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Vegetation and climate development on the North American Atlantic Coastal Plain from 33 to 13 million years ago (IODP Expedition 313)

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Abstract

We have investigated the palynology of sediment cores from Sites M0027 and M0029 of IODP Expedition 313 on the New Jersey shallow shelf, east coast of North America, spanning an age range of 33 to 13 million years before present. Additionally, a pollen assemblage from the Pleistocene was examined. The palynological results were statistically analyzed and complemented with pollen-based quantitative climate reconstructions. Transport-related bias of the pollen assemblages was identified via analysis of the ratio of terrestrial to marine palynomorphs, and considered when interpreting palaeovegetation and palaeoclimate from the pollen data. Results indicate that from the early Oligocene to the middle Miocene, the hinterland vegetation of the New Jersey shelf was characterized by oak-hickory forests in the lowlands and conifer-dominated vegetation in the highlands. The Oligocene witnessed several expansions of conifer forest, probably related to cooling events. The pollen-based climate data imply an increase in annual temperatures from ∼ 12 °C to more than 15 °C during the Oligocene.

The Mi-1 cooling event at the onset of the Miocene is reflected by an expansion of conifers and an annual temperature decrease by almost 3 °C, from 15 °C to 12.5 °C around 23 million years before present. Particularly low annual temperatures are also recorded for an interval around ∼ 20 million years before present, which probably reflects the Mi-1aa cooling event. Generally, the Miocene ecosystem and climate conditions were very similar to those of the Oligocene in the hinterland of the New Jersey shelf. Miocene grasslands, as known from other areas in the USA during that time period, are not evident for the hinterland of the New Jersey shelf.

Surprisingly, the palaeovegetation data for the hinterland of the New Jersey shelf do not show extraordinary changes during the Mid-Miocene climatic optimum at ∼ 15 million years before present, except for a minor increase in deciduous-evergreen mixed forest taxa and a decrease in swamp forest taxa. Pollen-based annual temperature reconstructions show average annual temperatures of ∼ 14 °C during the Mid-Miocene climatic optimum. We conclude that vegetation and regional climate in the hinterland

of the New Jersey shelf did not react as sensitively to Oligocene and Miocene climate changes as other regions in North America or Europe. An additional explanation for the relatively low regional temperatures reconstructed for the Mid-Miocene climatic optimum could be an uplift of the Appalachian Mountains during the Miocene. The Pleistocene pollen assemblage probably derives from the Marine Isotope Chron 7 or 5e and shows climate conditions similar to present-day.

1 Introduction

The Eocene, Oligocene, and Miocene witnessed the transition from warmer "greenhouse" to colder "icehouse" conditions (Zachos et al., 2001a, 2008) and a decreasing global sea level (e.g., Miller et al., 2005). These changes did not occur gradually or continuously, but with several reversals to warmer conditions, as well as short phases of rapid cooling (e.g., Zachos et al., 2001a; DeConto et al., 2008). The understanding of these changes and the driving factors is mainly based on the analyses of marine climate records, while examinations integrating terrestrial proxies, such as pollen from terrestrial vegetation, are still rare (e.g., Eldrett et al., 2009; Pross et al., 2012). This is particularly the case for Eastern North America, whereas several integrated studies for Eurasia have been published during the last two decades (e.g., Mosbrugger et al., 2005; Jiménez-Moreno et al., 2005, 2007; Larsson et al., 2011).

There is general agreement that the distribution of global vegetation changed significantly during the early Oligocene, with retreat of the tropical and paratropical biomes to the lower latitudes and an equatorward expansion of temperate vegetation (e.g., Willis and McElwain, 2002). Broad-leaved forests declined, and conifer forests in the Northern Hemisphere (including North America) migrated southwards (Janis, 1993). The late Oligocene was a time of global warming and retreat of ice sheets in Antarctica (Zachos et al., 2001a, 2008). Although this warming period took place under different circumstances (e.g., absence of ice sheets in the Northern Hemisphere and different continental configurations, Zachos et al., 2001a), it can to some degree be regarded as an analogue for the present day situation of increasing atmospheric CO_2 levels presumably resulting in increasing global temperatures (Zachos et al., 2008; Kump et al., 2009).

The transition to the Miocene was characterized by a cooling pulse, the Mi-1 event (Miller et al., 1987, 1991; Wright and Miller, 1992; Zachos et al., 2001b). Subsequently, starting at ~ 20 million years before present (Ma), global temperatures increased until ~ 15 Ma (Zachos et al., 2001b), culminating in the Mid-Miocene climatic optimum between ~ 17 and ~ 14 Ma. This overall warm interval was, however, interrupted by several short cooling events (e.g., additional Mi-events; Miller et al., 1987, 1991; Pagani et al., 1999a). Furthermore, the Early Miocene witnessed the spread of biomes dominated by grasses (Poaceae; Jacobs et al., 1999; Willis and McElwain, 2002; Strömberg 2005). The loss of forest cover and spread of grass-dominated biomes during the Miocene may have weakened the biotic weathering feedback (Taylor et al., 2009) and thus contributed to the climate development from the Miocene until today (Pagani et al., 2009).

The Mid-Miocene climatic optimum was followed by a gradual cooling and ice sheet expansion during the late Miocene, while atmospheric CO_2 remained relatively stable compared to Eocene to early Miocene oscillations (Pagani et al., 2005). This cooling trend and increasing seasonality is generally reflected in pollen records from fluvial deposits from the middle Atlantic margin (Pazzaglia et al., 1997), but these records could only roughly be correlated with marine records. Pollen-based results for the same region presented by Groot (1991) are somewhat contradictory, indicating stable climate conditions at the close of the Miocene. However, the records described by Groot (1991) lack consistent age models and can thus not be compared directly with other climate archives. The late Miocene witnessed the spread of C4 plants (i.e., plants better adapted to drought and low atmospheric CO_2 concentrations; Ehleringer and Monson, 1993; Cerling et al., 1997). The triggering mechanism for this spread is still under debate (e.g., Jacobs et al., 1999; Pagani et al., 1999b).

In short, there remains a lack of studies that integrate changes in the marine realm (e.g., water temperatures and sea-level changes) and related vegetation and climate developments in the terrestrial realm during the Eocene, Oligocene and Miocene. There is a particular scarcity of such studies for Eastern North America, even though the North Atlantic Ocean plays an important role in the climate development in Eastern North America, Europe and North Africa (e.g., Pearson and Palmer, 2000).

An ideal approach for studies integrating marine and terrestrial ecosystem and climate changes is the examination of terrestrial and marine palynomorphs in marine sediments. Methods have been developed to calculate quantitative climate data (e.g., temperature, precipitation, and seasonality) from pollen assemblages. One of these methods is the "nearest-living-relative"/"co-existence" or "mutual climate range" method (e.g., Kershaw, 1997; Mosbrugger and Utescher, 1997; Utescher et al., 2009; Thompson et al., 2012; Reichgelt et al., 2013): climatic limits of fossil plant taxa are assumed to be similar to those of their nearest living relatives. Therefore, the intervals of climate parameters for a given fossil flora, in which a maximal number of nearest relatives can coexist, can be considered the best possible description of the palaeoclimate under which the fossil flora lived (Thompson et al., 2012).

The analysis of terrestrial palynomorphs from marine sediments allows a direct land-sea correlation via the comparison with marine palynomorphs and further marine proxies (e.g., Heusser and Shackleton, 1979; Kotthoff et al., 2008a, b; Eldrett et al., 2009; Pross et al., 2012). Furthermore, the ratios of non-saccate/bisaccate pollen and the ratios of terrestrial/marine palynomorphs reflect changes in terrigenous sediment influx into the marine realm, and can be used to reconstruct site-shoreline distances and sea-level fluctuations (e.g., McCarthy and Mudie, 1998; McCarthy et al., 2003). One drawback of climate and sea-level reconstructions based on marine palynomorph records is the alteration of the palynological record due to differential preservation and transport characteristics of pollen taxa. These taphonomic problems can however be minimized/controlled by (a) choosing research areas characterized by high sedimentation rates where oxidation of palynomorphs is less pronounced (e.g., Kotthoff et al., 2008a); (b) sites sufficiently proximal to the coastline to minimize transportation bias (e.g., Mudie and McCarthy, 1994); and (c) sedimentary settings that have remained tectonically stable.

These criteria have been met in the New Jersey shallow shelf area (NJSS; North American east coast, Fig. 1; Mountain et al., 2010) since the early Burdigalian when the clinoform or rollover migrated past Site 27 (Figs. 1 and 2; McCarthy et al., 2013). The potential of this region for palaeoclimate research and for sea-level reconstruction has already been shown for records from the coastal plain and the continental slope (Miller and Sugarman, 1995; Miller et al., 1996). The cores recovered from the NJSS in the framework of IODP Expedition 313 in 2009 (Figs. 1 and 2, Sites M0027, M0028, M0029) offer an excellent opportunity to execute palynological analyses.

In the light of the above, the New Jersey shelf is an ideal research area to study the palaeovegetation and palaeoclimate development in coastal Eastern North America during the Oligocene and particularly the Miocene. In the context of IODP Expedition 313, numerous proxies have been analyzed, and a robust age model was developed based on paleontological, sedimentological, and geochemical data (Mountain et al., 2010; Browning et al., 2013; Miller et al., 2013a, b). Here, we present a new pollen record from the New Jersey shelf, covering the interval from ~ 33 to ~ 13 Ma, complemented with a pollen assemblage from Pleistocene sediments. With this record, we can reconstruct a longer and more continuous history of the vegetation and climate development during this interval than could earlier palynomorph-based examinations for coastal Eastern North America.

2 Geographical and geological setting

Hole M0027A was drilled into the New Jersey shallow shelf at 39°38.046′ N and 73°37.301′ W at 33.5 m water depth and a site-shoreline distance of ~ 50 km (Fig. 1). The total penetration reached 631 mbsf, with a drilled interval of 547 m. The hole was aimed at sampling a thick early Miocene succession, but relatively thin and incomplete

Pleistocene, late to middle Miocene and Oligocene sediments were also recovered. No Pliocene sediments were found (Mountain et al., 2010).

The modern annual precipitation in the coastal regions of New Jersey is ~ 1100 mm, and average annual temperatures are ~ 12 °C (climate.rutgers.edu/stateclim/). The modern- vegetation of New Jersey is dominated by oak-pine forests (deciduous forest of Davis and Webb, 1975). Southwards, oak-hickory-pine forests are dominant (Davis and Webb, 1975).

3 Material and methods

3.1 Age model

The age model for Site M0027 is based on integrated microfossil biostratigraphy (dinoflagellate cysts, diatoms, calcareous nannofossils), strontium isotopes, and sequence stratigraphy (e.g., Browning et al., 2013; Miller et al., 2013a, b). According to the age model, the lowermost part of the record could be Priabonian. Pronounced hiatuses occur during the early Rupelian, and most of the Chattian and Aquitanian. However, Site M0027 yields continuous records for the late Rupelian (~ 29.3 to ~ 28.2 Ma), the very late Chattian and transition to the Aquitanian (~ 23.5 to ~ 23 Ma), the early Burdigalian (~ 20.9 to ~ 19.2 Ma), and, with some shorter hiatuses, the late Burdigalian to early Serravallian (~ 18 to ~ 13.2 Ma) (Miller et al., 2013b). Additionally, material was recovered for the very early Rupelian (possibly also the late Priabonian) and for the Pleistocene, probably marine isotope chron (MIC) 7 or MIC5e (Miller et al., 2013a).

3.2 Processing and counting

Sediments of ~ 5 cm^3 volume, equivalent to ~ 8 g weight, were processed for palynological analysis at Brock University using standard techniques, including treatment with warm, dilute (0,02 %) sodium hexametaphosphate, weak (10 %) HCl and concentrated HF, and sieving through Nitex mesh to retain the > 15 µm fraction. Samples were mounted on glass slides using glycerine jelly. Palynomorphs were identified at 400×/500× magnification using a Zeiss AxioScope, or under oil immersion at 1000× magnification for verification where necessary.

Seventy-seven samples from Site M0027 were analyzed for their palynomorph content. We differentiated between ∼ 70 pollen types. Since the time interval analyzed covers ∼ 33 to ∼ 13 Ma together with one sample from the Pleistocene, we have generally assigned the pollen grains to extant botanical groups if possible. This approach allows the reconstruction of the palaeoecology and the application of techniques useful for palaeoclimate reconstructions (cf. Jiménez-Moreno et al., 2005; Larsson et al., 2011). In the framework of another study (Fang et al., 2013), 35 additional samples from Site M0029 were analyzed with similar methods. Since Site M0029 is characterized by a particularly thick middle Miocene succession, we have incorporated the palynological results of seven samples from this site in our study. In addition to pollen grains, plant spores, fungal remains, foraminifer test linings, and dinoflagellate cysts (dinocysts) were counted. We used the total number of non-saccate pollen grains as reference sums for all percentage calculations (Figs. 2 and 3). The data used for this study will be stored in the PANGEA database.

3.3 Transport validation

Due to the particularly efficient airborne transport, longer floating time in the water column and high resistance to oxidation, bisaccate pollen is generally over-represented in marine pollen assemblages and shows significant relative increase compared to other pollen types with increased distance from the coastline (e.g., Mudie, 1982; Mudie and McCarthy, 1994; McCarthy et al., 2003; Kotthoff et al., 2008a). It has been shown that terrestrial modern pollen assemblages in Eastern North America, including coastal and continental shelf sediments, reflect the modern vegetation with exception of the genera *Pinus* (pine) and *Picea* (spruce), whose bisaccate pollen often originate from very distant regions (e.g. Davis and Webb, 1975; Mudie, 1982). In light of this, we have excluded bisaccate pollen from the reference sum on which pollen percentage calculations and climatic analyses are based. However, high percentages of bisaccate pollen, e.g., *Pinus* pollen, are not necessarily tied to transport effects (Hooghiemstra, 1988); they can certainly also be related to climate-based changes in hinterland vegetation and, as shown for the Pleistocene by Lacourse et al. (2003) and Kotthoff et al. (2008a), increased *Pinus* pollen percentages can also be related to extension of *Pinus* forests onto shelfal areas during sea-level lowstands. Herein, we use estimates of the site-shoreline distance based on the ratio of non-saccate pollen to marine palynomorphs (dinocysts, acritarchs, and foraminifer test linings) to validate the relevance of high bisaccate-pollen percentages, assuming that over-representation of bisaccate pollen is lower in samples with small relative abundances of dinocysts and foraminifer test linings. This approach attempts to identify "real" peaks in bisaccate pollen and thus discover changes in conifer-forest development. Transport-related bias can to a lesser degree also influence nonsaccate pollen assemblages. For example, it appears likely that high percentages of large, nonsaccate grains like *Carya* (hickory; Plate 1), in some cases represent downslope mass transport prior to progradation of the shelf break past Site M0027 (McCarthy et al., 2013). Comparison of the percentages of large nonsaccate grains, such as *Carya* (hickory), *Tilia* (linden), *Nyssa* (tupelo), and *Fagus* (beech), i.e. taxa indicating slightly different environmental parameters, can to some degree be used to overcome this problem. A detailed review of the marine and terrestrial palynology at Sites M0027 and M0029, including transportation effects, is given elsewhere (McCarthy et al., 2013).

3.4 Pollen differentiation

For pollen identification, we used several works of Krutzsch (1963a, b, 1967, 1970, 1971) and also descriptive publications and pollen keys of, e.g., McAndrews et al. (1973), Frederiksen (1979, 1980), Traverse (1994), Pazzaglia et al. (1997), Beug (2004), and Jarzen et al. (2010). We have counted pollen of *Podocarpus* (i.e., *Podocarpidites*) separately, however, it should be noted that *Podocarpus* grains are very similar to *Pinus* grains and cannot be distinguished in all cases. Both genera contain several species that are very variable in pollen morphology, and the palynomorph *Podocarpidites* includes both “*Podocarpus*” as well as *Pinus* (Nichols and Brown, 1992), and may also represent related genera in the Podocarpaceae and not *Podocarpus* sensu strictu (Greenwood et al., 2013). The genus *Pinus* was particularly rich in species in North America throughout the Cenozoic (e.g., Stults et al., 2010). During the counting process, we have separated *Pinus* grains into two types (compare Sect. 4.2.1), one type comprising species with smaller grains and relatively larger sacci.

We have aimed at a differentiation between different *Tsuga* pollen types. Several authors distinguish numerous *Tsuga* (*Zonapollenites*) species for the Miocene (e.g., Krutsch, 1971), but we decided to assign *Tsuga* pollen grains to three types similar to present-day species. While *Tsuga mertensiana* pollen can be separated from other *Tsuga* species by its bisaccate morphology, present-day *T. canadensis* and *T. heterophylla* pollen (Fig. 4) cannot easily be discriminated. Both are monosaccate, verrucate and characterized by an encircling frill-like structure. We used a more differentiated “frill” and the presence of microechinate processes on the muri to assign monosaccate *Tsuga* grains to the *T. heterophylla* type, following e.g. White and Ager (1994) and Barnett (1989).

Arecipites, other Arecaceae and the “*Monocolpopollenites* type” were counted separately, but grouped together as “monocolpate” for the pollen diagram (Fig. 5). The differentiation of *Arecipites*-, *Monocolpopollenites*- and *Liliacidites*-related pollen grains is a matter of debate, e.g., there is uncertainty concerning the presence of *Arecipites* grains with reticulate structure (compare Krutzsch, 1970; Nichols et al., 1973). We have followed the approach of Krutzsch (1970) and in some cases assigned monocolpate grains with a fine reticulate structure (compare Fig. 4) to *Arecipites,* but grains with a reticulum formed of clearly visible clavae and baculae were assigned to *Liliacidites* (e.g., Nichols et al., 1973). Generally, the morphology of Arecaceae pollen grains is highly diverse (e.g., Harley and Baker, 2001). Grains assigned to “other Arecaceae” were mainly monocolpate, in rare cases monoporate. Our conservative approach to identifying palm pollen in the New Jersey record may have yielded cooler temperature estimates for some samples due to palms being not identified as such, but as *Liliacidites*.

Taxodium pollen was differentiated from other inaperturate pollen types, but particularly when pyrite grains were present inside the pollen grains (compare Sect. 4 and Fig. 4), the identification was hampered, so that in some samples, *Taxodium* pollen may have been assigned to the “other inaperturate pollen type”. Therefore, in the pollen diagram (Fig. 5) pollen of the *Inaperturopollenites* type was grouped together with *Taxodium* and *Cupressacites* due to the morphological similarities of these pollen types (see also Larsson et al., 2011). Inaperturate grains were assigned to *Sequoia* when a long papilla was preserved (e.g., Krutzsch, 1971), in contrast to the shorter, often invisible papilla present in *Taxodium* and related taxa. The differentiation of *Sequoia* pollen is important since this taxon is not directly associated with swamps, unlike *Taxodium* and *Cupressacites*. Therefore *Sequoia* is associated with the conifer forest type, and not with the swamp/wet forest type (see Fig. 6).

While it is generally possible to distinguish *Nyssa* pollen grains from *Fagus* pollen grains (e.g., McAndrews et al., 1973; Traverse, 1994; Beug, 2004), the differentiation was hampered in a few samples with slightly degraded pollen or pollen grains filled with pyrite (see Fig. 4). We have nevertheless decided to aim at a differentiation, since *Nyssa* is rather associated with swamp vegetation, while *Fagus* is characteristic of mid-latitude deciduous forests.

We differentiated several *Quercus*/*Quercoidites* pollen types, proposing that smaller *Quercus* pollen with more rugulate structure may be related to modern red-oak taxa such as *Quercus incana* (“Bluejack Oak”), which is an understorey taxon adapted to dry and sandy soils, while bigger grains with a scabrate surface (Fig. 4) may be more closely related to large, arboreal forms such as modern *Q. alba*. While doubting that present-day red and white oaks can be separated via light microscopy, Solomon (1978) also points to the generally rugulate structure of red oak pollen in contrast to white oak pollen. For Fig. 5, we have assigned the identified types to two groups, with *Quercus*

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type A containing smaller and sometimes rugulate grains in contrast to bigger, never regulate grains. *Zelkova* and *Ulmus* were not separated and all counted as *Ulmus*.

Generally, we have applied names of modern pollen types to the grains encountered. This approach is justifiable: While palynological studies for the Palaeocene and Eocene of Eastern North-America revealed nowadays extinct species, and taxa that cannot be undoubtedly related to modern taxa (e.g., Frederiksen, 1979, 1991; Nichols and Brown, 1992), most modern genera were already established during the Oligocene and particularly the Miocene and identifiable from pollen (e.g., *Fagus*; Denk and Grimm, 2009), and have previously been used for palaeoclimate reconstructions (e.g., Groot, 1991; Eldrett et al., 2009).

3.5 Vegetation types

To analyze changes in ecosystems in the hinterland of the New Jersey shelf, we have assigned the pollen and spores encountered in this study to groups based on the modern ecology of related genera (Table 1), following similar approaches of, e.g., Jiménez-Moreno et al. (2005) and Larsson et al. (2011). While we have not assigned the same taxa to different vegetation types, several of the taxa mentioned in Table 1 can occur in different ecosystems. For example, the tupelo tree (*Nyssa*) is present within several vegetation types in recent South-Eastern North America; however, *Nyssa* is particularly frequent in swamp associations due to its tolerance of wet soils and is therefore best placed into the swamp forest vegetation type. Similarly, Cupressaceae, including *Taxodium*, occur in a variety of environments, but the majority of North American species rather prefer wet conditions and include swamp taxa. Generally, the assignment to vegetation types allows a clearer interpretation of the pollen data and comparison with other palaeobotanical records.

3.6 Statistical methods

Since the assignment to certain vegetation types can in some cases be arbitrary, the pollen dataset was subjected to principal component analysis (PCA) to identify characteristic pollen associations statistically (Fig. 6) and compare them to assumed vegetation types (See Sect. 3.5). In this type of analysis, the number of variables of the dataset is reduced via the extraction of uncorrelated axes (the principal components). In Q-mode, the inclusion of a taxon in a principal component is set by its score value and the value of the component on a sample by its loading. The explained proportion of the total variance of the data matrix can be calculated for each new component. For further details on the methodological aspects of PCA see Leyer and Wesche (2007). In case of the dataset for Site M0027, bisaccate pollen was excluded from the analyses due to its over-representation in the pollen record. Analyses were run separately for the Oligocene, early Miocene, late Miocene, and for all samples combined. In a first set of analyses, covering only a part of the record, several *Quercus* pollen types were differentiated. These analyses suggested that small, rugulate *Quercus* pollen was a significant part of an "understorey factor" containing herbaceous forms and/or Ericaceae. However, with the complete record, this signal was not as clear and the different *Quercus* pollen types dominated several components and suppressed signals of other taxa. Generally, the assignment to different *Quercus* types is problematic due to the large number of Miocene types (e.g., Liu et al., 2007). The PCA analysis depicted in Fig. 3 and discussed in Sect. 4.3 is thus based on a dataset with combined *Quercus* pollen.

3.7 Quantitative climate reconstructions

Climate was reconstructed by applying bioclimatic analysis (Kershaw, 1997 as modified by Greenwood et al., 2005; Reichgelt et al., 2013), a form of "nearest living relative" (NLR) analysis or mutual climate range technique (Thompson et al., 2012) to the spore-pollen record of land vegetation. Spore and pollen taxa with known NLR were identified from the fossil assemblages. Climatic profiles were then assembled from both published and unpublished sources for each NLR with respect to various climate parameters such as mean annual temperature (MAT), coldest month mean temperature (CMMT), warmest month mean temperature (WMMT), and mean annual precipitation (MAP). Each profile contains the maximum and minimum values for a range of climate and related environmental variables with respect to an individual NLR taxon, based on their present-day distribution. For this study, the majority of climate profiles were obtained from Thompson et al. (1999, 2000, 2012) for trees and shrubs, and the online database of Natural Resources Canada (2012) for non-trees, supplemented by data from sources outlined in Pross et al. (2012) and Reichgelt et al. (2013).

To determine the climate envelope that accommodated a majority of taxa from a given fossil assemblage with respect to a given climate parameter, the zone of overlap was calculated using the 10th percentile (as lower limit) and 90th percentile (as upper limit) of the total range for all NLRs represented in that sample (Greenwood et al., 2005; Reichgelt et al., 2013). This calculation removes or down-weights outliers; NLR taxa whose climate profile is at the extremes of the range of all taxa in the assemblage and is comparable to the weighted MCR method of Thompson et al. (2012). The estimate in bioclimatic analysis is presented as the midpoint between the lower and upper limits, with the error spanning from the lower to the upper limit (Greenwood et al., 2005; Pross et al., 2012; Thompson et al., 2012; Reichgelt et al., 2013). With this approach and by using mainly the climate profiles from Thompson et al. (1999, 2000, 2012), we avoid problems discussed by Grimm and Denk (2012), who showed that MAT ranges provided for NLR in the widely-used PALEOFLORA database (http://www.palaeoflora.de) are partly inaccurate and that the precision reached with the coexistence approach based on this database is low. Thompson et al. (2012), however, demonstrated for modern North American and Pleistocene vegetation assemblages; (1) that there was a high degree of correlation between observed climatic values (including CMMT and MAT) and estimates from MCR approaches, (2) that estimates with sample NLR ≤ 10 were much less precise than for samples where $n \sim 20$ NLR, and (3) that presence-absence comparisons vs. those based on taxon abundance avoid assumptions of fossil and modern vegetation being analogous. Their analysis also showed that MCR analysis of modern Eastern North American coniferous forests and broadleaf forests (30–47° N) yielded accurate and precise temperature estimates. We used only samples with at least 11 NLRs with climate profiles for our analysis, with the majority of the samples analysed with 17 or more NLRs with climate profiles. Whereas genera are typically used for NLRs in bioclimatic analysis (e.g., Reichgelt et al., 2013), in the present analysis *Tsuga* was differentiated by species. *Pinus* pollen was excluded from the reconstructions due to its over-representation in marine pollen records as also done by Eldrett et al. (2009), whereas *Podocarpus* was excluded due to concerns over the correct botanical affinity of these grains (Greenwood et al., 2013, compare Sect. 3.4).

Thompson et al. (2012) demonstrated that the extremes of the modern climate range (i.e., 0 % and 100 %) of NLRs yield wide climate estimates and so recommended assigning the 10th and 90th percentiles to the range of climatic tolerance of plant genera to increase precision. The weighting (i.e., exclusion of outliers) in bioclimatic analysis (sensu Greenwood et al., 2005) based on the 10th and 90th percentiles yields a warm estimate where a predominance of taxa with high minima are present, and a predominance of taxa with low minima yields a cool estimate. Particularly high temperature reconstructions in the bioclimatic analysis were therefore tied to the occurrence of thermophilic taxa such as palms (Arecaceae/*Arecipites*-pollen type; Arecaceae MAT 11.2–28.9 °C, CMMT 2.1–27.2 °C), together with mesothermic taxa with only moderate tolerance of cold winters (e.g., *Nyssa*, MAT 4.5–23.0 °C, CMMT −10.4–18.9 °C and *Taxodium*, MAT 12.6–26.6 °C, CMMT −1.4–25.4 °C), whereas samples with notably cool estimates lacked these taxa (or contained only a few) and were rich in taxa with low winter tolerances (e.g., *Alnus* MAT −12.2–20.9 °C, CMMT −30.9–14.1 °C, *Fraxinus* MAT −2.3–24.4 °C, CMMT −23.8–18.1 °C, and *Populus* MAT −12.2–25.5 °C, CMMT −31.0–13.6 °C).

4 Results

4.1 Sedimentology/taphonomy

As discussed in McCarthy et al. (2013), taphonomy can have a major impact on the palynological record of continental margins, reflecting differential transport and differential preservation of palynomorphs. The assessment of the importance of these factors at Site M0027 through the Miocene assists in making the interpretation of environmental change more robust. Figure 3 highlights intervals characterised by several palynological indicators of high flux of terrigenous palynomorphs, particularly of large angiosperm pollen that tend to settle quickly in coastal settings (Mudie and McCarthy, 1994; McCarthy and Mudie, 1998), as well as heavier phytoclasts that tend not to be transported past the shelf break except by mass wasting (McCarthy et al., 2013). These are far more common below ∼ 425 mbsf in Hole M0027A, after which Site M0027 was for the most part shoreward of the shelf break and thus not subject to the intense mass wasting events that characterise the thick, prograding sequence m5.8 in particular (compare Fig. 2). A taphonomic approach would advocate focusing on the samples in this sequence that are richer in marine palynomorphs and amorphous organic matter (AOM) in drawing conclusions about palaeovegetation and palaeoclimate. The majority of the late Burdigalian through Langhian sediments at Site M0027, in contrast, appear to have been deposited on the shelf during high sea level intervals, and thus are more likely to reflect palaeovegetation, making palaeoenvironmental reconstructions more reliable. It must be considered though that, since high sea level may be paired with an increased site-shoreline distance (McCarthy et al., 2013), samples from these sediments may reveal a greater degree of long-distance transport bias.

4.2 Quantitative palynology

4.2.1 General palynology

Because pollen behaves aerodynamically and hydrodynamically like silt particles (Traverse, 2008) muddy sediments contain abundant, well-preserved palynomorphs, as long as the rate of sediment accumulation is relatively high. Particularly good palynomorph preservation and high concentration is observed for sediments from the early Burdigalian at Site M0027. As discussed in Sect. 4.1, this interval (around ~ 490 to ~ 425 mbsf) may also be characterised by common mass transport deposition. For some samples, identification was hampered due to the occurrence of pyrite grains inside palynomorphs, indicative of reducing conditions, which also tend to promote palynomorph preservation.

In most of the analyzed samples, *Quercus* (oak) pollen is the dominant pollen type; the values vary between 40 % and 80 % (Fig. 5), except for the uppermost sample from Core 9 (19.54 mbsf) from Site M0027, which contains only 15 % *Quercus* pollen. The assumption that smaller, rugolate *Quercus* grains may be associated with generally dryer conditions could not be verified (compare Sect. 4.3).

Decreases in *Quercus* pollen during the Oligocene/Miocene are generally paired with increases in *Carya* (hickory) pollen and/or inaperturate pollen percentages. The *Quercus*/*Carya* pollen ratio may to some degree change due to taphonomic effects, since *Carya* pollen grains are generally larger than other non-saccate pollen grains (see Sect. 3.3). Rarely occurring pollen (e.g., *Ginkgo*, *Populus*, *Carpinus*) is not depicted in the pollen diagram (Fig. 5) but is discussed in the respective sections. *Podocarpus* pollen was also rare, with percentages below 1 %. Due to this rare occurrences and its similarity to *Pinus* pollen, this taxon was also not depicted in Fig. 5. *Pinus* was separated into two types, but the percentage curves for both types showed almost identical signals, therefore, they were merged in Fig. 5. Pteridophyte spores are generally rare, with the exception of the uppermost sample analysed (19.54 mbsf).

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Climate development on the NA Atlantic Coastal Plain

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Dinoflagellate cysts (dinocysts) show significant variations during the Oligocene and Miocene, with particularly high values at ~ 620, around 550, 480, and 350 mbsf, while the interval between 300 and 250 mbsf is characterized by particularly low dinocyst abundances. In most cases, the relative abundance of foraminifer test linings correlates very well with those of the dinocysts, indicating that the signal of marine vs terrestrial palynomorphs is consistent and can be used as a proxy for site-shoreline distance. A notable exception is the sample from the Pleistocene (19.54 mbsf), which shows high percentages of dinocysts, but low foraminifer percentages (Fig. 5). The dinocyst assemblage in this sample is nearly monospecific, suggesting a bloom of *Bitectatodinium tepikiense* Wilson obscuring the normal taphonomic signature. Comparison with calculations of palaeo-water-depth for Sites M0027 and M0029 based on benthic foraminifers has shown that high marine/terrestrial palynomorph ratios generally correlate well with deeper water/distal settings (McCarthy et al., 2013).

4.2.2 ~ 627 to ~ 540 mbsf, Eocene (Priabonian)?, Oligocene (Rupelian, ~ 33 to ~ 28 Ma)

The marine palynomorphs (depicted in foraminifer test lining percentages and the dinocyst/nonsaccate pollen ratio, Fig. 5) show a decreasing trend from ~ 627 to ~ 580 mbsf and a subsequent increasing trend up to ~ 538 mbsf (sequence boundary O6). Bisaccate pollen generally shows a very similar trend of changing abundance. Notable exceptions are two samples at ~ 626 and ~ 624 mbsf with very low bisaccate pollen percentages (paired with relatively high percentages of swamp taxa pollen; Fig. 6) and one sample at ~ 576 mbsf with particularly high *Pinus* percentages. The sample at ~ 576 mbsf is furthermore characterized by very low pollen percentages of swamp taxa and increased herbaceous pollen percentages. Pollen of deciduous-evergreen forest taxa show percentages varying between 67 and 86 %. Dominant pollen taxa in this association are *Quercus* (oak) and *Carya* (hickory) and, to a lower degree, *Ulmus* (elm) and *Tilia* (linden). Increases in *Carya* pollen are generally coupled with decreases in *Quercus*, *Ulmus*, and *Tilia* pollen and vice versa. Due to the similar pollen morphologies of *Carya* and *Tilia*, these signals are probably not mere transport signals, but reflect real changes in vegetation. *Ginkgo* pollen is also present in some samples from this interval, but is generally rare.

4.2.3 ∼ 540 to ∼ 509 mbsf, Oligocene/early Miocene (late Chattian to early Aquitanian, ∼ 28 to ∼ 23 Ma)

There are no strata in the age range ∼ 28 to ∼ 24 Ma at site M0027 according to the age model of Browning et al. (2013). The sediments between ∼ 539 and ∼ 509 mbsf probably represent the time interval from ∼ 23.4 to ∼ 23 Ma and thus the transition from the late Chattian to the Aquitanian. This interval is represented by four samples in our records. The third of these samples (from below) shows a high peak of bisaccate pollen (> 200 %), while marine palynomorphs do not show such extraordinarily high values. The high percentages of bisaccate (namely *Pinus*) pollen are paired with occurrences of *Tsuga* (hemlock) pollen, relatively high *Carya* pollen percentages and a significant decrease in pollen of other arboreal taxa (particularly *Quercus*, *Tilia*, *Ulmus*). Furthermore, this interval shows the only significant occurrences of coastal/steppic pollen taxa (here: Chenopodiaceae) in the Oligocene sediments.

4.2.4 ∼ 509 to ∼ 422 mbsf, Early Miocene (Aquitanian/early Burdigalian, ∼ 21 to ∼ 19 Ma)

This interval consists of two sequences (m6, m5.8) and was analyzed at a particularly high resolution due to good palynomorph preservation and high content of pollen (Fig. 5). Marine palynomorphs show generally low values with exception of a few samples around ∼ 480 mbsf. There are occurrences of *Tsuga* pollen surpassing 2 % of the nonsaccate pollen assemblage at ∼ 475 mbsf. This relative increase in *Tsuga* pollen is expressed to a higher degree at site M0029 (around ∼ 733 mbsf/∼ 20.1 Ma, with almost 10 % of nonsaccate pollen). A similar peak is also revealed at Site M0028A at a depth of ∼ 620 mbsf (Fig. 2; Mountain et al., 2010). For all Sites, the hemlock peak is coeval with a strong increase in bisaccate pollen (mainly *Pinus*, at ~ 475 to ~ 470 mbsf at Site M0027), but a minor increase in marine palynomorphs, indicating that the increase in *Pinus* pollen is not simply taphonomically induced.

Generally, *Pinus* shows a decreasing trend for this interval. The *Pinus* pollen increase around 475 mbsf is coeval with an increase in *Carya* (over 18 %), Ericaceae, and *Nyssa* pollen, while Fagaceae, including *Quercus*, show a significant decrease from ~ 79 to ~ 45 %. Between ~ 467 and ~ 423 mbsf, there are still minor fluctuations in the pollen percentages of single taxa, but the percentages of combined deciduous-evergreen forest taxa remain relatively stable.

The pollen record also reveals occurrences of rare deciduous tree taxa such as *Populus*, *Juglans*, and *Corylus*. As discussed above (Sect. 4.1), some of the changes in pollen percentages between ~ 490 and ~ 425 mbsf, particularly the peak occurrence of *Carya* and *Nyssa* pollen, may be partly tied to the phenomenon of mass wasting events. Pollen concentration is extraordinarily high around ~ 450 mbsf, while the number of marine palynomorphs is particularly low in the same interval. The interval from ~ 410 to ~ 365 mbsf at Site M0027, consisting of medium to coarse-grained sand, is barren of palynomorphs.

4.2.5 ~ 360 to ~ 260 mbsf, Early Miocene (late Burdigalian ~ 19 to ~ 16.5 Ma)

This interval is represented by nine samples in the pollen record from Site M0027, and complemented with two samples from Site M0029 that have been positioned according to sequence stratigraphy and the age model by Browning et al. (2013). A significant change in pollen assemblages occurs around 300 mbsf, with a decline in *Quercus* and additional Fagaceae pollen and a coeval increase of *Carya*, *Nyssa*, and *Fagus* pollen. The interval from ~ 360 to ~ 250 mbsf is the first containing consistent occurrences of Poacea (grass) pollen, but the percentages never exceed 2.5 % for all samples analyzed. The second half of the interval is characterized by a significant increase in *Quercus* pollen percentages.

4.2.6 ∼ 250 to ∼ 79 mbsf, Middle Miocene (Langhian/Serravallian, Tortonian? ∼ 16 to ∼ 11.6 Ma)

Nineteen samples from Site M0027 and five samples from Site M0029 represent the interval between ∼ 16 to ∼ 11.6 Ma (∼ 250 to ∼ 80 mbsf) in our pollen record. Between ∼ 250 and ∼ 199 mbsf (∼ 16 to ∼ 13 Ma), *Quercus*/Fagaceae pollen and combined pollen percentages of deciduous-evergreen mixed forest taxa decrease. Samples from ∼ 199 mbsf to ∼ 190 mbsf show strong variation in pollen percentages of deciduous-evergreen forest taxa (Fig. 8). In addition to relatively frequent *Ulmus* (elm) pollen, the sediments between ∼ 250 and ∼ 79 mbsf also contain small amounts of *Tilia*, *Alnus*, *Carpinus* and *Ostrya* pollen grains. The samples between ∼ 210 and ∼ 190 mbsf reveal a decrease of conifer (mainly *Pinus*) pollen and strong increase in fungal remains.

The pollen dataset from Site M0027 contains another sample from sequence m1 (∼ 79.6 mbsf) which probably has an age of ∼ 11.6 Ma (Browning, personal communication, 2010). This sample is not particularly different from older Miocene samples and characterized by low percentages of bisaccate pollen and marine palynomorphs, and also high percentages of fungal remains.

4.2.7 Pleistocene

Pliocene sediments are not confirmed from the New Jersey shallow shelf (Mountain et al., 2010). The uppermost sample analyzed herein (∼ 19.5 mbsf), dated as Pleistocene (probably MIC 7 or 5e; Miller et al., 2013a), shows a pollen association that in several aspects is different from the Miocene samples. Particularly characteristic is a peak in *Betula* (birch) pollen of almost 20 %. Furthermore, bisaccate pollen percentages are extremely high within this sample (Fig. 5). *Picea* pollen, while rarely present in the Miocene and Oligocene samples, is a significant part of the bisaccate association in the Pleistocene. Percentages of nonsaccate tree pollen are low, with *Quercus* values decreasing to less than 30 %. A surprising finding is the presence of *Engelhardia*/*Momipites* type pollen (see below). The pollen concentration is particularly low in this sample. The high percentages of dinocysts in this sample consist almost exclusively of cysts of *Bitectadinium tepikiense* (Fig. 4), a taxon that is an indicator of rather cool water conditions and of meltwater influence (e.g., Bakken and Dale, 1986). The nearly monospecific nature of the assemblage suggests a bloom in relatively low salinity surface waters.

While the dinocyst/nonsaccate pollen ratio is very high for this sample, the percentages of foraminifer test linings do not exceed 10 %. Furthermore, fungal remains show relatively high percentages, and percentages of trilete spores exceed 60 %, pointing to a strong terrestrial influence.

4.3 Statistical analyses and palaeoenvironment

The analysis depicted in Fig. 6 reveals 5 factors. Factor 1 ("*Quercus* factor") contains *Quercus* with a score of 8.9. All other taxa show scores below 0.4. Factor 1 explains 45.7 % of the total variance. Factor 2 ("*Carya* factor") contains *Carya* with a score of 9.8, and *Quercus* with a score of 4.4. All other taxa do not exceed 0.4. Factor 2 explains 32.1 % of the total variance. Together, the *Quercus* and *Carya* factors explain more than 70 % of the variance, indicating the dominance of these taxa in the nonsaccate pollen associations. The two factors show counter-balanced signals for most of the Oligocene and Miocene.

Factor 3 ("*Taxodium* factor") explains 11.2 % of the total variance. The highest score is held by combined *Taxodium*/*Cupressacites*/*Inaperturopollenites* pollen (9.8). Associated (with scores > 0.4) are *Quercus* (score: 2.5), Magnoliaceae (score: 2.2), and small tricolpate pollen grains (*Quercoidites*?; score: 1.1). These taxa generally indicated humid conditions. The *Taxodium* factor has particularly high values for the lowermost (Priabonian?) sample analyzed, notably low values occur during the Rupelian (around 28 Ma) and the late Burdigalian (around 17.8 Ma; Fig. 6). A notable increase during the Miocene occurs around ~ 15 Ma.

Factor 4 ("*Nyssa* factor") explains 11.2 % of the total variance. This factor is dominated by *Nyssa* (score: 7.9) and *Fagus* (score: 6.0). This may indicate that *Nyssa* and

Fagus were not successfully separated. However, analyses based on samples from the Oligocene and early Miocene revealed that *Nyssa* and *Fagus* were not characteristic of the same factor. In the analysis depicted in Fig. 6, Factor 4 also contains *Quercus* (score 3.0) and Cyperaceae (score: 1.3). Generally, this factor contains taxa preferring humid conditions. A particularly significant increase is present in samples around ∼ 200 mbsf, paired with a decrease in conifer forest taxa pollen percentages (Fig. 6).

Factor 5 ("*Betula* factor") contains

a. forest/understorey taxa: *Betula* (score 7.9; note that some *Betula* taxa also indicate steppic conditions), *Corylus* (score 4.6), combined *Quercus* (score 1.8), *Engelhardia*/*Momipites* punctatus type (score 1.4; maybe reworked), *Ulmus* (score 1.1), Ericaceae (score 1.1), and small tricolpate grains (*Quercoidites*?; score: 1),

b. herbaceous taxa indicating deforestation/steppic conditions: Asteracaea (score: 2.7), Chenopodiaceae (score: 1.3), *Artemisia* (score: 1.0), and small, probably herbal, tricolporate grains (score: 1.0).

Although the *Betula* factor dominates only the Pleistocene sample at ∼ 19.5 mbsf (Fig. 6), it explains 4.5 % of the total variance. We have therefore decided to keep the 5-factor analysis containing this factor, because it reveals an association characteristic for the Pleistocene (interglacial) conditions. The factor analysis underlines the dominating role of *Quercus* and *Carya* among trees with nonsaccate pollen grains, and the importance of taxa associated with humid conditions, which are probably associated with swamps and river-near plant associations.

4.4 Pollen-based climate reconstructions

Pollen-based temperature values are generally well constrained for the record from Site M0027, with uncertainties generally varying between 2 to 5 °C for mean annual temperatures (Fig. 7). Mean temperatures of the warmest month generally show less variation between samples than those of the coldest month. The mean annual precipitation curve for Site M0027 is less variable than the reconstructed temperatures.

The values vary between ~ 1100 and ~ 1250 mm a^{-1}, which is within the range of the values encountered today in New Jersey.

The pollen-based climate reconstructions indicate relatively warm temperatures for the lowermost, probably Priabonian-aged sample (MAT: ~ 15 °C, CMMT: ~ 6 °C). MAT values for the subsequent samples from the early and middle Oligocene vary around ~ 13.5 °C until a relatively abrupt increase to more than 15 °C between ~ 570 and ~ 540 mbsf (around 28 Ma; Figs. 7 and 8). Even higher MATs around 17 °C have been reconstructed for two samples around ~ 535 mbsf (~ 23.4 MA), followed by a rapid decline to ~ 13 °C at the transition to the early Miocene (Fig. 8).

For the time interval reflected in sequence m6 and the lower part of m5.8 (reflected in 32 samples), average MATs of ~ 14 °C have been reconstructed. Two particularly cool intervals are revealed, at between ~ 493 and ~ 488 mbsf (20.1 Ma) and at ~ 438 mbsf (~ 19.7 Ma). The first of these two intervals is also characterized by particularly low MAP values (~ 1031 mm). A very warm interval with MATs surpassing 17 °C is reflected in samples from neighbouring Site M0029 (around ~ 18.5 Ma).

Reconstructions for the following interval from ~ 18 Ma to ~ 16.6 Ma (~ 335 to ~ 250 mbsf) reveal a cooling trend to MATs of ~ 12 °C. Between ~ 16 and 14.5 Ma (~ 255 to ~ 225 mbsf), averaged MATs are ~ 14 °C, but the MAT values vary significantly between ~ 10 °C (for an interjected sample from site M0029) and ~ 16 °C. The subsequent time interval (~ 14.5 to ~ 12 MA; ~ 225 to ~ 80 mbsf) shows slightly higher average MAT (~ 14.9 °C), with peak values (> 16 °C) at ~ 13 MA (around ~ 208 mbsf).

The climate reconstructions for the sample at ~ 19.5 mbsf (Pleistocene, MIC 7 or 5e) show a MAT of ~ 11.8 °C and a CMMT of ~ 1.3 °C, values consistent with present day climate of New Jersey.

5 Discussion and comparison with other vegetation records

The quantitative climate reconstructions presented here (Figs. 7 and 8) are based on the "nearest living relative" (NLR) approach. They are best understood as an integrated climate signal over the whole pollen catchment area, including lowland and mountainous areas. The relative abundances are not considered – only presence and absence. This makes the climate reconstructions less susceptible to transport-related and taphonomic bias, but in some cases decreases the precision of the reconstructions. Pollen percentages as depicted in Figs. 5 and 6, on the other hand, show shifts in palaeovegetation (such as migration of conifer forests to lowland areas or spread of swamp vegetation) which could also point to regional climate changes; however, seemingly climate-induced changes in pollen assemblages may sometimes be related to transport effects and taphonomy. Furthermore, the pollen assemblages may also be altered by regional landscape changes, e.g., alterations in river systems, and by sea-level related movements of the coastline (compare McCarthy et al., 2013).

In the following, we present an interpretation of the vegetation and climate development in the hinterland of the New Jersey shelf, integrating the relative abundances of terrestrial and marine palynomorphs and the pollen-based quantitative climate analyses with further results from IODP Expedition 313. The results and interpretations are compared with other palynomorph records from Eastern/Central North America and Europe. Finally, we compare the climate results from New Jersey with global climate records, particularly oxygen isotope records.

5.1 Eocene(?), Oligocene (Rupelian, ~ 33 to ~ 28 Ma)

The lowermost sample analyzed (~ 626 mbsf) implies that conifer forests were restricted to mountainous areas during the very late Eocene/very early Oligocene. This is because even though high relative abundances of marine palynomorphs, particularly foraminifer test linings, imply a particular long site-shoreline distance and thus a greater degree of transport bias, bisaccate pollen percentages are very low. Mean annual temperatures were relatively high compared to the following part of the early Oligocene (Fig. 8). It cannot be unambiguously determined whether the lowermost sediments from Site M0027 are from the Priabonian or the early Oligocene (Browning et al., 2013). But if the lowermost sample analyzed herein is of Priabonian age, then the results are congruent with results of Eldrett et al. (2009), who found a decrease of annual temperature of ~ 3 °C (from ~ 13 to ~ 10 °C) at the transition from the Eocene to the Oligocene in the high latitudes, based on the NRL method applied to sediments from the Norwegian-Greenland Sea. The relatively minor changes in pollen associations (excluding the rapid decrease in swamp/wet forest taxa, Fig. 6) between the samples at ~ 627 and ~ 624 mbsf may contradict an Eocene age for the oldest samples, since studies from Southeastern North America (St. Stephens Quarry, Fig. 1, No. 1) indicate significant changes in marine ecosystems. Oboh et al. (1996) also could not find significant palaeobotanical changes at the Eocene–Oligocene boundary in records from South-Eastern North America (including St. Stephens Quarry), indicating a decoupling of marine and terrestrial ecosystem changes across the Eocene–Oligocene boundary.

The decreasing trend in marine palynomorphs from ~ 627 to ~ 580 mbsf (~ 33 to ~ 28.8 Ma; Fig. 5) indicates a shortening site-shoreline distance, with a subsequent lengthening of the distance up to ~ 538 mbsf, which is coeval with higher MATs. The similar trends in marine palynomorphs and bisaccate pollen suggest that the increases and decreases of bisaccate pollen, particularly *Pinus* pollen, are mainly transport-induced. Two samples with very low bisaccate pollen percentages at ~ 626 (see above) and ~ 624 mbsf, and one sample with particularly high *Pinus* percentages at ~ 576 mbsf, probably record real vegetation signals. The changes between the *Quercus*- and *Carya*-factors (Fig. 6) during the Rupelian (and also during phases of the Burdigalian) are probably to some degree caused by transport effects, since the *Carya* is characterized by relatively large, robust pollen grains

Generally, the lowland vegetation was dominated by oak-hickory (*Quercus*-*Carya*) forests (with changing frequency of elms and lindens). While *Alnus* (alder) is common in Western and Northern North-American records from the Eocene/Oligocene, its presence in Oligocene sediments from Southeastern North America has to our knowledge not yet been confirmed, and evidence from the Eocene is rare. *Alnus* pollen was identified by Gray (1960) in Eocene sediments from Alabama (Fig. 1, No. 13), but Frederiksen (1979) found *Alnus* pollen in Palaeocene, but not Eocene samples in Virginia (Oak Grove, Fig. 1, No. 7), and studies from the Eocene of Florida (Jarzen and Dilcher, 2006; Fig. 1, No. 3) did not reveal the presence of this genus. Swamp vegetation was widespread during the late Eocene and the early Oligocene, whilst the following intervals witnessed only slight variations until the Middle Miocene.

5.2 Oligocene/Miocene transition (late Chattian/early Aquitanian, ∼ 23 Ma)

The findings described in Sects. 4.2.3 and 4.4 indicate that the time interval from ∼ 23.4 to ∼ 23 Ma (∼ 535 to ∼ 523 mbsf) was characterized by warm temperatures, and a long site-shoreline distance (probably paired with a sea-level high stand), but that a sudden cooling (Fig. 8) of 3 to 4 °C led to an expansion of conifer forests, including a spread of *Tsuga*. The *Tsuga* pollen grains found within this interval probably belong to different species (*T. canadensis*, *T. heterophylla*, and *T. mertensiana*). These findings are consistent with phylogenetic results by Havil et al. (2008), implying that the split of these species occurred during the Eocene/Oligocene. The increase in *Tsuga* pollen is of particular interest since this genus, particularly *Tsuga heterophylla*, can tolerate cool climates, but needs humidity and cannot tolerate persistent drought (e.g., Havill et al., 2008). As temperatures dropped at ∼ 23.4 Ma, the site-shoreline distance shortened, as indicated by the decrease in marine palynomorphs, particularly foraminifer test linings (Fig. 5). According to McCarthy et al. (2013, compare Fig. 3), the shortening in site-shoreline distance was coupled with a fall in sea level.

5.3 Early Miocene (Aquitanian/early Burdigalian, ∼ 21 to ∼ 19 Ma)

The frequent occurrences of *Tsuga* pollen at all three Sites around ∼ 20 Ma (∼ 492 and ∼ 475 mbsf at Site M0027, Figs. 2 and 6), paired with very high percentages of *Pinus* pollen (at Site M0029 at around ∼ 733 mbsf and at Site M0028A at a depth of ∼ 620 mbsf) are probably partly caused by over-representation due to the good transport properties of these pollen types – particularly given the location beyond the clinoform rollover at all three sites. Nonetheless, considering the coeval decrease in deciduous-evergreen forest, we infer that around ∼ 20 Ma cooler, but humid conditions prevailed in the hinterland of the New Jersey shelf, causing a migration of conifer taxa to the lowlands. Indeed, the carbon-isotope curve for Site M0029 reveals a very significant negative excursion at the same time, which may indicate a rapid turn to more humid conditions (cf. Fang et al., 2013).

The site-shoreline distance probably continued to shorten during the related interval as implied by decreasing abundances of marine palynomorphs. Using also foraminifer-based water-depth calculations, McCarthy et al. (2013) infer a generally falling sea level for this interval (Fig. 3). The pollen record may thus represent a particularly local signal here that may have been altered by changes in river systems. The sediment record indeed indicates a significant change in the environment to decreasing river influence between ∼ 480 and ∼ 470 mbsf (Miller et al., 2013b). Additionally, the alteration of the pollen assemblages due to mass-transport effects (particularly between ∼ 490 to ∼ 425 mbsf, see Sects. 4.1 and 4.2.4) must be considered for the sediments deposited during the Aquitanian/early Burdigalian. The presence of *Populus* and other rare pollen taxa encountered in Neogene sediments from Site M0027 is corroborated by plant macrofossil findings of Stults and Axsmith (2009, 2011) from Alabama. *Fagus* and *Juglans* pollen was also found in the Early Miocene Brandon lignite from Vermont, an area north of New Jersey (Fig. 1, No. 16) (Traverse, 1994).

5.4 Early Miocene (late Burdigalian ∼ 19 to ∼ 16.5 Ma)

The combined decline in inaperturate pollen and *Quercus* pollen and coeval increase of *Carya*, *Nyssa*, and *Fagus* pollen indicates that this change is partly caused by transport effects, since all the *Carya*, *Nyssa*, and *Fagus* are characterized by relatively large grains. The relatively weak changes in bisaccate pollen percentages and marine palynomorphs over this interval point to only minor changes in the site-shoreline distance. Therefore, the changes in the tree pollen assemblages are probably also reflecting true vegetation signals. The very warm MATs surpassing 17 °C indicated for samples from

Site M0029 (around ~ 18.5 Ma) are congruent with results from European records, for which even higher MATs have been reconstructed (e.g., around ~ 18.3 °C in a Danish record by Larsson et al., 2011, and around ~ 18.5 °C from Spain, recorded by Jiménez-Moreno et al., 2007). More surprising is the cooling trend revealed for the following interval from ~ 18 Ma to ~ 16.6 Ma, culminating in MATs of ~ 12 °C. Such a decrease is not revealed in records from Europe. The occurrences of Poaceae pollen indicate that grasses were present within the vegetation in the Atlantic Coastal Plain during the early Miocene, but the Site-M0027 pollen record implies that they did not become an important factor until at least the early Pleistocene.

5.5 Middle Miocene (Langhian/Serravallian, ~ 16 to ~ 11.6 Ma)

Generally, the pollen assemblages found in the middle Miocene sediments from Site M0027 are very similar to those found in the neighbouring pollen record from the York Quarry (Fig. 1, point 9) with *Quercus*, *Carya*, and *Pinus* being dominant taxa, and the consistent presence of Taxodiaceae, Cupressaceae, *Ulmus*, *Ilex*, *Liquidambar*, *Pterocarya*, and *Castanea*-like pollen (Pazzaglia et al., 1997). The Langhian/Serravallian pollen percentages and pollen-based climate reconstructions from Site M0027 imply several changes in ecosystems, particularly spreads in swamp forests and understorey plants. Similarly, climate conditions varied significantly. Between ~ 15 to ~ 12 Ma, there is a generally shortening site-shoreline distance as implied by the decreasing percentages of bisaccate pollen and marine palynomorphs. The high abundance of fungal remains in the samples around ~ 194 mbsf and at ~ 79.6 mbsf also points to an increased terrigenous influence, though the pollen concentration is not very high in this sample. The similarity of the sample at ~ 79.6 mbsf to the Miocene samples below indicates that it is also of Miocene age. The relatively high MATs (~ 13.2 °C) for this sample fit well with palaeoflora-based estimations from New Jersey (Pine Barrens; Fig. 1, No. 14). The palaeoflora suggests warm and temperate conditions for this region at ~ 11 Ma (Greller and Rachele, 1984). Based on the palynoflora, Rachele (1976) estimated the annual precipitation to 1270 mm, average January temperature to 6 °C and average July temperature to 24 °C. These results cannot directly be tied to the record from Site M0027, but match relatively well with our results for the sample at ~ 79.6 mbsf (~ 1195 mm, ~ 2.7 °C, ~ 23.1 °C). Our results are furthermore consistent with findings by McCartan et al. (1990) who analyzed a palaeoflora from upland deposits of the Southern Maryland Coastal Plain (Fig. 1, No. 8). The climate was probably warmer in Southeastern North America. Palaeobotanical records from the Middle Miocene Alum Bluff Flora (Fig. 1, No. 12) indicate warm-temperate conditions (e.g., Jarzen et al., 2010).

The plant associations found in early/middle Miocene sediments from the NJSS are very similar to those encountered in similar-aged marine/marginal marine sediments from Atlantic Western Europe (e.g., Larsson et al., 2011). However, the MATs reconstructed for the Miocene of the Atlantic Coastal Plain (averaged MAT to ~ 14.0 °C for the interval from ~ 16.5 to ~ 14 Ma and ~ 14.9 °C thereafter) are colder by 1 to 3.5 °C compared to records from Denmark (~ 17.5 °C, Larsson et al., 2011), Serbia (~ 15.5 °C, Utescher et al., 2007), or Bulgaria (~ 15 °C, Utescher et al., 2009), with European records from higher altitudes showing lower temperatures. This seeming discrepancy in annual temperature between the Atlantic Coastal Plain and Europe is discussed in detail in Sect. 5.7.

5.6 Pleistocene

The findings described in Sect. 4.2.7 are consistent with a pollen record from the neighbouring York Quarry (Bryn Mawr Formation; Fig. 1, point 9), which shows increased pollen percentages of *Betula* (birch) for Pliocene and Pleistocene samples (Pazzaglia et al., 1997). Birches are particularly speciated in North America, with species as *B. nana* and *B. minor* prevailing under cool/dry conditions, and others being a typical part of swamp vegetation (e.g., *B. pumila*), or pioneer taxa (e.g., *B. papyrifera*). The increase in swamp forest implied in Fig. 6 may to some degree be artificial, since it is mainly based on the increase in *Betula* pollen, while other swamp taxa do not show significant increases. Thus, the implied spread of *Betula* in the hinterland of the NJSS may at least partly be tied to a spread of pioneer species adapted to dry rather than humid conditions (compare Fig. 4, image 6 showing a small *Betula* pollen grain from the Pleistocene sample). This interpretation is also corroborated by the fact that factor 5 (*Betula* factor) identified in the statistical analyses (Sect. 4.3) also comprises partly steppe taxa like Asteraceae and Chenopodiaceae.

Generally, the palynoflora identified for the Bryn Mawr Formation by Pazzaglia et al. (1997) is very similar to that from ∼ 19.5 mbsf in core 9 from Site M0027. The high percentages of *Picea* in the respective sample support the assignment to the Pleistocene, since *Picea* pollen is very rare in older Pliocene sediments from the Bryn Mawr Formation (Pazzaglia et al., 1997). The pollen assemblages from this core are also congruent with results from McCarthy and Gostlin (2000) for Pleistocene samples from neighbouring ODP Hole 1073A (Fig. 1). Pollen-based qualitative climate reconstructions by Groot (1991) for several sites in the Atlantic Coastal Plain (e.g., Fig. 1, No. 6, 7, 8, 15) indicate relatively warm temperatures for the late Miocene and Pliocene, and a warm-temperate climate at least during the early Pleistocene. However, the relatively warm temperatures reconstructed for the sample at ∼ 19.5 mbsf (MAT: 11.8 °C, CMMT: 1.3 °C) indicate that it does not reflect glacial conditions, but rather mild conditions of an interglacial or interstadial. This is congruent with results of Miller et al. (2013a), who assign the associated core to MIC 7 or MIC 5e. The presence of now-extinct/exotic taxa like *Engelhardia* is however surprising if the age assignment of Miller et al. (2013a) is correct (compare Pazzaglia et al., 1997; Rich et al., 2002). It must be considered that these pollen types occur in the sample due to reworking (see Sect. 4.4). We have therefore excluded *Engelhardia* from the quantitative climate calculations for this sample.

5.7 Further comparison with global signals and outlook

The pollen-based quantitative climate record presented here for Site M0027 must remain fragmentary due to several hiatuses and the insufficient pollen preservation in coarse-grained sediments, even if the sample resolution will probably be increased during subsequent studies. The age model established by Mountain et al. (2010) and

Browning et al. (2013) still allows a comparison with supra-regional climate records (Fig. 8).

If directly compared to global climate changes as revealed for the marine realm in oxygen-isotope values (Zachos et al., 2001a, 2008; Cramer et al., 2009), the averaged mean annual temperature record shows similar signals during the Palaeogene. The transition from the Priabonian to the early Oligocene is reflected in a temperature decrease (Fig. 8) and probably a shift to less humid conditions as indicated by the decrease in swamp/wet forest taxa (Fig. 6). Around ~ 29 Ma, an increase in MATs is congruent with a slight decrease in the oxygen-isotope values. Unfortunately, the interval from 28 to 26 Ma is not yet recovered from the NJSS, but the Mi-1 cooling event Mi-1 (Miller et al., 1987, 1991; Wright and Miller, 1992) is reflected by shifts in palaeovegetation (Figs. 5 and 6) and a rapid fall in MATs (Figs. 7 and 8; compare Sect. 5.2).

For the early Miocene, there are still many congruencies between the results from the NJSS and the global marine signals. We suggest that the significant drop in mean annual and winter temperatures, and coeval spread of conifer forests between ~ 20.1 to ~ 20 Ma (around ~ 488 mbsf) is the local expression of the coeval Mi1aa-event (Pekar and DeConto, 2006). Considering that the strontium-isotope- and microfossil-based age control could be erroneous by 0.5 to 1 Ma for the samples between ~ 500 and ~ 400 mbsf (around ~ 20 Ma), the subsequent coolings at around 19.7 Ma may also still be tied to this event. The MAT decrease and subsequent rapid increase between ~ 19 and ~ 18 Ma to very high temperatures (~ 17 °C), and even the following decline, are also congruent with the oxygen isotope data (Fig. 8).

However, for the interval between ~ 16 to 14.5 Ma (~ 255 to ~ 225 mbsf at Site M0027), which should reflect the MMCO, there is no clear congruency between the regional signals from the NJSS and the global signal reflected in the oxygen-isotope record (Fig. 5). The deciduous-evergreen forest taxa pollen curve seems to some degree to resemble the isotope curve, but the averaged MATs over the MMCO imply a temperature of only ~ 14 °C, (less than in preceding intervals). The minimum oxygen-isotope values, which should imply particularly warm temperatures, are not reflected in the MAT curve (Fig. 8).

One possible explanation for this discrepancy could be a problem in the age model. The strontium-isotope- and microfossil-based age control could be erroneous by 1 to 1.5 Ma for the samples between ∼ 225 and ∼ 190 mbsf (sequences m5, m4.5, and 4.1). If shifted by 1.5 Ma to the past, the samples from these depths could reflect the second part of the MMCO at ∼ 15 Ma. But even if this was true, there would still be a discrepancy with the first part of the MMCO at ∼ 16.5 Ma. For this time, the age control is particularly good (Browning et al., 2013).

Another possible explanation would be that the hinterland of the NJSS was not very susceptible to global climate changes during the middle Miocene. Climate model results (e.g. Herold et al., 2011, 2012) seem to indicate that climate at the Eastern US coast could have remained relatively stable during the MMCO, while the Northern North American (Canadian) coast and the regions around the Gulf of Mexico could have experienced significantly different temperatures during the Miocene compared to today. However, the climate models used in the studies of Herold et al. (2011, 2012) also indicate minor changes for Western Europe, which is not congruent with results from European pollen records showing very warm conditions during the middle Miocene (e.g., Utescher et al., 2007; Larsson et al., 2011; compare Sect. 5.5).

Another option to explain the surprisingly low temperatures reconstructed for the hinterland of the NJSS would be topographical changes resulting in regional vegetation and climate changes. Climate model results by Herold et al. (2009) imply for the Miocene that topographical lowering of high mountain ranges like the Andes and the Tibetian plateau can significantly increase regional temperatures. Vice versa, an uplift of mountain ranges could cause a shift in vegetation and a temperature decrease. Poag and Sevon (1989) discuss an uplift phase of the Appalachian Mountains (Fig. 1) during the middle Miocene. Such an uplift could be a possible explanation for the surprisingly low temperatures reflected in the pollen record from the NJSS, since the Appalachians are close to its catchment area. The findings for the post-MMCO interval and the

Pleistocene sample (at ~ 79.5 mbsf) are congruent with findings from other regional records, and the results for the samples from the Pleistocene support the findings of Mountain et al. (2013a).

The current research state probably does not allow a final interpretation. During future research, the Oligocene and Miocene palynomorph assemblages of Site M0027 will be analysed in a higher resolution. Particularly the interval covering the MMCO will be the focus of further studies.

6 Conclusions

The approach of including marine-palynomorph assemblages into our analyses to identify transport-related bias allows separation of seeming from real shifts in the palaeovegetation of the Oligocene and Miocene Atlantic Coastal Plain. It is concluded that this region was characterized by oak-hickory forest, and that conifers dominated the higher altitudes in the hinterland. The Oligocene witnessed several expansions of temperate conifer forest, which in some cases can be tied to cooling events. The transition between Oligocene and Miocene sediments at the NJSS is probably the regional expression of the Mi-1 cooling event. It is reflected by an expansion of conifers and an annual temperature decrease by almost 3 °C to 12.5 °C around 23 Ma.

There was little change in terrestrial ecosystem and climate conditions between the Oligocene and the Miocene. The pollen associations found in Miocene sediments are generally congruent with results from other North American pollen records. The quantitative climate results for the Miocene are in accordance with other reconstructions from the Atlantic Coastal Plain, but comprise a longer time interval. Further Miocene cooling events could be identified, particularly the Mi-1aa cooling event at around ~ 20 Ma. While the mean annual temperatures in the region were generally warmer than today (around ~ 14 °C) during the Oligocene and Miocene, they were significantly lower than temperatures reconstructed for European records.

There is no clear expression of the MMCO reflected in the pollen record from the NJSS. We conclude that vegetation and regional climate in the hinterland of the New Jersey shelf may not have reacted as sensitive to Oligocene and Miocene climate changes as other regions in North America or Europe. An additional explanation for the relatively low regional temperatures reconstructed for the MMCO could be an uplift of the Appalachian Mountains during the middle Miocene.

An Oligocene/Miocene expansion of grasslands is not evident for the hinterland of the NJSS. The Pleistocene pollen assemblage probably derives from the Marine Isotope Chron 7 or 5e and shows climate conditions similar to present-day.

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Table 1. Assignment of Pollen types found at Site M0027 to vegetation types.

Vegetation type	Conifer-forest	High-altitude conifer forest	Swamp/wet forest	Deciduous-evergreen mixed forest	Mesophytic understorey plants	Coastal or steppic taxa
associated pollen	*Cedrus* *Pinus* *Sciadopitys* *Sequioa* *Tsuga* *Podocarpus*	*Abies* *Picea* *Larix*	*Alnus* *Betula* *Cupressacites* Cyrillaceae *Inaperturopollenites* *Myrica* *Nyssa* *Salix* *Sapotaceae* *Symplocos* Type *Taxodium* Type	*Monocolpopollenites* Arecaceae v. *Arecepites* *Podocarpus* *Acer* *Carpinus* *Carya* *Castanea* *T.-cingulum* type *Corylus* *Engelhardia* Ericaceae Fagaceae v. *Fagus* *Ilex* *Liquidambar* *Platycarya* *Populus* *Pterocarya* *Quercus* *Quercoidites* *Tilia* *Ulmus* T.	Pteridophyta *Sphagnum* *Osmunda* *Artemisia* Compositae v. *Dryas* Poaceae *Sparganium* Umbelliferae	Chenopodiaceae *Ephedra*

T. = type, v. = varia

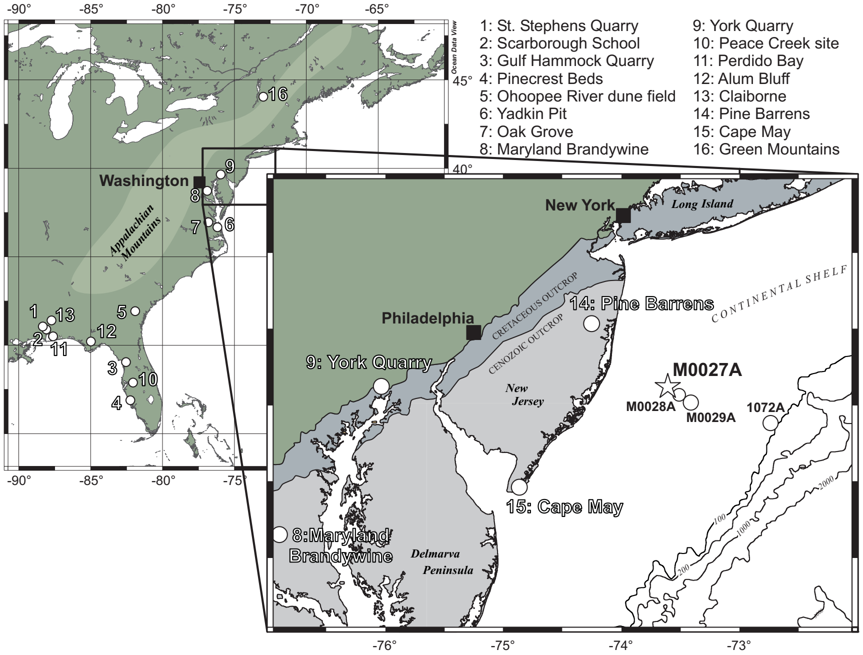

Fig. 1. Map of Eastern North America with a zoom into the area around New Jersey. White points indicate plant macrofossil outcrops, pollen profiles, and drilling sites referred to (1: Oboh et al., 1996; 2, 10, 11: e.g., Stults et al., 2010; 3, 8, 12: e.g., Jarzen et al., 2010; 4: Hansen et al., 2001; Jarzen and Dilcher, 2006; 5: Rich et al., 2002, 6: Groot, 1991; 7: Frederiksen, 1991; 9: Pazzaglia et al., 1997; 13, 14, 15: e.g., Rachele, 1976; 16: Traverse, 1994) and the white star indicates the position of Site M0027 (after Mountain et al., 2010; Schlitzer, 2011). Black squares mark the position of major cities.

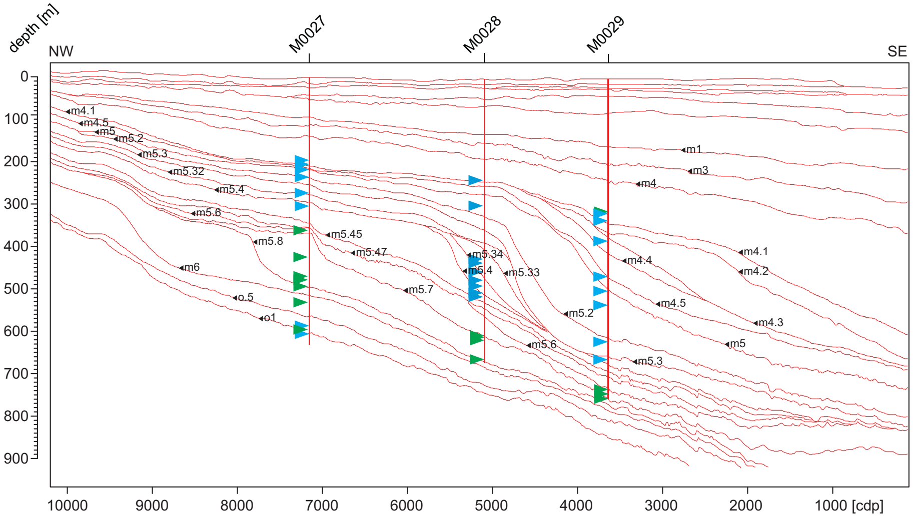

Fig. 2. Depth-converted seismic stratigraphic framework for IODP expedition 313 boreholes (after Mountain et al., 2010 and Fang et al., 2013). Depths of samples with *Ulmus* pollen percentages > 2,5 % are marked with blue triangles, samples with *Tsuga* percentages > 1 % are marked with green triangles (bisaccate pollen excluded from reference sum). Pollen data for Sites M0028 and M0029 were gathered in the framework of the IODP expedition 313 onshore science party (Mountain et al., 2010), additional pollen data for Site M0029 derive from Fang et al. (2013).

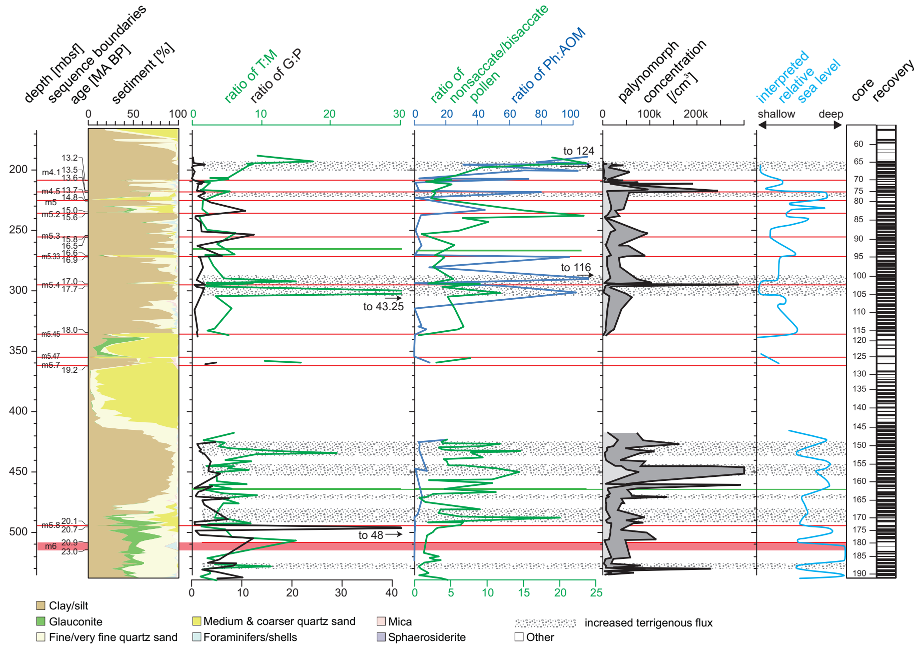

Fig. 3. Ratio of terrestrial vs. marine palynomorphs (black line: T:M), gonyaulacoid vs. protoperidinioid dinocysts (green line: G:P), phytoclast vs. amorphous organic matter (blue line: Ph:AOM) and nonsaccate (generally angiosperm) vs. bisaccate pollen (green line: Ang:Bisac), absolute abundance (concentration per cm^3) of of palynomorphs (marine: dinocysts + acritarchs, pale grey; terrigenous: pollen + embryophyte spores, dark grey), and estimated relative sea level vs. depth for Site M0027 (~ 530 to ~ 170 mbsf). Stipple highlights coeval peaks in T:M, Ph:AOM, and Ang:Bisac that in combination record increased terrigenous flux to Site M0027. These are generally associated with peaks in total palynomorph abundance (concentration) and very low G:P, recording rapid burial inhibiting oxidation. Reflectors m6 to m4.4 are sequence boundaries identified during IODP Expedition 313 and subsequently adjusted (Mountain et al., 2010; Miller et al., 2013b). Adapted from McCarthy et al. (2013).

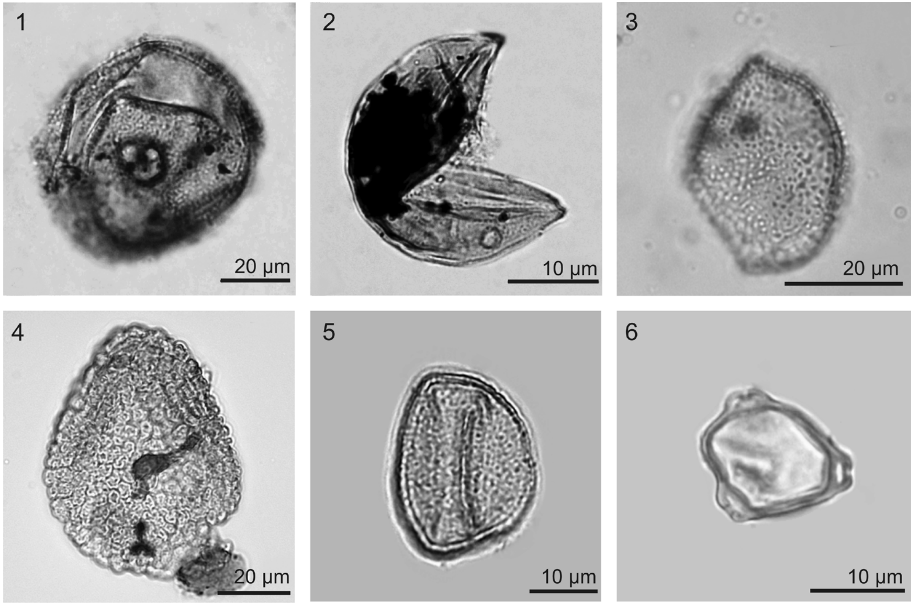

Fig. 4. Palynomorphs from Sites M0027 and M0029, New Jersey shallow shelf. 1: Dinocyst (*Bitectadinium tepikiense*, Site M0027, core 9, ~ 19.5 mbsf), 2: pyrite-filled *Inaperturopollenites* type (Site M0027, core 80, ~ 225 mbsf), 3: *Arecipites* type (Site M0027, core 115, ~ 332 mbsf), 4: *Tsuga heterophylla* type (Site M0029, core 209, ~ 733 mbsf), 5: *Quercus* type (Site M0027, core 67, ~ 200 mbsf), 6: *Betula* type (Site M0027, core 9, ~ 19.5 mbsf).

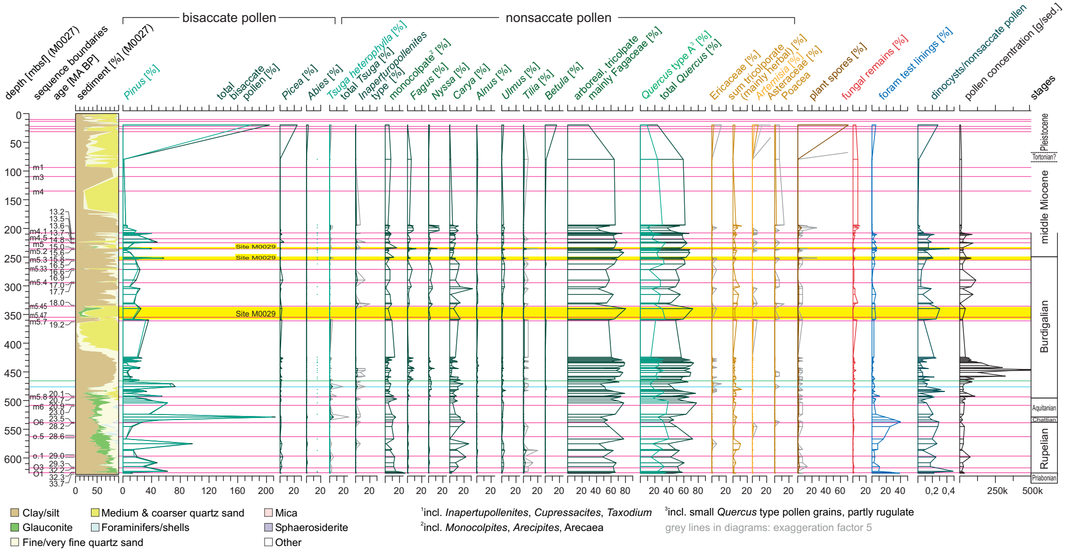

Fig. 5. Sedimentological and palynological results for Site M0027. Shown vs. depth: lithology, sequence boundaries, selected pollen types, further palynological proxies (percentages are based on the sum of non-saccate pollen for all palynomorph percentages), dinocyst/pollen ratio, pollen concentration (for some samples, the weight was estimated based on the sample volume), stages. Yellow bars mark samples from Site M0029 from sequences not preserved at Site M0027. For taxa with low occurrences, exaggeration lines (x5) are shown in grey. Sequence ages are based on Browning et al. (2013).

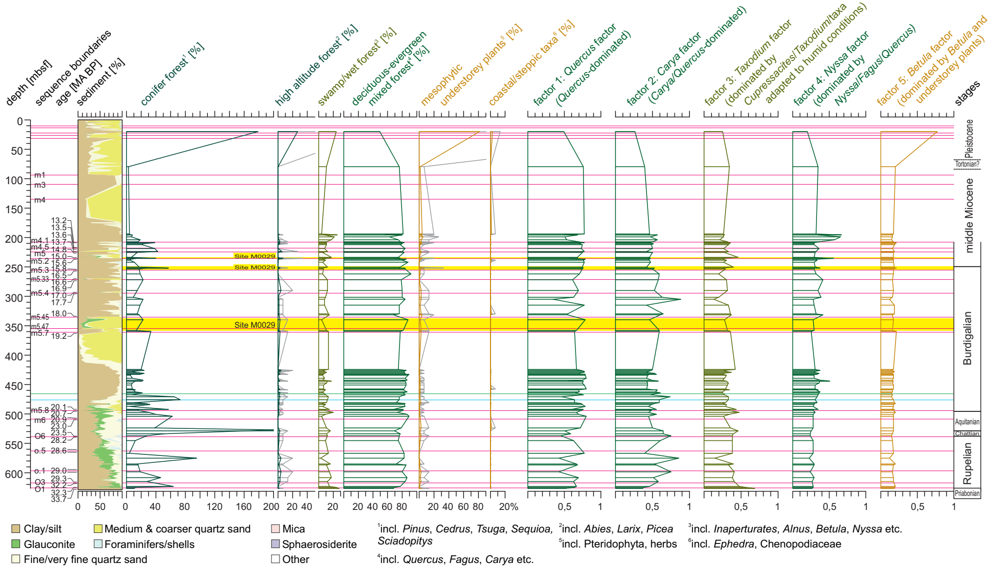

Fig. 6. Lithology and palynological results for Site M0027. Shown vs. depth: lithology, sequence boundaries, pollen percentages integrated into vegetation types, factor analysis results (5 factors; spores and bisaccate pollen excluded), stages. Yellow bars mark samples from Site M0029. Sequence ages are based on Browning et al. (2013).

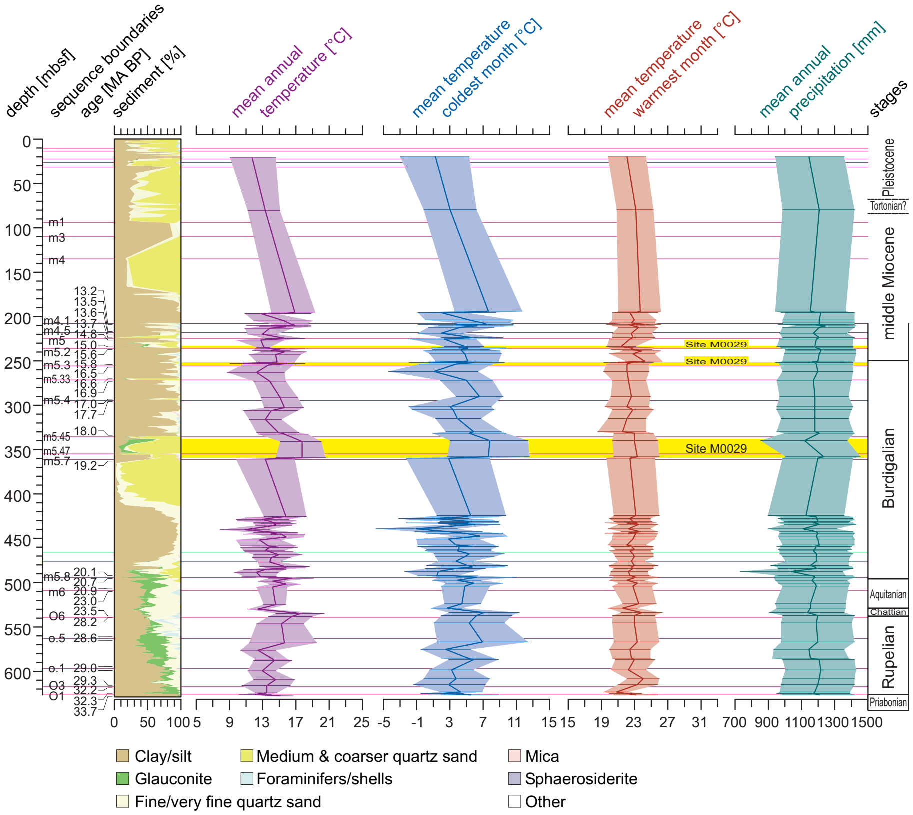

Fig. 7. Sedimentological and pollen-based climate results for Site M0027. Shown vs. depth: sedimentology, sequence boundaries, mean annual temperature, mean temperatures for coldest and warmest month, annual precipitation, stages. Yellow bars mark samples from Site M0029. Sequence ages are based on Browning et al. (2013).

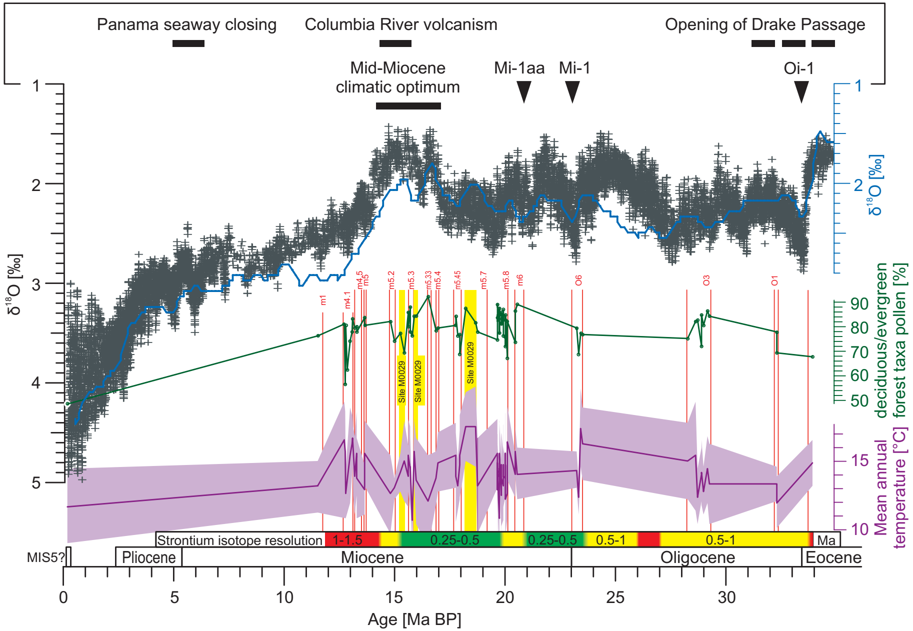

Fig. 8. Pollen-based mean annual temperature reconstruction and deciduous/evergreen forest taxa pollen percentages for Site M0027 (yellow bars mark samples from Site M0029) vs. age compared to a stacked and smoothed oxygen isotope record from the Pacific (after Cramer et al., 2009), global oxygen isotopes after Zachos et al. (2001, 2008), and global events. Age model for Eocene to Miocene samples after Browning et al. (2013), ages for sequence m4.1 are based on comparison with Site M0029. Strontium isotope age resolution after Browning et al. (2013); green: 0.25 to 0.5 Ma, yellow: 0.5 to 1.0 Ma, red: > 1.0 Ma. The age of the uppermost sample is based on Miller et al. (2013a).