

## Quantification of Calabrian vegetation in Southern Primory'e (Far East of Russia) using multiple proxies



Olesya V. Bondarenko<sup>a</sup>, Nadezhda I. Blokhina<sup>a,\*</sup>, Angela A. Bruch<sup>b</sup>, Alexandra-J. Henrot<sup>c</sup>, Torsten Utescher<sup>d,e</sup>

<sup>a</sup> Institute of Biology and Soil Science, Far Eastern Branch, Russian Academy of Sciences, Prospect Stoletiya Vladivostoka 159, Vladivostok 690022, Russia

<sup>b</sup> Senckenberg Research Institute, Heidelberg Academy of Sciences and Humanities, ROCEEH Research Center "The Role of Culture in Early Expansions of Humans", Senckenberganlage 25, 60325 Frankfurt M., Germany

<sup>c</sup> Unité de Modélisation du Climat et des Cycles Biogéochimiques (UMCCB), Université de Liège, Quartier Agora, Bât. B5c, Allée du Six Août 19C, B-4000 Liège, Belgium

<sup>d</sup> Senckenberg Research Institute and Natural Museum, Senckenberganlage 25, 60325 Frankfurt M., Germany

<sup>e</sup> Steinmann Institute, University of Bonn, Nussallee 8, 53115 Bonn, Germany

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### ABSTRACT

Early Pleistocene vegetation dynamics in the Russian Far East (southern Primory'e) are studied using multiple quantitative techniques on various palaeobotanical organ types. Vegetation data for this time interval were obtained from a total of 8 macrofloras (fruits and seeds, woods, and leaves) and 18 microfloras collected from a 10 m thick, terrigenous succession exposed in the Pavlovskoe brown coal field. According to magnetostratigraphy, the studied section covers the last 250 kyr of the Calabrian (1.0 to 0.781 Ma) and includes the early/middle Pleistocene boundary. In this first integrative study on quantification of palaeovegetation of the Russian Far East, we apply the following methods: Plant Functional Type (PFT) Approach, Integrated Plant Record (IPR) vegetation analysis, and ecological Coexistence Approach (CA<sub>eco</sub>) on the different organs, partly originating from the same layer.

The investigation documents the following outcomes: 1) Vegetation types obtained from the various methods are proven to be largely consistent. All data indicate the presence of more forested conditions and show no xeric, open woodland throughout the section. 2) Vegetation as reconstructed using the various methods generally is in good agreement with the recently published climate evolution throughout the section. 3) There is a cyclic evolution of PFT diversity which is in line with climate data. 4) The changes of vegetation types obtained from IPR analysis relate to cooling/drying trends of the climate evolution.

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### 1. Introduction

The modern status of the natural environment characteristic of the Russian Far East (RFE) is determined by its development associated with global and regional climate changes in the Quaternary. Globally, the Quaternary Period was characterized by sharp, intense and multiple changes of climate expressed as alternations of cold and warm phases (Williams et al., 1988; Frenzel et al., 1992; Lisiecki and Raymo, 2005; Velichko, 2009) and associated with strong fluctuations of the global sea-level (Lambeck et al., 2002). At the same time, the climate in the south Far East is supposed to reflect the varying intensity of the warm Kuroshio and cold, subarctic currents (e.g., Gallagher et al., 2009; Matthiessen et al., 2009). Moreover, the climate here is tied to the history of the East Asian Monsoon System (EAMS) (An et al., 2001).

In the south Far East, directionally rhythmic climate changes in the Pleistocene were characterized by increasing continentalization and accompanied by repeated reorganizations of vegetation zones and belts. In this region, large-scale climate changes were registered by alternately increasing oceanic (in warm phases) or continental (in cold phases) influences (Korotkii et al., 1980, 1996; Golubeva and Karaulova, 1983).

According to Korotkii et al. (1996), the most significant changes in the structure of vegetation of the southern part of the RFE were observed in ecotones (for example, near the upper boundary of the forest or in the coastal zone). They consider that in the upper mountain belt, this is due both to an overall increase in the severity of the climate and the nature of its winter mode (woody plants rapidly dying at low temperatures and strong winds). The influence of the EAMS particularly affected the formation of vegetation in the coastal zone of Primory'e. The coastal zone was under the influence of strong winter winds (even under relatively mild winters) and quite cool summers. Long, strong and cold mists displaced woody vegetation inland. In the coastal zone, and within the large inland depressions, changes of vegetation manifested themselves more actively due to changes in the water

\* Corresponding author.

E-mail addresses: [laricioxylon@gmail.com](mailto:laricioxylon@gmail.com) (O.V. Bondarenko), [blokhina@biosoil.ru](mailto:blokhina@biosoil.ru) (N.I. Blokhina), [angela.bruch@senckenberg.de](mailto:angela.bruch@senckenberg.de) (A.A. Bruch), [alexandra.henrot@ulg.ac.be](mailto:alexandra.henrot@ulg.ac.be) (A.-J. Henrot), [t.utescher@uni-bonn.de](mailto:t.utescher@uni-bonn.de) (T. Utescher).

regime in the river valleys and on wide watershed areas (Korotkii et al., 1996).

Unfortunately, in most parts of the southern RFE, the Plio-Pleistocene transition corresponds to a long stratigraphic gap, due to erosional dissection of the area with amplitudes of incision up to 130–150 m (Khudjakov et al., 1972; Korotkii et al., 1980; Korotkii and Pavlutkin, 1984). Lack of geological and palaeobotanical data complicates detailed reconstruction of the vegetation and climate of the early Pleistocene.

However, Pleistocene deposits are widespread in Primory'e, especially in its southern part. They were studied most completely within the Khanka Plain (43°20'–46°N and 131°–133°25'E) located in the south-western part of Primory'e between the spurs of the Sikhote-Alin Range and the mountains of Northeast China, and in the foothills and lower mountains of the southern Sikhote-Alin. In the western part of the Khanka Plain, early Pleistocene sediments were recovered from wells, whereas within the southern Sikhote-Alin they were accessible in sections of terraces (Korotkii and Karaulova, 1970; Khudjakov et al., 1972; Golubeva and Karaulova, 1983).

Vegetation development of southern Primory'e in the early Pleistocene has been reconstructed by Golubeva (1972a, 1972b, 1973, 1976), Golubeva and Karaulova (1983), Karaulova (1973), Korotkii and Karaulova (1970), Korotkii et al. (1996), etc. only on the basis of palynological data. Generally, the palynological data indicate that in the Pleistocene forests persisted in the territory of Primory'e, but in cold cycles their diversity gradually declined as most thermophilic elements were lost. Based on palaeomagnetic studies pollen assemblages dated as belonging to the Matuyama epoch (about 1.6–0.9 Ma), a spread of plant communities consisting of representatives of the modern Manchurian flora reached latitudes 42–45°N. These polydominant deciduous forests included species of *Fagus*, *Castanea*, *Zelkova*, *Pterocarya*, *Nyssa* and exotic species of *Pinus* while typical Neogene exotics such as *Ginkgo*, *Sciadopitys*, *Engelhardia* were absent. These taxonomically diverse forests thrived in the territory of the Khanka plain (Golubeva and Karaulova, 1983; Korotkii and Pavlutkin, 1984; Korotkii et al., 1996).

Spore and pollen assemblages from sediments dated to the early Pleistocene (about 0.8 Ma) demonstrate that broadleaved deciduous forests containing various species of Korean and Japanese *Pinus*, *Tsuga* and *Cryptomeria* as an admixture were widespread in the southern Primory'e (Golubeva and Karaulova, 1983). In general, at latitudes 42–45°N, the early Pleistocene forests were comparable in their structure with modern deciduous forests of the northern part of Honshu Island (Karaulova, 1974; Golubeva and Karaulova, 1983; Korotkii et al., 1996). Probably, in the southern part of the Khanka Plain and its surrounding foothills, steppe vegetation already existed. The forests consisted of various species of *Quercus* and *Betula* with an undergrowth of *Corylus* and *Syringa*. In the mountains of the western Sikhote-Alin, where humidity was higher, the forests consisted of *Castanea*, *Tilia*, *Juglans mandshurica*, *Carpinus* and exotic species of *Pinus*. Vegetation was similar to modern continental interior vegetation of the moderately warm subzone of North China and North Korea (Golubeva and Karaulova, 1983). In more northern regions of Primory'e, and at higher elevations in montane regions, there was a gradual impoverishment of the flora (Karaulova, 1974; Golubeva and Karaulova, 1983; Korotkii et al., 1996).

The beginning of the middle Pleistocene (about 0.7 Ma) was marked by a radical transformation of the landscapes. In Primory'e (between latitudes 40–47°N), broadleaved forests consisting mainly of modern species became the predominant vegetation type on the plains (Korotkii et al., 1996). In the Sikhote-Alin, penetration of cold adapted shrubs (representatives of hypo-arctic flora) and the formation of treeless mountain peaks (at altitudes above 1.500 m) occurred in this time (Korotkii et al., 1996).

Today, the Khanka Plain is a very notable part of Primory'e regarding its landscape, climate, soil and vegetation. The territory is quite flat and represents a complex combination of interconnected ancient lacustrine, alluvial and denudation-dealluvial surfaces. In general, Primory'e is

strongly influenced by the EAMS, however, the Khanka Plain is characterized by a specific climate. Irregularity of precipitation, high amplitudes of seasonal and daily temperatures, and winter drought are the most strongly pronounced here. Moreover, recurrent droughts caused by intrusion of dry air masses flowing from Northeast China and Mongolia are very typical for the Khanka Plain (Belyanin, 2009). Therefore, the modern vegetation of the Khanka Plain consists of xerophytic and mesophytic types, which are in contact and form complex combinations (Kurentsova, 1962, 1968; Korotkii, 2002).

Interregional comparisons of vegetation types and changes of the assemblages through time on the basis of qualitative, mainly palynological, data are difficult to assess because the analysis of spatial vegetation patterns and temporal evolution trends require the quantification of vegetation change. In comparison to the vast literature resources on the palaeobotanical record and phytogeography of RFE in general and Primory'e in particular, palaeovegetation reconstructions in this region are still rare. Until now, only Popova et al. (2013) has quantitatively reconstructed vegetation change in Siberia and the northeast of Russia during the Cenozoic based on diversity of Plant Functional Types (PFTs) of carpoifloras.

Therefore, our work is the first integrative study on quantification of palaeovegetation of southern Primory'e at the end of the early Pleistocene (1.0–0.781 Ma) encompassing Plant Functional Types (PFTs), Integrated Plant Record-vegetation analysis (IPR), and ecological Coexistence Approach (CA<sub>eco</sub>) methods based on different plant organs, sometimes originating from the same depositional layers. The results are discussed in the context of palaeoclimate data.

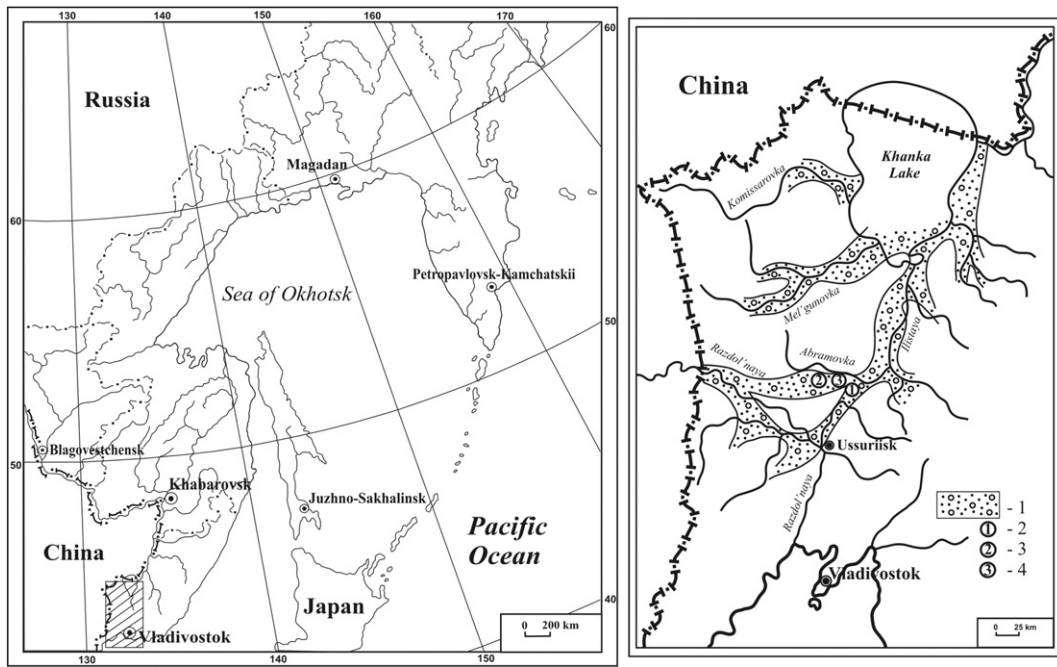
## 2. Study area

### 2.1. Geological settings

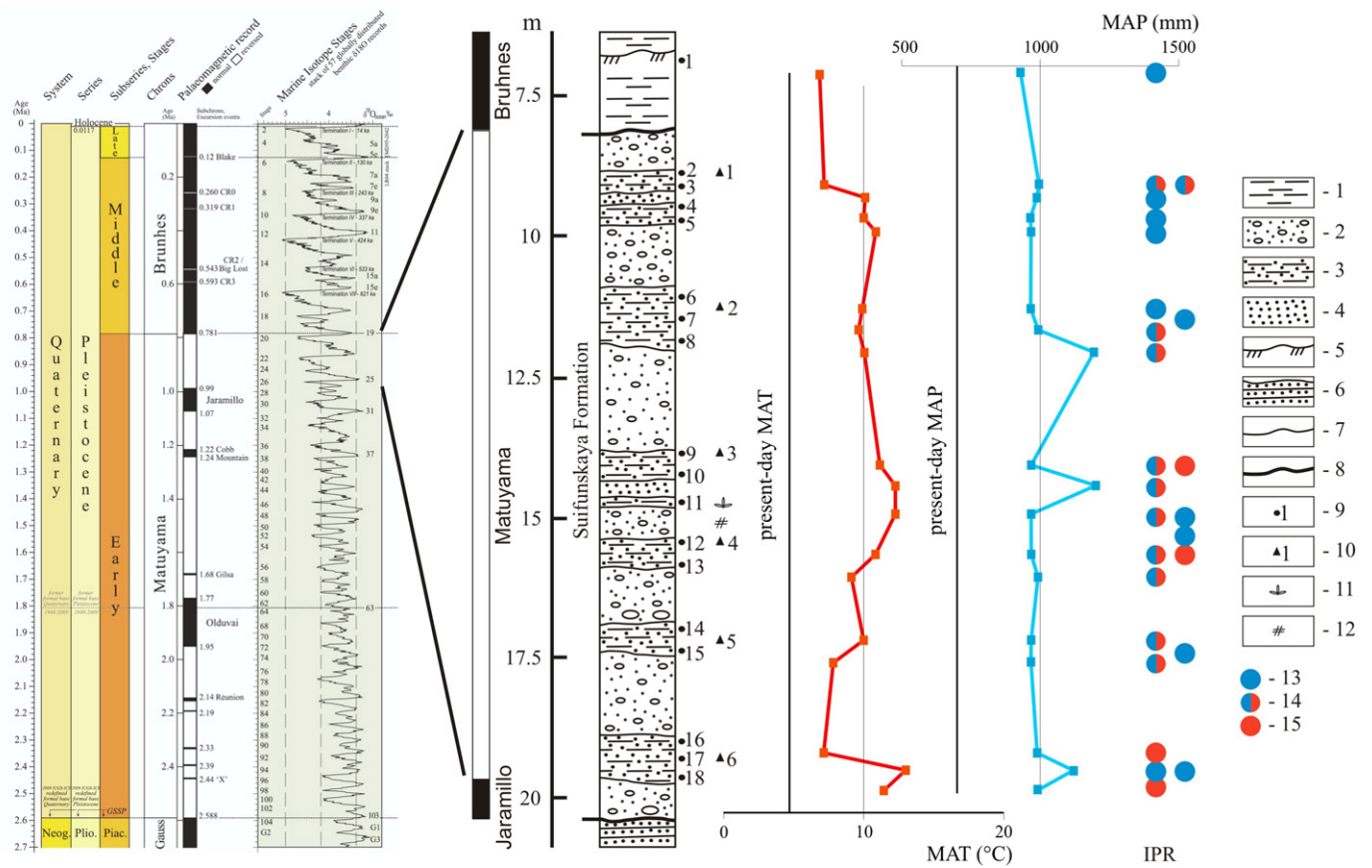
The Pavlovskoe brown coal field is located 35 km north-east of Ussuriisk city in the Primorskii Region (or Primory'e) of the RFE (Fig. 1). It covers a total area of ~150 km<sup>2</sup>, and belongs to the “structural-formational zone” of the Neoproterozoic Khankaiskii massif (Bersenev, 1969; Pavlutkin and Petrenko, 2010). The Pavlovskoe brown coal field comprises the Pavlovskii Basin and several separate small sub-basins located close to one another (Cherepovskii, 1997). The Pavlovskii Basin hosts the Pavlovskii-II open-cast coal mine. The Southern, Eastern and Northern sub-basins are included in the open-cast coal mine Pavlovskii-I. The Luzanovskii sub-basin is the location of the Luzanovskii open-cast coal mine (Cherepovskii, 1997).

The Pavlovskii Basin, as well as all sub-basins mentioned above, is filled with late Oligocene to Quaternary strata, unconformably resting on Palaeozoic basement. The Cenozoic deposits exposed in the open-cast mines are subdivided into three formations: Pavlovskaya, Ust'-Suifunskaya and Suifunskaya (Krasnyi, 1994; Cherepovskii, 1997; Klimova and Feoktistov, 1997).

The Pavlovskaya Formation is composed of fine to medium-grained siliciclastic sediments, brown coals, and tuffites, which mainly occur in the upper part. The age of the Pavlovskaya Formation is uppermost Oligocene to uppermost middle Miocene (Krasnyi, 1994). The overlying Ust'-Suifunskaya Formation with an erosional base, consists of cross-bedded sandstones and gravels dating to the late Miocene (Krasnyi, 1994). The deposits of the overlying Suifunskaya Formation are distributed within the middle reaches of the Razdol'naya River Basin extending northward to Khanka Lake within Khanka Plain (Fig. 1). Depending on the part of the basin, the Suifunskaya Formation unconformably rests on sediments of various composition and age, from Palaeozoic granites to weakly calcareous, late Miocene volcanic tuffites and late Pliocene red clays. The Suifunskaya Formation is placed in the early Pleistocene (Calabrian), and its thickness ranges from 10 to 20 m (Pavlutkin and Petrenko, 2010).



**Fig. 1.** Map showing location of the study area: 1 – distribution of the sediments of the Suifunskaya Formation (Pavlutkin et al., 1988); 2 – Pavlovskii-I open-cast coal mine; 3 – Pavlovskii-II open-cast coal mine; 4 – Luzanovskii open-cast coal mine.



**Fig. 2.** Lithological profile of the Suifunskaya Formation and correlation with the International Chronological Chart, palaeomagnetic chronozones, marine isotope stages, curves for MAT and MAP as reconstructed from palynofloras using the CA (Bondarenko et al., 2013) and Integrated Plant Record vegetation analysis: 1 – sandy clays; 2 – gravels; 3 – silts; 4 – sands; 5 – palaeosoil; 6 – sandstones; 7 – lithological boundaries; 8 – stratigraphic boundaries; 9 – palynoflora; 10 – capoflora; 11 – leaf flora; 12 – xyloflora; 13 – broad-leaved deciduous forest; 14 – ecotone between broad-leaved deciduous and mixed mesophytic forest; 15 – mixed mesophytic forest.



## 2.2. Studied section and age control

The studied section, no. 9035 of the Suifunskaya Formation (cf. Figs. 1 and 2; coordinates: 44°05'N 132°05'E), was measured in the Pavlovskii-II open-cast coal mine (Pavlutkin et al., 1988; Pavlutkin, 1997, 1998; Pavlutkin and Petrenko, 2010). In this section, the deposits of the Suifunskaya Formation, attaining a thickness of ca. 10 m, unconformably rest on coarse-grained, unconsolidated sandstones of the late Miocene Ust'-Suifunskaya Formation. The sandy clays on top of the profile are wide-spread in southern Primory'e and dated as middle – late Pleistocene (Korotkii, 1970; Pavlutkin, 1984).

According to Pavlutkin (Pavlutkin et al., 1988, 1991; Pavlutkin, 1998; Pavlutkin and Petrenko, 2010), the section exposes a series of fluvial sedimentary cycles, which are composed of cross-bedded gravels and small-pebble conglomerates. Silts deposited on top of each cycle contain spores and pollen and plant detritus. Layers with coarse-grained gravels in the middle part of the formation contain fossil woods (Fig. 2).

Traditionally, the Suifunskaya Formation was considered to be of Pliocene age (Krasnyi, 1958, 1994; Cherepovskii, 1997; Klimova and Feoktistov, 1997), though some researchers (Ganeshin and Smirnov, 1960; Ganeshin, 1961; Chemekov, 1962) defined its age as Pliocene – early Pleistocene. This is primarily due to the fact that the Geological Survey of the USSR and then of the Russian Federation up to 2011 placed the Neogene-Quaternary boundary at 0.7 Ma.

According to Pavlutkin (Pavlutkin, 1997, 1998; Pavlutkin and Petrenko, 2010), the Suifunskaya Formation belongs to the Calabrian, based on evidence from regional geology and pollen zonation. The pollen zonation established for the studied profile can be correlated with palynozones of the later part of Calabrian in Northern Japan (Kitagawa et al., 1988) and Northeast China (Li and Wang, 1982; Zhou et al., 1983). For more details see Pavlutkin (1997, 1998). Moreover, recent palaeomagnetic studies suggest that the basal part of the Suifunskaya Formation, having normal polarity, corresponds to the Jaramillo magnetic subchronozone, at 1.0 Ma; the profile part between depth levels 19 and 8 m in the studied section exhibits reverse polarity, and is placed in the Matuyama magnetic chronozone (Pavlutkin and Petrenko, 2010). The transition to sandy clays on top of the Suifunskaya Formation marks the early/middle Pleistocene boundary in southern Primory'e, at 0.781 Ma. According to Pavlutkin (1984), palaeomagnetic studies on these sandy clays show that all samples analyzed have normal polarity and correspond to the Brunhes magnetic chronozone. Based on these data, the studied section represents a time-span of about 250 ka (Fig. 2). However, the sedimentary facies, representing a fluvial, braided river environment with coarse-grained channel fills, suggests the presence of gaps in the record.

## 3. Materials

Plant fossil records from the Suifunskaya Formation of the Pavlovskoe brown coal field are represented by different organ types, namely wood remains, leaf impressions, fruits and seeds, and spores and pollen.

The xyloflora (XF) was collected and studied by several authors (Blokhina and Bondarenko, 2004, 2005, 2008; Blokhina et al., 2003, 2005; Bondarenko, 2006, 2007). According to geologists (Krasnyi, 1958, 1994; Pavlutkin et al., 1988; Cherepovskii, 1997; Pavlutkin, 1997, 1998), the fossil woods originate from a single level (Fig. 2), which can be identified in all adjacent open-cast mines of the Pavlovskoe brown coal field (Fig. 1). Fossil woods can be referred to 35 taxa (Appendix Tables 1 and 2). The abundant wood fragments are lignitic, light- to dark-brown in colour, and usually range in diameter from 3 to 5 cm up to 15–18 cm, and from 6 to 9 cm up to 23 cm in length. A few logs of 40–50 cm in diameter and 3–6 m in length were also found. Wood fragments, branches and logs were found horizontally aligned with respect to the bedding plane, with beds inclined 270° from east to west. Wood was found at the same level within the

Pavlovskii-I, the Pavlovskii-II and the Luzanovskii open-cast coal mines. Out of a total of 373 wood specimens studied, 335 were anatomically well preserved and were identified in this study.

According to Pavlutkin (Pavlutkin et al., 1988; Pavlutkin, 1997, 1998), the leaf flora (LF), carpofloras (CFs) and palynofloras (PFs) originate from the same section (no. 9035) located within the Pavlovskii-II open-cast coal mine.

Information about the LF was taken from Pavlutkin (1997, 1998), Klimova (1997), and Klimova and Feoktistov (1997). The impressions come from a single level (Fig. 2) and can be referred to 48 taxa (Appendix Tables 1 and 2) that were identified by Klimova (Klimova and Feoktistov, 1997).

The information regarding the CFs was taken from Pavlutkin et al. (1988) and Krasnyi (1994). The fruits and seeds were found at six levels (Fig. 2) and belong to 120 taxa (Appendix Tables 1 and 2) identified by Dorofeev (cit. by Pavlutkin et al., 1988).

PFs data are taken from Pavlutkin et al. (1988, 1991) and Krasnyi (1994). The microflora comes from a total of 18 levels (Fig. 2) and yields evidence for 53 taxa (Appendix Tables 1 and 2) identified by Belyanina (Pavlutkin et al., 1988). According to (Pavlutkin et al., 1988), the youngest PF 1 sample at the depth level 7.0 m originates from the basal part of the sandy clays (Fig. 2).

Palaeoclimate data reconstructed for the Calabrian of southern Primory'e using the Coexistence Approach (CA) are taken from Bondarenko et al. (2013) (Fig. 2).

## 4. Methods

### 4.1. PFT (plant functional type) approach

The PFT concept goes back to works of Prentice (e.g., Prentice et al., 1992; 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 on the Neogene palaeobotanical record was first introduced by Utescher et al. (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 1). The allocation of fossil taxa to the single PFTs is based on interpretation of their NLRs (Appendix Table 3), 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). This methodology is similar to the CA used in palaeoclimate reconstructions from palaeobotanical records. In cases when several classes of PFTs are possible for a taxon, only those that can coexist with the other classes identified at the site are retained. It narrows the range of plant types present at the site by suppressing extreme end members, such as cold boreal/temperate and tropical PFTs. The coexistence is used to evaluate the likelihood for the presence of each PFT at the site, according to the six following categories: absent, inconsistent, unlikely, likely, very likely, present. First, all PFTs to which at least one taxon has been unequivocally assigned are considered as present. Similarly, all PFTs that have not been allocated any taxa are considered as absent. Then, all remaining PFTs are tested for consistency with all other present or potentially present PFTs. This procedure results in the tested PFTs being classified in one of the remaining categories: inconsistent, unlikely, likely, very likely. The presence/absence status of the PFTs then was decided from these likelihood levels, by retaining the first three categories for the absence and the last three for presence (Appendix Table 4).

The PFT approach requires only information on presence and absence of taxa and thus is robust towards taphonomic bias. The approach

**Table 1**  
PFT classification used for the present study (Popova et al., 2013).

	PFT No.	PFT	
Herba	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	
Aquatic	23	Broadleaved summergreen temperate cool trees	
	24	Broadleaved summergreen temperate warm trees	
	25	Broadleaved raingreen tropical trees	
	26	Broadleaved evergreen tropical trees	
	27	Aquatic components	

can be applied on all types of fossil floras providing an adequate size of the sample.

#### 4.2. Integrated plant record (IPR)

The Integrated Plant Record vegetation analysis (IPR-vegetation analysis) 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 (CONIFER), 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, i.e. azonal woody component (AZW), azonal non-woody component (AZNW) and aquatic component (AQUA). The component PROBLEMATIC TAXA includes 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. Allocation of the fossil taxa to the components is given in Appendix Table 5. 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 proportions of the components were calculated for each level and are given in Table 2.

Based on relative proportions of the components the following six zonal vegetation types have been distinguished (Kovar-Eder and

Kvaček, 2007; Kovar-Eder et al., 2008): zonal temperate to warm-temperate broad-leaved deciduous forests (broad-leaved deciduous forests, BLDF), zonal warm-temperate to subtropical mixed mesophytic forests (mixed mesophytic forests, MMF), zonal subtropical broad-leaved evergreen forests (broad-leaved evergreen forests, BLEF), zonal subtropical, subhumid sclerophyllous or microphyllous forests (subhumid sclerophyllous forests, ShSF), zonal xeric open woodlands (open woodland), and zonal xeric grasslands or steppe (xeric grassland). Recently, Teodoridis et al. (2011) additionally defined ecotones between the BLDF and MMF and the BLEF and MMF.

Ten zonal taxa are regarded as a minimum to perform this method. The reliability of the results increases with increasing number of zonal taxa preserved.

#### 4.3. Quantification of vegetation density ( $CA_{eco}$ )

A method to quantify openness of vegetation based on plant fossils was introduced by Bruch et al. (2012) making use of remotely sensed data on vegetation cover, photosynthesis activity and vegetation density (leaf area index, LAI). The ecological Coexistence Approach ( $CA_{eco}$ ) is based on the methodology of the Coexistence Approach (CA) (Mosbrugger and Utescher, 1997; Utescher et al., 2014) relying on the assumption that since the Neogene the ecological requirements of plant taxa have remained similar to those of their nearest living relatives (NLRs).

With the CA, for each environmental parameter analyzed, the ranges in which a maximum number of NLRs of a given fossil flora can coexist is determined independently and considered the best description of the palaeoenvironmental situation under which the given fossil flora lived; considering only the presence of taxa in a fossil flora, not their abundances.

Distribution maps for NLR taxa which relate to the fossil wood record were compiled from botanical literature (Table 3). Those maps were digitized, georeferenced in GIS by using the program ESRI ArcView, and transformed into shapefiles. Depending on the different sources, the maps include distribution information with very variable spatial resolution. Sokolov et al. (1949, 1951, 1954, 1958) gives global distribution areas (polygons), Sokolov et al. (1977, 1980, 1986) give point data for the territory of former USSR with an accuracy of approx. 20 km. Point shapefiles were buffered by 20 km. Those shapefiles were intersected with a remotely sensed global raster dataset based on the ECOCLIMAP data of Masson et al. (2003) that was transposed to a resolution of 10 arc min. From the resulting raster data, all grid cells that exceeded the altitude range of the analyzed plant taxon were excluded from further consideration, as far as such information was available (Table 3). The maximum and minimum values of the extracted data were calculated for each parameter and taken as the ecological boundaries of the taxon (Table 4).

The three vegetation parameters considered here are LAI, vegetation cover and greenness. They are given in annual mean values and were taken as indicators of the size of biomass on the land surface (e.g., Wittich, 1997). The vegetation cover and greenness (photosynthesis activity) parameters are given in values between zero (no vegetation) and one (complete vegetation cover and maximum photosynthesis activity, respectively). The LAI as a measure for canopy density gives the ratio of leaf area to per unit ground surface area (e.g., Kraus, 2008; Zheng and Moskal, 2009). In the ECOCLIMAP data set of Masson et al. (2003), the dimensionless variable of LAI ranges from zero (no leaves, i.e. no vegetation) up to 5.7583 in tropical rainforests with a more than five times larger leaf area than ground area, e.g. with a dense multi-storey canopy. By measuring vegetation density, canopy density, and photosynthesis activity, the three parameters considered also give an estimate of the openness of the habitats preferred by the respective taxon.

After determining the requirements concerning openness of habitat for as many taxa of the fossil flora as possible, the application of the  $CA_{eco}$  follows the same procedure as the classical CA. It takes advantage

**Table 2**  
IPR-vegetation analysis: proportions of the components.

Depth, m	Flora	CONIFER	BLD	BLE	SCL	LEG	ZONAL PALM	ARB FERN	D-HERB	M-HERB	BLD prop, %	BLE prop, %	SCL + LEG prop, %	ZONAL HERB prop, %
7.0	PF1	5	6.28	0.45	0.78	0	0	0	2.11	3.36	83.62	5.99	10.39	30.42
8.8	CF1	3	1.5	0.5	0	0	0	0	1	1.7	7.5	25	0	35.06
	PF2	7	6.08	0.25	0.58	0	0	1	0.66	4.91	76.86	3.16	7.33	27.2
9.1	PF3	5	4	0	0	0	0	1	1.66	4.16	80	0	0	36.79
9.5	PF4	5	8.78	0.45	0.78	0	0	1	1.86	5.11	79.75	4.09	7.08	30.33
9.8	PF5	4	7.58	0.25	0.58	0	0	1	1.66	4.16	80.55	2.66	6.16	30.26
11.0	PF6	7	9.53	0.2	0.53	0	0	1	1.86	5.11	84.64	1.78	4.71	27.62
11.3	CF2	6	2.5	0.5	0	0	0	0	1	3.7	83.33	16.67	0	34.31
11.5	PF7	6	5.53	0.2	0.53	0	0	1	2.11	4.61	76.17	2.75	7.3	33.63
11.9	PF8	5	6.58	0.25	0.58	0	0	1	1.66	4.16	78.24	2.97	6.9	30.26
14.0	CF3	5	0.5	0.5	0	0	0	0	2.29	3.99	50	50	0	51.14
	PF9	8	11.78	0.95	1.08	0	0	1	2.11	5.36	79.54	6.41	7.29	24.67
14.4	PF10	6.5	11.28	0.95	1.08	0	0	1	2.11	5.36	78.83	6.64	7.55	26.41
14.8	LF	3.5	10.83	0.33	0	0	0	0	0	0.5	97.04	2.96	0	3.3
	PF11	4.5	9.78	0.45	1.58	0	0	1	2.11	5.36	76.35	3.51	12.33	30.14
15.0	XF	21	10	0	0	0	0	0	0	0	100	0	0	0
15.5	CF4	5	1	0.5	0	0	0	0	1.63	2.83	66.67	33.33	0	40.69
	PF12	6	6.58	0.25	0.58	0	0	1	1.66	4.91	78.24	2.97	6.9	31.31
15.9	PF13	6	4.33	0	0.33	0	0	1	1.66	4.91	76.5	0	5.83	36.04
17.0	PF14	7	9.78	0.95	1.08	0	0	1	2.11	3.36	76.35	7.42	8.43	21.64
17.3	CF5	5	3.5	0	0	0	0	0	2.59	4.89	100	0	0	46.81
17.5	PF15	7	10.28	0.45	1.58	0	0	1	1.86	3.11	77.24	3.38	11.87	19.66
19.0	PF16	6	6.78	0.45	1.08	0	0	1	2.11	3.36	72.82	4.83	11.6	26.32
19.4	CF6	2	10.83	0.5	0.33	0	0	0	4.96	5.96	92.88	4.29	2.83	44.43
	PF17	9.5	12.11	0.78	1.08	0	0	1	2.11	3.36	80.89	5.21	7.21	18.27
19.8	PF18	8.5	8.11	1.28	1.08	0	0	1	2.11	3.36	70.71	11.16	9.41	21.5

of the program ClimStat to calculate the range in which the maximum number of taxa can coexist, independently for each parameter considered. Those coexistence intervals provide a quantitative description of the environmental situation under which the given fossil flora lived.

The method relies strongly on the modern distribution of plants. In addition to uncertainties related to the relatively coarse resolution of the available distribution maps, anthropogenic disturbances add considerable problems and present distributions are not necessarily a reflection of potential vegetation. In addition, anthropogenic disturbances can also affect the remotely sensed data. Irrigation will increase values because it promotes more lush vegetation cover than would occur naturally; forest clearance will reduce values. In any case, the resulting range of the vegetation parameter for a taxon will become wider than under natural conditions, and so will the resulting coexistence intervals. Therefore, the results for vegetation parameters will not be wrong, but simply less distinct. Even with such shortcomings, CA<sub>eco</sub> seems to be an adequate method and, at present, one of the few available to directly quantify vegetation parameters.

## 5. Results

### 5.1. Plant functional types (PFTs)

Palaeovegetation data from the Suifunskaya Formation using the PFT Approach were obtained for 6CFs, one LF and one XF – macrofloras and 18 PFs – microfloras (Appendix Tables 3 and 4, Fig. 3). The number of fossil taxa in a sample is higher than the number of encountered PFTs, therefore we consider our results are meaningful.

The proportion of aquatic plants (PFT 27) varies from 6.1 to 10.8% in the microfloras and from 23.5 to 54.1% of total diversity of the flora in the macrofloras, except for the xyl- and leaf floras, in which the PFT is absent (Fig. 4). After the likelihood procedure, the diversity of herbaceous PFTs in the microfloras varies from 20.2 to 36.5%, in the macrofloras – from 41.2 to 66.7%; shrub PFTs are presented 3.9–22.2 and 5.6–47.6% in the micro- and macrofloras; arboreal PFTs content 44.4–68.5 and 14.1–93.7% in the micro- and macrofloras correspondently. Diversity of the arboreal component (PFTs 12–26)

ranges 44.4–68.5 and 14.1–93.7% in the micro- and macrofloras correspondently (Fig. 4).

Evergreen angiosperm plants are represented mainly in lower part of the section and in very low proportion from 2.1 to 4.8% (Fig. 3). In microfloras the evergreen plants are represented by PFTs 8 and 21 at the depth levels 19.0 and 17.5 m, in macrofloras – by PFT 8 at the depth levels 19.4, 17.3, 14.8, 14.0 and 11.3 m and PFT 7 at the depth levels 15.5 and 8.8 m (Fig. 3). Conifers are represented by PFT 13 at all levels and PFT 17 at almost all levels both in micro- and macrofloras; PFT 15 in microfloras appears at the depth levels 14.8 and 11.9 m, in macrofloras – at the depth levels 17.3, 14.0 and 11.3 m. The PFT 18 is only represented in microfloras at the depth levels 17.5, 14.0 and 11.9 m (Fig. 3).

### 5.2. Integrated plant record (IPR)

To apply IPR-vegetation analysis, all macrofloras (6CFs, one LF and XF) and microfloras (18 PFs) were analyzed (Appendix Table 5). The number of zonal taxa in each macroflora ranged 7.7–31.0 (mean 16.4). The analysis of 16 microfloras was based on 15.8–30.3 (mean 22.7) zonal taxa. Ten zonal taxa are regarded as a minimum to perform this method, therefore a mean number of zonal taxa of 20.8, according to Kovar-Eder et al. (2008), was sufficient for all the floras to yield reliable results, except the CF1 at the depth level of 8.8 m (7.7 zonal taxa only).

The relative proportions of the components are given in Table 2. Based on the relative proportions of the components, two zonal vegetation types and one ecotone between them were revealed for the early Pleistocene of southern Primory'e (Fig. 2).

The first vegetation type is zonal, warm-temperate to subtropical mixed mesophytic forest (= mixed mesophytic forest, MMF), with the following proportions of components: BLD < 75%, BLE < 30%, SCL + LEG < 20% of zonal woody angiosperms. Zonal herbs constitute <30%.

The second vegetation type is zonal, temperate to warm-temperate broad-leaved deciduous forest (= broad-leaved deciduous forest, BLDF). In this type, the BLD component is >80% of the zonal woody angiosperms and the zonal herb component is ≤30%.



**Table 3**  
Sources of information for NLR(s) of fossil wood taxa.

Fossil taxon	NLR(s)	Source of distribution map	Altitudinal range, m	Source of altitudinal range
<i>Abies aff. sachalinensis</i> Fr. Schmidt	<i>Abies sachalinensis</i> Fr. Schmidt	Sokolov et al. (1977)	0–1650	iucnredlist
<i>Abies chavchavadzeae</i> Blokh. et O.V. Bondarenko	<i>Abies magnifica</i> Murr. <i>Abies grandis</i> Lindl.	Little (1971); Sokolov ed., 1949 Little (1971)	1400–2700 0–1800	iucnredlist iucnredlist
<i>Acer aff. tegmentosum</i> Maxim.	<i>Acer tegmentosum</i> Maxim.	Sokolov (1958); Sokolov et al. (1986)	500–1000	wikipedia.de
<i>Betula aff. davurica</i> Pall.	<i>Betula davurica</i> Pall.	Sokolov (1951)	400–1300	eFloras
<i>Laricioxylon aff. chelebaevae</i> Blokh.	<i>Larix lyallii</i> Parl.	Little (1971)	1520–2440	iucnredlist
<i>Laricioxylon aff. korfiense</i> Blokh.	<i>Larix occidentalis</i> Nutt. <i>Larix leptolepis</i> Gord.	Little (1971); Sokolov (1949) Sokolov (1949)	600–2100 500–2900	iucnredlist iucnredlist
<i>Laricioxylon aff. sichotealinense</i> Blokh.	<i>Larix gmelinii</i> (Rupr.) Rupr. <i>Larix sibirica</i> Ledeb.	Sokolov et al., 1977 Sokolov (1949)	300–1800 500–2400	iucnredlist iucnredlist
<i>Laricioxylon blokhinae</i> O.V. Bondarenko	<i>Larix olgensis</i> A. Henry <i>Larix leptolepis</i> Gord.	Sokolov (1949) Sokolov (1949)	400–1800 500–2900	iucnredlist iucnredlist
<i>Laricioxylon pavlovskense</i> Blokh. et Bondar.	<i>Larix occidentalis</i> Nutt. <i>Larix gmelinii</i> (Rupr.) Rupr. <i>Larix olgensis</i> A. Henry	Little, 1971; Sokolov (1949) Sokolov et al., 1977 Sokolov (1949)	600–2100 300–1800 400–1800	iucnredlist iucnredlist iucnredlist
<i>Larix gmelinii</i> (Rupr.) Rupr. foss.	<i>Larix gmelinii</i> (Rupr.) Rupr.	Sokolov et al., 1977	300–1800	iucnredlist
<i>Larix olgensis</i> A. Henry foss.	<i>Larix olgensis</i> A. Henry	Sokolov (1949)	400–1800	iucnredlist
<i>Malus mandshurica</i> (Maxim.) Kom. foss.	<i>Malus mandshurica</i> (Maxim.) Kom.	Sokolov et al. (1980, 1986)	100–2100	eFloras
<i>Microbiota decussate</i> Kom. foss.	<i>Microbiota decussate</i> Kom.	Sokolov (1949)	800–1200	iucnredlist
<i>Micromeles alnifolia</i> (Siebold et Zucc.) Carr. foss.	<i>Micromeles alnifolia</i> (Siebold et Zucc.) Carr.	Sokolov (1954)	500–2300	eFloras
<i>Padus aff. maackii</i> (Rupr.) Kom.	<i>Padus maackii</i> (Rupr.) Kom.	Sokolov (1954)	800–2000	eFloras
<i>Picea jezoensis</i> (Siebold et Zucc.) Carr. foss.	<i>Picea jezoensis</i> (Siebold et Zucc.) Carr.	Sokolov (1949)	0–2700	iucnredlist
<i>Picea koraiensis</i> Nakai foss.	<i>Picea koraiensis</i> Nakai	Sokolov (1949)	400–1800	eFloras
<i>Piceoxylon pavlovskense</i> Blokh. et Bondar.	<i>Picea koraiensis</i> Nakai <i>Picea jezoensis</i> (Siebold et Zucc.) Carr.	Sokolov (1949) Sokolov (1949)	400–1800 0–2700	eFloras iucnredlist
<i>Piceoxylon ussuriense</i> Blokh. et Bondar.	<i>Picea sitchensis</i> (Bong.) Carr. <i>Picea koraiensis</i> Nakai <i>Picea rubens</i> Sarg.	Little (1971) Sokolov (1949) Little (1971); Sokolov (1949)	0–900 400–1800 0–1500	iucnredlist eFloras iucnredlist
<i>Pseudotsugoxylon pavlovskense</i> Blokh. et Bondar.	<i>Pseudotsuga menziesii</i> (Mirb.) Franco <i>Pseudotsuga macrocarpa</i> (Vasey) Mayr	Little (1971) Little (1971)	240–2100 0–3650	Little (1971) Little (1971)
<i>Pyrus ussuriensis</i> Maxim. foss.	<i>Pyrus ussuriensis</i> Maxim.	Sokolov et al. (1980)	0–750	Kharkevich (1996)
<i>Quercus primorica</i> Bondar., Blokh. et Snezhk.	<i>Quercus mongolica</i> Fisch. ex Ledeb. <i>Quercus crispula</i> Blume <i>Quercus dentate</i> Thunb.	Sokolov (1951) Sokolov et al. (1986) Sokolov (1951)	200–2500 0–400 100–2700	eFloras Kharkevich (1991) eFloras
<i>Sambucus</i> sp.	<i>Sambucus coreana</i> (Nakai) Kom. et Aliss. <i>Sambucus racemosa</i> L.	Sokolov et al. (1986) Sokolov et al. (1986)	500–1600 0–2000	eFloras Shishkin (1958)
<i>Ulmus japonica</i> (Rehd.) Sarg. foss.	<i>Ulmus japonica</i> (Rehd.) Sarg.	Sokolov et al. (1977)	0–2300	eFloras
<i>Ulmus laciniata</i> (Trautv.) Mayr foss.	<i>Ulmus laciniata</i> (Trautv.) Mayr	Sokolov (1951)	700–2200	eFloras

### 5.3. Quantification of vegetation density ( $CA_{eco}$ )

Using the  $CA_{eco}$  method, vegetation data were only obtained for the XF from a single depth level 15.0 m within the Suifunskaya section. The results of the quantification of vegetation density with  $CA_{eco}$  based on the fossil wood assemblage are given in Table 4. Based on these data, greenness values 65.0–71.9% and vegetation cover 90.1–95.0% document dense vegetation. The coexistence interval for LAI ranges from 2.4 to 2.9 indicates a forested environment. All data are considerably higher than present day values in the Primory'e region.

## 6. Discussion

### 6.1. Comparison of vegetation data from different organs and methods

The early Pleistocene vegetation of southern Primory'e was reconstructed using different types of fossil plant records and methods. Each type of palaeovegetation proxy has its advantages and limitations.

One main advantage of all three methods applied in the present study is that they can be employed independently for different organ assemblages, i.e., leaves, seeds and fruits, pollen and spores, and potentially wood, thus taking advantage of the complementary information offered by different sources.

The percentage of aquatic plants, as local components, is low and varies weakly in the microfloras, whereas in the carpofloras the percentage of aquatic plants is much higher and varies significantly along

the section. These data agree with lithological and facies data derived from the Suifunskaya Formation (Pavlutkin et al., 1988) and suggest the existence of a broad river system in the deposition area (Pavlovskoe brown coal field) (Pavlutkin et al., 1988; Blokhina and Bondarenko, 2011). The ratio of non-aquatic herb and shrub PFTs to tree diversity provides important information for assessing the openness of the landscape (Popova et al., 2013). The high proportion of arboreal PFTs (44.4–68.5 and 14.1–93.7% in the micro- and macrofloras correspondently) does not indicate open woodland throughout the section.

The PFT analysis has a high ecological resolution, shows the character of changes in the structure of vegetation and allows comparison between the ecospectra of the fossil floras and climatic fluctuations. The allocation of evergreen plants throughout the section coincides with the small-scale temperature variability, with two distinct warm phases at the depth levels 19.4–19.8 and 14.0–14.8 m and a third, less clear, at the depth level 9.1–9.8 m (Fig. 2) reconstructed by Bondarenko et al. (2013). According to the reconstruction provided by Bondarenko et al. (2013), there is no evidence for a significant large-scale temperature trend in the section. The basal part of the middle Pleistocene might have been cooler compared to the Calabrian but here results are based on a single sample only. Nevertheless, the character of changes in the structure of vegetation is not always comparable to the direction and amplitude of climatic fluctuations. The overall decline of precipitation reconstructed for the Calabrian of southern Primory'e (Bondarenko et al., 2013) is not reflected in changes of vegetation structure throughout the section. Drought tolerant PFTs represented by PFTs 2 and 15 in our record reach only minor proportions or occur sporadically, respectively.

**Table 4**

Ranges of vegetation density parameters of NLRs for the studied fossil taxa: GREEN – greenness; LAI – leaf area index; VEGCOV – vegetation cover).

Fossil taxon	GREEN_MIN	GREEN_MAX	LAI_MIN	LAI_MAX	VEGCOV_MIN	VEGCOV_MAX
<i>Abies</i> aff. <i>sachalinensis</i> Fr. Schmidt	0.2818	0.7719	0.7321	3.2167	0.6929	0.9500
<i>Abies</i> <i>chavchavadzeae</i> Blokh. et O.V. Bondarenko	0.2403	0.9198	0.6050	5.3239	0.4524	0.9675
<i>Acer</i> aff. <i>tegmentosum</i> Maxim.	0.3893	0.7719	1.1793	3.2167	0.5594	0.9500
<i>Betula</i> aff. <i>davurica</i> Pall.	0.1067	0.7719	0.2256	3.2167	0.2650	0.9500
<i>Laricioxylon</i> aff. <i>chelebaevae</i> Blokh.	0.2824	0.7710	0.7204	3.2111	0.6700	0.9500
<i>Laricioxylon</i> aff. <i>korfiense</i> Blokh.	0.1957	0.8780	0.4870	4.3268	0.3526	0.9500
<i>Laricioxylon</i> aff. <i>sichotealinense</i> Blokh.	0.0002	0.7719	0.0005	3.2167	0.0005	0.9500
<i>Laricioxylon</i> <i>blokhinae</i> O.V. Bondarenko	0.5519	0.8780	1.9031	4.3268	0.7503	0.9500
<i>Laricioxylon</i> <i>pavlovskiensis</i> Blokh. et Bondar.	0.0002	0.7719	0.0005	3.2167	0.0005	0.9500
<i>Larix</i> <i>gmelinii</i> (Rupr.) Rupr. Foss.	0.0002	0.7719	0.0005	3.2167	0.0005	0.9500
<i>Larix</i> <i>olgensis</i> A. Henry foss.	0.6315	0.7191	2.4016	2.9200	0.8245	0.9500
<i>Malus</i> <i>mandshurica</i> (Maxim.) Kom. foss.	0.2818	0.7431	0.7321	3.0531	0.6801	0.9500
<i>Microbiota</i> <i>decussata</i> Kom. foss.	0.6496	0.7635	2.4463	3.1627	0.9010	0.9500
<i>Micromeles</i> <i>alnifolia</i> (Siebold et Zucc.) Carr. foss.	0.4013	0.8609	1.1208	4.1506	0.5594	0.9500
<i>Padus</i> aff. <i>maackii</i> (Rupr.) Kom.	0.4426	0.7719	1.2646	3.2167	0.5959	0.9500
<i>Picea</i> <i>jezoensis</i> (Siebold et Zucc.) Carr. foss.	0.0047	0.7719	0.0122	3.2167	0.0148	0.9500
<i>Picea</i> <i>koraiensis</i> Nakai foss.	0.3893	0.7719	1.1793	3.2167	0.5594	0.9500
<i>Piceoxylon</i> <i>pavlovskiensis</i> Blokh. et Bondar.	0.0015	0.9345	0.0032	5.4750	0.0036	0.9500
<i>Piceoxylon</i> <i>ussuriense</i> Blokh. et Bondar.	0.2583	0.7719	0.7511	3.2167	0.3915	0.9500
<i>Pseudotsugoxylon</i> <i>pavlovskiensis</i> Blokh. et Bondar.	0.0463	0.9387	0.1228	5.4750	0.1097	0.9750
<i>Pyrus</i> <i>ussuriensis</i> Maxim. foss.	0.4357	0.7641	1.3999	3.1719	0.5576	0.9500
<i>Quercus</i> <i>primorica</i> Bondar., Blokh. et Snezhk.	0.0938	0.9786	0.1968	5.2424	0.2337	0.9798
<i>Sambucus</i> sp.	0.4524	0.7501	1.3552	2.9041	0.5261	0.9500
<i>Ulmus</i> <i>japonica</i> (Rehd.) Sarg. foss.	0.2818	0.7663	0.7321	3.1844	0.5566	0.9500
<i>Ulmus</i> <i>laciniata</i> (Trautv.) Mayr foss.	0.0004	0.7719	0.0008	3.2167	0.0010	0.9500
Coexistence intervals	0.6496	0.7191	2.4463	2.9041	0.9010	0.9500
Modern values in Primorskii Region	0.2177	0.4195	0.5154	1.0416	0.5857	0.9500

This indicates that in the Calabrian, southern Primory'e had no distinct dry seasons, even during the cooler and drier glacial phases.

As regards the small-scale temperature variability in the Suifunskaya section PFT spectra indicate that the diversities of plants making up herbaceous undergrowth and shrub layer correlate best with the Calabrian climate cycles reconstructed by Bondarenko et al. (2013): high proportions of these components coincide with two distinct warm phases at depth levels 19.4–19.8 and 14.0–14.8 m. Obviously, warm and very humid conditions of the interglacials had a favourable impact on the diversity on the understory plants.

Zonal vegetation is best represented by the microfloras (Krassilov, 1972). With a zonal herb proportion in our microfloras ranging from 18.3 to 36.8% a close forest cover seems likely throughout the Calabrian in the Primory'e region. In the early Pleistocene, the topography of the area was pronounced with wide plains lying in between hills (Denisov, 1965; Lebedeva, 1956, 1957). This agrees with lithological and facies data derived from the Suifunskaya Formation and characteristics associated with the buried plant remains given in Pavlutkin et al. (1988). Moreover, rivers and winds brought pollen partly from higher altitudes of the Sikhote-Alin Range area. All the spectra based on the microflora point to a mixed deciduous conifer forest with a temperate to warm temperate character and a diverse, mainly deciduous, undergrowth. Conifers are mainly represented by PFT 13 (needleleaved evergreen temperate cool trees, in the present materials mainly Pinaceae), and a provenance (at least in part) from elevated areas cannot be excluded. Broadleaved evergreen PFTs are represented in the primary PFT dataset for most of the low diversity samples but are excluded from most of the levels when applying the PFT coexistence table (see above). Hence, the PFT approach does not suggest the existence of MMF vegetation in the study area throughout the late Calabrian.

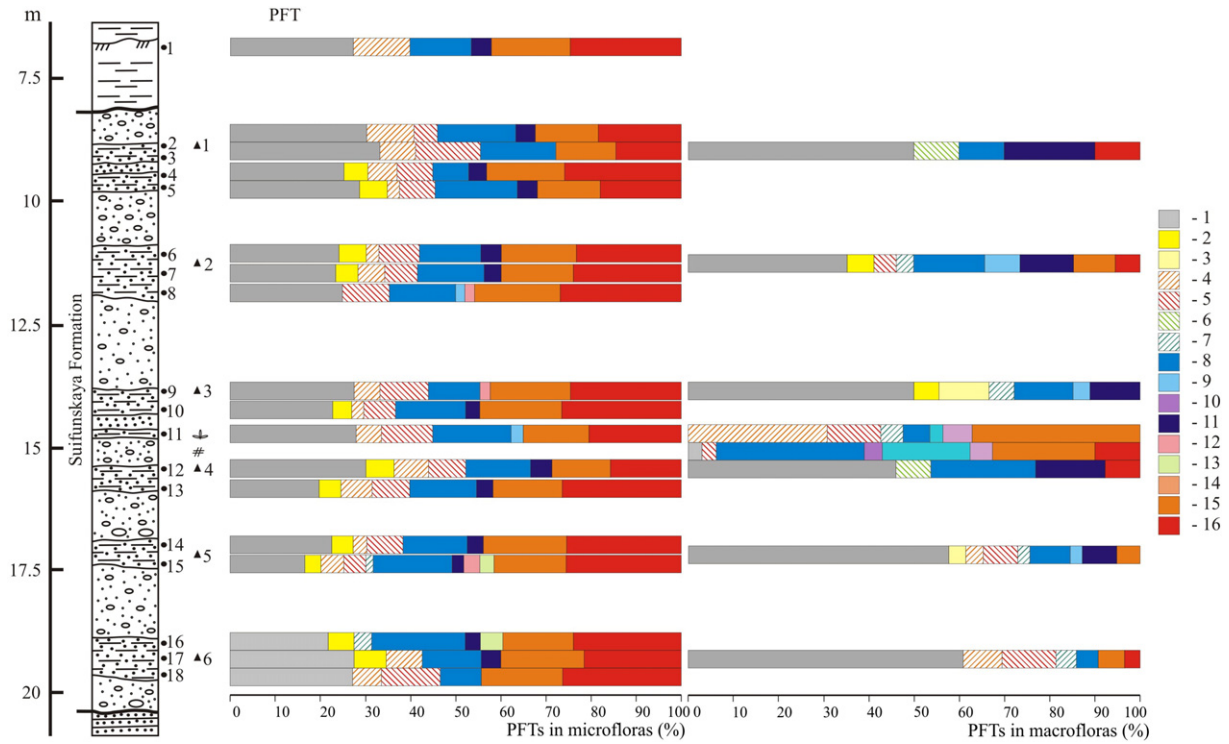
The levels with PFT spectra from multiple plant organ types provide an insight into how PFT richness in each case is represented and the same time underline the importance of a multiproxy record for a complete reconstruction. The leaf record best resolves local arboreal vegetation, which probably represents a riparian margin type of temperate character including mainly PFTs 5 and 25 and includes thermophilous needleleaved summergreen swamp trees (PFT 18). In the XF, conifer PFTs dominate the spectrum, especially PFT 13 has a high diversity,

possibly pointing to (partial) allocation and transport of the logs to the site of deposition by a watercourse over some distance (200–300 km) from somewhere in the nearest spurs of the southern Sikhote-Alin Range as suggested by Blokhina and Bondarenko (2011). Moreover, according to the climate analysis (Bondarenko et al., 2013), the wood assemblage represents a cooler climate, probably existing at a higher altitude. The CFs tend to reflect local vegetation (Krassilov, 1972) and their spectra display the highest proportions of zonal herbs when compared to the other organ types (34.3–51.1%). The fact that most of the zonal herbs belong to the mesic PFT 1 may point to a permanently humid habitat for most of these components and not to xeric, open vegetation types when taking into account the spectra of the coeval microfloras. When compared to the microfloras, the carpofloras of our record better represent the diversity of conifer PFTs. Moreover, the only evidence for PFT 7, broadleaved evergreen boreal/temperate cold shrubs, here represented by Ericaceae, is obtained from 2 carpofloras, recorded in a glacial phase depth levels 15.5 and 8.8 m.

IPR-vegetation analysis has a coarser ecological resolution in comparison to the PFT approach but facilitates observing major biome changes. Unlike in the PFT approach where the presence of the BLE component (represented by the thermophilous PFTs 19, 20, 26) is considered unlikely for most of the levels (see above), IPR vegetation analysis is based on the total score obtained for BLE, thus including also cases where taxa cannot be clearly allocated to BLE or BLD, respectively. Hence, IPR vegetation analysis reveals BLDF/MMF and MMF vegetation types for the majority of studied levels and suggests an overall warmer aspect of the vegetation in the late Calabrian when compared to the PFT approach.

Warm phases of the Calabrian climate (at depth levels 19.4–19.8, 14.0–14.8 and 9.1–9.8 m) are mainly characterized mainly by MMF and BLDF/MMF, whereas in the cooler, drier phases and towards the top of the section, MMFs disappear. This gradual change of vegetation type through the section with MMF more frequently encountered in the lower part and the dominance of BLDF towards the top correlates with the overall cooling trend expressed in the isotope record (Fig. 2). With zonal herb proportions ranging from 18.3 to 36.8% in the microfloras no open woodland is reconstructed throughout the section using the IPR-vegetation analysis.

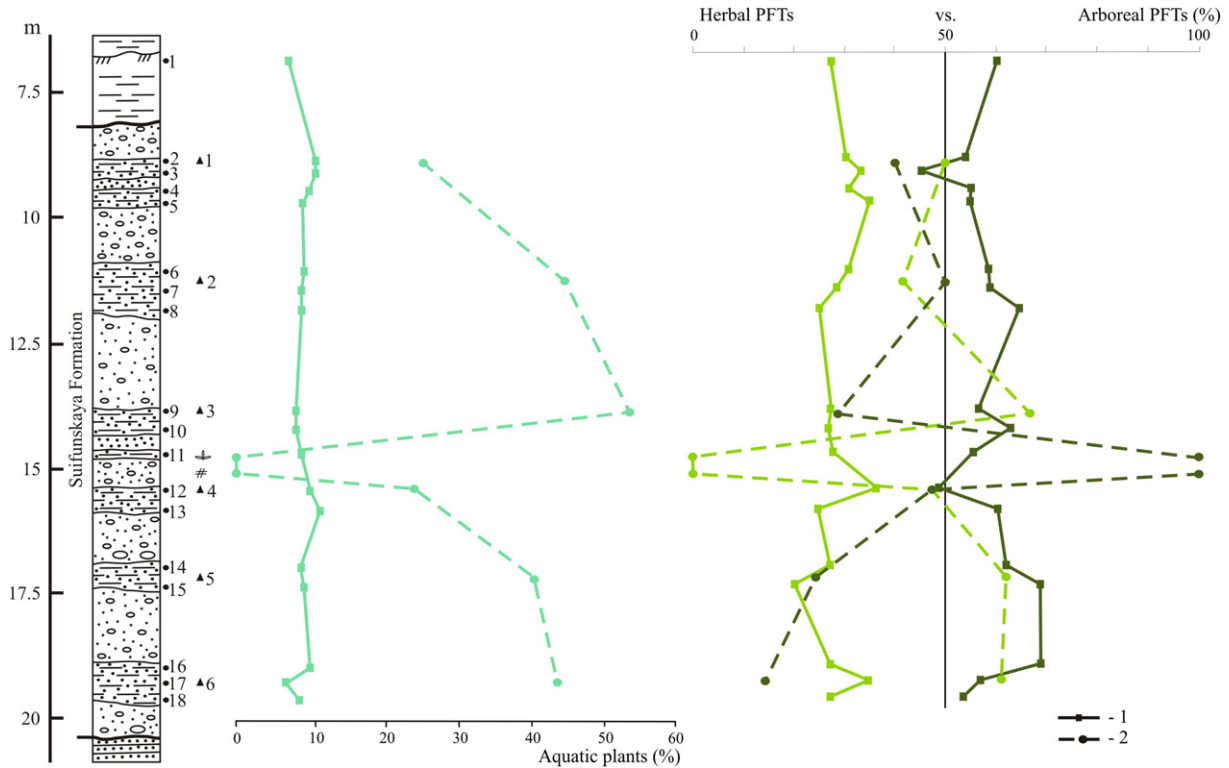




**Fig. 3.** Lithological profile of the Suifunskaya Formation and correlation with PFT diversity spectra after likelihood procedure: 1 – PFT 1; 2 – PFT 2; 3 – PFT 3; 4 – PFT 5; 5 – PFT 6; 6 – PFT 7; 7 – PFT 8; 8 – PFT 13; 9 – PFT 15; 10 – PFT 16; 11 – PFT 17; 12 – PFT 18; 13 – PFT 21; 14 – PFT 22; 15 – PFT 23; 16 – PFT 24.

The CA<sub>eco</sub> method was employed for the XF only to test the potential to estimate vegetation density based on parameters of palaeo-values for vegetation cover, photosynthesis activity and LAI. Compared to modern data from the area all three parameters show significantly higher palaeo-values for vegetation cover, photosynthesis activity and LAI. This documents a distinctly higher vegetation density at the time of

deposition of the XF, similar to more coastal regions today. Although the quantification of vegetation density based on fossil wood is biased towards tree and shrub taxa and may overestimate vegetation cover, earlier climate reconstructions based on this material showed warmer and wetter conditions than today (Bondarenko et al., 2013), which is in good accordance with a generally higher vegetation density.



**Fig. 4.** Proportion of aquatic, herbal and arboreal PFTs: 1 – microfloras; 2 – macrofloras.

## 6.2. 6.2. Comparison with modern vegetation of southern Primory'e

The modern vegetation of the Khanka Plain consists of xerophytic and mesophytic types (forest, wooded steppe, steppe, meadow, and swamp), which are in contact and form complex combinations (Kurentsova, 1962, 1968; Korotkii, 2002). However, steppe vegetation groups are less common. They are represented by small areas of meadow and mountain steppes that are preserved among farmlands and on steep, south-facing slopes of the hills (Korotkii, 2002). With the economic development of the Khanka Plain, meadow steppes were the first to be subjected to radical transformation resulting from plowing and cattle grazing. Therefore, today they do not play a significant role in the composition of vegetation in Primory'e (Kurentsova, 1973; Korotkii, 2002).

Our palaeobotanical data indicate the presence of more forested conditions within the studied territory during the early Pleistocene than at present and show no xeric, open woodland throughout the section (Figs. 2, 4). This might point to the fact that the xerophytic vegetation within the Khanka Plain appeared after the Calabrian and probably was caused by a decline of precipitation, especially in dry seasons. According to our reconstruction (Bondarenko et al., 2013), the climate of the southern Primory'e was significantly warmer and wetter in Calabrian time compared to the present.

The vegetation history of Primory'e in the Pleistocene and Holocene has been discussed in the works of Korotkii et al. (1980, 1996), and Golubeva and Karaulova (1983). They also demonstrated the presence of more forested conditions and no xeric, open vegetation: a progressive impoverishment of the polydominant broad-leaved forests during the Pleistocene, a gradual replacement of *Betula-Ulmus* forests by broad-leaved forests in the early Holocene, and then by mixed coniferous broad-leaved forests of the present type.

Palynological studies of cultural layers of ancient settlements in southern Primory'e might point to the fact that the xerophytic vegetation within the Khanka Plain appeared in more recent times. Based on these studies, several phases of steppe formation during the last 6000 years were revealed by Verkhovskaya and Esipenko (1993), and Verkhovskaya and Kundyshev (1993). According to these authors, the wooded steppes with dominating of *Betula* became widespread in southern Primory'e at least twice. According to Verkhovskaya (1990, 1997), the first phase of steppification occurred around 5000 BCE, followed by an expansion of forests culminating at 2500 BCE. A second phase of steppe formation ended near 800–900 BCE. According to archaeological data (Andreev, 1960; Vostretsov, 1996), the appearance of ancient people in southern Primory'e coincides with these steppification phases.

## 7. Conclusions

Calabrian vegetation of southern Primory'e, as reconstructed using multiple proxies, was denser than seen today. All data indicate the presence of more forested conditions and do not indicate open woodland throughout the section. The appearance of xerophytic vegetation within the Khanka Plain probably was caused by a reduction of precipitation after the Calabrian, especially in dry seasons. The changes of vegetation types generally relate to cooling/drying trends of the climate.

Our vegetation analysis is consistent with climate evolution and cyclicity previously reconstructed for the late Calabrian. Both, the PFT approach and IPR vegetation analysis do not reflect any substantial vegetation changes throughout the glacial/interglacial cycles in the late Calabrian of Southern Primory'e. PFT spectra from multiple plant organ types provide insights into how PFT richness in each case is represented, and underline the importance of a multiproxy record for a more complete reconstruction. Using the PFT technique pollen floras are considered most suitable to resolve the character of zonal vegetation. The likelihood analysis performed here is useful to remove non-representative data, but this procedure also tends to underestimate the

biodiversity of the palaeoflora by suppressing most of the cold or tropical PFTs. Biomes obtained from IPR vegetation analysis generally are in good agreement with the reconstructed climate evolution throughout the section but the resulting types may be biased towards too high an estimate of BLE components. Though only available for a single flora LAI data obtained with  $CA_{eco}$  are consistent with the results from the other approaches of vegetation reconstruction and provides an independent, complementary estimate of landscape openness.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.09.017>.

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