between c. 24 and c. 23 m (see Fig. 3).

*B. botryococcus* today has an almost cosmopolitan distribution under very different climatic conditions, but optimal growth conditions have been recorded from shallow lakes at low precipitation (Guy-Olson 1992; Batten & Grenfell 1996). The variability in the distribution of *Botryococcus* in the studied segment of the core can therefore be interpreted in terms of a transition between fully humid and less humid conditions as observed during the Middle Messel Formation (Lenz et al. 2011), which may have been connected to periodic lake-level fluctuations.

Although frequency fluctuations of *Botryococcus* are evident in the core segment, the question remains whether the observed frequency fluctuations of the other palynomorphs are truly significant or due to regular background variations in the pollen rain. Considering the pollen diagrams in which the frequency classes of Gauch (1982) are plotted (Figs 3b and 4b), it becomes obvious that slight but significant short-term frequency fluctuations of the mass pollen *P. plicatus* become obvious only in the OSB (Fig. 4b). Because they remained unaffected by the short-term climate changes *T. liblarensis* + *T. cingulum* are not significant for most of the studied sections and therefore not suited for the analysis of sub-Milankovitch cycliclity. However, all other taxa show at least some significant fluctuations that are more emphasized by assigning the percentage values to frequency classes (Fig. 3b).

**Principal component analysis**

Our interpretation of the pollen diagrams is supported in detail by principal component analysis (PCA) including 43 taxa or groups of taxa from 102 samples for the core segment and 48 taxa or groups of taxa out of 91 samples for the OSB.

The bivariate plots for the core segment show that samples that plot on the positive side of PCA axis 1 (eigenvalue: 8.19, 18.99% of total variance) are clearly separated from a large group of samples that plot on the negative side (Fig. 5a). This is mainly based on the presence of *Botryococcus*, which plots on the positive end of axis 1 (Fig. 5b). Typical elements of the paratropical rainforest such as the myricaceous pollen *Triatriopollenites rarensis* and *Triatriopollenites bititus* as well as *Labropollis laabraferus* of unknown botanical affinity are found on the negative side of axis 1.
A separation of samples is not obvious along PCA axis 2 (eigenvalue: 3.98, 9.24% of total variance). Nevertheless, some taxa or groups of taxa are found on the negative side of axis 2, which can be attributed to areas at the margin of the maar lake and immediately around, such as fern spores (Laevigatosporites spp., Leiotriletes spp.) as well as the sum of all spores including the rare fern and moss spores. Furthermore, typical elements of a Nyssa–Taxodium swamp forest plot on the negative part of axis 2 with Inaperturopollenites spp. (Cupressaceae–Taxodiaceae) and Nyssapollenites kruschii (Nyssaceae). Altogether a vegetation in the shallow water and swampy areas at and around the margin of the lake may be distinguished. This is supported by Ovoidites, representing cysts of the freshwater alga Spirogyra (Zygnemataceae), which today prefers shallow, stagnant, clean and oxygen-rich water in lake margin situations (van Geel & Grenfell 1996). In contrast, the positive side of axis 2 is characterized by typical elements of the surrounding forest such as Polyporopollenites spp. (Ulmaceae) and Triatriopollenites excelsus and T. excelsus minor (both Myricaceae).

The PCA of the palynological data from the OSB shows a similar picture. However, owing to the shorter timespan covered there is no clear separation of groups of samples (Fig. 6a), which indicates that there is less difference between the samples compared with the differences between the samples from the studied segment of the core. Furthermore, Botryococcus, which is responsible for the greatest variance in the core samples, is almost completely missing in the OSB.
Nevertheless, palynomorphs of plants from the margin of the lake and immediately surrounding areas such as spores (Leiotriletes spp., Laevigatosporites spp., ’sum of spores’) plot on the positive side of PCA axis 1 (eigenvalue: 3.09, 9.38% of total variance) and on the positive side of PCA axis 2 (eigenvalue: 2.9, 8.83% of total variance) and are separated from the elements of the paratropical rainforest, which can be found on the negative sides of both axes (Fig. 6b).

In contrast, the dominant elements of the palynomorph spectra of both sample sets, Plicatopollis plicatus and Tricolpopollenites liblarensis + Tricolporopollenites cingulum, do not contribute to the variance in both datasets owing to their hardly significant frequency fluctuations and have therefore not been plotted in Figures 5b and 6b.

Although the first two PCA axes reflect only 28.23% of the total variation in the core samples and only 18.2% in the OSB samples, scree plots of the PCA analyses (Figs 5a and 6a) indicate that not more than two principal components are significant in both datasets. These relatively low values for total variation can be ascribed to the great number of taxa and frequent 0% values in the datasets. Furthermore, these low values indicate that both records are uniform and only few elements such as fern spores show a distinct response to environmental or climatic changes.

**Time series analyses**

Based on the pollen diagrams and the results of the PCA a number of palynomorph taxa can be identified that show relatively strong...
frequency variations in both sample sets from the Middle Messel Formation and thus contribute to the greatest variance in the dataset, such as the various fern spores. This led to a total of 26 taxa (or groups of taxa), which were selected for time-series analyses (Tables 1 and 2). The results from eight of them are presented in Figures 7 and 8.

Significant and partly significant cycles have been assigned to nine cycle groups. Based on the median values three millennial-scale cycles with cycle lengths of c. 19, c. 7.4 and c. 1.64 kyr have been identified only in the studied segment of the core (Table 1). On the other hand, the centennial-scale cycles with lengths of c. 7.4, c. 2.3 kyr may be distinguished in both sample sets (Tables 1 and 2).

All nine cycles are characterized not by a single strong signal but by broadened peaks or a range of peaks with an average cycle length. This frequency variation is described with measures for location and spread in Table 3.

**Discussion**

**Significance of the Messel sub-Milankovitch cycles**

Many of the cycles that are identified as significant in the time series of the core segment and the OSB hardly reach or exceed the 95% confidence line and only a few signals exceed the 99% significance level, which defines a highly significant cycle. Nevertheless, it must also be considered that owing to its natural variability, which may be produced by local, non-climatic disturbance, occasional over-representation of particular pollen types (Jacobsen & Grimm 1986) and many infrequently occurring taxa (Birks & Gordon 1985), the pollen rain contains a high level of statistical noise. In this context ‘noise’ means therefore the component of variation arising from random effects on pollen production, dispersal and deposition (Prentice 1980). This may dampen the signal strength of true periodic changes in the vegetation. Therefore, significant cycles above a confidence limit of 99% are not to be expected very often. Thus, peaks with a confidence interval (CI) >95% were considered significant cycles that are described here for Lake Messel. The timescale is normally estimated spectrum with effects such as reduction of the confidence line and only a few signals exceed the 99% confidence limit in the REDFIT analyses. Normal type indicates significant cycles above the 95% confidence limit in the REDFIT analyses. Italic type indicates cycles that are partly exceeding the 95% confidence line in the wavelet analysis.

Significance of the Messel sub-Milankovitch cycles

| Species                          | Cycle 1 | Cycle 2 | Cycle 3 | Cycle 4 | Cycle 5 |
|----------------------------------|---------|---------|---------|---------|---------|
| Botryococcus                     | 20400   | –       | –       | –       | –       |
| Emmapolli s pseudoemana          | –       | –       | –       | 2600    | 1900    |
| Inaperturopollites sreensis       | –       | –       | –       | 4800    | –       |
| Tricolporopollites excelsus      | –       | 3500    | –       | 2300    | –       |
| Tetracolporopollenites spp.      | –       | 4700    | –       | 2500    | –       |
| Labrapollis labraserus           | –       | –       | 2100    | 2300    | –       |
| Luevagaposprites spp.            | 19000   | 5600    | –       | –       | 1590    |
| Leiotriletes spp.                | 17800   | 7000    | –       | 2300    | 1630    |
| Mornipites spp.                  | –       | –       | 3700    | –       | 1450    |
| Monocolpopollonesites tranquillus| –       | 5200    | –       | 2200    | –       |
| Nyssapolli s kruschii            | –       | –       | –       | 2300    | –       |
| Pentapolli s pentangulus         | –       | –       | –       | 8400    | 2250    |
| Phytosporites labdacus           | 17900   | 6800    | –       | –       | 1640    |
| Platycaryapollonesites spp.      | 19000   | –       | –       | –       | –       |
| Plicapollis plicatus             | 23800   | –       | 3400    | 2250    | –       |
| Pterocyapollonesites stellatus   | 21400   | –       | 4400    | –       | 1760    |
| Platylongisulcites microechinatus| –       | –       | 3700    | –       | 2500    |
| Sum of spores                    | 17800   | 7300    | 3600    | 2300    | –       |
| Tetracolpopollonesites spp.      | –       | –       | 3900    | –       | 1460    |
| Triatripoll excelsus minor       | 17800   | –       | –       | 2000    | 1700    |
| Triatripoll rurensis/butitius     | –       | 9500    | 2750    | 2500    | 1740    |
| Tricolpolp. retiformis           | –       | 10200   | –       | 2400    | 1580    |
| Tricolporop. marcodorenis        | –       | 8600    | –       | 2400    | 1490    |
| Tricolporop. mircroreticulatus   | –       | –       | –       | 2400    | 1750    |
| Tricolporop. parmarulatus        | 14300   | 7500    | 4200    | –       | 1640    |
| Tricolporopollenites. satzveyensis/edmundii | 20400 | 8400  | 3600    | –       | 1830    |
| Tricolporop. sole de portai      | –       | –       | 3100    | –       | 1480    |

Cycle values in years. Bold type indicates highly significant cycles above the 99% confidence limit in the REDFIT analyses. Normal type indicates significant cycles above the 95% confidence limit in the REDFIT analyses. Italic type indicates cycles that are partly exceeding the 95% confidence line in the wavelet analysis.

Sub-Milankovitch cyclicity in the Palaeogene greenhouse world
do not follow a certain trend, they do not obscure cycles (Weedon 2003).

Nevertheless, time series of random data show that some frequencies will appear statistically significant above the 95% confidence limit just by chance (Thomson 1990). A strong argument that most of the here described cycles are more than random is that they occur independently in the majority of the 26 analysed taxa. For example, the c. 3.6 kyr, c. 2.3 kyr and c. 420 year cycles occur in 54% and the c. 210 year cycle in 84% of the studied taxa (Tables 1 and 2).

Only the significance of the c. 1.64 kyr and the c. 159 year cycles is disputable. If the sample distances of c. 700 years in the core segment and c. 70 years in the OSB are considered, both periodicities correspond to a two-sample cycle. This could indicate that this cycle is a mathematical artefact that appears statistically significant just by chance and not a true climate cycle.

**Orbital cyclicity**

Within the range of the Palaeogene greenhouse phase, the influence of orbital cyclicity in the Milankovitch range of eccentricity, obliquity and precession on the terrestrial vegetation is so far known only from frequency fluctuations in pollen assemblages from the Middle Messel Formation at Messel (Lenz et al., 2011, 2015). Eleven of the 26 studied taxa (or groups of taxa) show a partially highly significant cycle of c. 19 kyr (Table 1) in the studied core segment, which corresponds to short precession, for which a linkage to the Palaeogene climate has already been proven by several studies (e.g. Westerhold et al. 2007, 2008; Zachos et al. 2010; Lenz et al. 2011). However, a pronounced reaction of the terrestrial flora to precession-paced climate change is primarily known from Pliocene and Pleistocene records (e.g. Willis et al. 1999; Magri & Tzedakis 2000; Popescu et al. 2006; Fletcher & Sánchez Goñi 2008; Joannin et al. 2011).

It is widely accepted that changes in the orbital parameters strongly affect climate on Earth, especially by influencing the distribution and amount of incident solar energy (Zachos et al. 2001). Orbital precession in particular influences the distribution and amount of precipitation, especially with respect to seasonality (Merlis et al. 2013). However, some palaeoclimate proxy records as well as climate model simulations also suggest annual changes in mean precipitation or in net precipitation (precipitation minus evaporation) in response to orbital precession (e.g. van Vugt et al. 2001; Popescu et al. 2006; Huang et al. 2008).

The short precession cycle occurs in less than 50% of the studied taxa. This may be explained by the fact that it may have preferentially induced pronounced changes in lake level by distinct changes in humidity and precipitation. Therefore, the elements of the lake shore were especially affected, whereas much of the vegetation of the paratropical rainforest around remained unaffected.

Among the palynomorphs showing a significant precession signal in Messel, the spores of ferns are of special interest, as ferns preferentially induced pronounced changes in lake level by distinct changes in humidity and precipitation. Therefore, they would have been sensitive to fluctuations in lake

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**Table 2. Results of time series analysis of 26 taxa (or groups of taxa) from a 1 m thick oil shale block from the Eocene maar lake of Messel (OSB, 1 cm sample interval)**

| Species                        | Cycle 3 | Cycle 4 | Cycle 6 | Cycle 7 | Cycle 8 | Cycle 9 |
|-------------------------------|---------|---------|---------|---------|---------|---------|
| Botryococcus                  | –       | –       | –       | 500     | 190     | 166     |
| Emmatropollenites pseudoelemma| –       | 2600    | –       | –       | 280     | 154     |
| Inaperturapollenites spp.     | –       | –       | –       | 600     | 270     | 175     |
| Labrapollis labraferus        | –       | –       | –       | –       | 350     | 205     |
| Laevigatosporites spp.        | 3100    | –       | –       | –       | –       | 210     |
| Leionitrites spp.             | –       | 910     | –       | –       | 180     | –       |
| Moneipites spp.               | –       | –       | –       | –       | –       | –       |
| Monocolpapollenites tranquillus| –       | –       | 370     | –       | –       | 158     |
| Nyssaapollenites kruschii     | –       | –       | –       | –       | 207     | 155     |
| Pentapollenites pentangulosis | –       | –       | –       | 340     | 230     | –       |
| Pityosporites labdacus        | –       | –       | 700     | 420     | –       | –       |
| Platycaryapollenites spp.     | –       | –       | –       | 480     | –       | 172     |
| Plicapollis pseudeexcelsus    | –       | 910     | –       | –       | 290     | –       |
| Plicatopollis plicatus        | –       | 2800    | 1000    | 580     | 202     | –       |
| Pierocaryapollenites stellatus| –       | –       | –       | –       | 180     | 161     |
| Punctilongisulcites microechinatus| –   | –       | –       | 460     | 245     | 150     |
| Sum of spores                 | –       | –       | –       | 800     | 200     | –       |
| Tetracolporopollenites spp.   | –       | –       | 1200    | 510     | 191     | –       |
| Triatriopoll. excelsus minor  | 3400    | –       | –       | –       | 230     | –       |
| Triatriopoll. rurensis/bituitus| –       | –       | –       | 360     | 210     | 160     |
| Tricolporop. retiformis       | –       | –       | –       | 350     | 220     | –       |
| Tricolporop. marcodauensis    | –       | –       | –       | 380     | –       | 155     |
| Tricolporop. microreticulatus | –       | –       | –       | –       | –       | 265     |
| Tricolporop. parvularius      | –       | –       | 870     | –       | –       | 270     |
| Tricolporopollenites. satzveyensis/edmundii| –   | –       | –      | 580     | 340     | 160     |
| Tricolporop. sole de portai   | –       | –       | –       | 730     | 295     | –       |

Cycle values in years. Bold type indicates highly significant cycles above the 95% confidence limit in the REDFIT analyses. Normal type indicates significant cycles above the 95% confidence limit in the REDFIT analyses. Italic type indicates cycles that are partly exceeding the 95% confidence line in the wavelet analysis.
Fig. 7. Time series analyses of characteristic palynomorphs from the core segment between 26.97 and 16.68 m depth (102 samples) and the oil shale block (OSB, 91 samples). (a) *Botryococcus* (green alga); (b) sum of spores (sum of all trilete and monolete fern and moss spores); (c) *Inaperturopollenites* spp. (Taxodiaceae); (d) *Pityosporites* sp. (Pinaceae). Continuous wavelet time–frequency spectra (Morlet wavelets) of abundance class values are shown on the left (core segment) and on the right (OSB) side. To reduce wraparound effects, the time series are padded with zeros. Therefore, the cone of influence indicates the region where boundary effects are present. Bold contours correspond to power that is significant at 95% confidence level. Significant periods are marked by dotted lines. The numbers point to the respective significant cycles of the REDFIT periodograms. In the periodograms (middle top: core segment; middle bottom: OSB) significant peaks passing the 95% (lower line) or 99% (upper line) Monte Carlo corrected confidence interval are indicated by frequency and periodicity values. Numbers in grey boxes quote the oversample/segment numbers, which are used to reduce red noise.
Time series analyses of characteristic palynomorphs from the core segment between 26.97 and 16.68 m depth (102 samples) and the oil shale block (OSB, 91 samples). (a) Punctilongisulcites microechinatus (Hydrocharitaceae); (b) Triatriopollenites rurensis/bituitus (Myricaceae); (c) Pentapollenites sp. (unknown parent plant); (d) Tricolporopollenites parmularius (Eucommiaceae). Continuous wavelet time–frequency spectra (Morlet wavelets) of abundance class values are shown on the left (core segment) and on the right (OSB) side. To reduce wraparound effects, the time series are padded with zeros. Therefore, the cone of influence indicates the region where boundary effects are present. Bold contours correspond to power that is significant at 95% confidence level. Significant periods are marked by dotted lines. The numbers point to the respective significant cycles of the REDFIT periodograms. In the periodograms (middle top: core segment; middle bottom: OSB) significant peaks passing the 95% (lower line) or 99% (upper line) Monte Carlo corrected confidence interval are indicated by frequency and periodicity values. Numbers in grey boxes quote the oversample/segment numbers, which are used to reduce red noise.
level and changes in humidity. A temporary rise of the lake level owing to an increase in precipitation could therefore have resulted in more extended swampy areas supporting ferns. The Pinaceae (Pityosporites spp.) also show a highly significant precession signal. In contrast to the plants of the paratropical rainforest they should have been better adapted to less humid conditions (Lenz et al. 2011). Therefore, they show distribution maxima when the climate became drier, whereas plants sensitive to more humid conditions were suppressed. Accordingly, this is reflected by the opposite frequency of fern spores and Pityosporites spp. in the core segment (Fig. 3b).

A precession-paced distribution is also obvious for the green alga Botryococcus with peaks in abundance during frequency maxima of fern spores and minima of Pinaceae pollen (Fig. 3b). Therefore, periodic changes of lake chemistry and higher nutrient availability owing to increased precipitation during times of higher seasonality and more extended areas of shallow water are considered as possible causes for a precession-paced accumulation of Botryococcus. However, the PCA of the samples from the core segment (Fig. 5) shows that Botryococcus and swamp elements are uncorrelated although the distribution of both is influenced by precipitation. Nevertheless, strong seasonal nutrient supply in the lake affected only the pelagic environment and induced blooms of Botryococcus (Tyson 1995; Batten 1996; Sarmaja-Korjonen et al. 2006), whereas the vegetation at the edge of the lake was unaffected during these short periods.

**Solar activity**

Both solar cycles and centennial- to millennial-scale variations of ENSO are considered as possible causes for the other significant cycles in the core and OSB records. Varve analyses from the oil shale of Messel have already proved interdecadal and multidecadal variations with periods of 10–11 and 17–25 years, as well as around 50 and 80 years (Lenz et al. 2011), which correspond to solar variations such as the Schwabe cycle (11 years), the Hale cycle (22 years) and the Gleissberg cycle (80–90 years). Therefore, an influence of solar activity on the climate and thus on the vegetation in Messel can be assumed.

In the OSB record centennial-scale variations with cycles of 210, c. 420 and c. 890 years are found that are also known from Neogene and Quaternary records and have been considered to represent centennial-scale solar cycles. For example, a c. 208 year cycle (De Vries or Suec cycle) is documented in various Holocene and Pleistocene records and commonly believed to be one of the most pronounced solar cycles (Damon & Sonett 1991; Stuiver & Braziunas 1993; Wagner et al. 2001). Several studies have shown that this quasi-200 year cycle may have a climate response in various parameters such as temperature, precipitation or atmospheric and oceanic circulation (Raspopov et al. 2008) and is, for example, related to periods of drought in Central and North America (Yu & Ito 1999; Hodel et al. 2001). Evidence for climatic and solar variations related to the De Vries cycle has not only been found in Holocene and Pleistocene records (e.g. Wagner et al. 2001; Prasad et al. 2004) but was also reported for various proxies from the late Miocene Pannonian Lake (Kern et al. 2012).

The longer centennial-scale cycles of c. 420 and c. 890 years that are found in the OSB record almost match frequencies of 500–550 and 1000 years, which have been reported from Holocene and Pleistocene records and were linked to solar activity by Stuiver et al. (1995) and Chapman & Shackleton (2000). In particular, the c. 1000 year cycle, which is known from the Holocene in the GISP2 δ¹⁸O record (Stuiver et al. 1995), the atmospheric Δ¹³C record (Stuiver et al. 1998; Nederbragt & Thuro 2005) and varied sequences in the Santa Barbara Basin (Nederbragt & Thuro 2005), was attributed to solar activity as an external forcing of climate change (Nederbragt & Thuro 2005). Both cycles are also significant in the Miocene Pannonian Lake (Kern et al. 2012). The results of our study now indicate that both unnamed centennial-scale cycles as well as the De Vries cycle were already significant and strongly expressed in Palaeogene times, indicating that they are not linked to a specific climate system such as greenhouse or icehouse.

Among the millennial-scale variations that are significantly expressed in the core and in the OSB mainly the c. 2.3 and c. 7.4 kyr cycles are considered as solar in origin. The so-called Hallstatt cycle (2.1–2.5 kyr) modulates the c. 200 year de Vries cycle (Damon & Sonett 1991), indicating a close correlation of the various solar cycles, but was so far only known from Holocene (Damon & Sonett 1991; Charcátová 2000; Nederbragt & Thuro 2005; Debrt et al. 2007), Pliocene (Kloosterboer-van Hoeve et al. 2006) and Miocene (Kern et al. 2012) records. Our analyses now show that the Hallstatt cycle, for which a link to wind stress and variations in humidity or aridity is indicated (Nederbragt & Thuro 2005), already existed in the Palaeogene.

The c. 7.4 kyr cycle from the core segment almost matches a cycle of c. 6 kyr, which can be identified in reconstructed numbers of sunspots (Xapsos & Burke 2009). However, the impact of this Xapsos cycle on climate and vegetation remains unknown. A slightly longer cycle of 10 kyr, which influenced precipitation and soil moisture (and therefore implies changes in the vegetation), is known from the Pliocene of Ptolemais (Greece) (Kloosterboer-van Hoeve et al. 2006), but it has been linked to atmosphere–ocean interactions in the North Atlantic (Kloosterboer-van Hoeve et al. 2006) not necessarily based on solar influence. For the Eocene, comparable depositional cycles of c. 10 kyr indicate millennial-scale fluctuations of lake levels in the Green River Formation in North America (Pietrus et al. 2003; Machlus et al. 2008). However, these cycles were probably linked to orbital forcing (half-precession cycle) and not to solar activity (Pietrus et al. 2003).

Nevertheless, the centennial-scale variations and the Hallstatt cycle in the palynomorph record at Messel may indicate a strong influence of solar activity on the vegetation. The maar lake was an ideal trap reflecting the influence of solar activity, as sea and lake levels are particularly sensitive to its variations (Yousef 2006; Bruckman & Ramos 2009). This is due to the fact that precipitation can be affected by solar activity via cosmic rays stimulating cloud formation (Friis-Christensen & Svensmark 1997). However, the response of precipitation to solar forcing is more complicated as compared with a temperature response, because precipitation intensity depends on changes in the atmospheric circulation and physical and chemical conditions of the atmosphere (Raspopov et al. 2008).

| Cycle | Cycle 1 | Cycle 2 | Cycle 3 | Cycle 4 | Cycle 5 | Cycle 6 | Cycle 7 | Cycle 8 | Cycle 9 |
|-------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| Mean (in years) | 19,055 | 7608 | 3672 | 2343 | 1656 | 890 | 438 | 231 | 160 |
| Median (in years) | 19,000 | 7400 | 3600 | 2300 | 1640 | 890 | 420 | 210 | 159 |
| Standard deviation (SD) | 2456 | 1482 | 604 | 203 | 137 | 160 | 99 | 42 | 8 |
| Standard error (SE) | 740 | 428 | 151 | 44 | 33 | 57 | 25 | 8 | 2 |

Table 3. Measures of location (mean, median) and spread (standard deviation, standard error) for the nine significant sub-Milankovitch cycles from the maar lake of Messel
Significant solar-cycle-related changes in lake level as well as in lake ecology have been documented for the Holocene (e.g. Vos et al. 1997; Yousef 2006; Di Rita 2011) and the Miocene (Kern et al. 2012). They were mainly linked to decadal and multidecadal solar cycles such as the Schwabe cycle (e.g. Yousef 2006). However, it is documented that longer solar cycles have also affected lake levels. For example, Stager et al. (2005) recognized a relationship between solar variability and centennial-scale fluctuations in the level of Lake Victoria, Central Africa, during the last millennium, and Garcin et al. (2006) for the last 45 kyr in Lake Masoko, Tanzania, whereas Magny (1993) showed that fluctuations of lake levels in the Jura and French Subalpine Ranges followed the 2.3 kyr Hallstatt cycle. It is therefore not surprising that palynomorphs of elements from the vegetation of the lake margin such as various fern spores, pollen of aquatic plants such as Hydrocharitaceae (Punctilongisulcites microechinatus) or palm pollen (Monocolopollenites tranquillus) show significant centennial- and millennial-scale cycles in the core and OSB records at Messel (Table 1). Surprisingly, some palynomorphs most probably originating from plants of the surrounding paratropical rainforest, which should not have been directly influenced by lake-level fluctuations, also show significant centennial- and millennial-scale cycles. This is true for some juglandaceous pollen (e.g. Plicatopollis plicatus, Platycarycopollenites spp.), whereas pollen of other Juglandaceae such as Pterocarycopollenites spp. does not show these cycles. This indicates a complex behaviour of the vegetation including different responses of single taxa to changes in precipitation as caused by solar activity.

Pollen of Pinaceae as represented by Pityosporites spp. is also characterized by significant centennial cycles around 500 years as well as by the Xapsos cycle. Because their parent plants most probably flourished in the hinterland their variations in frequency may therefore not only reflect changes in precipitation and/or humidity but also include a component related to wind intensity and direction, which may have influenced pollen transport to the site. Kern et al. (2013) assumed that these effects may also be linked to the influence of solar cycles because changing wind intensity and direction could be due to a feedback mechanism between cosmic rays and cloud formation (Friis-Christensen & Svensmark 1997).

However, the strength of the relationship between solar activity and the Earth’s climate as well as the respective response of the vegetation is still contentious. For example, Telford et al. (2015) demonstrated that many records from the Holocene do not show a significant influence of solar activity and concluded that this is a strong indication for the fact that either the solar cycles have limited influence on the Earth’s climate or solar forcing is effective only in geographically limited regions.

**Evidence for an Eocene Super ENSO?**

Most of the significant cycles that can be recognized at Messel correspond to solar cycles as known from the Holocene. However, varve analyses of the laminated oil shale from the Middle Messel Formation clearly show the influence of an Eocene ENSO, as the significant biennial and decadal components of the time series are almost identical to modern variations of ENSO (Lenz et al. 2010). Furthermore, the significant interdecadal and multidecadal variations in the oil shale that are comparable with known solar cycles such as the Schwabe and Gleissberg cycles (Lenz et al. 2010) also show similarities to the modern Pacific Decadal Oscillation (PDO, Mantua et al. 1997) or Northern Pacific Oscillation (NPO, Gershunov & Barnett 1998), which are both characterized by variations between 17 and 28 years (Biondi et al. 2001) as well as 50 – 70 years (Minobe 1997). Gershunov & Barnett (1998) proved that the PDO has a modulating effect on the climate patterns resulting from ENSO, which does not necessarily mean that the PDO controls ENSO, but rather that both interact with each other. Therefore, comparable climate patterns could have existed in Eocene times, especially as Huber & Caballero (2003) were able to model a robust ENSO for the Eocene. Accordingly, centennial- and millennial-scale ENSO variations as proven for the Quaternary (Moy et al. 2002; Stott et al. 2002; Turney et al. 2004), may have occurred in the Eocene as well.

Today, ENSO has effects on the global climate mainly on the annual to decadal scale by its oscillation in a 2 – 7 year rhythm (Rasmussen et al. 1990), but for the Quaternary (sub)millennial-scale ENSO-related cycles have also been described. For example, the c. 890 year cycle from Messel approximately matches the c. 1000 year cycle that has been described by Heusser & Sirocko (1997) for the past 24 kyr in southern California. The 1470 year cycle, which is the most important millennial-scale cycle of the Quaternary and is known as Bond cycle in the Holocene (Bond et al. 1995) and represented by Dansgaard–Oeschger events in the Pleistocene (Schulz 2002), has been related to ENSO by some researchers (e.g. Turney et al. 2004). A similar 1500 year cycle is known from the Miocene and has been interpreted as an ‘Earth-system-immanent-cycle’ independent from solar forcing (Kern et al. 2012). The 1.64 kyr cycle from the core segment may correspond to this cycle; however, this should be treated with caution because of the proximity to the Nyquist frequency, which is generally regarded as a frequency of twice the sampling distance (Weedon 2003).

The 3.6 kyr cycle of the core record matches a quasi-periodicity of climate variability between 2.5 and 4.0 kyr, which has been described for the past 25 kyr from Southern Africa and was interpreted in terms of changes in the frequency of wetter and drier conditions (Holmgren et al. 2003). A non-linear response to the precession cycle as described by Pestaix et al. (1988), solar forcing or millennial-scale teleconnections of an ENSO-like character have also been suggested as possible explanations for these climate variations (Holmgren et al. 2003). Furthermore, millennial-scale fluctuations of ENSO with a periodicity of c. 3 kyr were identified by Horikawa & Ito (2004) in Pleistocene shelf successions from Japan.

Considering the varve analyses showing annual to decadal variations of ENSO and PDO (Lenz et al. 2010), the occurrence of the c. 890 year cycle in the OSB record as well as the c. 1.64 and c. 3.6 kyr cycles in the core record may suggest an influence of annual- to millennial-scale ENSO effects on the vegetation around the Eocene lake at Messel. As a consequence, the millennial-scale variations at Messel could be described as an Eocene ‘Super ENSO’; the term ‘Super ENSO’ was introduced by Stott et al. (2002) for millennial-scale patterns of ENSO in the Quaternary to distinguish them from the modern short-term ENSO.

Nevertheless, an unequivocal assignment of the centennial- and millennial-scale cycles from Messel to solar activity or atmosphere–ocean interaction such as ENSO is difficult because solar and geomagnetic modulation of the cosmic-ray flux and variations in ocean circulation act in overlapping time domains and are not always independent of each other (Stuiver & Braziunas 1993; Wiles et al. 2004). At least for the Holocene the interaction of ENSO as well as PDO and solar activity has been described (Stuiver & Braziunas 1993). Therefore, an interaction of both climate driving mechanisms may probably have led to climate variability in the Eocene at Messel.

**Vegetation response to sub-Milankovitch cyclicity in Messel**

As is to be expected for the relatively short time series of 6.3 and 70 kyr from a greenhouse climate there are no changes in the taxonomic composition of the vegetation. The pollen diagrams of both sample sets show quantitative changes of only some of the taxa (Figs 3 and 4). On the one hand, this may be regarded as characteristic for a stable climax vegetation; on the other, it may be
considered to be a sign of a relatively minor influence of sub-Milankovitch cyclicity on the vegetation. Nevertheless, all of the 26 analysed taxa that show significant variation in the PCA (Figs 5 and 6) reveal a distinct pattern of cyclic changes proving an influence of periodic climate variations on the vegetation at centennial and millennial scales during the Palaeogene greenhouse climate.

However, not all of the cycles are expressed in all of the taxa. This suggests that the parent plants of these palynomorphs responded differently to climate variability. This is probably due to the fact that the various palynomorphs were derived from plants occupying different habitats in the Eocene vegetation at Messel. This is proven by PCA (Figs 5 and 6), which mainly separates the elements of marginal swampy areas of the lake (e.g. ferns) and a swamp forest (e.g. Taxodiaceae, Nyssaceae) from the elements of the paratropical rainforest around. This can be interpreted in terms of humidity and precipitation mainly influencing lake level and, as a consequence, elements of the vegetation at the edge of the lake, whereas elements of the rainforest remained either unaffected or responded with delay.

Although long-term changes of the climatic conditions such as caused by short precession and longer sub-Milankovitch cycles clearly had a significant impact on the vegetation owing to changes in lake level or humidity, it is an interesting question whether there was a vegetation response to relatively short-term climate variations in a stable climax system such as the Eocene paratropical rainforest at Messel. However, it is known that sudden climate change can have a significant impact on the composition of the vegetation within a few decades owing to ‘migration’ of plant taxa even in tropical climates (Hughes et al. 2004). Furthermore, short-term reactions of the vegetation as reflected by pollen precipitation may not necessarily have been caused by changes in the quantity and/or distribution of the parent plants within the vegetation. Quantitative shifts of the pollen rain may also have been caused by climate-stress-induced alterations of flowering behaviour in plants with a corresponding change in pollen production. Stress-induced effects on flowering behaviour or seed production are well known from modern plant communities subject to anthropogenic climate change (Wada & Takeno 2010). In addition to changes in light intensity or nutrition, climate variations such as changes in precipitation or temperature can also cause stress-induced flowering (Nir et al. 1972; Hopkinson 1977; Hirai et al. 1994). Above all, variation between more seasonal and more balanced precipitation, which obviously occurred in the Eocene of Messel (Lenz et al. 2015), may have had an influence on the length of the flowering and the resting periods of tropical trees and thus on pollen production (see Borchert 1983).

Furthermore, solar activity can affect cloud formation, which has an influence on rainfall patterns and the amount of sunlight reaching the surface, which may in turn lead to changes in heating and evaporation on land and water (Frisch-Christensen & Svensmark 1997). This could influence wind activity and direction, with changes in the air-borne input of palynomorphs as possible consequences (Kern et al. 2013). This has been suggested by Kern et al. (2013) as the cause for short-term changes in the quantity of various palynomorphs as derived from the pollen rain of a subtropical to tropical vegetation from the upper Miocene of the Pannonian Lake in Austria. Here, the pollen of Pinaceae (Picea, Cathaya), Poaceae and Fabaceae are characterized by cyclic fluctuations in frequency within 80–200 years reflecting an influence of solar activity in the range of the lower (50–80 years) and upper (90–120 years) Gleissberg cycles (Kern et al. 2013).

Similar wind-induced effects may also have influenced the composition of the pollen rain at the Eocene maar lake of Messel.

Conclusions

Sub-Milankovitch cyclicity has been recognized in a paratropical rainforest around the Eocene maar lake of Messel by time series analyses of frequency data of various palynomorphs in two high-resolution studies on different scales. They clearly show that short-term climate variations can be related to solar activity or to a centennial- to millennial-scale Eocene ‘Super ENSO’.

It is striking that the nine significant sub-Milankovitch cycles from Lake Messel match cyclicties that are well known especially from Quaternary and modern archives. The centennial-scale cycles of c. 210, c. 420 and c. 890 years as well as the millennial-scale cycles of c. 2.3 and c. 7.4 kyr correspond well to solar cycles as known from Holocene records, whereas the c. 1.64 and c. 3.6 kyr as well as the c. 890 year cycles match the Holocene millennial-scale ENSO of the Pacific. Therefore, an interaction of internal and external climate forcing is suggested to account for natural climate variability even in the early Middle Eocene at Messel. Along with the evidence from the Holocene and Pleistocene, almost identical records of centennial- and millennial-scale cycles from the Pliocene (Kloosterboer-van Hoeve et al. 2006), from the Miocene (Kern et al. 2012) and from the Eocene of Messel (present study) show that this pattern of cyclic climate fluctuations represents a pervasive and persistent system not only for the modern climate and the Quaternary icehouse, but also for the entire Neogene and the Palaeogene greenhouse world. This is firm evidence for at least about 50 myr of stability in the driving forces of natural climate change on Earth.

In particular, the influence of solar activity on the climate and the environment is a complex process, especially as the mechanisms behind this are still enigmatic and poorly understood (Kern et al. 2012). However, a significant influence of solar activity on the formation of clouds is well known, and this affects patterns of precipitation and heating of the Earth’s surface, both triggering wind direction and intensity as well as humidity (Frisch-Christensen & Svensmark 1997).

The influence of an Eocene ENSO, on the other hand, is shown by a global climate model that is based on variations in sea surface temperatures (SST; Huber & Caballeri 2003). Such changes in SST distribution are accompanied by changes in the atmospheric convection, which alters the global climate via atmospheric teleconnections. Shifts of climate belts particularly involving changes of the seasonal precipitation in a monsoonal climate may have been possible consequences affecting Central Europe during the Eocene. The above-mentioned teleconnections have previously been related to an annual- to decadal-scale ‘Eocene ENSO’ variability (Lenz et al. 2010); however, they now turn out to be a manifestation of climate forcing by a centennial- to millennial-scale Eocene ‘Super ENSO’.

Nevertheless, regardless of the causes for climate change in the Eocene at Messel, (seasonal) precipitation changed in particular. This led to lake-level fluctuations directly affecting the vegetation on and immediately around the lake shore. Distinct quantitative fluctuations of the pollen rain originating from plants of the surrounding paratropical rainforest may not necessarily reflect actual changes in the quantitative composition of the rainforest, but rather stress-induced flowering behaviour affecting pollen production or wind-induced effects on pollen transport and precipitation.

The results of our study clearly suggest that fundamental climate forcing mechanisms have not changed from the Palaeogene greenhouse until today regardless of the actual climate system.

In view of the rarity of suitable terrestrial records from the Palaeogene greenhouse world our study must be regarded as an initial step in the recognition of short-term climate change in this period of time. It is necessary to identify and study more high-resolution terrestrial records from the last natural greenhouse, especially as the knowledge of natural climate change in deep time provides important information for understanding and forecasting the effects of a future anthropogenic greenhouse climate on Earth.
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