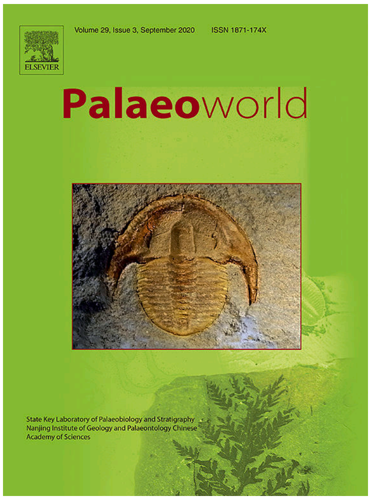

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Early Paleogene plant biomes of the Pacific side of Eurasia

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Abstract

Major plant biome changes in East Asia during the early Paleogene are studied using the Integrated Plant Record vegetation analysis for the first time based on paleobotanical records. The paleobotanical record employed for the reconstruction comprises 110 paleofloras covering the early Paleocene to early Eocene, a time-span of ca. 17 Myr. Our data indicate the presence of more forested conditions over East Asia during the early Paleogene than at present. The early Paleogene vegetation cover in the study area fundamentally differed from modern and was much more homogeneous compared to the modern one. Mixed mesophytic zonal vegetation dominated on the Pacific side of Eurasia during the early Paleogene. Thermophilous mixed mesophytic forests were distributed even at very high latitudes, but at the same time, ecotone between the mixed mesophytic / broadleaved evergreen forests and broadleaved evergreen forest were confined to regions south of 50°N. The proportions of sclerophyllous plants are low in general, even in the mid-latitudes. The localities with open woodlands are all located south of ca. 45°N. The observed vegetation patterns and their changes throughout the early Paleogene in many cases can be correlated with climate patterns and the overall continental paleoclimate evolution as reconstructed from the paleobotanical record. The higher-than-present spatial homogeneity of early Paleogene vegetation coincides with shallow temperature gradients and a significantly more humid regional rainfall pattern over East Asia during the early Paleogene.

Keywords: Vegetation types; vegetation patterns; Integrated Plant Record (IPR); early Paleogene; East Asia

1. Introduction

Vegetation is an integral part of the structural and functional organization of any ecosystem. At the same time, vegetation is the most visible component of the ecosystem, reflecting changes in regional ecological status. At present, the vegetation cover of the Pacific coast of Eurasia is one of the most interesting world phenomena in terms of both biological diversity and ecosystem organization. The vegetation cover of East Asia has the world's longest continuous latitudinal forest vegetation gradient (more than 60°), which stretches from the forest border in the Arctic to the southern tip of the Malaysian Peninsula. The sublongitudinal gradient along the western coast of the Pacific Ocean is represented by all varieties of vegetation from the humid subtropical forests of southeastern China and Japan to the cold deserts of Mongolia (Krestov, 2006). In the south of the Russian Far East, two large floristic areas — namely, Circumboreal and Eastern Asiatic — merge and partly overlap (Takhtajan, 1978; Krestov, 2006), and the study of their interaction in time and space will make it possible to understand the general patterns of florogenesis. Contrasting climatic conditions, high species diversity and a significant number of "Tertiary" relics in the vegetation cover of East Asia have long been the object of close attention.

Globally, early Paleogene climate was relatively stable, warm and moist; the Polar Regions were mostly ice-free and covered with coniferous and deciduous forests (Willis and McElwain, 2002). These Paleocene and Eocene polar broadleaved deciduous forests grew in winter darkness and mesothermal humid climate (Willard et al., 2019). These were very low diversity forests with little habitat variation, very few climbers and more open structure (Collinson, 1992; Collinson and Hooker, 2003). The warm temperatures worldwide gave rise to thick tropical, subtropical and deciduous forest around the globe. Paleocene forests were probably denser than those of the Cretaceous. Angiosperms, first seen in the Cretaceous, continued to develop and proliferate. In general, the Paleocene was marked by the development of modern plant families and genera (Collinson, 1990, 2000, 2001). The first broadleaved subtropical evergreen (rain) forests appeared in the Paleocene and evolved during the Eocene (Willis and McElwain, 2002), but were variable in time and space (Collinson, 1992; Collinson and Hooker, 2003). They are therefore potentially important for the interpretation of plant biomes and their response to global change and provide a unique opportunity for modeling climate changes and understanding the response of the Earth system to various driving forces (Flato et al., 2013; Lunt et al., 2021). Thus, early Paleogene floras provide the potential for detailed interpretation of plant biomes and their responses to global change, such as warm climate thermal maxima and tectonic events. The knowledge of vegetation evolution during the early Paleogene provides unique perspectives for the modeling of actual global changes and helps probe the integrated response of the Earth system to various driving forces (Zachos et al., 2008; Utescher et al., 2009).

By contrast, our knowledge about plant biomes on the Pacific side of Eurasia during the early Paleogene is still fragmentary and debated. Only recently, quantitative paleoclimate and vegetation studies have been conducted for regions of the southern Russian Far East (RFE) revealing major plant biome changes throughout the Paleogene (Bondarenko et al., 2019, 2020a, 2020b, 2021, 2022; Bondarenko and Utescher, 2023). Using quantitative reconstruction, Li et al. (2022) showed vegetation patterns within China during the Eocene.

Moreover, we reconstructed detailed temperature patterns (Bondarenko and Utescher, 2022), precipitation gradients (Bondarenko and Utescher, 2024a), and Plant Functional Types (PFT-based) vegetation patterns (Bondarenko and Utescher, 2024b), based on the same set of floras used in this study. Following up the PFT analysis (Bondarenko and Utescher, 2024b), we aim to test the performance of the Integrated Plant Record vegetation analysis (IPR) — technique that includes a biomization procedure that allows to compare and evaluate the results obtained with both methods.

All vegetation data presented in the following are reconstructed using a single approach (IPR) applicable on every plant organ type. The studied paleobotanical record comprises data of published paleobotanical sites from Eastern Siberia, RFE, China, and Japan (Fig. 1). Based on a total of 110 reasonably well-dated palyno- and leaf floras, coherent IPR vegetation data sets are presented for three stratigraphic levels, namely the lower Paleocene, upper Paleocene, and lower Eocene, covering a time-span of ca. 17 Myr.

2. Materials and methods

2.1. Floral record

The paleobotanical records on the Pacific side of Eurasia studied herein originate from 73 localities (Fig. 1, Appendices A, B). The early Paleogene deposits of China are widely distributed and generally represent terrestrial facies conditions. The early Paleogene deposits of Eastern Siberia and RFE are also widely distributed, and are dominated by terrestrial facies conditions. For details on the Paleogene strata of the study area the reader is referred to Bondarenko and Utescher (2022). We use regional stratigraphic schemes to allocate the paleobotanical sites to three time slices. The stratigraphic correlation chart is combined from Quan et al. (2012a, 2012b) for China, Kezina (2005), Pavlyutkin and Petrenko (2010) for the continental part of the south RFE, Gladenkov et al. (2002) for Sakhalin Island, Gladenkov et al. (2005) for the Kamchatka Peninsula, and Grinenko et al. (1997) for the continental part of the north RFE and Eastern Siberia. Age control of the selected early Paleogene fossil floras of eastern Eurasia is based on a variety of stratigraphic data obtained from radiometric dating, well log correlations, and regional sequence-stratigraphical concepts, considering the position of volcanogenic units and main phases of peat formation, vertebrate fauna, mollusks, foraminifera, and regional and inter-regional pollen zonation (Table S1). The stratigraphic schemes of Eastern Siberia and RFE have been tied to the International Stratigraphic Chart (Grinenko et al., 1997; Gladenkov et al., 2002, 2005; Kezina, 2005; Pavlyutkin and Petrenko, 2010; Cohen et al., 2013) and allow for dating the flora-bearing horizons at stage level. For some of the floras, stratigraphic ages are constrained by radiometric dating (Appendix A).

In this study, all paleofloras were carefully re-evaluated regarding the validity of taxonomic identifications and Nearest Living Relatives (NLRs) of the fossil taxa. We analysed 110 floras including 79 palynofloras (PF), 30 leaf floras (LF) and one carpoflora (CF) with respect to paleoclimate considering three time slices, namely the early Paleocene, late Paleocene, and early Eocene. The floras cover a total time-span of ca. 17 Myr, ranging from the Danian to Ypresian. The assignment of the paleofloras to the three time slices considered here is based on published stratigraphic information and compiled in Table S1. In many cases, flora-bearing horizons originate from longer successions that are tied to regional stratigraphy and partly cover the lower Paleocene to lower Eocene (e.g., Kolyma1, Slezovka15, Erkovtsy, etc.) thus facilitating a consistent sample selection. The individual floras are listed in Appendix A together with information on basin provenance, type of flora, stratigraphic age, method of dating, and references.

2.2. Plant biome reconstruction — IPR

The IPR is a semi-quantitative method first introduced by Kovar-Eder and Kvaček (2003) to assess zonal vegetation based on the fossil plant record (leaf, fruit, and pollen assemblages). In order to employ the IPR, thirteen basic taxonomic-physiognomic groups, termed components, defined to reflect key ecological characteristics of an assemblage (Kovar-Eder and Kvaček, 2003, 2007; Kovar-Eder et al., 2008; Teodoridis et al., 2011) are used: conifer component (CONIF), broad-leaved deciduous component (BLD), broad-leaved evergreen component (BLE), sclerophyllous component (SCL), legume-like component (LEG), zonal palm component (ZONPALM), arborescent fern component (ARBFERN), dry herbaceous component (D-HERB), mesophytic herbaceous component (M-HERB). Azonal components, commonly growing in riparian and coastal stands, include azonal woody component (AZW), azonal non-woody component (AZNW) and aquatic component (AQUA). The component PROBLEMATIC TAXA include elements with uncertain taxonomic-physiognomic affinity. For further analysis, all taxa (but not their abundances) of every single assemblage have to be assigned to those components and their relative proportions have to be calculated as explained below.

To characterize zonal vegetation, the following proportions of components are regarded as relevant: (a) the proportion of the BLD, BLE, and SCL+LEG components of zonal woody angiosperms, where “zonal woody angiosperms” means sum of BLD+BLE+SCL+LEG+ZONPALM+ARBFERN components; (b) the proportion of the ZONAL HERB (D-HERB+M-HERB) component of all zonal taxa, where “zonal taxa” means sum of the CONIF+BLD+BLE+SCL+LEG+ZONPALM+ARBFERN+D-HERB+M-HERB components. The reliability of the results increases with increasing numbers of zonal taxa preserved. Ten zonal taxa are regarded as a minimum to perform this method (Kovar-Eder et al., 2008). Recently, Kovar-Eder and Teodoridis (2018) raised the former threshold to 15 zonal taxa for the application of the IPR-vegetation analysis.

Based on relative proportions of the components, the following six zonal vegetation types are distinguished (Kovar-Eder and Kvaček, 2007; Kovar-Eder et al., 2008): zonal temperate to warm temperate broadleaved deciduous forests (broadleaved deciduous forests, BLDF), zonal warm temperate to subtropical mixed mesophytic forests (mixed mesophytic forests, MMF), zonal subtropical broadleaved evergreen forests (broadleaved evergreen forests, BLEF), zonal subtropical, subhumid sclerophyllous or microphyllous forests (subhumid sclerophyllous forests, ShSF), zonal xeric open woodlands (OWl), and zonal xeric grasslands or steppe (Gl or St). Teodoridis et al. (2011) additionally defined ecotones between the BLDF and MMF and the BLEF and MMF and recently, Kovar-Eder and Teodoridis (2018) defined an ecotone between the MMF/ShSF (Table S2).

The complete flora lists, assigned NLRs and their allocation to the components are given in Appendix A. The number of taxa assigned to the components for each flora is given in Table S3. The proportions of the components for definition of zonal vegetation types are given in Table S4. The zonal vegetation types distinguished in this study are listed next to mean values of climate variables, namely MAT and MAP (Table S5). The variation of components in the micro- and macrofloras is shown in Fig. 2. To visualize the results, a series of paleogeographic maps is provided and discussed below. The maps, allowing to trace the evolution of the IPR vegetation types throughout the early Paleogene, are based on the relative proportions of the components for each paleoflora (Figs. 3–5). For the technical preparation of the maps, ArcMAP 10.4 was used. We use rotated coordinates (using ODSN Plate Reconstruction Service for 55 Ma and hotspot reference frame I) for the paleosites (Figs. 3–5), because in the study area the paleogeographic situation did not undergo any significant changes during the time span investigated here.

2.3. The PFT approach

Although the PFT Approach is not employed in this study, we provide a short outline to facilitate understanding of the discussion and methodological inter-comparisons we presently carry out. The PFT concept goes back to the works of Prentice et al. (1992) and Prentice and Webb (1998), and has been widely used to describe vegetation cover in vegetation modelling. A PFT is defined using traits and climatic thresholds of key taxa, and combines species related by morphological and phenological traits (François et al., 2011). The application of the PFT technique was first introduced by Utescher et al. (2007) on the Neogene paleobotanical record. The study of Bondarenko and Utescher (2024b), based on the same set of floras used in the present study, employs an extended PFT classification scheme described in detail in Popova et al. (2013), comprising 26 herbaceous to arboreal PFTs based on physiognomic characters and bioclimatic tolerances of plants, complemented by an aquatic PFT. The allocation of fossil taxa to the single PFTs is based on interpretation of their NLRs, and follows the procedure described in Utescher and Mosbrugger (2007) and Utescher et al. (2007). The PFT approach requires only information on presence and absence of taxa and thus is relatively robust against taphonomic bias. The approach can be applied to all types of fossil floras with an adequate sample size. Based on the scores of PFTs, PFT diversity spectra (ecospectra) are calculated for each flora. interpretation of the ecospectra in terms of vegetation is supported by multivariate statistics (e.g., cluster analysis; cf. Utescher et al., 2007).

3. Results

To apply IPR-vegetation analysis, 110 floras were analyzed. For the early Paleocene, a total of 25 floras were utilized, all from within a relatively narrow latitudinal range from 41.50°N to 67.06°N (Figs. 3C, 4C). For the late Paleocene, the compilation comprises 21 floras ranging from 41.50°N to 71.50°N (Figs. 3B, 4B). The early Eocene record includes 64 floras covering the widest latitudinal range, from 19.38°N to 75.53°N (Figs. 3A, 4A).

The total number of all fossil taxa per site varies between 9 and 97 (Table S3). When ten zonal taxa are regarded as a minimum (Kovar-Eder et al., 2008), a mean number of zonal taxa of 29.39 for all the floras was sufficient to yield reliable results, except the early Paleocene LF 7 (8.5 zonal taxa), early Eocene PF 38 (7.96 zonal taxa) and LF 23 (8.0 zonal taxa). When 15 zonal taxa are regarded as a minimum (Kovar-Eder and Teodoridis, 2018) seven microfloras and eight macrofloras are insufficient to yield reliable results. The number of zonal taxa (Table S3) in each microflora ranged from 7.96–75.56 (mean 32.46, std. 12.90). The analysis of macrofloras was based on 8.0–50.64 (mean 22.54, std. 11.69) zonal taxa.

The components used for calculation of the proportions also vary in the micro- and macrofloras (Fig. 2, Table S3). The CONIF component in microfloras ranges from 0 to 10, in the macrofloras — 0–15.5 zonal taxa. The BLD component is present in all micro- (3.28–26.07 zonal taxa) and macrofloras (1.75–28.24 zonal taxa). The BLE component in the microfloras varies from 1.08 to 11.69, whereas in the macrofloras — from 0 to 8.13, but mostly does not exceed 3 zonal taxa. The SCL component ranges from 0 to 2.69 in the microfloras and from 0 to 1.99 zonal taxa in the macrofloras. The LEG component occurs rarely: 0–1 in microfloras, 0–4 zonal taxa in the macrofloras. The ZONALPALM component occurs in 21 microfloras (1–4 zonal taxa) and only in one macroflora. The ARBFERN component occurs only in microfloras (0.33–3 zonal taxa) and is absent from the macrofloras. The D-HERB component in the microfloras varies from 0 to 2.45, in the macrofloras — from 0 to 0.83 zonal taxa. The M-HERB component is 0–12.03 zonal taxa in the microfloras and 0–13.58 zonal taxa in the macrofloras.

Generally, for the early Paleogene of the Pacific side of Eurasia, five zonal vegetation types and two ecotones were revealed based on the relative proportions of the components (Figs. 3, 4, Table S4). Warm temperate to subtropical mixed mesophytic forest (= mixed mesophytic forest, MMF) was evidenced by most floras (55 out of 110). The floras assigned to this zonal vegetation type are characterized by proportions of the BLD component from 60.2% to 74.2%, BLE component — 7.3–29.7%, SCL+LEG component — 0–18.6%, and 0–27.6% of herbs. Twenty six out of 110 floras are assigned to warm temperate broadleaved deciduous forest (BLDF) and characterized by proportions of the BLD component from 80.9% to 100%, BLE component — 0–14.8%, and 0–25.7% of herbs. Only one flora is assigned to the warmest, zonal vegetation type of subtropical broadleaved evergreen forests (broadleaved evergreen forests, BLEF) with a proportion of the BLD component higher than 45%. Only five floras were assigned to open woodlands (proportion of herbs from 31.3% to 35.1%). The highest proportion of herbs (42.6–59.7%) characterize two floras assigned to grasslands (Fig. 5, Table S4). The ecotone MMF/BLEF was revealed by 11 floras, characterized by 39.7–64.3% of BLD, 30.3–37.6% of BLE, 2.3–14.8% of SCL+LEG, and 0–23.1% of herbaceous components. The ecotone BLDF/MMF was revealed by 10 floras, characterized by 75.3–79.9% of

BLD, 7.5–24.3% of BLE, 0–12.6% of SCL+LEG, and 0–23.1% of herbaceous components.

4. Discussion

4.1. Comparison of micro- and macrofloras

The IPR claims to reconstruct vegetation independent from the type of flora, so this method was developed to assess major vegetation types. It applies a semi-quantitative evaluation based on the autecology of taxa and leaf physiognomy (Kovar-Eder and Kvaček, 2003, 2007; Kovar-Eder et al., 2008; Teodoridis et al., 2011). Nevertheless, the fossil plant record is usually strongly influenced or even dominated by intrazonal taxa (mainly wetland taxa), masking zonal taxa which are characteristic of mesophytic environments (Kovar-Eder and Teodoridis, 2018). In our results based on micro- and macrofloras, there are also some distinct differences. In the microfloras the number of zonal taxa is more stable in comparison with the macrofloras (Table S3). In turn, this suggests a more even and constant supply of fossil material from pollen compared to leaves. In addition, a greater number of microflora localities suggests more opportunities for pollen storage compared to leaves. However, some taxa are poorly represented or not preserved, even in microfloras.

IPR data are not independent from organ type regarded in each case (Kovar-Eder and Kvaček, 2003). Nevertheless, as seen from our results (Fig. 2, Table S3), the components used for calculating the proportions vary in the micro- and macrofloras. Moreover, the proportions calculated for determination of the zonal vegetation types also differ in the micro- and macrofloras (Figs. 3, 4, Table S4). Leaf floras seem to be biased towards higher BLD and lower BLE proportions, microfloras have a lower proportion of LEG but a higher proportion of SCL components, the ZONALPALM and ARBFERN components occur only in the microfloras in our record. The ZONAL HERB proportions are represented in the microfloras by up to 32%, in the macrofloras — up to 60%. As a result, micro- and macrofloras can sometimes show the same types of vegetation (Ozero Toni, Table S4). However, based on micro- (Fig. 3) and macrofloras (Fig. 4), different types of vegetation may be reconstructed. More often, the difference lies in the character of the reconstructed vegetation. For example, a warmer type based on macroflora (Novosibirskie Islands, Table S4), or a cooler type based on macroflora (Smolyaninovo, Table S4). Sometimes different organ types even show different basic biome type, such as forest based on microflora and open vegetation based on macroflora (Erkovtsy, Table S4).

Despite the fact that, in general, leaf floras have a cooler aspect, and the BLD forest biome is more often reconstructed based on leaves (Fig. 4), as seen in the Table S5, the climatic parameters for leaf floras do not correspond to a temperate character, and, as in microfloras, indicate warm mean annual temperatures. Bondarenko et al. (2019) noted the same pattern for the Paleogene of Primorye. This may result from taphonomic as well as edaphic reasons. Kovar-Eder and Kvaček (2007) assume that the differences of relative proportions of the components in the micro- versus the macrofloras are probably related to the lower taxonomic resolution of the pollen record and to the fact that pollen assemblages may be much more strongly influenced by long-distance transport than the leaf floras. Microfloras may also comprise components originating from different stands and altitudes, a problem that may flaw IPR reconstructions but largely cannot be avoided because the delimited taxonomic resolution does not allow for an unequivocal identification of altitudinal elements.

It should be noted that the taphonomic factor affects the vegetation type reconstruction (with both IPR and PFT) more than the climate reconstruction. Therefore, even floras that are very warm in terms of climatic values (e.g., Krasnoyarka, Table S5) sometimes show vegetation types having a more temperate aspect. Therefore, the IPR approach performs well with both micro- and macrofloras, but there is a bias, comparable to that already known from the PFT technique (Utescher et al., 2021). As has been shown in various previous studies using integrative approaches such as the IPR and PFT technique (e.g., Kovar-Eder et al., 2008; Popova et al., 2017; Bondarenko et al., 2019, 2020b; Utescher et al., 2021) taphonomy may affect the results obtained in vegetation reconstruction even though both methods use diversity instead of richness of components. To quantify taphonomic effects, floral lists for various organ types would be required from the same site, in the best case originating from the same stratigraphic level in order to rule out short-term climatic signals, absent in the present record. At the same time, the fact that the IPR and PFT approaches do not take into account the richness of vegetation components may reduce its ecological resolution. As an advantage, the approaches potentially are more robust to errors induced by differing primary productivity of plants or transport properties of their organs thus making floras of different organ type inter-comparable. Nonetheless, it has to be stressed that the reconstructed vegetation types are based on taphocoenoses and hence potentially represent a composite assemblage that may represent various vegetation types (Utescher et al., 2021).

4.2. Vegetation patterns

Today, the vegetation of Asia is divided into five major zones based on the richness and types of flora of each region: taiga and tundra in the north, deserts and steppes in the central and western parts, tropical rain or dry forests in the south, temperate mixed forests in the east, tropical rain forests in the southeast (Krestov, 2006). According to our results, the early Paleogene vegetation cover in the study area fundamentally differed from the modern one. Although five IPR zonal vegetation types and two ecotones (Fig. 3) were revealed for the early Paleogene of eastern Eurasia, the vegetation patterns reconstructed for the three time slices were much more homogeneous compared to today. The MMF zonal vegetation type dominated over the Pacific side of Eurasia during the early Paleogene, as evident from the microfloras, and occurs in the early and late Paleocene and early Eocene. Thermophilous MMFs were distributed even at very high latitudes, at the same time MMF/BLEF and BLEF were confined to regions south of 50°N. Obviously, the BLEF could be expected also for South China, but there are many localities plotting as more temperate MMFs. The SCL+LEG proportions are low in general, even in the mid-latitudes, where seasonally dry or even larger scale desert conditions have been suggested as evidenced by evaporites and dune systems preserved in Paleogene strata of Southwest China (He et al., 2022). In the actual reconstruction, the scarcity of the SCL+LEG component may be a taphonomic effect related to the poor representation of SCL key taxa (e.g., lauraceous pollen) in the fossil pollen record. Nevertheless, OWl reconstructed for three early Eocene localities, all located south of ca. 45°N

(Fig. 3), may point to regional open landscapes. A recent study based on the application of the PFT technique on Eocene sites of China supports the assumption of regionally more open conditions in the study area to the south of ca. 50°N. The reconstructed patterns show a zone with dry shrub or open woodland in the northwest, and a zone of humid broadleaved forest in the southeast of China while this gradient became more distinct during the Eocene (Li et al., 2022).

Based on the low zonal herb proportions (Fig. 5), the vast majority of sites of our record classify as forest vegetation in the IPR analysis. The results obtained from the early Paleogene floral record of East Asia largely coincide with data obtained by other plant-based reconstructions. Prevailing forest vegetation has been indicated by Grinenko et al. (1989, 1997), Collinson (1990, 2000, 2001), Fradkina (1995, 1996), Kodrul (1999), Collinson and Hooker (2003), Akhmetiev (2004), Ablaev et al. (2005), Utescher and Mosbrugger (2007), Brea et al. (2011), Suan et al. (2017), Bondarenko et al. (2019, 2020b, 2022), Li et al. (2022) (only eastern and southeastern sites), Xie et al. (2022), and Bondarenko and Utescher (2023, 2024b).

The main discussion relates to the type of forest vegetation. IPR results indicate MMF and BLDF as main plant biomes for the study area. In contrast to our data, Collinson (1990, 2000, 2001) indicated a thick tropical, subtropical and deciduous forest cover in the Paleocene around the globe. Graham (1999) and Brea et al. (2011) indicated tropical and subtropical forests worldwide, mainly populated by conifers and broadleaved trees. Willis and McElwain (2002) show that in the Paleocene even the Polar Regions were covered with coniferous and deciduous forests. Some of those reconstructions are not supported by our results.

Using PFT diversity spectra as proxies for vegetation type, the early Paleogene zonal vegetation was generally represented by a warm temperate and subtropical mixed evergreen-deciduous type (Bondarenko and Utescher, 2024b). Based on IPR data, there is no evidence for a zonal arrangement of vegetation belts in the early Paleocene, at least at the high and middle latitudes, where sites are available, while in the late Paleocene the conifer rich MMF subtype prevailed at high latitudes. Hence, our data do not support the model of Wolfe (1985) suggesting (para)tropical vegetation extending to Arctic Asia (high diversity on non-tropical PFTs) or the reconstruction by Collinson and Hooker (2003) (BLDFs for the Paleocene at higher and high latitudes). Golovneva et al. (2023), based on data from the early Paleocene circum-Arctic sites, pointed to highly uniform, temperate and extremely humid conditions around the margins of the early Cenozoic Arctic Ocean. The landmasses around the Arctic Ocean were covered with lush vegetation, represented by conifer and deciduous angiosperm forests. Our results largely coincide with the model of Akhmetiev (2004) suggesting the emergence of a regionally poorly differentiated, large-leaved mesophytic vegetation at higher latitudes of the Northern Hemisphere in the early Paleocene. According to Fradkina (1995), the Paleocene vegetation of the high latitudes (above 60°N) was represented by coniferous forests (mainly *Pinus* Linnaeus and Taxodioideae Endlicher ex Karl Koch), and in lowland areas — deciduous forests with a significant proportion of evergreen elements which is in good agreement with our reconstruction.

Regional studies carried out on the Paleocene floral record of Primorye, located around 50°N, employing PFT diversity spectra, indicated the prevalence of mixed evergreen-deciduous forests of warm temperate character (Bondarenko et al., 2020b).

Based on the IPR method, these plant biomes varied from the MMF/BLEF ecotone to the BLDF/MMF ecotone (Bondarenko et al., 2020a). For southern Primorye, at ~44°N–46°N, Bondarenko et al. (2019, 2021) reconstructed a temperate BLDF based on macrofloras, most probably representing intrazonal wetland vegetation, and a MMF based on microfloras, representing the dominant zonal vegetation type.

As indicated by our data, the early Eocene vegetation in the study area had a warmer and more homogenous aspect compared to that of the Paleocene. This warm aspect of Eocene vegetation has been reported previously. According to Wolfe (1985) and Akhmetiev (1987) tropical and paratropical vegetation widely extended into the higher northern latitudes, up to ca. 60°. On the other hand, Utescher and Mosbrugger (2007) report dominantly warm temperate vegetation types most probably growing under humid conditions for the early and middle Eocene mid-latitudes of the Northern Hemisphere, apart from more sclerophyllous vegetation, restricted to smaller areas. Most sites considered there are indeed characterized by high diversity percentages of evergreen trees, but even in early to middle Eocene localities which had been classified as “paratropical” (cf. Wolfe, 1985) temperate, extra-tropical deciduous elements may reach high diversities as well (e.g., South Greenland, mid-latitudes of Western Asia). The distribution of temperate vegetation, namely the MMF and temperate mixed needle-leaved forest in the reconstruction of Utescher and Mosbrugger (2007) correspond to the zonal extension of both the polar BLDF and the paratropical forest in the reconstruction of Wolfe (1985) for the Paleocene and early Eocene. Also, the subdivision into a needle-leaved type covering the highest northern latitudes and a mainly BLDF type in the northern mid-latitudes as proposed by Wolfe (1985) is evident from the reconstruction by Utescher and Mosbrugger (2007) based on PFT diversity data. Another early Eocene vegetation map for the Northern Hemisphere was presented by Collinson and Hooker (2003) showing polar BLDFs at high and middle latitudes, a mixed vegetation of temperate deciduous broadleaved elements with warm temperate to subtropical elements at mid-latitudes, and a BLEF growing in a wet and tropical climate in southern China, while isolated records of thermophilic floras are reported from Japan and Kamchatka. Such clear zonal arrangement of vegetation belts are not seen in our IPR data. Especially, floras having clear BLE spectra are absent from our record. However, it has to be stated that our early Eocene data cover in the southern part of the study area is quite incomplete, while data for the Paleocene are barren completely. Akhmetiev (2004) suggested the evolution of seasonally dry vegetation during the early Eocene stretching from the Amur region into northern and central parts of China (our floras Shulan, Huanghua, Shache, Wutu, Lanzhou).

Regarding regional scale reconstructions of the early Eocene vegetation of high latitudes (above ~60°N) our results coincide with those of Fradkina (1995) suggesting mainly mixed coniferous and BLDFs with a significant participation of evergreens of up to 7% in the palynological data. Early Eocene pollen records of northern Yakutia (Eastern Siberia), quantitatively studied using the PFT and IPR techniques, revealed cyclic variations of MMFs during warmer intervals to BLDF/MMF ecotone during cooler episodes (Bondarenko et al., 2022; Bondarenko and Utescher, 2023). These types are also observed for northern Yakutia in the reconstruction of Bondarenko and Utescher (2024b). For Primorye, located today at ~44°N–46°N, various detailed studies were presented (Bondarenko et al., 2019, 2021), based on the same localities as presently used. Based on the IPR, MMF/BLEF ecotones based on microfloras, and temperate BLDFs based on macrofloras were reconstructed and are largely in line with the our PFT approach-based results (Bondarenko and Utescher, 2024b).

Various qualitative and semi-quantitative reconstructions of the Eocene vegetation of China have already been published (Sun and Wang, 2005; Ma et al., 2012; Su et al., 2020), but probably due to uncertainties arising from dating accuracy, area range, and methodology, the detailed evolution of vegetation patterns in China during the Eocene is still debated (Sun and Wang, 2005; Ma et al., 2012). The dispute is whether the vegetation pattern of the Eocene East Asia is an east-west differentiation or a tripartite latitudinal zonal arrangement (Sun and Wang, 2005; Ma et al., 2012). Ma et al. (2012) compiled 19 Paleogene pollen records and analyzed the Paleogene vegetation pattern using the percentages of each pollen type classified by life forms. They suggest a noticeable vegetation difference between eastern and western China persisting throughout the Eocene (Ma et al., 2012). According to Xie et al. (2022), during the PETM the palynological assemblage of Jianghan Basin (central China) was characterized by diverse and abundant tropical and subtropical broadleaved tree pollen, providing strong evidence of a diverse south subtropical forest ecosystem that once existed in so-called arid belt of central China. For the early Eocene, the PFT-based vegetation reconstruction suggests a vegetation distribution having some aspects of non-zonality. An arid vegetation zone, represented by shrub mixed with evergreen broadleaved and deciduous broadleaved forest or open woodland with mesophytic to xeric herbs, was located in the interior to the west. For the eastern seaboard, more humid and temperate broadleaved deciduous lowland forest with conifers or subtropical multilayered forest formed the humid vegetation zones in the north of the study area and the south, respectively (Xie et al., 2022).

In contrast to the non-zonal vegetation pattern of Xie et al. (2022), zonal Eocene vegetation with three latitudinally distributed zones over China was suggested by the qualitative study, mainly based on species selected as drought indicators such as *Ephedripites* (Sun and Wang, 2005; Xie et al., 2020). According to them, a subtropical humid vegetation zone was located in the north, (sub-)tropical (semi-)arid vegetation zone was present at mid-latitudes. In contrast, a tropical humid vegetation zone existed in the south (Sun and Wang, 2005). Recent vegetation reconstructions based on integrated modeling results and qualitative paleobotanical data have also suggested similar vegetation distribution (Li et al., 2022).

4.3. Comparison of PFT and IPR vegetation

A recent study (Bondarenko and Utescher, 2024b) using the PFT approach and based on the same floral record allows for comparison of the results obtained from both methods. The IPR vegetation reconstruction (cf. section 2.2.) allows to directly assess vegetation types by using thresholds of zonal vegetation components that are calibrated with modern East Asian vegetation stands. The PFT approach (cf. section 2.3.) does not employ fixed thresholds as no standardized biomisation procedure, and so, the researcher is free to assign PFT spectra obtained for each flora to any vegetation unit. Moreover, the IPR analysis attempts to identify non-zonal elements to exclude them from further calculations, while the PFT approach in its 26 classes version, as in Bondarenko and Utescher (2024b), does not discern zonal and non-zonal PFTs. Thus, the IPR appears to reconstruct vegetation more precisely and effectively compared to the PFT technique. However, IPR results may be biased by incorrect interpretation of fossils in terms of the zonal-non-zonal aspect or the restricted applicability of the inherent modern calibration data set on past phytocoenoses, while the PFT technique can be regarded more robust in this context. Therefore, it can be suggested to apply both approaches as complementary methods.

In the present record, all floras allocated to the BLDF and one flora classified as ecotone between BLDF and MMF using the IPR method fall into the group of BLDF and transitional BLDF to MMF vegetation using the PFT approach (Bondarenko and Utescher, 2024b). With the exception of three floras allocated to the open woodlands, floras identified as MMF/BLEF, MMF and ecotone between BLDF and MMF based on the IPR approach fall into the large group of MMF varieties as identified using the PFT approach (Bondarenko and Utescher, 2024b).

In summary, it is shown that the vegetation established by the PFT method tends to be more temperate compared to IPR vegetation analysis. This is supported by a study on the vegetation in the Paleogene of Primorye (Bondarenko et al., 2021), where IPR vegetation analysis also shows a warmer aspect of the vegetation when compared to the PFT approach. This effect can be explained by the fact that in the IPR, potentially temperate, mainly broadleaved deciduous elements are a priori excluded from the identification procedure of the biome type, for being scored as non-zonal. Moreover, it is shown that the IPR may yield a higher spatial heterogeneity in reconstructed vegetation types (e.g., Primorye, Figs. 3, 4) while the PFT approach provides more homogeneous vegetation patterns (Bondarenko et al., 2021; Bondarenko and Utescher, 2024b), which is generally more in line with the reconstructed climate patterns (Bondarenko and Utescher, 2022, 2024a). The observed heterogeneity in the IPR is partly a result of predefined thresholds. Partly it is caused by the bias introduced by the differing representativeness of plant organs with respect to the functional types preserved in each case in the sedimentary record (Fig. 2). The IPR was designed as an intergrative analysis tool to jointly reconstruct vegetation from all types of plant organs (Kovar-Eder and Kvaček, 2003), hence, we follow this concept in the present study. In addition, in the PFT technique, the organ type has a distinct impact on the results. Therefore, Bondarenko and Utescher (2024b) treated micro and macrofloras separately in order to ensure a sound statistical analysis.

4.4. Correlation with climate patterns

It is known that vegetation changes are mostly induced by climate change (Askin and Spicer, 1995; Lu et al., 2023). The observed vegetation patterns and their changes through the early Paleogene in many cases can be correlated with climate patterns and the overall continental paleoclimate evolution as reconstructed from the paleobotanical record. The higher-than-present spatial homogeneity of early Paleogene vegetation coincides with shallow temperature gradients (Bondarenko and Utescher, 2022) and significantly wetter-than-present conditions in inland regions north of 50°N and at high latitudes of East Asia during the early Paleogene (Bondarenko and Utescher, 2024a).

Paleotemperature reconstructions for the presently studied paleobotanical sites (means of mean annual temperature – MAT and cold month mean temperature – CMMT; cf. Bondarenko and Utescher, 2022) indicate the existence of two different regional climatic zones in the Paleocene representing in each case the cooler and warmer (subtropical) part of warm temperate climate of the Koeppen-Geiger system. In the early Eocene, the gradient became more clearly pronounced and in addition, a cool temperate zone can be distinguished (cf. fig. 3 in Bondarenko and Utescher, 2022). Also mean values of mean annual precipitation (MAP) demonstrate a clear regional subdivision (especially pronounced in the early Eocene) into two zones located to the north and south of ca. 50°N paleolatitude, which is also expressed by mean precipitation of dry and wet months data (Bondarenko and Utescher, 2024a). Between both zones, within the range of ca. 5° to the south and north from 50°N paleolatitude, a transition zone can be distinguished where both floras existing under wetter and drier conditions occurred. According to Bondarenko and Utescher (2024a), the MAP gradient became more pronounced in the early Eocene and was northwest-southeast oriented, whereas in the mid-latitudes and a larger zone with a distinctly seasonal rainfall pattern appeared which probably became more pronounced during the Eocene. In Tibet/western China, the Eocene encompasses significant changes in topography and tectonic uplift processes causing the establishment of a Mediterranean type climate (Zhao et al., 2023). The generally high precipitation level reported for the high and higher mid-latitudes of the Pacific areas of Eurasia throughout the early Paleogene (Bondarenko and Utescher, 2024a) is combined with high temperatures, and a shallow thermal gradient (Bondarenko and Utescher, 2022).

In general, the major plant biome changes reconstructed for the Pacific coastal areas during the early Paleogene (especially in the early Eocene), show a very smooth differentiation into two vegetation zones: BLDF/MMF and MMF in the northern part, and MMF, MMF/BLEF and BLEF in the southern part (Table S5), which coincide with the climate patterns. The presence of mangroves in our early Eocene records, already known from previous studies, is largely in line with our climate reconstruction and can be related to hyperthermal events such as the PETM and ETM (Bondarenko and Utescher, 2022). The distribution of swamp taxa (*Glyptostrobus* Endlicher and *Taxodium* Richard) is well correlated with our wetter zone located to the north of 50°N paleolatitude and distribution of coals and/or oil shales. The distribution of the xerophytic taxon *Ephedra* Linnaeus largely defines the drier zone located to the south of 50°N paleolatitude and coincides with the regional distribution of red bed sediments and/or evaporites (Bondarenko and Utescher, 2024a).

In various earlier publications, East Asian Paleogene climates were subdivided into three latitudinal zones controlled by the planetary wind system (e.g., Liu, 1997; Wang et al., 1999; Akhmetiev, 2004; Zhang et al., 2012). These zones are, at least partly, defined by hydrological constraints. Lithologically, two humid zones located separately in the south and north are characterized by the occurrence of coals and/or oil shales, while the third broad arid zone resided in the middle largely designated by widespread red beds and/or evaporites along ca. 30°N paleolatitude (ranging between ~25°N and ~35°N), possibly driven by subtropical highs (Liu, 1997; Wang et al., 1999; Zhang et al., 2012).

Based on the PFT approach, Li et al. (2022) suggest the existence of a northwestward zone of dry shrub or open woodland and a southeast zone of humid broadleaved forest in China from the early to late Eocene. This hydrological distribution is consistent with mammal distribution, lithological indicators and geochemical proxies. The reconstructed early Eocene vegetation pattern coincides with our results showing a declining MAP gradient from the eastern coastal areas to the western continental region (Bondarenko and Utescher, 2024a).

Terrestrial ecosystems are greatly affected by climate, particularly temperature and precipitation (Whittaker, 1975). As can be seen (Fig. 6), the marked area of average min and max values of MAT and MAP for the early Eocene of East Asia corresponds to four modern plant biomes, namely the tropical deciduous and temperate forests, savanna and steppe. Due to the comparatively moderate early Eocene MAP (Bondarenko and Utescher, 2024a), the southernmost sector of our sites partly plots in the modern steppe/savanna sectors, but most of our localities indicate forest, according to the IPR. At the same time, Li et al. (2022) indicate a zone of dry shrub or open woodland in the northwest of China during the Eocene.

More insight into the relationship of early Paleogene vegetation and modern vegetation units in the study area is obtained when plotting the climatic envelopes calculated from the single floras (Bondarenko and Utescher, 2022) on a diagram showing modern vegetation of Pacific Eurasia in the field of MAT and mean annual range of temperatures (MART) (Wolfe, 1979). Due to the high early Eocene temperature level and low seasonality, our sites plot in the upper left corner of MAT-MART chart (Fig. 7), in the realm of modern broadleaved evergreen forest and coolest parts of paratropical forests, while modern MMFs comparable to the reconstructed phytocoenoses (mixed broadleaved-evergreen and deciduous; mixed broadleaved-evergreen and coniferous) exist under cooler conditions and partly under raised seasonality of temperature. On the one hand, this may explain the occurrence of broadleaved evergreen components even in floras at higher and very high latitude. On the other hand, it exemplifies that Cenozoic phytocoenoses may have substantially differed from modern ones regarding their taxonomic composition and hence, comparisons regarding their climatic envelope have to be treated with care.

The MAT-MART chart (Fig. 7) also provides clues regarding the absence/scarcity of sites with unequivocal tropical vegetation from the Eocene of South China as was also reported by Li et al. (2022). Climate conditions reconstructed for the southernmost sector (cf. Fig. 7, north of ~22°N) with MAT < 22°C and CMMT < 18°C (Bondarenko and Utescher, 2022) would not have supported tropical vegetation. Warmer conditions likely existed further to the south, but in this context, it should be mentioned that there is evidence for cooler than expected near-equatorial temperatures, e.g., from the early Eocene of Rajasthan, India (Shukla et al., 2014) and the middle Eocene of Hainan Island, South China (Spicer et al., 2014), despite Paleogene climates being generally considered warmer than present. However, in our reconstructed time-interval, only a few localities at lower latitudes are available and more research is required to include more well-dated sites in order to fill this knowledge gap.

5. Conclusions

The exceptionally rich paleobotanical record of East Asia holds the key for reconstructing the detailed early Paleogene regional vegetation evolution in space and time. The high diversity of the paleofloras and up-to-date taxonomy result in useful vegetation interpretations. Our vegetation maps for the first time allow quantifying major plant biome changes in space and time on the Pacific side of Eurasia over the early Paleogene.

Based on the low zonal herb proportions, our data indicate that the Pacific side of Eurasia during the early Paleogene was mainly covered by forest vegetation. The results obtained from the IPR-vegetation analysis of the early Paleogene floral record of East Asia do not contradict the data obtained by other researchers, except for the presence of distinctly arid mid-latitudes and widespread tropical forests north of ~20°N, which are not supported by our IPR data.

According to our results, the early Paleogene vegetation in the study area fundamentally differed from that of the modern. Regarding our IPR patterns, the vegetation in the early Paleogene was much more homogeneous compared to modern vegetation, although five zonal vegetation types and two ecotones were revealed for the early Paleogene of eastern Eurasia. The MMF zonal vegetation type dominated on the Pacific side of Eurasia during the early Paleogene. As evident from the microfloras, the MMF occurs in the early and late Paleocene and early Eocene. Thermophilous MMFs were distributed even at very high latitudes while MMF/BLEF and BLEF were confined to regions south of 50°N. The SCL+LEG proportions are low in general, even in the mid-latitudes. The OWl localities are all located south of ca. 45°N.

The proportions calculated for determining of the zonal vegetation types differ in the micro- and macrofloras. Despite the fact that, in general, leaf floras have cooler aspect, and the BLD forest biome is more often reconstructed based on leaves, the climatic parameters for leaf floras do not correspond to a temperate character, and, as microfloras, they show a high MAT. Therefore, even floras that are very warm in terms of climatic values sometimes show cooler types of vegetation. This may partly relate to a riparian imprint in many of the studied fossil floras.

The observed vegetation patterns and their changes through the early Paleogene, in many cases, can be correlated with climate patterns and the overall continental paleoclimate evolution as reconstructed from the paleobotanical record. The higher-than-present spatial homogeneity of early Paleogene vegetation coincides with shallow temperature gradients and a significantly more humid regional rainfall pattern over East Asia during the early Paleogene.

The vegetation established by the IPR method tends to be warmer compared to PFT vegetation analysis because various temperate taxa are not considered in biome reconstruction for being classified azonal. The IPR appears to reconstruct vegetation more precisely and effectively compared to the PFT technique, due to the integrated calibration technique using modern vegetation data. However, IPR results may be biased by incorrect interpretation of fossils in terms of the zonal-non-zonal aspect or the restricted applicability of the inherent modern calibration data set on past phytocoenoses while the PFT technique can be regarded more robust in this context. Therefore, it can be suggested to apply both approaches as complementary methods.

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Figure captions

Fig. 1. Location of the selected early Paleogene sites of the Pacific side of Eurasia. See Appendices A, B for list of all the sites and the floral data.

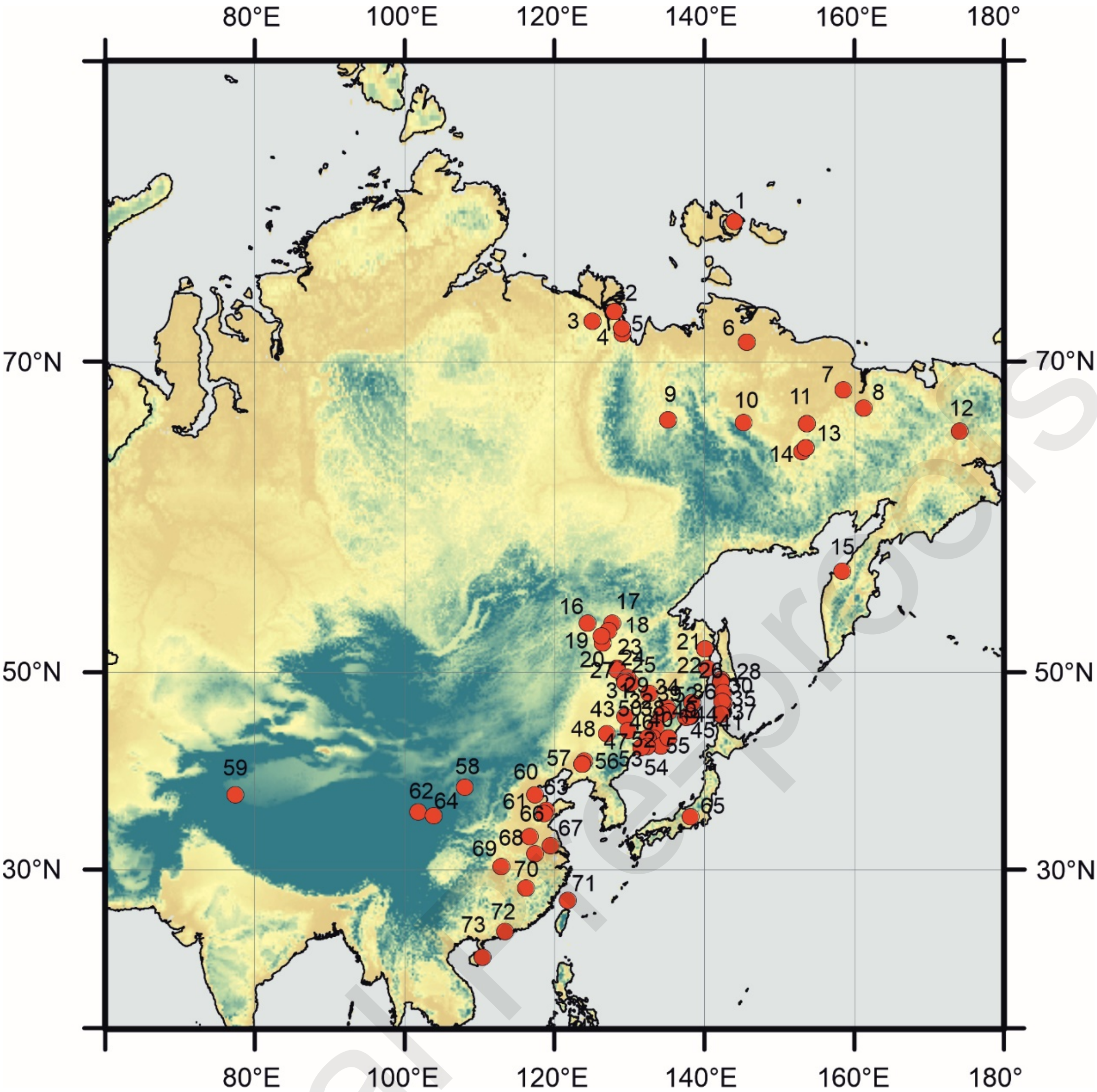

Fig. 2. Representation of IPR components in macro- and microfloras. Mean proportions calculated based on 110 early Paleocene to early Eocene localities yielding both macro- and microfloras.

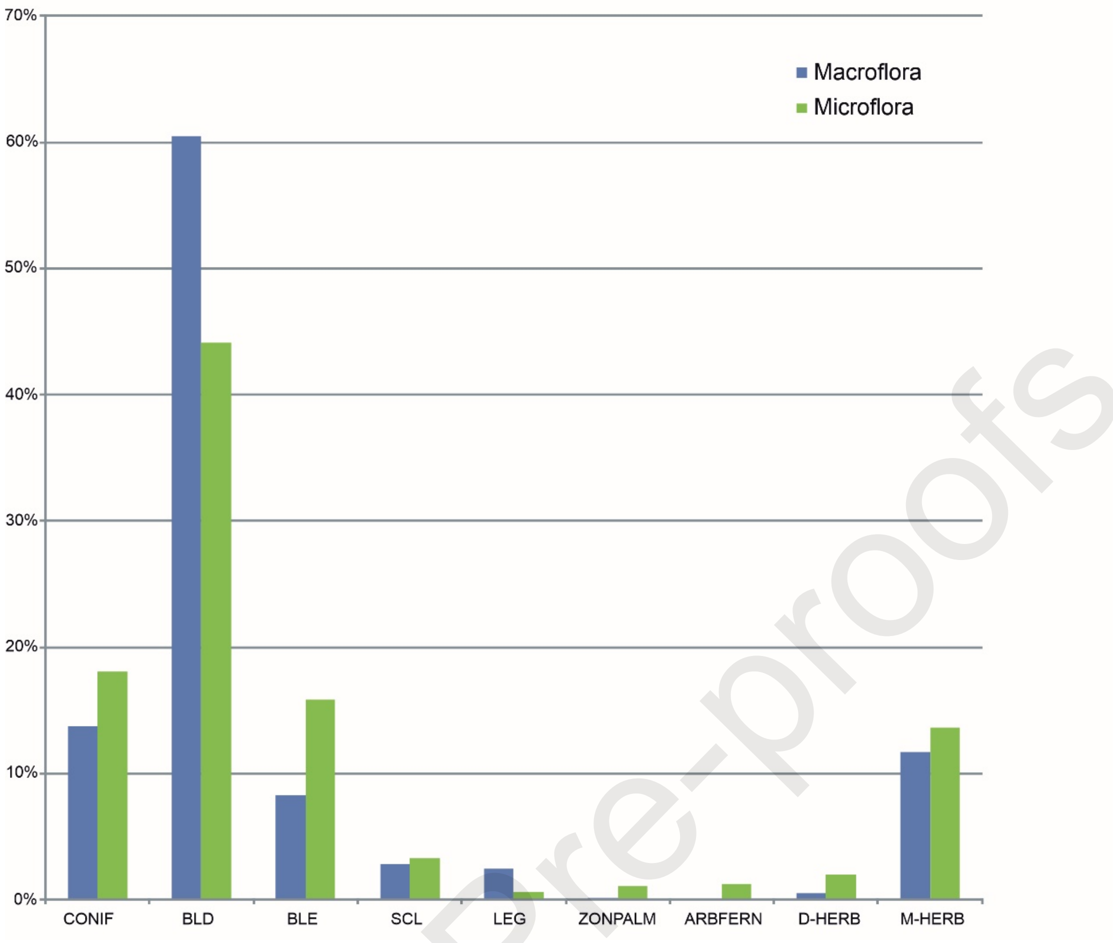

Fig. 3. Proportions of the IPR components and corresponding zonal vegetation types in the early Paleogene of East Asia based on microfloras.

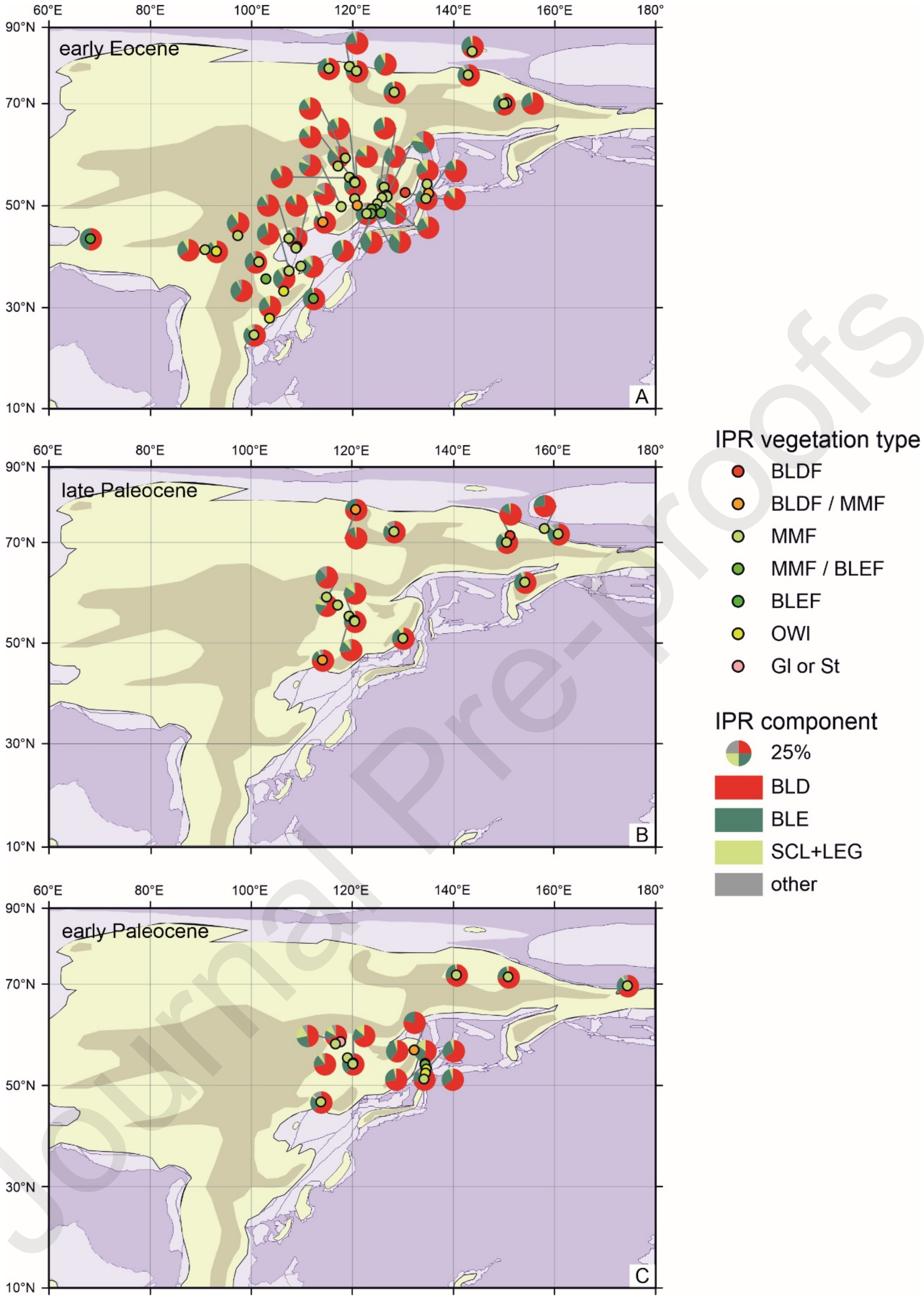

Fig. 4. Proportions of the IPR components and corresponding zonal vegetation types in the early Paleogene of East Asia based on macrofloras.

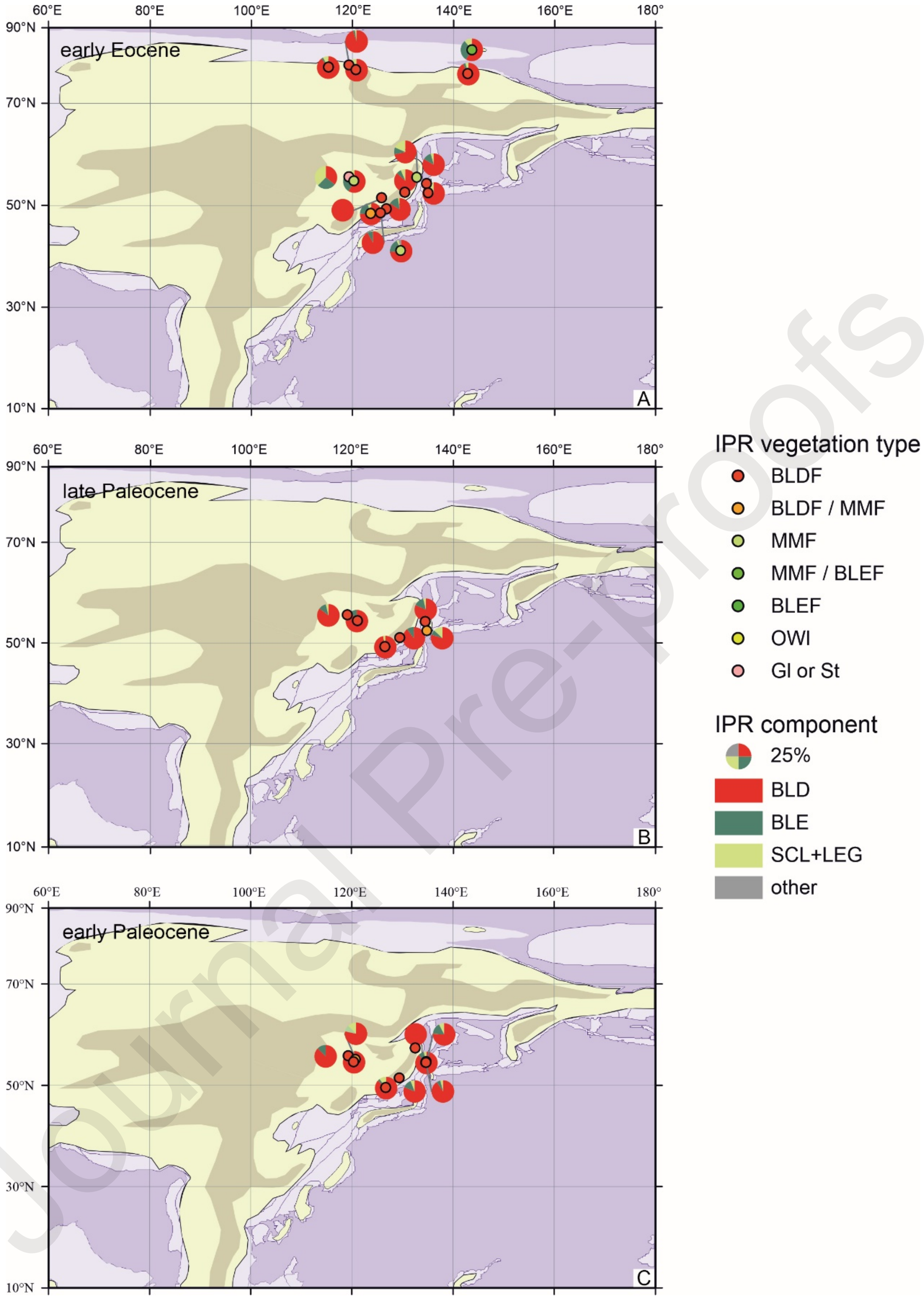

Fig. 5. Proportions of the herbaceous and arboreal components and corresponding zonal vegetation types in the early Paleogene of East Asia.

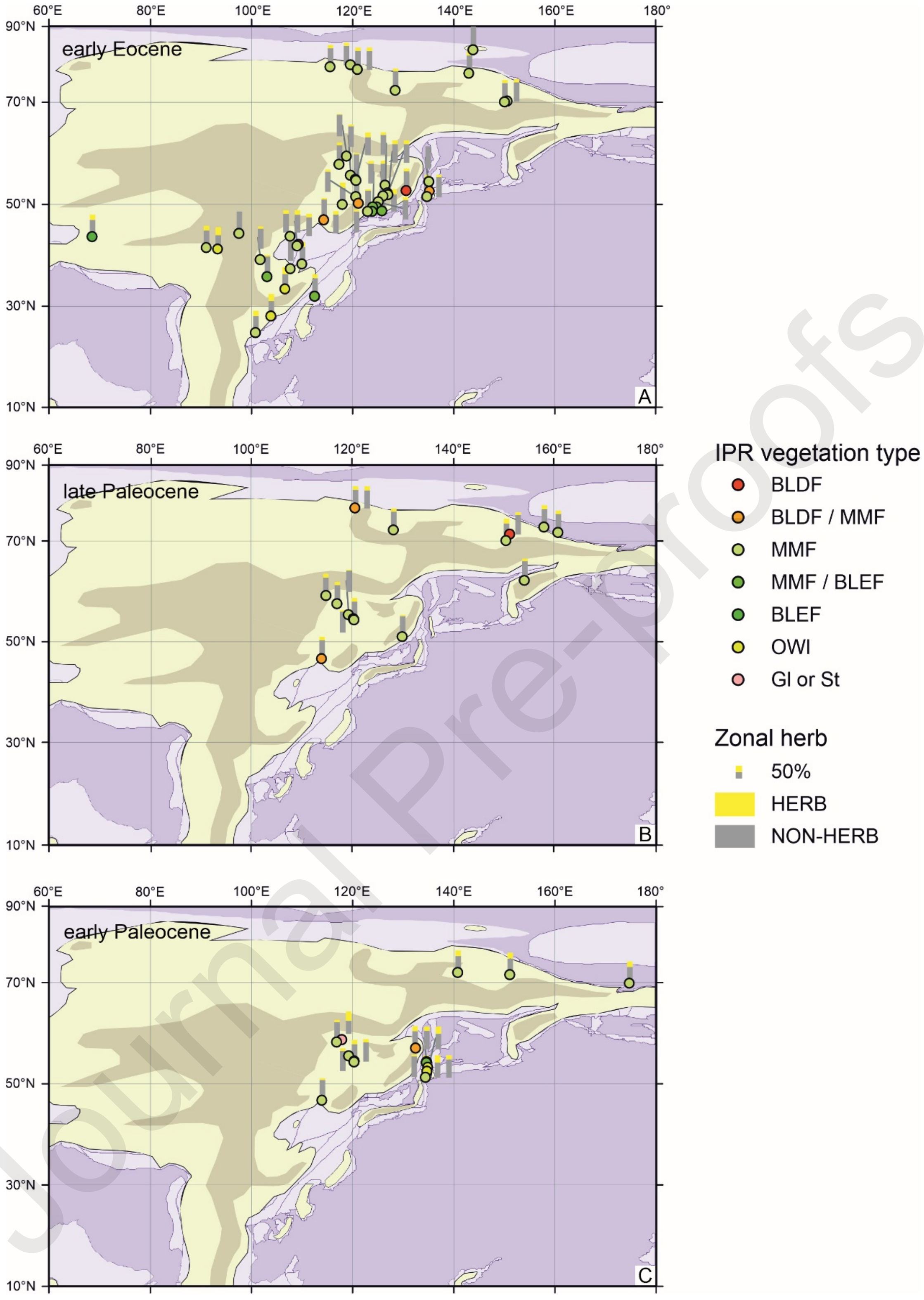

Fig. 6. Modern biomes on axes of MAT and MAP (from Whittaker, 1975). The highlighted area shows MAT and MAP reconstructed for the early Paleogene of East Asia by Bondarenko and Utescher (2022, 2024a).

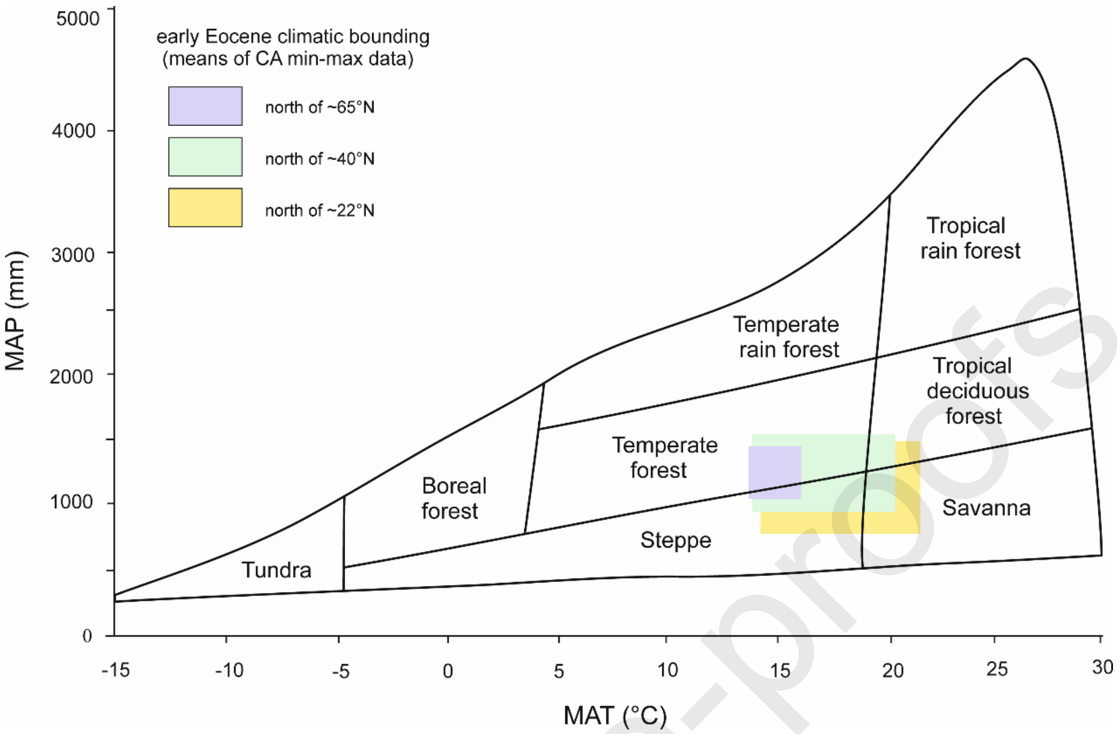

Fig. 7. Modern forest biomes on axes of MAT and MART (from Wolfe, 1979). The highlighted area shows MAT and MAP reconstructed for the early Paleogene of East Asia by Bondarenko and Utescher (2022, 2024a).