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Paleogene vegetation changes in Primorye, Far East of Russia: A study based on diversity of plant functional types

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Paleogene vegetation changes in Primorye (Far East of Russia) are studied using the Plant Functional Types (PFT) Approach, for the first time applied on the large palaeobotanical records of this region. The palaeobotanical data for this reconstruction are based on the analysis of 30 palynofloras and 24 leaf floras covering the Early Palaeocene to Late Oligocene. The vegetation reconstruction at the level of PFTs in general points to the presence of mesophytic forest vegetation in Primorye throughout the Paleogene. While in the Palaeocene vegetation of Primorye was of temperate deciduous type, warm temperate-mixed evergreen-deciduous forests dominated in the Eocene and Early Oligocene. In the Late Oligocene, the vegetation of Primorye was again primarily deciduous, mixed evergreen-deciduous forests persisted at places. The observed vegetation patterns and their changes through time in many cases can be correlated with spatial climate patterns and the overall continental palaeoclimate evolution, as recently reconstructed from the same palaeobotanical record. The higher-than-present spatial homogeneity of Paleogene vegetation coincides with shallow temperature gradients and a significantly more humid regional rainfall pattern over Primorye during the Paleogene.

KEYWORDS

PFT diversity, PFT structure, spatial gradient, temporal trend, vegetation type

1 | INTRODUCTION

The Paleogene (65.5–23.03 Ma) globally was an interval of significant climatic and biotic reorganization (Akhmetiev, 2004). Vegetation dynamics in the Paleogene were associated with global and regional climate changes that took place in this time span (Akhmetiev, 2004). The global climate during the Paleogene was characterized as being in a worldwide warm and equable greenhouse state, punctuated by intermittent hyperthermals, and the transition to an icehouse (Eldrett, Greenwood, Harding, & Huber, 2009; Zachos, Dickens, & Zeebe, 2008).

The relatively stable Palaeocene, followed by a global warming trend, was punctuated by the Palaeocene—Eocene Thermal Maximum (PETM, 55.5 Ma) which displayed the highest temperature in the Cenozoic (Zachos et al., 2008). At that time vegetation was adapted to a warm, moist global climate, and forested areas expanded to the poles, which were free of ice (Willis & McElwain, 2002). The Palaeocene and Eocene polar broad-leaved deciduous forests grew in winter darkness and mesothermal humid climate. Those were very low-diversity forests with little habitat variation, very few climbers and more open structure (Collinson, 1992; Collinson & Hooker, 2003).

The first broadleaved subtropical evergreen (rain) forests appeared in the Palaeocene and evolved during the late Palaeocene and Eocene (Willis & McElwain, 2002). The Late Palaeocene and Eocene broadleaved subtropical evergreen forests were variable in time and space. Most evergreen thermophilous forests were highly diverse, multistratal, rich in climbers, with closed structure and would have provided many varied habitats. In several areas, subtropical vegetation contained sclerophyllous elements at different times in the Eocene (Collinson, 1992; Collinson & Hooker, 2003).

A global cooling trend setting in after the Middle Eocene Climatic Optimum (MECO) culminated in the Oi 1 glacial event at the Eocene–Oligocene transition (EOT) (Bijl et al., 2009; Zachos et al., 2008). Accordingly, from the late Middle Eocene, subtropical evergreen forest vegetation gradually changed into vegetation characterized by the loss of paratropical elements and increasing proportion of temperate deciduous elements resulting in the establishment of broadleaved mixed deciduous and evergreen forests in the Oligocene (Collinson, 1992). The Late Eocene and Oligocene vegetation developed as climate changed, and therefore was variable due to its transitional nature; however, broadly it represented mixed mesophytic forest vegetation. This Late Eocene and Early Oligocene mixed broadleaved deciduous and evergreen forest vegetation had medium to high diversity, with the proportions of different elements varying through time and different geographic areas. This vegetation had lower diversity, contained fewer lianas and climbers and possibly had a more open structure than the subtropical forests. Some seasonality was present, being induced either by changes in temperature or water availability or both (Collinson, 1992).

In the Oligocene, the vegetation of most parts of Eurasia reflected a humid warm temperate climate but with sclerophyllous elements becoming more significant in abundance or diversity. It was dominantly forest vegetation (possibly shrubland in places) but with relatively open structure (Collinson, 1992). In some regions, climate tended to become drier after the start of the Oligocene (Sun et al., 2014).

Thus, Paleogene floras provide the potential for detailed interpretation of plant biomes and their response to global change, such as warm climate thermal maxima and tectonic events. Therefore, the knowledge of the vegetation evolution during the Paleogene provides unique perspectives for the modelling of actual global changes and helps to probe into the integrated response of the Earth system to various driving forces (Collinson, 1992; Utescher, Mosbrugger, Ivanov, & Dilcher, 2009; Zachos et al., 2008).

The Primorye Region (or Primorye) is located in the south of the Russian Far East (RFE), on the coast of the Sea of Japan, bordering the Eurasian continent and the Pacific Ocean. Located in the transitional zone "continent-ocean," this territory constantly experiences the influence of oceanic-atmospheric and continental-atmospheric events (Gerasimov, 1969). The study of the vegetation dynamics of Primorye in the geological past, in particular in the Paleogene, promotes the understanding of the formation of modern vegetation in this region.

The evolution of Paleogene climates in eastern Eurasia in general and Primorye in particular is tied to the history of the East Asian Monsoon and is complicated by tectonic events such as uplift of the Tibetan Plateau, and the Sea of Japan back-arc opening (Akhmetiev, 2004, 2015; Akhmetiev & Zaporozhets, 2017; An, Kutzbach, Prell, & Porter, 2001; Liu et al., 2015; Liu & Yin, 2002; Pavlyutkin & Golozubov, 2010; Quan, Liu, & Utescher, 2012a, 2012b; Sato et al., 2006; Tada, Zheng, & Clift, 2016; Yamanoto & Hoang, 2009). Moreover, past climates of eastern Eurasia are supposed to reflect the varying intensity of the warm Kuroshio and cold subarctic currents (Gallagher et al., 2009; Matthiessen, Knies, Vogt, & Stein, 2009).

Vegetation dynamics in the Paleogene can be reconstructed from the palaeobotanical records. Primorye is one of the RFE regions, where large burials of Paleogene plants are concentrated; therefore, the Paleogene flora of Primorye was a subject of extensive taxonomic studies the results of which were presented in the works of Ablaev (1974, 1977, 1978, 2000), Ablaev and Akhmetiev (1977), Ablaev, Li, Vassiliev, and Wang (2005), Ablaev, Li, and Wang (2006), Akhmetiev (1973, 1974, 1988, 1993), Akhmetiev, Bolotnikova, Bratseva, and Krassilov (1978), Akhmetiev, Bratseva, and Klimova (1973), Akhmetiev and Shyvareva (1989), Baskakova and Gromova (1979, 1982, 1984), Baskakova and Lepekhina (1990), Bolotnikova (1979), Bolotnikova and Sedykh (1987), Bolotnikova (1988, 1989, 1993, 1994), Borsuk (1952), Gromova (1980), Klimova (1981, 1988), Klimova, Kramchanin, and Demidova (1977), Klimova and Tsar'ko (1989), Koshman (1964), Krassilov (1989a, 1989b), Kundyshev and Petrenko (1987), Kundyshev and Verkhovskaya (1989), Mikhailov, Feoktistov, and Klimova (1989), Pavlyutkin (2002, 2007a, 2007b, 2011), Pavlyutkin, Chekryzhov, and Petrenko (2012, 2014), Pavlyutkin, Nevolina, Petrenko, and Kutub-Zade (2006), Pavlyutkin and Petrenko (1993, 1994, 1997, 2010), Rybalko, Ovechkin, and Klimova (1980), Tashchi, Ablaev, and Mel'nikov (1996), Varnavskii, Sedykh, and Rybalko (1988), Verkhovskaya and Kundyshev (1989), etc.

However, these works are mainly devoted to the description of plant fossil remains, new fossil taxa, taxonomic diversity of Paleogene plants, or palaeofloristic aspects. The knowledge on Primorye vegetation dynamics in the Paleogene is still very poor and fragmentary. For example, Krassilov and Alekseenko (1977) attempted a reconstruction of a sequence of plant community change in southern Primorye involving different dominants. Ablaev (2000) described plant communities that existed within the territory of the Artemo-Tavrichanskii Basin (southern Primorye) in the middle Eocene. Pavlyutkin (2007a) reconstructed a domination of broadleaved forests with a very small admixture of conifers within the area of the Artemo-Tavrichanskii Basin in the late Eocene. Ablaev and Vassiliev (1998), and later Pavlyutkin (2011) described the early Oligocene temperate warm coniferous-broadleaved and broadleaved deciduous vegetation associated with some evergreen representatives within the Khasanskii Basin (southern Primorye). Lopatina (2004), based on macro- and microflora, reconstructed a coniferous-broadleaved polydominant forest at the end of the late Eocene and in the early Oligocene in northern Primorye. Bolotnikova (1979) described the Paleogene vegetation that existed on the west coast of the Sea of Japan within the territory of southern Primorye on the basis of palynological data: from mixed forests with tropical and subtropical elements in the Palaeocene to coniferous-deciduous forests with some admixture of subtropical plants in the Oligocene.

In summary, partly contradictory and fragmentary results are obtained from these qualitative interpretations of macro- and microfloral successions, and quantitative studies integrating over various types of floras were largely missing so far. Only recently, Bondarenko, Blokhina, Mosbrugger, and Utescher (2019) provided a first coherent palaeoclimate reconstruction for the Paleogene of Primorye based on the palaeobotanical record. Moreover, major plant biome changes in Primorye during the Paleogene were studied by Bondarenko, Blokhina, and Utescher (2019) using the Integrated Plant Record vegetation analysis and discussed in the palaeoclimatic context. Here, we apply a complementary method, the Plant Functional Type (PFT) Approach that can also be applied on micro- and macrofloras and allows for an interpretation of vegetation at the level of PFTs and to trace diversity changes in time and space. Based on a total of 54 reasonably well-dated pollen and leaf floras (LF) from 19 basins, diversity patterns are reconstructed for seven stratigraphic levels and dynamics are traced over a time-span of ca. 42 myr, in total. Moreover our study allows for discussion of advantages and drawbacks of two well-established methods of quantitative biome reconstruction from the palaeobotanical record.

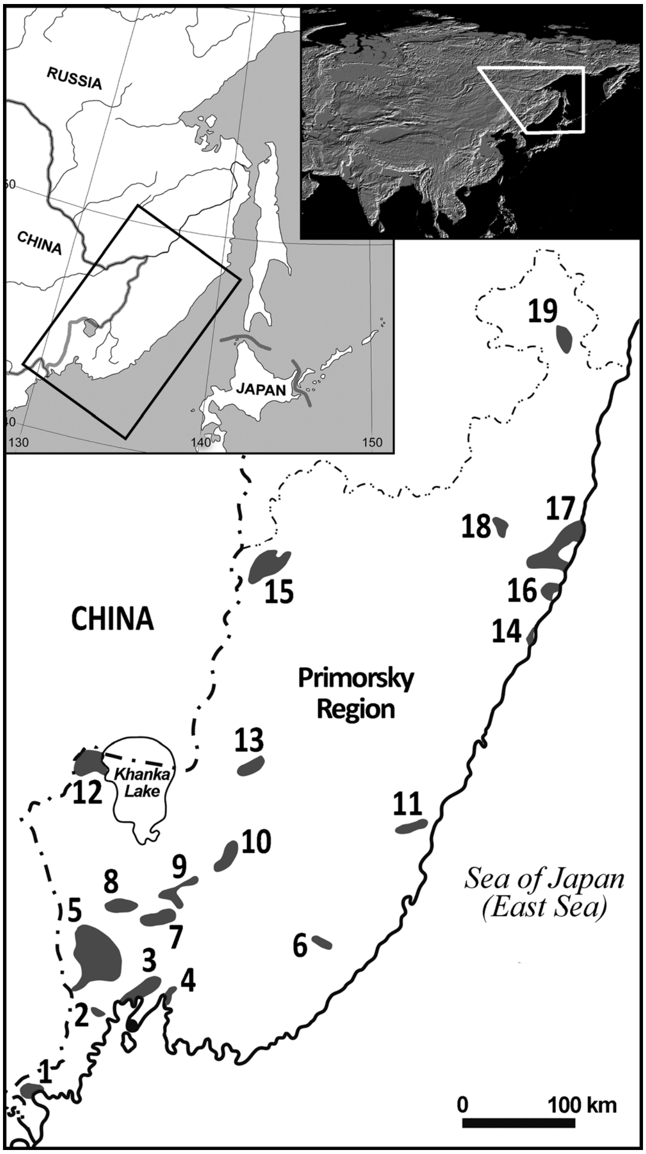

FIGURE 1 Map showing the location of the Primorye Region within the Far East of Russia and the location of the studied basins. Filled areas: the basins after Pavlyutkin and Petrenko (2010). 1—Khasanskii, 2—Ambinskii, 3—Artemo-Tavrichanskii, 4—Shkotovskii, 5—Pushkinskii, 6—Vanchinskii, 7—Ivanovskii, 8—Pavlovskii, 9—Snegurovskii, 10—Chernyshevskii, 11—Zerkal'nenskii, 12—Tur'erogskii, 13—Krylovskii, 14—Kemskii, 15—Nizhnebikinskii, 16—Amginskii, 17—Maksimovskii, 18—Svetlovodnenskii, 19—Ozero Toni. The single floras are listed in Table 1, together with information on basin provenience, type of flora, stratigraphic age, method of dating, and references. The complete flora lists, assigned NLRs and their allocation to the PFTs are given in Data S1

2 | STUDY AREA

The palaeobotanical records of Primorye studied herein originate from 19 basins (Figure 1). The Paleogene strata of Primorye comprise volcanic and sedimentary deposits, unconformably overlying Mesozoic basement. The sedimentary facies includes fine- to coarse-grained continental clastics and intercalated lignites excavated in several active opencast mines. For some of the basins, mainly generated by extensional tectonics (Pavlovskii, Pushkinskii and Maksimovskii basins), intercalated volcanoclastic layers and tholeitic lava flows (Maksimovskii Basin: Takhobinskaya and Kuznetsovskaya formations) allow for radiometric dating of the strata (Table 1 and Figure 2). The sedimentary successions in the individual basins are characterized by numerous unconformities related to regional tectonics and phases of rifting and subsidence (Pavlyutkin & Petrenko, 2010). When combining the strata of the individual basins a time-span of ca. 42 myr is represented, spanning the Early Palaeocene (Danian) to Late Oligocene (Chattian).

The regional stratigraphic correlation chart for the basins (Figure 2; adapted from Pavlyutkin & Petrenko, 2010) is based on a variety of stratigraphic data obtained from radiometric dating, well log correlations, regional sequence-stratigraphical concepts considering the position of volcanogenic units and main phases of peat forming, vertebrate fauna and regional and inter-regional pollen zonation (Akhmetiev, 1973; Chashchin et al., 2013; Pavlyutkin & Petrenko, 2010; Popov, Rasskazov, Chekryzhov, et al., 2005; Varnavskii et al., 1988). The stratigraphic scheme has been tied to the International Stratigraphic Chart (Cohen et al., 2013; Pavlyutkin & Petrenko, 2010) and allows for dating the flora-bearing horizons at the stage level (Figure 2). For some of the floras, stratigraphic ages are better constrained (cf. Table 1: radiometric datings for the Zanadvorovka, Gladkaya17, Kluch Stolbikova and Sobolevka floras).

3 | MATERIAL AND METHODS

3.1 | The floral record

The palaeobotanical record of Primorye is diverse and has been subject to extensive taxonomic studies (cf. Table 1 for references). In the present study, a total of 54 floras including 30 palynofloras (PF) and 24 LF were studied with respect to palaeoclimate at seven stratigraphic levels. The floras cover a total time-span of ca. 42 myr, ranging from the Early Palaeocene (Danian) to Late Oligocene (Chattian). The single floras are listed in Table 1, together with information on basin provenience, type of flora, stratigraphic age, method of dating, and references. The complete floral lists, assigned Nearest Living

TABLE 1 Palaeofloras studied

Stratigraphic level	Locality name (Lon/Lat)	Type of flora	Number of fossil taxa	Basin, formation	Age, method of dating	References
1. Late Oligocene	1. Zanadvorovka (131.40/43.20)	PF	30	Ambinskii, analog of Pavlovskaya	Chattian, K/Ar dating (24.0 ± 3.0 ma), RG, IRC	Pavlyutkin & Petrenko, 2010; Popov et al., 2005
	2. Pushkinskii9180 (131.50/43.30)	PF	30	Pushkinskii, Pavlovskaya	Chattian, RG, IRC	Pavlyutkin et al., 2012
		LF	28			
	3. Pavlovka9035-D (132.05/44.05)	PF	35	Pavlovskii, Pavlovskaya	Chattian, RG, IRC	Pavlyutkin & Petrenko, 2010
	4. Turii Rog8 (131.60/45.10)	PF	32	Tur'erogskii, analog of Pavlovskaya	Chattian, RG, IRC	Pavlyutkin & Petrenko, 2010
	5. Luchegorsk6212 (134.20/46.30)	PF	32	Nizhnebikinskii, Upper coal	Chattian, RG, IRC	Pavlyutkin & Petrenko, 2010
2. Early Oligocene	6. Kraskino9182/9196 (130.40/42.45)	PF	71	Khasanskii, Nizhnefatashinskaya	Rupelian, RG, IRC	Pavlyutkin et al., 2014
		LF	161			
	7. Pavlovka9035-D (132.05/44.05)	PF	37	Pavlovskii, Pavlovskaya	Rupelian, RG, IRC	Pavlyutkin & Petrenko, 2010
	8. Rettikhovka (132.40/44.10)	PF	36	Snegurovskii, analog of Pavlovskaya	Rupelian, RG, IRC	Ablaev, 1977; Akhmetiev et al., 1973; Klimova et al., 1977; Pavlyutkin & Petrenko, 1994, 2010
		LF	48			
	9. Voznovo9206 (135.30/44.15)	PF	79	Zerkal'nenskii, Voznovskaya	Rupelian, RG, IRC	Pavlyutkin et al., 2014
		LF	80			
	10. Tikhii Kluch (137.10/45.40)	LF	49	Kemskii, Kizinskaya	Rupelian, RG, IRC	Akhmetiev, 1988; Rybalko et al., 1980; Varnavskii et al., 1988
	11. Amgu9302 (137.36/45.60)	LF	62	Amginskii, Granatnenskaya	Rupelian, RG, IRC	Akhmetiev, 1988; Akhmetiev & Shyvareva, 1989; Klimova, 1981, 1988; Pavlyutkin et al., 2014
	12. Maksimovka (137.50/46.05)	LF	81	Maksimovskii, Maksimovskaya	Rupelian, RG, IRC	Akhmetiev, 1988; Rybalko et al., 1980; Varnavskii et al., 1988
3. Late Eocene	13. Gladkaya17 (130.50/42.40)	PF	41	Khasanskii, Khasanskaya (=Nazimovskaya)	Priabonian, K/Ar dating (35.6–36.0 ma), RG, IRC	Chashchin et al., 2013; Gromova, 1980; Pavlyutkin & Petrenko, 1997, 2010; Pavlyutkin et al., 2006, 2014
		LF	33			
	14. Tavrichanka9142 (131.50/43.20)	PF	46	Artemo-Tavrichanskii, Ust'-davydovskaya	Priabonian, vertebrate fauna, RG, IRC	Flerov et al., 1974; Pavlyutkin, 2007a; Pavlyutkin & Petrenko, 1993, 2010; Pavlyutkin et al., 2006; Yanovskaya, 1954
		LF	75			
	15. Shkotovo (132.15/43.20)	PF	26	Shkotovskii, Upper coal	Priabonian, RG, IRC	Pavlyutkin & Petrenko, 2010
	16. Ivanovka610 (132.30/43.60)	PF	50	Ivanovskii, analog of Pavlovskaya	Priabonian, RG, IRC	Pavlyutkin & Petrenko, 2010
	17. Pavlovka9035-D (132.05/44.05)	PF	50	Pavlovskii, Pavlovskaya	Priabonian, RG, IRC	Bolotnikova, 1993, 1994; Pavlyutkin & Petrenko, 2010; Varnavskii et al., 1988
		LF	25			
	18. Svetlyi (135.10/44.10)	PF	14	Zerkal'nenskii, Svetlinskaya	Priabonian, RG, IRC	Mikhailov et al., 1989; Pavlyutkin & Petrenko, 2010
		LF	22			
	19. Luchegorsk (134.20/46.30)	PF	61	Nizhnebikinskii, Bikinskaya	Priabonian, RG, IRC	Ablaev et al., 2006; Bolotnikova & Sedykh, 1987; Koshman, 1964; Kundyshev & Verkhovskaya, 1989
		LF	56			
	20. Salibeza (137.50/46.05)	LF	48	Svetlovodnenskii, Salibezskaya	Priabonian, RG, IRC	Klimova & Tsar'ko, 1989; Varnavskii et al., 1988

(Continues)

TABLE 1 (Continued)

Stratigraphic level	Locality name (Lon/Lat)	Type of flora	Number of fossil taxa	Basin, formation	Age, method of dating	References
4. Middle Eocene	21. Vol'no-Nadezhdinskoe (131.50/43.20)	PF	59	Artemo-Tavrichanskii, Nadezhdinskaya	Bartonian, RG, IRC	Akhmetiev et al., 1978; Pavlyutkin, 2007a; Pavlyutkin & Petrenko, 1993, 2010
		LF	25			
	22. Bolotnaya (131.05/43.20)	PF	45	Artemo-Tavrichanskii, Nadezhdinskaya	Lutetian, RG, IRC	Ablaev, 2000; Ablaev & Akhmetiev, 1977; Akhmetiev, 1973; Kundyshev & Petrenko, 1987; Pavlyutkin, 2007a; Pavlyutkin & Petrenko, 2010
		LF	75			
	23. Shkotovo (132.15/43.20)	PF	31	Shkotovskii, Nadezhdinskaya	Middle Eocene, RG, IRC	Baskakova & Gromova, 1982
	24. Terekhovka (131.30/43.40)	PF	44	Pushkinskii, Nadezhdinskaya	Middle Eocene, RG, IRC	Pavlyutkin & Petrenko, 2010
	25. Luchegorsk540/541 (134.20/46.30)	PF	33	Nizhnebikinskii, Luchegorskaya	Middle Eocene, RG, IRC	Pavlyutkin & Petrenko, 2010
5. Early Eocene	26. Tavrichanka9142 (131.50/43.20)	PF	58	Artemo-Tavrichanskii, Uglovskaya	Ypresian, RG, IRC	Pavlyutkin & Petrenko, 2010
	27. Smolyaninovo (132.30/43.20)	PF	56	Shkotovskii, Uglovskaya	Ypresian, RG, IRC	Baskakova & Gromova, 1979, 1984; Pavlyutkin & Petrenko, 2010; Tashchi et al., 1996; Varnavskii et al., 1988; Verkhovskaya & Kundyshev, 1989
		LF	42			
	28. Kluch Ugolnyi (134.10/43.30)	PF	19	Vanchinskii, analog of Uglovskaya	Ypresian, RG, IRC	Chekryzhov, Popov, Panichev, Seredin, & Smirnova, 2010; Pavlyutkin & Petrenko, 2010
		LF	20			
	29. Rettikhovka (132.40/44.10)	PF	56	Snegurovskii, analog of Uglovskaya	Ypresian, RG, IRC	Pavlyutkin & Petrenko, 2010
	30. Arsen'evka (133.10/44.10)	PF	57	Chernyshevskii, analog of Uglovskaya	Ypresian, RG, IRC	Bolotnikova, 1988
	31. Kluch Tuyanov (135.10/44.10)	LF	62	Zerkal'nenskii, Tuyanovskaya	Ypresian, RG, IRC	Baskakova & Lepekhina, 1990; Varnavskii et al., 1988
	32. Krylovskii524 (133.40/45.10)	PF	59	Krylovskii, Uglovskaya	Ypresian, RG, IRC	Pavlyutkin & Petrenko, 2010
	33. Luchegorsk540/541 (134.20/46.30)	PF	58	Nizhnebikinskii, Lower coal	Ypresian, RG, IRC	Pavlyutkin & Petrenko, 2010
		LF	12			
	34. Ozero Toni (138.30/47.40)	PF	32	Ozero Toni, Kizinskaya	Early Eocene, RG, IRC	Oleinikov & Klimova, 1977; Varnavskii et al., 1988
		LF	44			
6. Late Palaeocene	35. Ustinovka (135.10/44.10)	LF	25	Zerkal'nenskii, Tadushinskaya	Selandian, RG, IRC	Pavlyutkin & Petrenko, 2010
	36. Kluch Stolbikova (137.50/46.05)	LF	14	Maksimovskii, Kuznetsovskaya	Thanetian, K/Ar dating (55.0 ma), RG, IRC	Pavlyutkin & Petrenko, 2010; Varnavskii et al., 1988
	37. Kluch Kedrovyi (137.78/46.17)	PF	37	Maksimovskii, Kedrovskaya	Thanetian, RG, IRC	Varnavskii et al., 1988
7. Early Palaeocene	38. Ustinovka (135.10/44.10)	LF	31	Zerkal'nenskii, Bogopol'skaya	Danian, RG, IRC	Ablaev et al., 2005; Krassilov, 1989b
	39. Sobolevka (137.50/46.05)	LF	64	Maksimovskii, Takhobinskaya	Danian, K/Ar dating (64.0 ma), RG, IRC	Akhmetiev, 1973, 1988; Borsuk, 1952

Note: References and complete flora lists including Nearest Living Relatives allocated to single plant functional type are given in the Data S1.
Abbreviations: IRC, inter-regional correlation based on palaeobotany; LF, leaf floras; PF, palynofloras; RG, regional geology.

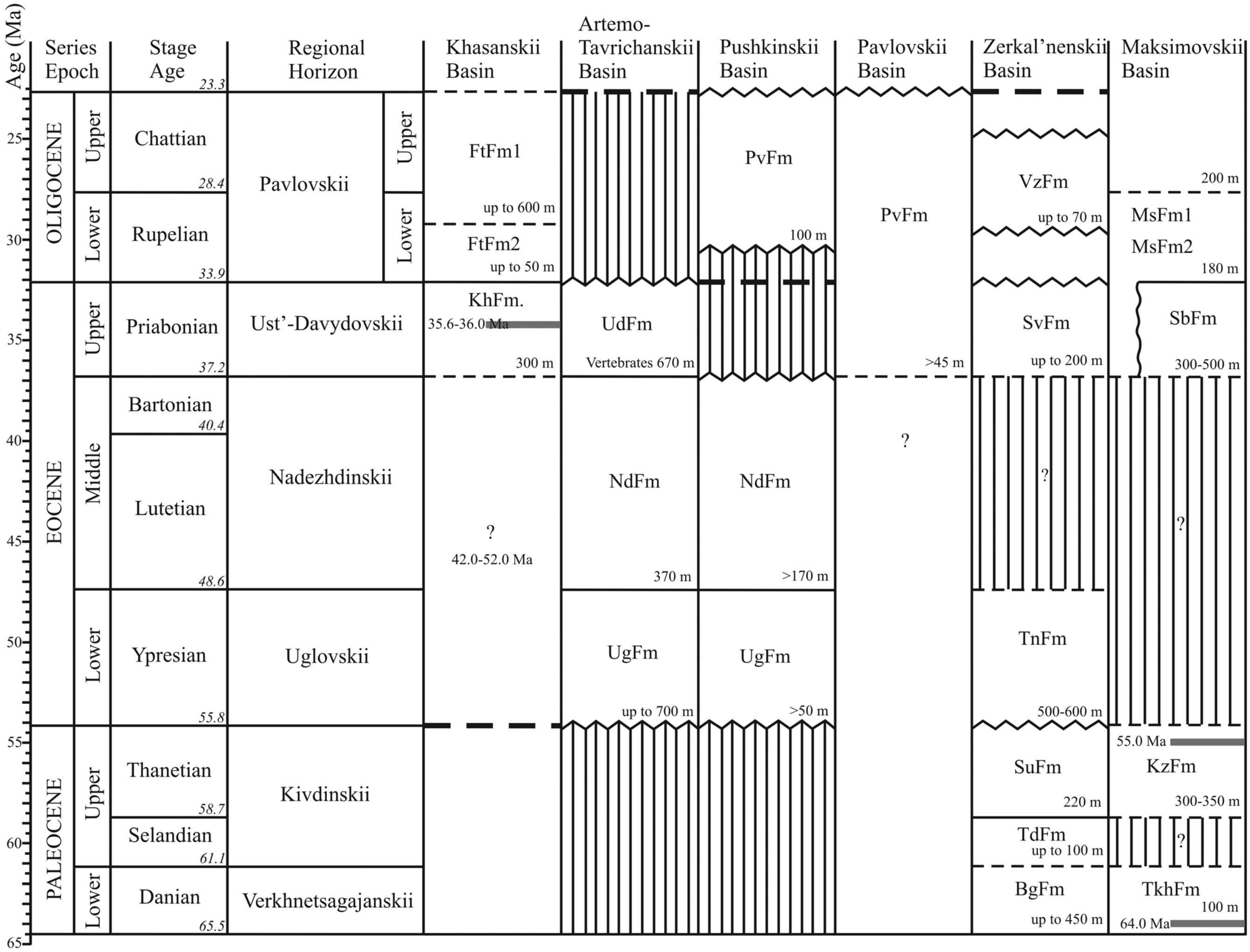

FIGURE 2 Regional stratigraphic chart for the Paleogene sediments of the Cenozoic basins of Primorye considered in this study (modified from Pavlyutkin & Petrenko, 2010), tied to the international standard (Cohen, Finney, Gibbard, & Fan, 2013). Details on the palaeofloras are given in Table 1. BgFm, Bogopol'skaya Formation; FtFm, Fatashinskaya Formation; KhFm, Khasanskaya Formation; KzFm, Kuznetsovskaya Formation; MsFm, Maksimovskaya Formation; NdFm, Nadezhdinskaya Formation; PvFm, Pavlovskaya Formation; SbFm, Salibezskaya Formation; SuFm, Suvorovskaya Formation; SvFm, Svetlinskaya Formation; TdFm, Tadushinskaya Formation; TkhFm, Takhobinskaya Formation; TnFm, Tuyanovskaya Formation; UgFm, Uglovskaya Formation; UdFm, Ust'-davydovskaya Formation; VzFm, Voznovskaya Formation

Relatives (NLRs) and their climatic requirements are given in the Data S1. For the climate data see Bondarenko, Blokhina, Mosbrugger, and Utescher (2019).

3.2 | Quantitative vegetation reconstruction—Application of the PFT approach

To reconstruct vegetation from the plant fossil record of Primorye, we use the PFT Approach. The PFT concept goes back to works of Prentice (Prentice et al., 1992; Prentice & Webb III, 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 on the Neogene palaeobotanical record was first introduced by Utescher, Erdei, François, and Mosbrugger (2007). The present study employs an extended PFT classification scheme described in details in Popova et al. (2013), comprising 26 herbaceous to arboreal PFTs based on physiognomic characters and bioclimatic tolerances of plants, completed by an aquatic PFT (Table 2). 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).

To exclude unlikely PFTs, we use the likelihood procedure according to François et al. (2011). The PFT presence/absence status is decided from these likelihood levels (Data S1). Henrot et al. (2017) set the thresholds for the presence in the data between unlikely and likely. The diversity spectra of the Paleogene floras analysed after the likelihood procedure is shown on Figure 3.

To interpret the PFT spectra of the fossil sites in terms of vegetation units, cluster analysis was performed using a data matrix with

TABLE 2 PFT classification used for the present study (Popova et al., 2013)

	PFT no.	PFT
Herbal	1	C3 herbs (humid)
	2	C3 herbs (dry)
	3	C4 herbs
Shrub	4	Broadleaved summergreen arctic shrubs
	5	Broadleaved summergreen boreal or temperate cold shrubs
	6	Broadleaved summergreen temperate warm shrubs
	7	Broadleaved evergreen boreal or temperate cold shrubs
	8	Broadleaved evergreen temperate warm shrubs
	9	Broadleaved evergreen xeric shrubs
	10	Subdesertic shrubs
	11	Tropical shrubs
Arboreal	12	Needleleaved evergreen boreal or temperate cold trees
	13	Needleleaved evergreen temperate cool trees
	14	Needleleaved evergreen trees, drought-tolerant
	15	Needleleaved evergreen trees, drought-tolerant, thermophilous
	16	Needleleaved evergreen subtropical trees, drought-intolerant
	17	Needleleaved summergreen boreal or temperate cold trees
	18	Needleleaved summergreen subtropical swamp trees
	19	Broadleaved evergreen trees, drought-tolerant
	20	Broadleaved evergreen trees, drought-intolerant, thermophilous
	21	Broadleaved evergreen subtropical trees, drought-intolerant
	22	Broadleaved summergreen boreal or temperate cold trees
	23	Broadleaved summergreen temperate cool trees
	24	Broadleaved summergreen temperate warm trees
	25	Broadleaved raingreen tropical trees
	26	Broadleaved evergreen tropical trees
Aquatic	27	Aquatic components

all common PFTs (PAST program package; single linkage between groups; squared Euclidean distance measure) following the procedure described in Utescher et al. (2007). The clusters obtained were then related to basic biomes according to the characteristics of their PFT spectra (Figure 4). The distribution of the obtained biomes is shown in a series of maps for seven Paleogene time slices (Figure 5). For selected PFTs, the evolution of mean diversity is shown in time series by using box plots (program SSCstat) providing additional information on statistical significance of the displayed gradients (Figure 6).

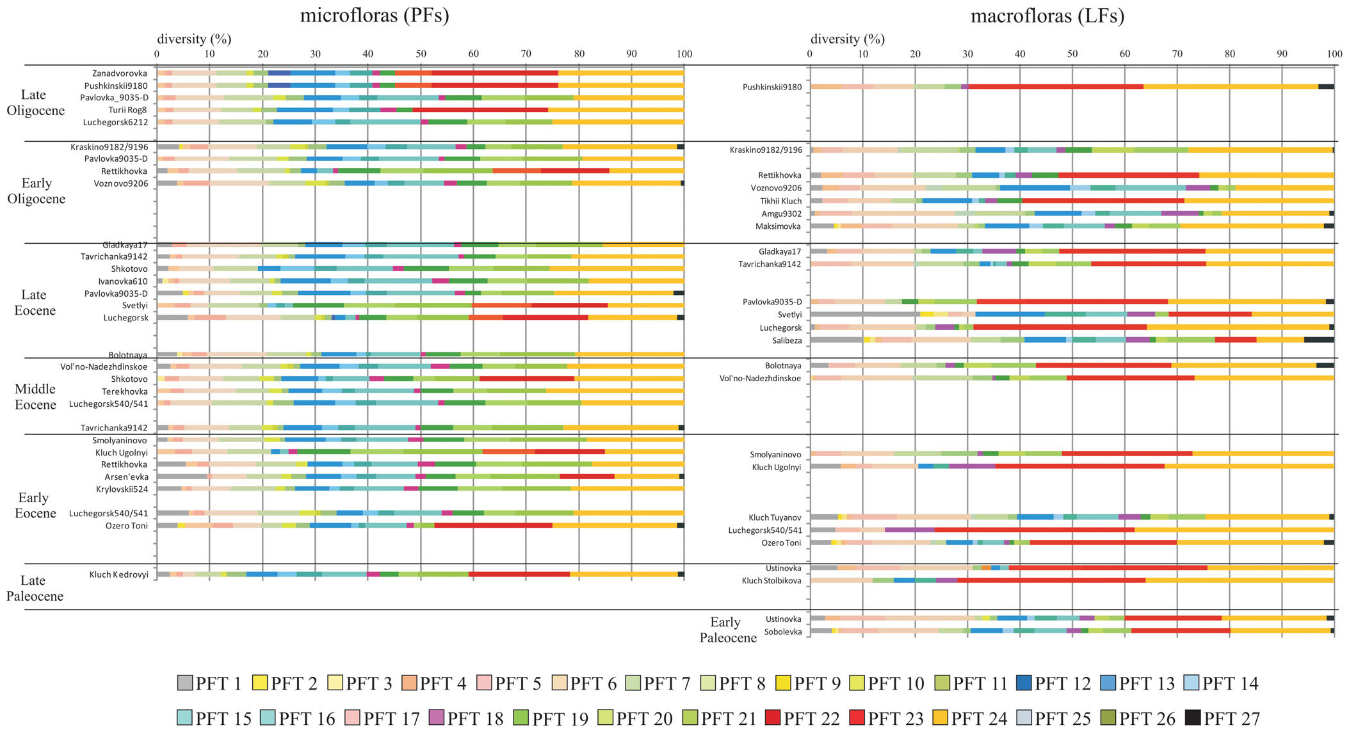

FIGURE 3 Ecospectra based on microfloras (PFs) and macrofloras (LFs). PFT 1—C3 herbs (humid), PFT 2—C3 herbs (dry), PFT 3—C4 herbs, PFT 4—broadleaved summergreen arctic shrubs, PFT 5—broadleaved summergreen boreal or temperate cold shrubs, PFT 6—broadleaved summergreen temperate warm shrubs, PFT 7—broadleaved evergreen boreal or temperate cold shrubs, PFT 8—broadleaved evergreen temperate warm shrubs, PFT 9—broadleaved evergreen xeric shrubs, PFT 10—subdesertic shrubs, PFT 11—tropical shrubs, PFT 12—needleleaved evergreen boreal or temperate cold trees, PFT 13—needleleaved evergreen temperate cool trees, PFT 14—needleleaved evergreen trees, drought-tolerant, PFT 15—needleleaved evergreen trees, drought-tolerant, thermophilous, PFT 16—needleleaved evergreen subtropical trees, drought-intolerant, PFT 17—needleleaved summergreen boreal or temperate cold trees, PFT 18—needleleaved summergreen subtropical swamp trees, PFT 19—broadleaved evergreen trees, drought-tolerant, PFT 20—broadleaved evergreen trees, drought-intolerant, thermophilous, PFT 21—broadleaved evergreen subtropical trees, drought-intolerant, PFT 22—broadleaved summergreen boreal or temperate cold trees, PFT 23—broadleaved summergreen temperate cool trees, PFT 24—broadleaved summergreen temperate warm trees, PFT 25—broadleaved raingreen tropical trees, PFT 26—broadleaved evergreen tropical trees, PFT 27—aquatic components [Colour figure can be viewed at wileyonlinelibrary.com]

4 | RESULTS

Palaeovegetation data of Primorye using the PFT approach were obtained for 30 PFs—PF and 24 LFs—LF (Data S1). The number of fossil taxa in each sample is higher than the number of encountered PFTs (Table 3); therefore, we consider that our results are meaningful.

Aquatic plants (PFT 27) are presented only in eight PF and 11 LF. The proportion of aquatic plants varies from 0.6 to 2.0% in the PF and from 0.3 to 3.4% of total diversity of the flora in the LF (Table 4). Herbaceous plants (PFTs 1–3) are presented only in 20 PF and 19 LF. The diversity of herbaceous PFTs in the microfloras varies from 1.9 to 9.4%, in the LF—from 0.5 to 26.3% of total diversity of the flora (Table 4). Shrubs (PFTs 4–11), in contrast to aquatic and herbaceous plants, are presented in all floras studied: 14.5–31.9 and 5.3–42.0% in the micro- and LF correspondently (Table 4). After the likelihood procedure, arboreal plants (PFTs 12–26) are presented in all floras studied. Arboreal PFTs content 63.8–81.9 in the PF and 53.4–85.7% in the LF (Table 4).

Needleleaved (PFTs 12–18) are presented in all micro- and macrofloras, except the Late Eocene LF 17. In PF, the proportion of conifers varies within the range of 4.8–32.1%, in LF—0.5–40.2% of total diversity of the flora (Table 4). Broadleaved deciduous plants (PFTs 4–6, 22–25) are present in all micro- and LF. The diversity of deciduous PFTs in the microfloras varies from 28.2 to 63.6%, in the LF—from 35.2 to 87.9% of total diversity of the flora (Table 4). Broadleaved evergreens (PFTs 7–9, 19–21, 26) are present in 20 of 24 LF. The proportion of broadleaved evergreens varies from 9.9 to 43.5% in the microfloras and from 2.6 to 34.9% of total diversity of the flora in the LF (Table 4).

Cluster analysis performed in this study is based on diversity data of all common PFTs. Groups of floras are obtained that are characterized by their specific diversity patterns. Two major groups are established and interpreted in terms of vegetation type (Figure 4).

The first group of clusters mainly includes LF representing the deciduous and mixed deciduous vegetation, and has a temperate character. The diversity spectra of the floras allocated to this cluster are characterized by very high percentages of broadleaved summergreen PFTs (4–6, 22–24) and can be subdivided into four subunits (forest types).

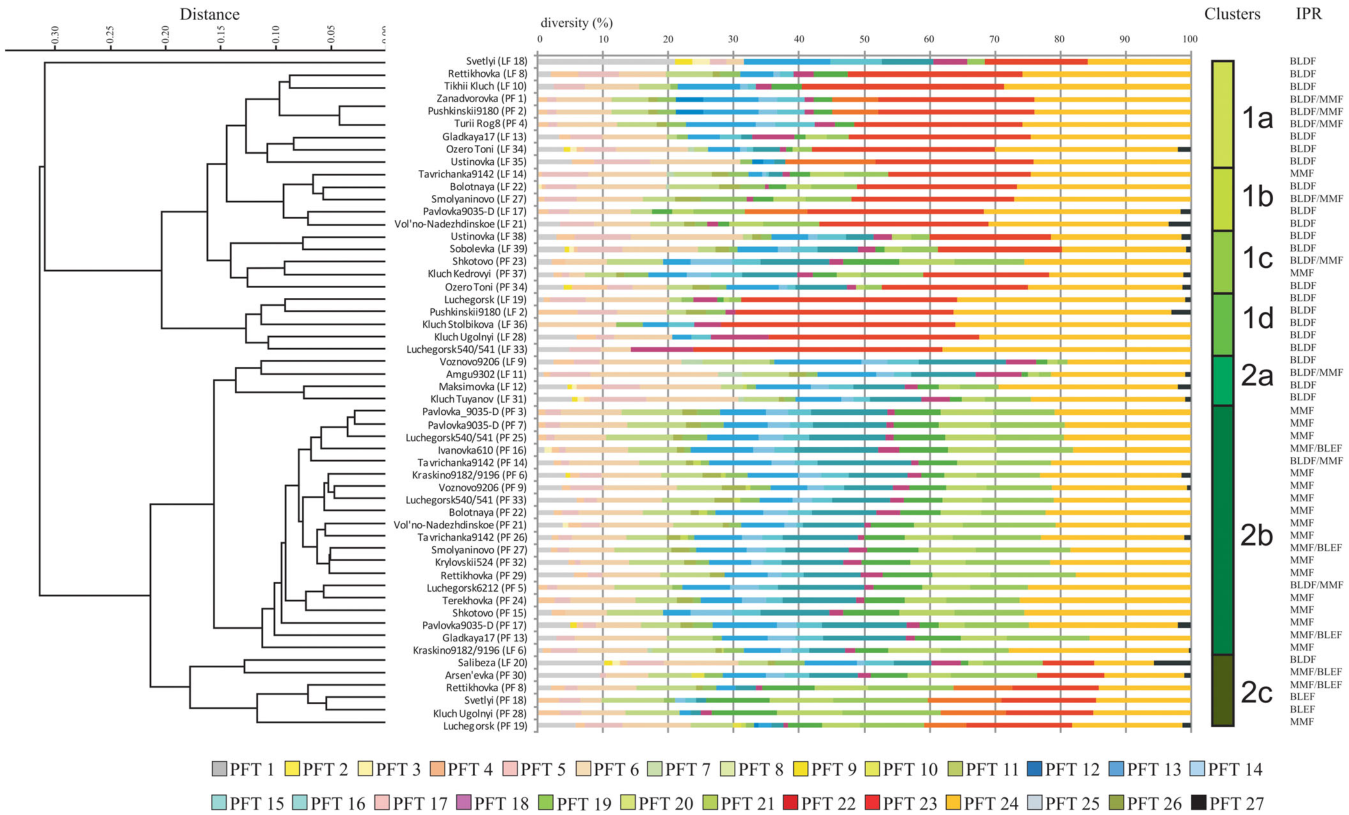

FIGURE 4 Vegetation units based on cluster analysis using a data matrix with all common PFTs. PFT 1—C3 herbs (humid), PFT 2—C3 herbs (dry), PFT 3—C4 herbs, PFT 4—broadleaved summergreen arctic shrubs, PFT 5—broadleaved summergreen boreal or temperate cold shrubs, PFT 6—broadleaved summergreen temperate warm shrubs, PFT 7—broadleaved evergreen boreal or temperate cold shrubs, PFT 8—broadleaved evergreen temperate warm shrubs, PFT 9—broadleaved evergreen xeric shrubs, PFT 10—subdesertic shrubs, PFT 11—tropical shrubs, PFT 12—needleleaved evergreen boreal or temperate cold trees, PFT 13—needleleaved evergreen temperate cool trees, PFT 14—needleleaved evergreen trees, drought-tolerant, PFT 15—needleleaved evergreen trees, drought-tolerant, thermophilous, PFT 16—needleleaved evergreen subtropical trees, drought-intolerant, PFT 17—needleleaved summergreen boreal or temperate cold trees, PFT 18—needleleaved summergreen subtropical swamp trees, PFT 19—broadleaved evergreen trees, drought-tolerant, PFT 20—broadleaved evergreen trees, drought-intolerant, thermophilous, PFT 21—broadleaved evergreen subtropical trees, drought-intolerant, PFT 22—broadleaved summergreen boreal or temperate cold trees, PFT 23—broadleaved summergreen temperate cool trees, PFT 24—broadleaved summergreen temperate warm trees, PFT 25—broadleaved raingreen tropical trees, PFT 26—broadleaved evergreen tropical trees, PFT 27—aquatic components. Clusters: 1a—mixed broadleaved deciduous—conifer forest, 1b—broadleaved deciduous forest with some broadleaved evergreens, 1c—mixed broadleaved deciduous forest with some broadleaved evergreens and conifers, 1d—broadleaved deciduous forest, 2a—mixed mesophytic deciduous forest, 2b—mixed mesophytic forest, 2c—mixed mesophytic deciduous evergreen forest. IPR: BLDF—zonal temperate to warm-temperate broad-leaved deciduous forests (broad-leaved deciduous forests), MMF—zonal warm-temperate to subtropical mixed mesophytic forests (mixed mesophytic forests), BLEF—zonal subtropical broad-leaved evergreen forests (broad-leaved evergreen forests), BLDF/MMF—ecotone between the BLDF and MMF, MMF/BLEF—ecotone between the MMF and BLEF [Colour figure can be viewed at wileyonlinelibrary.com]

4.1 | Cluster 1a: Mixed broadleaved deciduous—conifer forest (LFs, PFs)

In the floras allocated to Cluster 1a, broadleaved summergreen PFTs represent the dominant PFTs with respect to diversities between 63.9% and 87.9%, needleleaved PFTs reach also high diversities of up to 22.7%, broadleaved evergreen PFTs are absent or below 13.4%.

4.2 | Cluster 1b: Broadleaved deciduous forest with some broadleaved evergreens (LFs)

The floras of Cluster 1b are characterized by high diversities of broadleaved summergreen PFTs varying from 66.1 to 81.0%. Needleleaved PFTs in general have a low diversity (up to 6.3%) or are completely absent, broadleaved evergreen PFTs are varying from 17.5 to 25.0%.

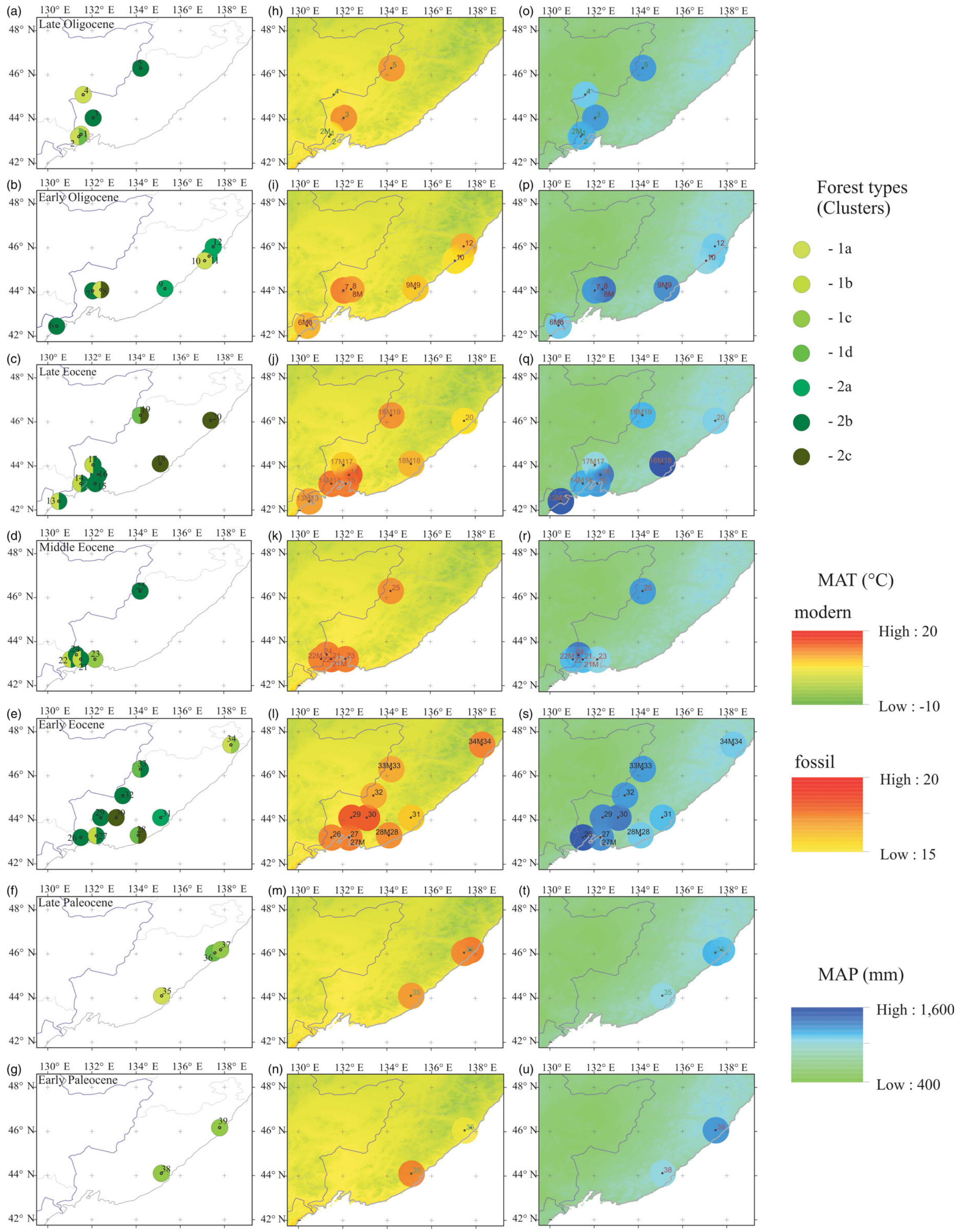

FIGURE 5 Distribution of vegetation types (a–g), Mean Annual Temperature (MAT) (h–p) and Mean Annual Precipitation (MAP) (q–z) in the Paleogene of Primorye in comparison with modern MAT and MAP: (a), h and q—late Oligocene, (b), i and r—early Oligocene, (c), j and s—late Eocene, (d), k and t—middle Eocene, (e), m and x—early Eocene, (f), n and y—late Palaeocene, (g), p and z—early Palaeocene. Clusters: 1a—mixed broadleaved deciduous—conifer forest, 1b—broadleaved deciduous forest with some broadleaved evergreens, 1c—mixed broadleaved deciduous forest with some broadleaved evergreens and conifers, 1d—broadleaved deciduous forest, 2a—mixed mesophytic deciduous forest, 2b—mixed mesophytic forest, 2c—mixed mesophytic deciduous evergreen forest. Maps are generated using ArcMAP 10.4. Modern climate data: WorldClim—Global Climate Data (www.worldclim.org). Small black discs with numbers refer to fossil sites in Table 1. Palaeoclimate data (coloured disks): interpolated means of coexistence intervals using Spatial Analyst (IDW method, power 2 and fixed search radius) [Colour figure can be viewed at wileyonlinelibrary.com]

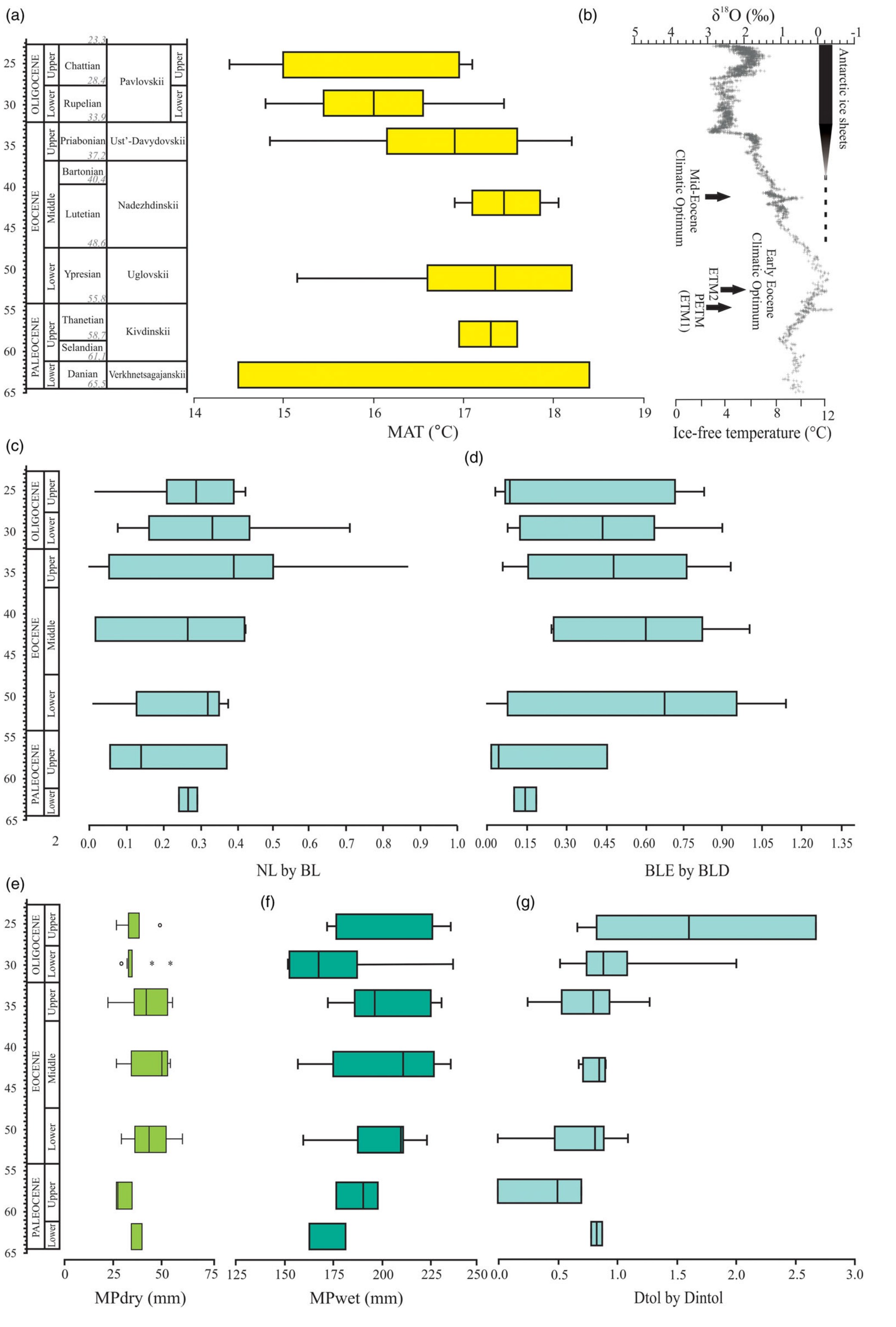

FIGURE 6 MAT records (a) next to the composite deep-sea benthic foraminiferal oxygen isotope record after Zachos et al. (2008) (b), and proportion of some groups of PFTs: needleleaved (NL) vs. broadleaved (BL) (c), broadleaved deciduous (BLD) vs. broadleaved evergreen (BLE) (d), drought-tolerant (Dtol) versus drought-intolerant (Dintol) (g) throughout the Paleogene reflecting changes in MPdry (e) and MPwet (f) [Colour figure can be viewed at wileyonlinelibrary.com]

4.3 | Cluster 1c: Mixed broadleaved deciduous forest with some broadleaved evergreens and conifers (LFs, PFs)

The floras of Cluster 1c are characterized by lowest diversities of broadleaved summergreen PFTs (44.6–67.1%) compared to other clusters of the deciduous vegetation group. Needleleaved (18.6–25.3%) and broadleaved evergreen PFTs (8.6–27.8%) in general have a high diversity.

4.4 | Cluster 1d: Broadleaved deciduous forest (LFs)

The floras of Cluster 1d are characterized by high diversities of broadleaved summergreen PFTs (79.4–87.2%). Needleleaved in general have a low diversity (1.5–14.7%), broadleaved evergreen PFTs are absent or below 6.1%. PFT composition and representation by LF only point to a riparian, intrazonal character of Cluster 1d floras.

TABLE 3 Number of fossil taxa allocated to PFTs next to the number of scores before and after likelihood procedure

		Palynofloras			Leaf floras		
Stratigraphic level	Locality name	Number of fossil taxa allocated to PFTs	Number of scores before likelihood procedure	Number of scores after likelihood procedure	Number of fossil taxa allocated to PFTs	Number of scores before likelihood procedure	Number of scores after likelihood procedure
1. Late Oligocene	1. Zanadvorovka	29	93	71	–	–	–
	2. Pushkinskii9180	29	93	71	28	82	66
	3. Pavlovka9035-D	34	119	86	–	–	–
	4. Turii Rog8	31	96	66	–	–	–
	5. Luchegorsk6212	31	96	68	–	–	–
2. Early Oligocene	6. Kraskino9182/9196	67	199	143	155	431	298
	7. Pavlovka9035-D	36	122	88	–	–	–
	8. Rettikhovka	30	106	99	47	136	97
	9. Voznovo9206	73	222	160	75	169	127
	10. Tikhii Kluch	–	–	–	48	115	84
	11. Amgu9302	–	–	–	61	153	112
	12. Maksimovka	–	–	–	81	221	153
3. Late Eocene	13. Gladkaya17	36	93	71	33	70	61
	14. Tavrichanka9142	41	113	84	70	225	192
	15. Shkotovo	22	64	47	–	–	–
	16. Ivanovka610	45	126	94	–	–	–
	17. Pavlovka9035-D	49	141	101	25	65	63
	18. Svetlyi	14	67	62	22	45	38
	19. Luchegorsk	58	170	154	53	124	109
	20. Salibeza	–	–	–	48	99	88
4. Middle Eocene	21. Vol'no-Nadezhdinskoe	52	150	106	25	66	58
	22. Bolotnaya	43	114	81	74	215	184
	23. Shkotovo	26	86	72	–	–	–
	24. Terekhovka	40	116	80	–	–	–
	25. Luchegorsk540/541	31	105	77	–	–	–
5. Early Eocene	26. Tavrichanka9142	50	135	96	–	–	–
	27. Smolyaninovo	49	144	103	40	124	100
	28. Kluch Ugolnyi	16	64	60	20	36	34
	29. Rettikhovka	48	125	91	–	–	–
	30. Arsen'evka	50	131	106	–	–	–
	31. Kluch Tuyanov	–	–	–	62	159	114
	32. Krylovskii524	53	149	107	–	–	–
	33. Luchegorsk540/541	52	138	100	12	23	21
	34. Ozero Toni	31	91	76	43	123	100
6. Late Palaeocene	35. Ustinovka	–	–	–	24	58	58
	36. Kluch Stolbikova	–	–	–	14	25	25
	37. Kluch Kedrovyi	36	104	83	–	–	–
7. Early Palaeocene	38. Ustinovka	–	–	–	30	82	70
	39. Sobolevka	–	–	–	63	169	147

Note: References and complete flora lists including Nearest Living Relatives used for vegetation analysis are given in Data S1.

The second group of clusters mainly comprises PF and represents the mixed evergreen-deciduous vegetation having a warm temperate character. The diversity spectra of the floras allocated to this cluster are characterized by lower percentages of broadleaved summergreen and higher percentages of broadleaved evergreen PFTs (7–9, 19–21) and can be subdivided into three forest types.

4.5 | Cluster 2a: Mixed mesophytic deciduous forest (LFs)

The floras of Cluster 2a are characterized by high diversities of broadleaved summergreen (38.6–49.7%) and needleleaved PFTs (23.7–40.2%) with lower diversities of broadleaved evergreen (15.7–19.3%).

TABLE 4 Proportions of the different groups of PFTs

Stratigraphic level	Locality name	Aquatic (PFT 27) PF	Aquatic (PFT 27) LF	Terrestrial (PFTs 1–26) PF	Terrestrial (PFTs 1–26) LF	Herbaceous (PFTs 1–3) PF	Herbaceous (PFTs 1–3) LF	Shrubby (PFTs 4–11) PF	Shrubby (PFTs 4–11) LF	Arboreal (PFTs 12–26) PF	Arboreal (PFTs 12–26) LF	Coniferous (PFTs 12–18) PF	Coniferous (PFTs 12–18) LF	Deciduous (PFTs 4–6, 22–25) PF	Deciduous (PFTs 4–6, 22–25) LF	Evergreen (PFTs 7–9, 19–21, 26) PF	Evergreen (PFTs 7–9, 19–21, 26) LF
1. Late Oligocene	1. Zanadvorovka	0	–	100	–	0	–	21.1	–	78.9	–	21.1	–	66.2	–	9.9	–
	2. Pushkinskii9180	0	3.0	100	97.0	0	0	21.1	28.8	78.9	68.2	21.1	1.5	66.2	86.4	9.9	6.1
	3. Pavlovka9035-D	0	–	100	–	0	–	27.9	–	72.1	–	26.7	–	33.7	–	36.0	–
	4. Turii Rog8	0	–	100	–	0	–	22.7	–	77.3	–	22.7	–	63.6	–	10.6	–
	5. Luchegorsk6212	0	–	100	–	0	–	22.1	–	77.9	–	29.4	–	36.8	–	32.4	–
2. Early Oligocene	6. Kraskino9182/9196	1.4	0.3	98.6	99.7	4.9	0.7	27.3	30.9	66.4	68.1	26.6	17.1	35.7	43.6	27.3	34.9
	7. Pavlovka9035-D	0	–	100	–	0	–	28.4	–	71.6	–	26.1	–	33.0	–	37.5	–
	8. Rettikhovka	0	0	100	100	2.0	2.1	25.3	28.9	72.7	69.1	7.1	11.3	49.5	70.1	39.4	13.4
	9. Voznovo9206	0.6	0	99.4	100	3.8	2.4	31.9	33.9	63.8	63.8	21.3	40.2	38.1	38.6	32.5	18.1
	10. Tikhii Kluch	–	0	–	100	–	2.4	–	19.0	–	78.6	–	14.3	–	72.6	–	9.5
	11. Amgu9302	–	0.9	–	99.1	–	0.9	–	42.0	–	56.3	–	31.3	–	47.3	–	17.9
	12. Maksimovka	–	2.0	–	98.0	–	5.9	–	27.5	–	64.7	–	24.8	–	49.7	–	15.7
3. Late Eocene	13. Gladkaya17	0	0	100	100	2.8	3.3	25.4	19.7	71.8	77.0	29.6	16.4	32.4	68.9	33.8	9.8
	14. Tavrichanka9142	0	0	100	100	2.4	0	23.8	32.3	73.8	67.7	32.1	6.3	34.5	66.1	28.6	24.5
	15. Shkotovo	0	–	100	–	2.1	–	17.0	–	80.9	–	27.7	–	34.0	–	36.2	–
	16. Ivanovka610	0	–	100	–	2.1	–	21.3	–	76.6	–	31.9	–	29.8	–	35.1	–
	17. Pavlovka9035-D	2.0	1.6	98.0	98.4	5.9	0	20.8	17.5	71.3	81.0	31.7	0	32.7	81.0	24.8	17.5
	18. Svetlyi	0	0	100	100	0	26.3	21.0	5.3	79.0	68.4	4.8	34.2	50.0	36.8	43.5	2.6
	19. Luchegorsk	1.3	0.9	98.7	99.1	5.8	0.9	27.3	22.9	65.6	75.2	5.2	3.7	57.1	87.2	28.6	5.5
	20. Salibeza	–	5.7	–	94.3	–	12.5	–	28.4	–	53.4	–	23.9	–	35.2	–	18.2
4. Middle Eocene	21. Vol'no-Nadezhdinskoe	0	3.4	100	96.6	4.7	3.4	26.4	22.4	68.9	70.7	19.8	1.7	36.8	67.2	36.8	22.4
	22. Bolotnaya	0	0	100	100	2.5	0.5	24.7	34.2	72.8	65.2	28.4	0.5	35.8	70.1	30.9	25.0
	23. Shkotovo	0	–	100	–	1.4	–	22.2	–	76.4	–	19.4	–	50.0	–	27.8	–
	24. Terekhovka	0	–	100	–	0	–	25.0	–	75.0	–	25.0	–	41.3	–	32.5	–
	25. Luchegorsk540/541	0	–	100	–	0	–	26.0	–	74.0	–	28.6	–	29.9	–	37.7	–
5. Early Eocene	26. Tavrichanka9142	1.0	–	99.0	–	2.1	–	21.9	–	75.0	–	26.0	–	33.3	–	35.4	–
	27. Smolyaninovo	0	0	100	100	1.9	0	22.3	32.0	75.7	68.0	26.2	1.0	28.2	68.0	42.7	24.0
	28. Kluch Ugolnyi	0	0	100	100	0	5.9	21.7	14.7	78.3	79.4	5.0	14.7	51.7	79.4	43.3	0
	29. Rettikhovka	0	–	100	–	5.5	–	23.1	–	71.4	–	24.2	–	30.8	–	39.6	–
	30. Arsen'evka	0.9	–	99.1	–	9.4	–	18.9	–	70.8	–	22.6	–	30.2	–	34.0	–

(Continues)

TABLE 4 (Continued)

Stratigraphic level	Locality name	Aquatic (PFT 27)		Terrestrial (PFTs 1–26)		Herbaceous (PFTs 1–3)		Shrubby (PFTs 4–11)		Arboreal (PFTs 12–26)		Coniferous (PFTs 12–18)		Deciduous (PFTs 4–6, 22–25)		Evergreen (PFTs 7–9, 19–21, 26)	
		PF	LF	PF	LF	PF	LF	PF	LF	PF	LF	PF	LF	PF	LF	PF	LF
	31. Kluch Tuyanov	–	0.9	–	99.1	–	7.0	–	32.5	–	59.6	–	23.7	–	47.4	–	19.3
	32. Krylovskii524	0	–	100	–	4.7	–	21.5	–	73.8	–	23.4	–	30.8	–	39.3	–
	33. Luchegorsk540/541	0	0	100	100	6.0	4.8	28.0	9.5	66.0	85.7	22.0	9.5	34.0	85.7	34.0	0
	34. Ozero Toni	1.3	2.0	98.7	98.0	5.3	6.0	23.7	20.0	69.7	72.0	19.7	12.0	60.5	73.0	10.5	7.0
6. Late Palaeocene	35. Ustinovka	–	0	–	100	–	5.2	–	27.6	–	67.2	–	5.2	–	87.9	–	0
	36. Kluch Stolbikova	–	0	–	100	–	0	–	16.0	–	84.0	–	12.0	–	84.0	–	0
	37. Kluch Kedrovyi	1.2	–	98.8	–	2.4	–	14.5	–	81.9	–	25.3	–	44.6	–	22.9	–
7. Early Palaeocene	38. Ustinovka	–	1.4	–	98.6	–	2.9	–	32.9	–	62.9	–	18.6	–	67.1	–	8.6
	39. Sobolevka	–	0.7	–	99.3	–	5.4	–	25.2	–	68.7	–	21.1	–	57.1	–	14.3

Note: References and complete flora lists including Nearest Living Relatives used for vegetation analysis are given in Data S1.

4.6 | Cluster 2b: Mixed mesophytic forest (mainly PFs)

The floras of Cluster 2b are characterized by high diversities of broadleaved summergreen (28.2–43.6%), needleleaved (18.2–42.7%) and broadleaved evergreen PFTs (17.1–32.1%).

4.7 | Cluster 2c: Mixed mesophytic deciduous evergreen forest (mainly PFs)

The floras of Cluster 2c are characterized by highest diversities of broadleaved summergreen PFTs (30.2–57.1%) compared to other clusters of the mixed mesophytic vegetation group. Broadleaved evergreen PFTs also have high diversities varying from 18.2 to 43.5%. Needleleaved PFTs have the lowest diversities (4.8–23.9%) compared to other clusters of this vegetation group.

5 | DISCUSSION

5.1 | Differences in micro- and macro-based vegetation data

The integration of micro- and macrofloras in the present analysis allows for a couple of general considerations regarding resolution and quality of the obtained data thus providing clues about the integrity of the vegetation reconstruction.

Aquatic plants, as local components, are present only in 8 PF and 11 LF. The proportion of aquatic plants is low (0–2.0%) and varies weakly in the microfloras. In the LF, the proportion of aquatic plants is somewhat higher and varies more significantly—from 0 to 5.7% (Table 4 and Figure 3). This is not surprising because aquatic plants are usually well represented only in carpofloras (Krassilov, 1972). However, the presence of aquatic plants agrees with lithological and facies data and suggests the existence of a broad river system in this area (Pavlyutkin & Petrenko, 2010).

Herbaceous plants are present only in 20 pollen floras and 19 LF. The proportion of herbaceous plants is low (0–9.4%) and varies weakly in the PF. In the LF, the proportion of herbaceous plants is higher (0–26.3%) and varies more significantly (Table 4 and Figure 3). Usually, herbs are not well represented in LF but diverse in PF and carpofloras (Popova, Utescher, Gromyko, Mosbrugger, & François, 2018; Utescher et al. (2020)). In our floras, high percentages of herbs are obtained in a single leaf flora only (the Late Eocene LF 18). In this leaf flora, 7 out of 22 taxa are allocated to PFT 1 and represented by Cyperaceae, *Equisetum*, *Lygodium*, *Onoclea*, *Osmunda*, *Phragmites*, and *Woodwardia*.

Shrubs, in contrast to aquatic and herbaceous plants, are present in all floras studied. The proportion of shrubby plants in the microfloras varies from 14.5 to 31.9%, while in the LF varies more significantly—from 5.3 to 42.0% (Table 4 and Figure 3). In the microfloras, deciduous and evergreen shrubs are about equally present, whereas in LF mainly deciduous shrubs are present (Figure 3).

When analysing diversities of tree (arboreal) and non-tree species, it is shown that the data are highly variable (Table 4 and Figure 3). There is evidence of a strong impact of type of the fossil flora on the relative diversity of arboreal species. In the Paleogene of Primorye, arboreal plants are present in all floras studied. The proportion of arboreal plants is high in both microfloras and in LF (Table 4 and Figure 3), and varies mainly within the range of 70–80%. According to Utescher et al. (2007), trees are very well represented in LF reaching 60–95% in most of the cases because their leaves might be relatively easily transported when compared to herbs, while in the palynological record herbaceous plants commonly are well represented and thus the relative tree diversities almost always stay below 55%.

Needleleaved PFTs are presented in all floras except for the Late Eocene LF 17. Conifers are presented in all microfloras and vary mainly within the range of 10–30%, except few floras. In LF, the proportion of conifers varies more significantly—from 1.5 to 40.2%, except the late Eocene LF 17 (Table 4 and Figure 3).

In the spectra (Figure 3), generally the arboreal plants in the microfloras are represented by broadleaved deciduous and evergreen and needleleaved plants about equally, whereas in LF they are presented mainly by deciduous arboreal plants. Proportions of all broadleaved deciduous and broadleaved evergreen plants (shrubs and arboreal plants together) demonstrate the same trend: in microfloras, they are well represented both by broadleaved deciduous and evergreen plants, whereas in LF they are represented mainly or sometimes only by deciduous plants.

Thus, in the LF, all studied groups of PFTs show higher variability. This can be expected because frequently macrofloras represent almost exclusively plant associations growing near water and reflect mainly an intrazonal vegetation and local conditions, while microfloras reflect the averaged composition of the vegetation of fairly large areas and represent zonal vegetation (Krassilov, 1972).

5.2 | PFT structure of plant assemblages

When regarding the diversity spectra of the Paleogene floras analysed (Figure 3), it is shown that broadleaved summergreen shrubs and trees (PFTs 6 and 23/24) are the most important functional types, followed by broadleaved evergreen shrubs and trees (PFTs 8/9 and 19–21) and needleleaved evergreens (PFTs 13–16 and 18). Needleleaved summergreen boreal trees (PFT 17) are completely absent in the spectra after the likelihood procedure, needleleaved evergreen boreal trees (PFT 12) are presented in few floras. Needleleaved summergreen subtropical swamp trees (PFT 18) are presented in all floras, except for one palynoflora (Figure 3). In some LF conifers are represented only by this PFT. The constant presence of these conifers in all studied floras throughout the Paleogene suggests a high humidity in general, and the existence of swamps at places. All tropical PFTs (PFT 25 and 26) are excluded when applying the likelihood procedure. Moreover, all taxa scoring for tropical PFTs may represent temperate types. The absence of tropical PFTs makes sense when considering the latitudinal position of the study area and the reconstructed palaeoclimate which does not support the occurrence of tropical plants (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019), but is in contrast with Bolotnikova (1979) and Lopatina (2004) suggesting the presence of tropical vegetation.

Herbaceous plants are mainly represented by humid herbs (PFT 1). This coincides with the reported high humidity throughout the Paleogene (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019). There is no evidence of any distinct dry signal from our data that can be discussed in the context of the climate drying noted for China after the start of the Oligocene (cf. Sun et al., 2014). Perhaps the studied floras do not cover this short period or it was not expressed in the territory of Primorye.

5.3 | Vegetation

Based on the low proportion of herbaceous PFTs (0–12.5%, excepting the Late Eocene LF 18 with 26.3%), our data indicate the presence of forest vegetation in Primorye during the Paleogene. The results obtained from the PFT approach are in accordance with data obtained from other methods. According to Bondarenko, Blokhina, and Utescher (2019) with zonal herb proportions ranging from 0 to 22%, except the Late Eocene LF 18 constituting 37.5% of herbs, no open woodland is reconstructed for the Primorye Region throughout the Paleogene based on the Integrated Plant Record (IPR)-vegetation analysis. Thus, a closed forest cover likely existed in Primorye throughout the Paleogene. In Western Siberia, however, Popova et al. (2013) point out a steep declining trend of the arboreal component, already setting in at the end of the Eocene.

Using diversity spectra as proxies for vegetation type, it can be stated that based on microfloras and LF, the vegetation of Primorye in the Palaeocene was of a temperate deciduous type. In the Eocene, on microfloras, zonal vegetation was generally of a warm temperate-mixed evergreen-deciduous type, with the exception of the Early Eocene PF 34 and Middle Eocene PF 23. On LF, vegetation of Primorye in the Eocene is generally deciduous, but some LF also show a mixed evergreen-deciduous type of vegetation. Most likely, the vegetation of Primorye in the Eocene and Early Oligocene had a mosaic distribution, that is, was generally of mixed evergreen-deciduous type, but in some places, for example, in more northern regions, vegetation was primarily deciduous. LF with mainly deciduous PFT spectra such as Cluster 1d floras most probably represent the intrazonal wetland vegetation. In the Late Oligocene, zonal vegetation in Primorye was mainly deciduous (PFs belonging to Cluster 1a), the mixed evergreen-deciduous vegetation was distributed only locally, namely in the inner part of Primorye (Figure 5).

The vegetational data obtained in the study by Bondarenko, Blokhina, and Utescher (2019) using the Integrated Plant Record vegetation analysis (IPR) and based on the same floral record allow for comparison of the results obtained from both methods. The vegetation established by the PFT method is in general more temperate and homogenous than the IPR-based reconstruction. Differences in the results obtained by different methods can be explained, firstly, by differences in allocation of taxa and thus the calculation of the proportions of certain groups and, secondly, differences in the thresholds of these proportions for distinguishing forest types. For example, in the PFT approach, the proportion of evergreens is calculated by summing up all arboreal zonal and azonal evergreen PFTs, whereas in IPR the broadleaved evergreen (BLE) components is the proportion of the BLE components to zonal woody angiosperms, for example, the sum of broadleaved deciduous, broadleaved evergreen, sclerophyllous, legume-like, zonal palm and arborescent fern (BLD + BLE + SCL + LEG + ZONPALM + ARBFERN) components. In addition, in the PFT approach, the threshold value for isolating deciduous vegetation, following Utescher et al. (2007) and according to the clusters (Figure 4), is not less than 60% of broadleaved deciduous PFTs, while in the IPR for this type of vegetation, the proportion of broadleaved deciduous components should not be lower than 80%.

With a seemingly external difference in the results obtained by these methods, all the floras allocated to the broadleaved deciduous forest (BLDF) and some floras in the ecotone between BLDF and mixed mesophytic forest (MMF) using the IPR method also fell into the group of deciduous (temperate) vegetation (Clusters 1a–1d) using the PFT approach (Figure 4). With the exception of one flora allocated to the BLDF (the Late Eocene LF 20) and two floras allocated to the BLDF/MMF (the Late Oligocene PF 5 and Late Eocene PF 14), all floras allocated to MMF, the ecotone between MMF and broadleaved evergreen forest (BLEF) and BLEF using the IPR approach fell into the second group of mixed evergreen-deciduous (warm temperate) vegetation (Clusters 2a–2c) using the PFT approach. Thus, the results obtained by different methods do not contradict each other. However, the PFT method shows more homogeneous vegetation, which is generally consistent with the reconstructed climate patterns (see below). This could probably be due to the fact that the PFT 25 and 26 were excluded during the likelihood procedure. According to Bondarenko, Blokhina, Bruch, Henrot, and Utescher (2017), IPR vegetation analysis also shows a warmer aspect of the vegetation in the Early Pleistocene when compared to the PFT approach. This effect can be explained by the fact that in the IPR, potentially azonal elements, including mainly broadleaved deciduous taxa, are a priori excluded when identifying the biome type.

The results obtained from the PFT method of the Paleogene floral record of Primorye in general do not contradict the vegetation reconstructions by other methods. However, vegetation is interpreted at the level of PFTs and thus does not allow for comparisons at the taxonomic level. Diverse mesic mixed forest types partly with thermophilous, evergreen tree taxa, as described from the Middle to Late Eocene and Early Oligocene of the Artemo-Tavrichanskii and Khasanskii basins (southern Primorye) (Ablaev, 2000, Pavlyutkin, 2007a) broadly agree with our reconstruction. The reconstruction of thermophilous vegetation, partly with predominance of evergreen plants, in Eocene coastal and lowland areas of southern Primorye provided by Bolotnikova (1979) coincides with high diversity of evergreen plants (from 18.2 to 42.7–43.5%) we observe in the floras of Clusters 2b and 2c. According to Soh et al. (2019), a rapid rise in CO_2 makes evergreen trees more efficient in water use than deciduous trees, especially in cooler parts of the world. A decline of hygrophilous plants and predominance of conifer forests at the end of the Oligocene, as suggested by Bolotnikova (1979) is not supported by our reconstruction (Figure 6).

According to Lopatina (2004), Amgu flora (the LF 11) demonstrates that in the Late Oligocene coniferous species played an important role in the plant cover. Light coniferous (a forest in which the main forest-forming species are photophilous conifers, such as pine and larch) and dark coniferous (a forest dominated by shade-tolerant conifers such as spruce and fir) forests predominated. Broadleaved deciduous species apparently did not form independent formations, but were accessory elements in coniferous-small-leaved forests. Taxodioideae continued playing a large role in the vegetation composition, and shrubs became more varied. Based on our data, there is no evidence for pure conifer forests in Primorye during the Paleogene. However, high diversity of conifers (above 30%) is observed for the Late Eocene LF 18 and Early Oligocene LF 9 and LF 11 (northeastern Primorye). Probably, *Taxodium* was mainly part of the intrazonal vegetation and did not form a zonal conifer forest.

The modern vegetation gradients of Primorye reflect the superimposition of the continental scale atmospheric circulation pattern such as monsoonal circulation and regional forcings. The modern vegetation of Primorye consists of mesophytic and xerophytic types (forest, wooded steppe, steppe, meadow, and swamp), which are in contact and form complex combinations (Kurentsova, 1968). Based on the present study, our palaeobotanical data in general demonstrate a mesophytic vegetation type in Primorye during the Paleogene while there is no evidence for xerophytic types and steppe.

5.4 | Climate

It is known that vegetation changes are often induced by climate change. Recently, the Paleogene climate dynamics in Primorye were studied using the Coexistence Approach, based on the same palaeobotanical records as presently used (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019; Utescher, Bondarenko, & Mosbrugger, 2015). The climatic inferences obtained are consistent with independently derived global trends, demonstrating general climate cooling throughout the Paleogene (Zachos et al., 2008). The data indicate that the Paleogene climate of Primorye was significantly warmer than present, in general, with the warmest conditions prevailing throughout the Eocene and in the southeast of the study area. Negligible Paleogene temperature gradients over Primorye have been related to global patterns and specific regional aspects (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019). Paleogene temperature gradients on the Northern Hemisphere were shallow in general as was reconstructed from palaeobotanical proxies (Greenwood & Wing, 1995; Utescher, Bruch, Micheels, Mosbrugger, & Popova, 2011). Shallow meridional gradients and considerably warmer-than-present higher northern latitudes were also obtained in some Eocene model runs under substantially raised atmospheric CO_2; however, equally connected to distinct warming of the tropics (Lunt et al., 2012).

TABLE 5 The characteristics of the forest types distinguished by cluster analysis next to means of climatic variables

			Forest characteristics			Means of climatic variables						
Vegetation type (cluster)	Forest type	Flora	Proportion of conifers, %	Proportion of BLD, %	Proportion of BLE, %	MAT, °C	CMMT, °C	WMMT, °C	MAP, mm	MPwet, mm	MPdry, mm	MPwarm, mm
1		LF 18	34.2	36.8	2.6	14.8	2.2	24.6	1,158	180	55	125
	1a	LF 8	11.3	70.1	13.4	14.8	8.0	25.8	1,329	167	32	158
		LF 10	14.3	72.6	9.5	15.2	4.4	26.0	1,059	160	45	130
		PF 1	21.1	66.2	9.9	15.0	4.5	24.0	1,188	225	38	148
		PF 2	21.1	66.2	9.9	15.0	4.5	24.0	1,188	225	38	148
		PF 4	22.7	63.6	10.6	15.0	4.5	24.0	1,132	176	38	148
		LF 13	16.4	68.9	9.8	17.6	9.3	25.6	1,307	212	22	154
		LF 34	12.0	73.0	7.0	15.1	3.9	25.9	1,047	159	30	152
		LF 35	5.2	87.9	0.0	16.9	3.8	25.3	1,045	176	27	142
		Min–max	5.2–22.7	63.6–87.9	0.0–13.4	14.8–17.6	2.2–9.3	24.0–26.0	1,045–1,329	159–225	27–55	125–158
	1b	LF 14	6.3	66.1	24.5	17.6	8.9	26.4	1,227	225	26	147
		LF 22	1.7	67.2	22.4	18.0	9.6	26.4	1,284	199	43	134
		LF 27	1.0	68.0	24.0	17.5	7.9	26.8	1,315	222	36	148
		LF 17	0.0	81.0	17.5	17.1	8.3	25.9	1,044	186	41	108
		LF 21	0.5	70.1	25.0	17.8	9.7	26.6	1,172	210	53	134
		Min–max	0.0–6.3	66.1–81.0	17.5–25.0	17.1–18.0	7.9–9.7	25.9–26.8	1,044–1,315	186–225	26–53	108–148
	1c	LF38	18.6	67.1	8.6	18.4	9.7	24.1	1,045	162	34	138
		LF 39	21.1	57.1	14.3	14.5	8.5	25.1	1,293	181	40	128
		PF 23	19.4	50.0	27.8	17.5	8.6	25.6	1,070	156	50	129
		PF 37	25.3	44.6	22.9	17.6	10.0	26.5	1,158	197	27	127
		PF 34	19.7	60.5	10.5	17.4	8.2	25.9	1,126	173	60	136
		Min–max	18.6–25.3	44.6–67.1	8.6–27.8	14.5–18.4	8.2–10.0	24.1–26.5	1,045–1,293	156–197	27–60	127–138
	1d	LF 19	3.7	87.2	5.5	17.2	8.3	25.7	1,198	175	36	119
		LF 2	1.5	86.4	6.1	14.4	2.2	26.1	1,229	171	49	126
		LF 36	12.0	84.0	0.0	17.3	6.7	25.9	1,210	190	35	145
		LF 28	14.7	79.4	0.0	17.2	6.2	24.4	1,122	180	37	136
		LF 33	9.5	85.7	0.0	15.2	5.4	24.2	1,159	198	36	150
		Min–max	1.5–14.7	79.4–87.2	0.0–6.1	14.4–17.3	2.2–8.3	24.2–26.1	1,122–1,229	171–198	35–49	119–150
2	2a	LF 9	40.2	38.6	18.1	15.4	4.3	25.2	1,134	152	35	160
		LF 11	31.3	47.3	17.9	15.4	4.8	26.3	1,137	152	34	146
		LF 12	24.8	49.7	15.7	16.5	7.8	25.6	1,126	161	34	137
		LF 31	23.7	47.4	19.3	15.9	9.0	25.6	1,170	187	41	160
		Min–max	23.7–40.2	38.6–49.7	15.7–19.3	15.4–16.5	4.3–9.0	25.2–26.3	1,126–1,170	152–187	34–41	137–160
	2b	PF 3	26.7	33.7	36.0	17.1	6.6	25.6	1,278	235	27	147
		PF 7	26.1	33.0	37.5	17.4	8.2	25.6	1,278	236	29	147

(Continues)

TABLE 5 (Continued)

Vegetation type (cluster)	Forest type	Flora	Forest characteristics: Proportion of conifers, %	Proportion of BLD, %	Proportion of BLE, %	Means of climatic variables: MAT, °C	CMMT, °C	WMMT, °C	MAP, mm	MPwet, mm	MPdry, mm	MPwarm, mm
		PF 25	28.6	29.9	37.7	17.1	6.8	25.6	1,278	235	27	147
		PF 16	31.9	29.8	35.1	18.2	9.6	26.1	1,404	210	50	153
		PF 14	32.1	34.5	28.6	16.9	7.9	27.3	1,554	226	45	147
		PF 6	26.6	35.7	27.3	16.9	6.1	27.4	1,163	151	35	125
		PF 9	21.3	38.1	32.5	16.0	6.1	27.3	1,323	187	33	120
		PF 33	22.0	34.0	34.0	16.6	8.1	26.2	1,278	209	43	147
		PF 22	19.8	36.8	36.8	17.4	7.8	25.2	1,170	175	34	153
		PF 21	28.4	35.8	30.9	16.9	7.9	27.3	1,554	226	54	147
		PF 26	26.0	33.3	35.4	17.3	7.2	27.3	1,554	210	45	147
		PF 27	26.2	28.2	42.7	18.2	9.6	26.2	1,295	192	44	153
		PF 32	23.4	30.8	39.3	16.6	8.1	25.5	1,278	211	29	153
		PF 29	24.2	30.8	39.6	18.2	8.9	26.1	1,351	210	53	154
		PF 5	29.4	36.8	32.4	16.9	6.1	25.6	1,278	221	33	147
		PF 24	25.0	41.3	32.5	17.3	6.5	26.2	1,404	210	50	147
		PF 15	27.7	34.0	36.2	17.6	8.5	25.9	1,278	195	42	147
		PF 17	31.7	32.7	24.8	16.5	8.3	24.9	1,373	187	40	160
		PF 13	29.6	32.4	33.8	16.9	7.6	27.3	1,554	226	54	147
		LF 6	17.1	43.6	34.9	16.3	6.1	26.2	1,118	179	35	125
		Min–max	17.1–32.1	29.8–43.6	18.2–42.7	16.0–18.2	6.1–9.6	24.9–27.4	1,095–1,554	151–236	27–54	120–160
	2c	LF 20	23.9	35.2	18.2	17.5	9.0	25.6	1,095	196	30	142
		PF 30	22.6	30.2	34.0	18.2	8.0	25.9	1,404	223	52	153
		PF 8	7.1	49.5	39.4	16.9	7.9	27.3	1,422	226	54	148
		PF 18	4.8	50.0	43.5	16.3	10.2	22.9	1,596	230	54	172
		PF 28	5.0	51.7	43.3	18.2	8.0	26.0	1,422	210	56	148
		PF 19	5.2	57.1	28.6	16.1	6.0	25.5	1,265	172	53	120
		Min–max	4.8–23.9	30.2–57.1	18.2–43.5	16.1–18.2	6.0–10.2	22.9–27.3	1,095–1,596	172–230	30–56	120–172

Note: References and complete flora lists including Nearest Living Relatives used for vegetation analysis are given in Data S1. Means of Coexistence Intervals (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019).

Moreover, the precipitation reconstruction points to conditions considerably wetter than at present (Utescher et al., 2014). A distinct increase in mean annual precipitation was reconstructed for the study area for the Early Eocene and moderately declined throughout the Oligocene (Utescher et al., 2014). The regional rainfall pattern fundamentally differed from modern conditions, and this holds for all studied variables. The inland region and the south of Primorye were significantly more humid than today. The Paleogene pattern was possibly related to an early established monsoon-type circulation over East Asia (Quan et al., 2012a; Quan, Liu, & Utescher, 2011) and enhanced flow of humid air masses from the Pacific to inland areas of northeast Asia, even though it is assumed that, prior to the back arc opening of the Sea of Japan (Maruyama, Isozaki, Kimura, & Terabayashi, 1997), the Paleogene coast line was located several 100 km to the east of our study area (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019). The enhanced flow was possibly enabled by a significantly flatter morphology of the Paleogene Pacific coastal realm (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019). Moreover, a weak Siberian High at that time led to more equable and humid climate conditions in the continental interior compared to the present-day situation (Popova, Utescher, Gromyko, Bruch, & Mosbrugger, 2012).

The observed vegetation patterns and their changes through time in many cases can be correlated with spatial climate patterns and the overall continental palaeoclimate evolution as reconstructed from the palaeobotanical record (Figure 5). More homogeneous vegetation is generally consistent with the reconstructed shallow Paleogene temperature gradients and significantly more humid palaeoclimate conditions in Primorye. In general, the mixed evergreen-deciduous type of vegetation corresponds to mean values of the MAT not lower than 15.4°C, CMMT not lower than 4.3°C, WMMT up to 27.4°C and MAP up to 1,596 mm. Deciduous type of vegetation is characterized by somewhat lower values: MAT from 14.4°C, CMMT from 2.2°C, WMMT up to 26.8°C and MAP up to 1,329 mm (Table 5). In turn, each of the seven forest types identified is characterized by a different set of climatic parameters. For example, forest types 2b and 2c are characterized by MAT values not lower than 16.0°C and CMMT not lower than 6.0°C, but differ in values of precipitation parameters—forest type 2c is characterized by higher values and narrower intervals for MAP, MPwet and MPdry (Table 5).

The change in the proportion of some groups of PFTs (needleleaved vs. broadleaved, broadleaved deciduous vs. broadleaved evergreen, drought-tolerant vs. drought-intolerant) throughout the Paleogene also reflects changes in some climatic parameters. The decreasing proportion and diversity of broadleaved evergreen plants and the increasing proportion of needleleaved plants from the Early Palaeocene to Late Oligocene coincides with the general climate cooling throughout the Paleogene (Figure 6). The constant presence of PFT 18 in all studied floras agrees with the precipitation reconstruction (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019) demonstrating considerably wetter conditions than at present. PFT 18 is also indicative for intrazonal swamp forest communities and thus points to the presence of inundated areas throughout the studied time-span (Figure 6). The increasing trend in the seasonality of precipitation (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019) is mirrored by an increase in the drought tolerant/drought intolerant PFTs proportion since the Early Eocene (Figure 6). Accordingly, Akhmetiev (2004) suggested the existence of more seasonal climate conditions for southern Primorye since the Middle Eocene.

As regards palaeoclimate evolution of Primorye throughout the Paleogene MAT means calculated from the microfloras have demonstrated the globally observed cooling trend (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019). This coincides with coeval major plant biome changes in Primorye, namely from the subtropical MMF/BLEF ecotone in the Late Palaeocene to the warm temperate BLDF/MMF ecotone in the Late Oligocene, as resulting from the application of the IPR on the microfloras (Bondarenko, Blokhina, & Utescher, 2019). Using the PFT technique, a comparable trend is reflected by steadily declining medians of the BLE/BLD proportion since the Early Eocene (Figure 6) pointing to an increasingly more temperate character of the phytocoenoses.

Except for warm peaks in the Late Palaeocene and Middle Eocene possibly corresponding to the PETM and climatic optimum in the Middle Eocene (MECO) LF tend to indicate somewhat lower temperatures in general and a less clear trend in palaeoclimate evolution (Bondarenko, Blokhina, Mosbrugger, & Utescher, 2019). Accordingly, results obtained from IPR analysis do not reflect major vegetation changes showing only one dominant type of temperate to warm-temperate forest for the studied time-span—the BLDF (Bondarenko, Blokhina, & Utescher, 2019). Based on the PFT approach most thermophilous LF (BLE component >20%) date to the Eocene (the LFs 14, 21, 22, 23, 27) and thus this technique better reflects the general picture. The possibly warmest leaf flora (the LF 6), however, dates to the early Oligocene. The cooler aspect of leaf flora ecospectra, in general, most likely can be explained by the fact that they usually have a riparian imprint while evergreens are comparatively rare in riparian settings (Krassilov, 1972). Moreover, leaves of deciduous plants are more likely to be buried than those of evergreen plants, while pollen show their presence more reliably (Krassilov, 1972).

6 | CONCLUSIONS

1. Our data in general demonstrate a mesophytic vegetation types in Primorye during the Paleogene. The observed vegetation patterns and their changes through time in many cases can be correlated with spatial climate patterns and the overall continental palaeoclimate evolution as reconstructed from the palaeobotanical record. Homogeneous vegetation is generally consistent with the conclusion about the shallow Paleogene temperature gradients and significantly more humid regional rainfall pattern over Primorye.

2. The more deciduous character of ecospectra obtained for LF are either related to taphonomical effects or indicate intrazonal wetland vegetation. This has to be considered when interpreting data obtained with statistical ordination methods such as cluster analysis.

3. In the Palaeocene, vegetation of Primorye was of a temperate deciduous type. In the Eocene and Early Oligocene vegetation had a mosaic distribution, that is, was generally of a warm temperate mixed evergreen-deciduous type, but in some places had a deciduous character. In the Late Oligocene, vegetation in Primorye was primarily deciduous, while at places, mixed evergreen-deciduous vegetation persisted.

4. The application of the likelihood procedure leads to more reliable ecospectra because it excludes PFTs that are incompatible with the palaeoclimatic settings of the study area. In the case of *Larix* the approach facilitates the identification of PFT outliers.

5. When comparing the results obtained with the PFT technique with IPR data it is shown that the IPR tends to reconstruct more thermophilous vegetation containing more broadleaved evergreen components because various deciduous taxa are excluded from scoring for being considered as azonal elements. This, however, may not be justified in each case because most of the excluded elements may also be part of the zonal vegetation.

6. The proportion of BLE among broadleaved component culminates in the Early and Middle Eocene, and this coincides with the warmest time-period in the study area as reconstructed with the CA.

7. The increase in drought tolerant PFTs in the Oligocene coincides with a lower MPdry level reconstructed for the same time-span. In combination with the relatively high MPwet level at that time a more seasonal character of climate may have evolved in the Oligocene.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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