VILNIUS UNIVERSITY

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DEVELOPMENT OF THE LATE GLACIAL AND HOLOCENE FOREST VEGETATION IN LITHUANIA, ACCORDING TO LRA (LANDSCAPE RECONSTRUCTION ALGORITHM) MODELLING DATA

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VILNIAUS UNIVERSITETAS

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VĖLYVOJO LEDYNMEČIO IR HOLOCENO MIŠKŲ AUGALIJOS RAIDA LIETUVOJE LRA (KRAŠTOVAIZDŽIO ATKŪRIMO ALGORITMO) MODELIAVIMO DUOMENIMIS

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INTRODUCTION

Pollen data is used for the reconstruction of vegetation of various geological periods from the birth of pollen analysis (von Post, 1916). It is one of the most widely used methods in Late Glacial and Holocene palaeoecology, as well as one of the most informative (Lowe, Walker, 1997). Plants produce pollen in extremely high amounts, and pollen is dispersed over a vast territory – up to thousands of kilometers from it‘s source. Furthermore, pollen is very well preserved in bog and lake sediments, where it can remain for thousands of years (Moore et al., 1991). Thus, by analyzing fossil pollen spectra, information on the past vegetation can be acquired.

Characteristics of the study object. Despite popularity of pollen analysis, reconstruction of past vegetation from pollen data presents a complicated task. The assumption that a pollen spectrum (pollen composition of one sample) unambiguously represents past vegetation, can not be followed when interpreting pollen data. The relationship between pollen and vegetation is not linear, and pollen composition differs from past vegetation composition because of number of reasons. One of the most important factors, influencing this difference, is difference in pollen productivity between different taxa (Andersen, 1970; Кабайлене, 1973; Sugita, 1994). Some taxa produce more pollen, while others produce less. For instance, insect-polinated plants tend to produce less pollen than wind-polinated plants (Faegri, Iversen, 1989). Preservation properties of pollen differ as well – aspen, ash, mapple are not so well preserved taxa (Moore et al., 1991). Another important factor is distance from pollen source. Evidently, the farther from the from the deposition site is a pollen producing plant, the less infuence pollen of that plant will have on pollen spectra in the deposition site. Therefore, it is often difficult to determine, whether a pollen spectrum is influenced by low quantity of plants growing in the distinct vicinity, or by large quantity of plants away from the deposition site. Such factors as plant age, growing conditions, pollen weight, morphology, mechanical properties, deposition speed, prevailing wind directions and turbulence, basin size influence pollen spectra as well (Jacobsen, Bradshaw, 1981; Кабайлене, 1973; Kabailienė, 1990; Sugita, 1994).

The quality of pollen data interpretation, and consequently, the quality of vegetation reconstruction, depends on precise determination of the relationship between vegetation in the vicinity of deposition site, and the corresponding pollen spectra. This complex relationship, in the beginning determined only intuitively (e.g., Firbas, 1934; Iversen, 1941; Faegri, Ottestad, 1948), started to be defined mathematically in the second half of 20th century. As numerical methods and information technology improved, increasingly sophisticated pollen-vegetation relationship models were being developed (Davis, 1963; Andersen, 1970; Кабайлене, 1969; 1973; Prentice, 1985; Sugita, 1994; Sugita et al., 1999). These models enabled increasingly precise vegetation reconstructions (Kabailienė, 1985; Bunting, 2003; Nielsen, 2003; Nielsen, Odgaard, 2005; Gaillard et al., 2010 ir t.t.).

The demand for detail past vegetation reconstructions constantly increases (Moore et al., 1991). However, most of investigations are still aimed at reconstruction of regional vegetation. Detail investigations are usually limited by the lack of pollen data and shortcomings of data processing methodology. These problems can be solved by using GIS on the accordingly created extensive pollen databases. GIS allows processing extensive amounts of spatial data, carry out spatial analysis, mathematical and statistical calculations, interpolation, as well as automating workflows and hence significantly increasing productivity (Maguire et al., 2005; Harder et al., 2011; Krivoruchko, 2011).

GIS is a relatively new technology, becoming increasingly important in various scientific disciplines. Despite of the significant potential, however, it is rarely applied in pollen studies. Mostly, GIS is used for mapping purposes, e.g. creation of isopollen or palaeovegetation maps (Hooghiemstra et al., 1987; Ren, Beug, 1999; Ralska-Jasiewiczowa et al., 2004 ir kt.). Potential of GIS analysis is only starting to be applied for pollen-vegetation relationship studies, but there are only a few attempts so far (Fyfe, 2006; Flantua et al., 2007). This study employs not only GIS possibilities of vizualization and analysis, but advantages of automated calculations as well, hence enabling high precision and detail of past vegetation reconstruction.

Practical significance of the study. Detail results of the Late Glacial and Holocene vegetation reconstruction in the territory of Lithuania are presented in this thesis. These results provide an important context for future paleogeographical and archaeological investigations in Lithuania. Lithuanian pollen database, successfully employed in this study, was designed to allow scalability, in terms of the amount and variety of stored information. Design of the database also enables other modern applications of data management, interpretation and precise (quantitative) modelling, that can be involved on demand in the future.

The aim of the study was precise and detail reconstruction of the Late Glacial and Holocene forest composition (most significant tree taxa), as well as it‘s changes in the territory of Lithuania, involving existing pollen-vegetation relationship models and advantages of GIS.

Study goals were the following:

1. Supplementing available Late Glacial and Holocene pollen data in Lithuania with the investigated sediment sequences from new cores.

2. Creating pollen database, that includes core and outcrop pollen data, corresponding Late Glacial and Holocene.

3. Creating isopollen maps for different periods of Late Glacial and Holocene in Lithuania.

4. Evaluating the effectiveness of the most widely used pollen-vegetation relationship models in the environment of Lithuania.

5. Reconstructing forest composition of Late Glacial and Holocene in Lithuania and determination of the most important tree migration patterns, using the acquired pollen data and the selected pollen-vegetation relationship function.

6. Creating palaeovegetation maps for the main tree taxa during different periods of Late Glacial and Holocene in Lithuania.

Defended highlights:

1. Application of GIS database along with automated GIS analysis and pollen-vegetation relationship functions enables detail reconstructions of past vegetation.

2. Simulation of pollen assemblages in the environment of Lithuania, according to different pollen-vegetation relationship functions showed that the most precise results are achieved using functions, developed by I. C. Prentice (1985, 1988) and S. Sugita (1993, 1994). Therefore, LRA (Landscape Reconstruction Algorithm; Sugita, 2007a; 2007b) model, which is based on the above mentioned pollen-vegetation relationship functions, is the most suitable for the reconstruction of past vegetation reconstructions in Lithuania.

3. Compiled isopollen maps correlate with the results of similar studies in neighbouring countries. Therefore, the created pollen database is suitable for past vegetation modelling.

4. Compiled palaeovegetation maps show differences in taxa composition in different parts of the territory of Lithuania. These differences are determined by climate change, plant migration and distribution of Quaternary sediments.

5. During the colder periods of the Late Glacial, as well as beginning of the Holocene, pioneer vegetation (birch) was more abundant in the northern part of Lithuania. When vegetation cover formed completely, it‘s differentiation was primarily determined by distribution of Quaternary sediments. In the second part of the Holocene, when human impact became increasingly intense, it eventually became dominant factor, influencing vegetation distribution.

Originality of work:

Five new pollen sequences are presented in this thesis. Relational pollen database has been created using GIS technology along with programming of spatial data management tools, which enabled considerable detalization of known information on Late Glacial and Holocene vegetation in Lithuania. The results of past vegetation reconstructions are presented as palaeovegetation maps, showing quantitative distribution of vegetation in the area.

Approbation of results:

Since 2000, when author has published first results of his work, presentations related to current study were given in five scientific conferences (in Lithuania, Poland, Estonia, Greece and Switzerland). Six publications were published individually or with co-authors, two of which published in *ISI Web of Science* journals.

Structure of the thesis:

The thesis consists of the introduction, four chapters, conclusions, reference list (244 references), and authors publication list (6 publications). Overall, there are 282 pages of the text, 127 figures and 15 tables.

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1. QUANTITATIVE RECOSTRUCTIONS OF PAST VEGETATION, ACCORDING TO POLLEN DATA

During the first decades after appearance of pollen analysis, knowledge of the relationship between pollen and vegetation has been rather superficial. However, pollen dispersal has been researched intensively during this period (Pohl, 1933; 1937; Rempe, 1937; Colwell, 1951; Wright, 1952).

An important improvement of pollen dispersal studies was facilitated by O. G. Sutton‘s (1953) work, where characteristics of solid particle movement in the air were defined. Sutton‘s formula was used in later studies to model pollen dispersal (Кабайлене, 1969; 1973; Prentice, 1985; Sugita, 1994; Sugita et al., 1999 et al.).

Another aspect, important for the interpretation of pollen data, was found by F. Fagerlind (1952). Essentially it was determined that pollen quantities described in percentages depend not only from vegetation and pollen dispersal, but on abundancy of other taxa as well. This issue, called “Fagerlind effect“, presented a challenge for pollen dispersal research, especially for quantitative vegetation reconstructions (Moore et al., 1991). Nowadays, this problem is largely solved by using Extended R-value (ERV) models.

First quantitative methods of vegetation reconstruction appeared in the second part of 20th century. M. B. Davis (1963) became a founder of pollen-vegetation relationship functions by describing R-value as:

$$R = P \cdot v$$

(where R – function, describing relationship between pollen and vegetation; P – pollen productivity; v – vegetation abundance). It has been argued later (Sugita, 1994), that this model is too simplified and it‘s significance is rather theoretical than practical.

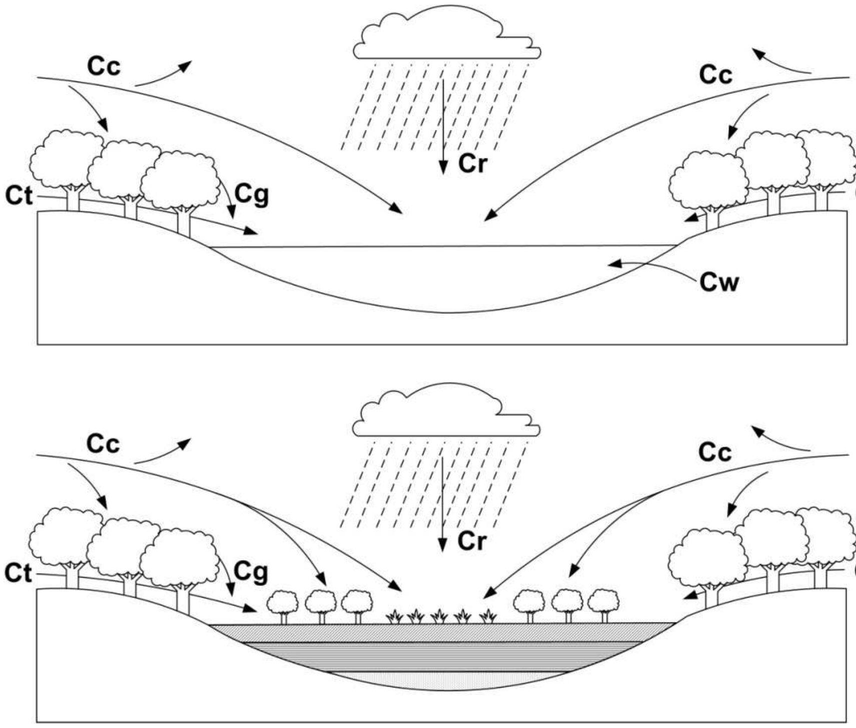


Fig 1. *Pollen source components in a small forest opening (according to Moore et al., 1991). Cc – canopy component; Cg – gravitational component; Cr – rain component; Ct – trunk space component; Cw – secondary component.*

H. Tauber (1965) presented model, showing different types of pollen source components for the site, located in the forest opening (Fig. 1). This model provided better knowledge of different ways of pollen dispersal and transport.

Another Danish scientist, S. T. Andersen (1970), investigated surface pollen in forest openings and compared them to the surrounding forest composition. He described pollen-vegetation relationship as productivity factor (P – pollen productivity of taxon; p – pollen abundance; a – vegetation abundance):

$$P = \frac{p}{a}$$

He also distinguished local and regional components (p_0 – background pollen):

$$P = \frac{p - p_0}{a}$$

An important step in researching pollen dispersal were investigations, carried out by M. Kabailienė (Кабайлене, 1969; 1973). She has modified Andersen‘s model into an Effective Productivity Model (EPM), which also evaluated pollen transport from the source to the site. This model was based on evaluation of vegetation within concentric rings around the site (Q – relational pollen productivity; S – vegetation proportion; ΔF(x) – pollen dispersal function):

$$Q = \sum_{0}^{\infty} S \cdot \Delta F(x)$$

Jacobsen and Bradshaw (1981) noted an importance of the size of investigated basin (Fig. 2), as one of the factors, influencing pollen-vegetation relationship. They determined, that for the basin of up to 100 m in size, most pollen is local. For 100-200 m sized basins – most pollen is extralocal, and in basins larger than 200 m, most pollen is regional.

The vast majority of fossil pollen records are represented in percentages. Due to the Fagerlind (1952) effect, it is difficult to interpret such data. To solve problems, caused by Fagerling effect, Extended R-value (ERV) models were developed. This approach is based on iterational solving of simultateous equations. ERV1 model (Parsons, Prentice, 1981) linearizes a non-linear proportional dataset, by making an assumption, that background pollen value is constant. ERV2 (Prentice, Parsons, 1983) model assumes that background component of a taxon is constant, compared to total abundance of a taxon. In ERV3 model (Sugita, 1994) it is assumed that pollen data is represented in proportions, and vegetation data – in absolute numbers. ERV models are being successfully applied until nowadays (Nielsen, Odgaard, 2005; Gaillard et al., 2008a; 2008b; Soepboer, Lotter, 2009; Gaillard et al., 2010 ir kt.).

In the light of earlier investigations, new pollen-vegetation relationship model was created (Prentice, 1985, 1988). This model also evaluates basin size. It describes abundance of pollen deposited in the center of the lake as ($y_{i,k}$ – pollen of taxon i, deposited at site k; P_i – pollen productivity of taxon i; R – basin radius; Z_{max} – distance, from which most of pollen comes; $x_{i,k}$ – abundance of vegetation of taxon i at distance z from the site; $g_i(z)$ – pollen dispersal finction):

$$y_{i,k} = P_i \cdot \int_R^{Z_{max}} x_{i,k}(z) \cdot g_i(z) \cdot dz$$

Pollen dispersal function is described as (γ – constant):

$$g_i(z) = \ b_i \cdot \gamma \cdot z^{\gamma-1} \cdot e^{-b_i \cdot z^{\gamma}}$$

b_i is determined ($v_{g,i}$ – pollen deposition speed; n, c_z, u – constant):

$$b_i \equiv \frac{4 \cdot v_{g,i}}{n \cdot \sqrt{\pi} \cdot c_z \cdot u}$$

Prentice’s model assumptions are the following: 1) dominant pollen transportation factors are wind above the canopy and gravitation beneath the canopy; 2) investigated basin is a circular opening in the canopy; 3) wind distribution in all directions is even. Despite the assumptions, which can not be completely fulfilled in the real environment, model is considered reliable as vegetation reconstruction tool in bog environment. This model was improved by S. Sugita (1993, 1994), so it would not only evaluate deposition in the center of the lake, but in all the basin area. For this reason it is recommended to be used in lake sediments.

Differences in canopy structure between continuous forest and open or semi-open territories can be related to differences in air turbulence, that affects pollen dispersal and deposition (Sugita et al., 1998). For this reason, models representing forest patchiness were developed – Fininte line source (FLS; Sugita et al., 1998) and Ring Source (RS; Sugita et al., 1999) models. Fundamental equations of these models are identical to those of Prentice’s model, though they use different pollen dispersal-deposition functions. Dispersal-deposition function of the RS model is the following (Cy, Cz - constant):

$$g_i(z) \equiv \left[\int_{z-R}^{z+R} \int_{-\sqrt{R^2-(x-z)^2}}^{\sqrt{R^2-(x-z)^2}} \int_{0}^{x} \frac{2 \cdot v_{g,i}}{\pi C_y C_z u (x-x^*)^{2-n}} e^{\frac{4 \cdot v_{g,i} \cdot (x-x^*)^{n/2}}{n \cdot u \cdot C_z \cdot \sqrt{\pi}}} e^{\frac{(y-\sqrt{x^* \cdot (2z-x^*)^2})}{{C_y}^2 \cdot (x-x^*)^{2-n}}} dx^* \cdot dy \cdot dx \right]$$

In the recent years, many studies related to pollen-vegetation relationship modelling, as well as reconstruction of past vegetation according to these models was carried out as part of POLLANDCAL and LANDCLIM 10000 projects. POLLANDCAL (2001-2005 m.) was aimed at the development and application of the new tools for the reconstruction of past vegetation (Middleton, Bunting, 2004; Bunting, Middleton, 2005; Sugita, 2007a; 2007b; Sugita et al., 2010), as well as landscape reconstructions (Nielsen, 2003; Nielsen, Odgaard, 2005; Sjörgen, 2006; Soepboer et al., 2008, ir kt.). LANDCLIM 10000 (2009-2011) was aimed at pollen-climate-landscape calibration, as well as small scale vegetation and landscape reconstruction in Europe during 10 000 – 6 000 BP (Kuneš et al., 2009; Gaillard et al., 2010; Mazier et al., 2010; Trondman et al., 2010). Similar study is carried out in this project, only higher detail and precision are emphasized in the present study.

2. MATERIALS AND METHODS

Four sediment cores were acquired for the purposes of this study, one sediment sequence (Dubičiai) sampled directly from the outcrop. Coring of sediments was carried out using Russian corer, taking sediments from two paralel cores. In addition, 17 surface pollen samples were collected. Largest part of surface samples was taken from lake surface sediments. Top 1 cm of sediment was extracted using gravity sampler from the approximate center of the lake. Part of surface samples were taken from moss polsters (according to methodology described by Moore et al., 1991), and one sample – using Tauber traps (1974) from pollen monitoring site.

Laboratory preparation of pollen samples followed standard procedure (Гричюк, 1940; Erdtman, 1936). Known quantity of *Lycopodium* marker spores

(Stockmarr, 1971) was added to each sample during preparation in order to assess pollen concentration. Number of terrestrial pollen counted was 1000 or 500 in every sample. Identification was based on pollen key (Moore et al., 1991) and reference slides of the Department of Geology and Mineralogy, Vilnius University. Pollen diagrams were created using *TILIA* and *TILIA Graph* programmes (Grimm, 1990, 1992). Stratigraphic cluster analyses (*CONISS*; Grimm, 1987) was involved in grouping local pollen assemblage zones. Pollen sums were calculated accoring to the methodology presented by B. Berglund ir M. Ralska-Jasiewiczowa (1986). Human impact in pollen diagrams was evaluated by distinguishing groups of indicator taxa (Behre, 1981; 1986; Berglund, Ralska-Jasiewiczowa, 1986).

Radiocarbon dating of sediments was carried out in Nature Research Centre, Institute of Geology and Geography. 7 sedment samples were dated from Dubičiai outcrop, 5 – from Kaciušiai core, 4 – from Perūnas core, and 18 from Amalvas core. Samples for dating were prepared with acid-alkaline-adid method. ^{14}C activity was determined by liquid scintillation counting method (Gupta, Polach, 1985; Арсланов, 1985; Kovaliukh, skripkin, 1994). *Oxcal v3.10* (Bronk Ramsey, 2001) programme has been used for calibration, along with *IntCal09* dataset (Reimer et al., 2009).

Pollen database was created using *ArcGIS Desktop 10.0* (*ArcEditor, Student License*) with *3D Analyst* and *Spatial Analyst* extensions (resources.arcgis.com). ESRI file geodatabase format has been chosen to store data – pollen counts, site metadata, radiocarbon dates, lithological descriptions, scanned pollen diagrams and references. The core of geodatabase is comprised of sites feature class (storing geographic location and metainformation of the investigated sites), three related tables (for storing counts, references and lithological descriptions), as well as scanned diagrams and publications, stored in the file system, and accessable from geodatabase via hyperlinks. Original pollen counts in their primary form are also stored outside geodatabase in *CSV* format.

During data input to the pollen database, site locations were determined from site descriptions or coordinates, provided in litterature. *CSV* files of pollen counts, reference list and lithological descriptions were created manually from manuscript counts or acquired from authors in digital form and loaded into geodatabase using *Python* scripts, created specifically for this purpose. All pollen counts were converted to percentages prior to loading.

Creation of isopollen maps was carried out from pollen database using *ArcGIS* geoprocessing models (Fig. 2) and *Python* scripts. Samples and taxa, corresponding requirements of the reconstruction were filtered from the main dataset, age information was calculated for each sample, and theoretical pollen assemblages were interpolated for the set of investigated time-windows of the Late Glacial and Holocene: 14 700 cal. BP, 14 000 cal. BP, 13 300 cal. BP, 12 100 cal. BP, 10 800 cal. BP, 9 500 cal. BP, 8 000 cal. BP, 6 500 cal. BP, 5 300 cal. BP, 3 300 cal. BP, 1 800 cal. BP and 500 cal. BP.

Modern vegetation maps were also created to carry out simulations of surface pollen spectra and compare them to the palynologically analyzed sample dataset. Vegetation maps were based on Forest Cadastre Integrated Information System (FCIIS) data, provided by National Forest Survey of Lithuania. Provided data contained forest parcel geography (more than a million parcels across Lithuania), and descriptive data, stored in related tables. Since the descriptive tables contained information about vegetation composition, it enabled creation of raster percentage maps for the main tree species of Lithuania. Raster grids were created with 10 m cellsize, however generalized versions of 100 m and 1000 m cellsize were used as well to facilitate further calculations. Creation of modern vegetation maps was carried out using *ArcGIS* geoprocessing models.

Pollen spectra were theoretically simulated at the points, where palynological investigation was carried out (fig. 3). Simulations were based on the created modern vegetation datasets, according to the most widely used pollen-vegetation relationship functions: bog-model by I. C. Prentice (1985), lake-model by S. Sugita (1994), effective productivity model by M. Kabailienė (Кабайлене, 1973), as well as more simple models 1/d (Prentice, Webb III, 1986) and 1/d^2 (Calcote, 1995; Webb III et al., 1981). Only *Pinus*, *Betula*, *Alnus*, *Picea* and *Quercus* taxa were simulated, as these are the most abundant in the territory of Lithuania nowadays. *ArcGIS* geoprocessing models and *Python* scripts were involved to carry out simulations.

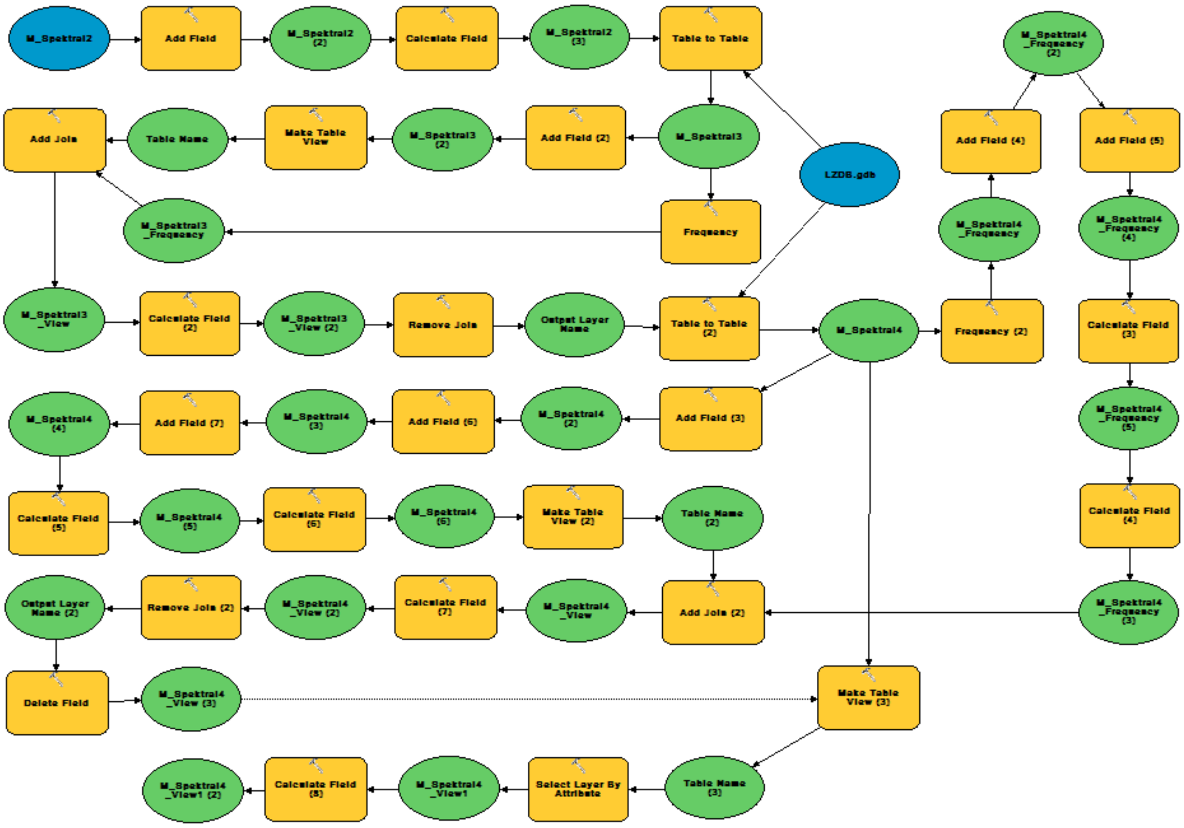


Fig. 2. *Graphical representation of the geoprocessing model „Eliminate pollen spectra“ – one of the models used for the creation of isopollen maps.*

Palaeovegetation maps were created according to pollen count data stored in pollen database. LRA 4.2.2 programme, comprising of two modules – REVEALS (Sugita, 2007a) and LOVE (Sugita, 2007b) – was used to carry out vegetation reconstructions at particular points. Consequently, vegetation data at points was used to interpolate values between them, and create palaeovegetation maps for the main tree taxa at time-windows of 14 000 cal. BP, 13 300 cal. BP, 12 100 cal. BP, 10 800 cal. BP, 9 500 cal. BP, 8 000 cal. BP, 6 500 cal. BP, 5 300 cal. BP, 3 300 cal. BP, 1 800 cal. BP and 500 cal. BP. Geoprocessing models and scripts were used for data pre-processing, as well as the creation of palaeovegetation rasters.

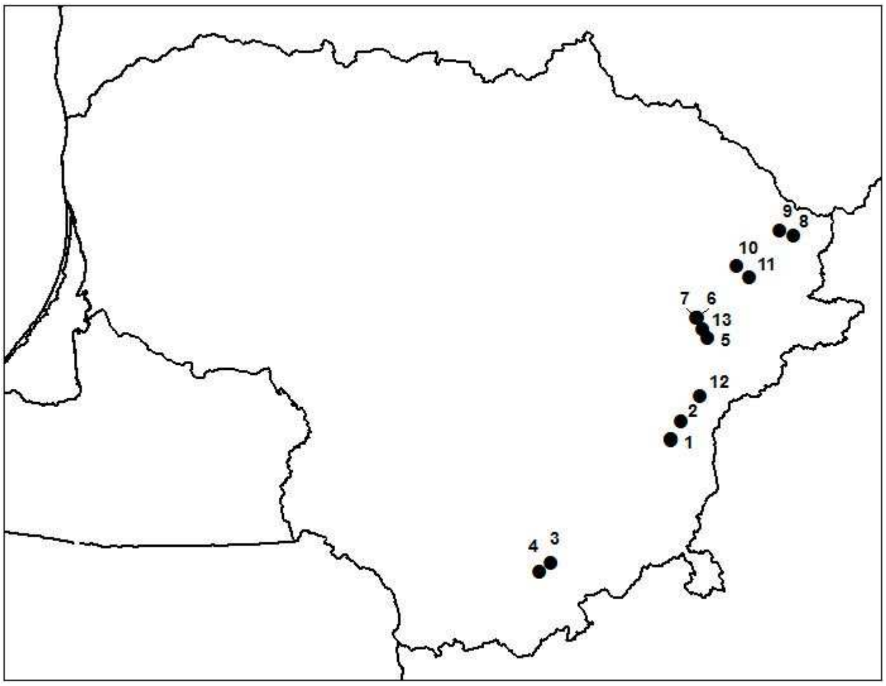


Fig. 3. *Surface pollen spectra investigation sites: 1 – Juodis lake; 2 – Gėlaitis lake; 3 - Gliūkaitis lake; 4 -Glėbas lake ; 5 - Baltelis lake; 6 - Elniukas lake; 7 – Žiotelės lake; 8 - Skaidrys lake; 9 - Davigiliai lake; 10 - Dagilėjus lake; 11 - Byvainis lake; 12 - Dumblelis lake; 13 - Ešerinis lake.*

3. RESULTS

Lithological descriptions, palynological investigations, and radiocarbon dating of sediments

All analyzed sequences have similar lithological pattern – soil or vegetation cover is lying on top (all cores were carried out from ground surface), then follows bog (peat), lake sediments (gyttja or lake marl), and eventually terigenous sediment (sand, silt and clay). Radiocarbon dating shows that sediments in the bottom of Dubičiai outcrop formed before 13 000 BP, Kaciušiai, Amalvas and Perūnas cores – before 10 000 – 11 000 BP. As pollen analysis, spanning larger sediment interval shows considerably higher content of herbs in the bottom of all sequences, it can be concluded that all sequences reach at least end of Late Glacial and cover most of the Holocene, except Dubičiai outcrop, where sedimentation took place from early stages of the Late Glacial till the beginning of the Holocene.

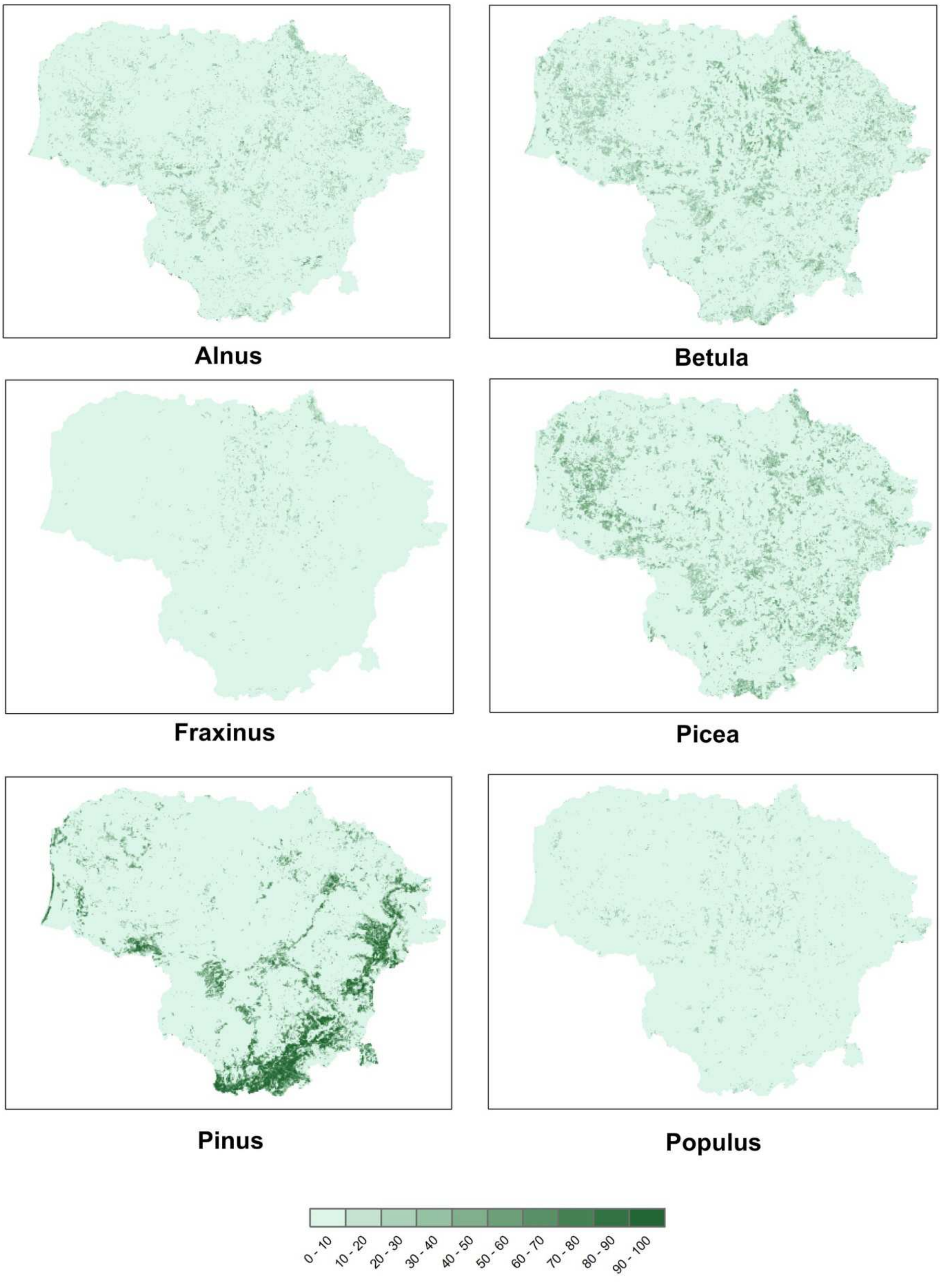
All analyzed pollen sequences have significant number of pollen samples and radiocarbon dates (except Šnieriškės core, which is not dated), thus providing additional well-dated, high-quality pollen data to the pollen database.

Modern vegetation maps

Modern vagetation maps were created for every taxon stored in FCIIS database. From the created raster maps of different taxa (Fig. 4) it is obvious that pine (*Pinus*) forests dominate in Lithuania, especially South-Eastern part. Spruce (*Picea*) distribution is more even, and it makes considerable amounts in all parts of Lithuania. Another significant taxon in the investigated area is birch (*Betula*). Highest amounts of birch are typical to central and western part of Lithuania, though it is significant virtually in all territory of Lithuania. Alder (*Alnus*) forest is mostly spread in South-West and North-East of Lithuania. In the South-East and North-West alder is distributed in much lower quantities. Other forest types – oak (*Quercus*), ash (*Fraxinus*), aspen (*Populus*) are rather limited, and they usually make relatively low percentages. Even lower quantities are characteristic to lime (*Tilia*) and hornbeam (*Carpinus*), which are more typical to southern part of Lithuania. Elm (*Ulmus*), willow (*Salix*) and beech (*Fagus*) are extremely fragmental and virtually indiscernable in vegetation maps.

Surface pollen assemblage simulation results

Surface pollen assemblage simulations (Fig. 5) yielded very different results at different sites. In ones (Gliūkaitis, Juodis, Glėbas, Kazimieriškė) average errors for one taxon were only few per cent, in others (Davigiliai, Perūnas) predicted values were extremely erroneous, i.e. close to the average random prediction error. In most simulations, different models at the same site gave similar results, i.e. if one model outputs results with low errors, other models also tend to output relatively precise results as well. Thus, it can be concluded that higher errors largely are not caused by differences in models, but probably by insufficient evaluation of environmental conditions and violations of model assumptions.



Alnus

Betula

Fraxinus

Picea

Pinus

Populus

Fig. 4. *Spatial distibution of Alnus, Betula, Fraxinus, Picea, Pinus and Populus in Lithuanian forests.*

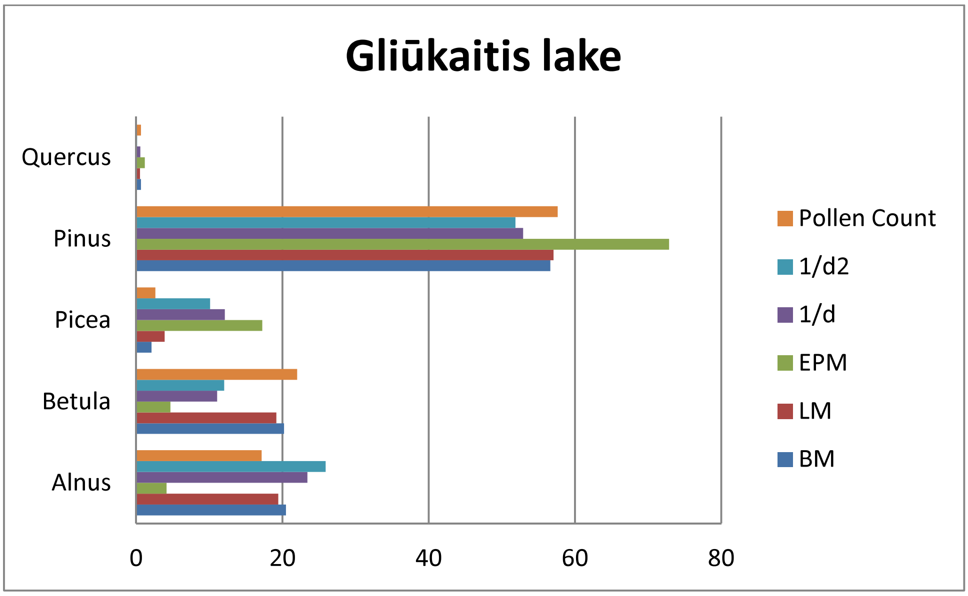


Fig 5. *Surface pollen assemblage simulation results in the Lake Gliūkaitis and their comparison to the assemblage, estimated by pollen analysis.*

In order to compare results of different models, simulation errors from all sites were averaged for every model (Table 1). It can be noticed in the table, that *Betula* was underestimated by all models, compared to palynological investigation results. *Picea* quantities were overestimated by all models, however BM (bog model) and LM (lake model) yielded relatively precise resuts. *Pinus* values were predicted rather precisely by BM and LM as well. *Alnus* values were underestimated by EPM (Effective productivity model), and overestimated by other models. *Quercus* values were most precisely predicted by 1/d, LM and BM.

Table 1. *Comparison of simuliation results for different pollen-vegetation relationship functions.*

Average	**BM**	**LM**	**EPM**	**1/d**	**1/d2**
Alnus	7.81	5.87	-4.06	8.87	8.38
Betula	-6.67	-8.60	-20.14	-16.20	-16.65
Picea	0.12	3.71	15.29	15.75	16.17
Pinus	-1.35	-1.03	8.39	-8.40	-7.59
Quercus	0.08	0.05	0.53	-0.02	-0.31
Average error	9.57	9.92	10.78	13.03	13.79

Overall simulation quality was evaluated with average errors for each taxon. Best results were achieved with BM (average 9.57 %) and LM (average 9.92 %) simulations. EPM average error was 10.78 %. The least precise were *1/d* and $1/d^2$ models (13.03 % and 13.79 % respectively). All predictions of BM and LM were similar to each other, as well as *1/d* and $1/d^2$ predictions.

Generally, errors of predictions with all models were rather high. Even if in some single cases simulation results matched the results of palynological investigation with a very low error, at some sites errors were close to ones of a random guess. It seems that in most cases, local conditions and their evaluation had the most impact on simulation errors. One of the possible sources of errors could be insufficiently detail evaluation of basin bank vegetation. Even though vegetation that is growing on basin banks should have significantly higher influence on pollen spectra than vegetation growing 10-20 meters away from the bank (Tauber, 1965), such detail neither is represented vegetation dataset, nor it is evaluated by any of the used pollen-vegetation relationship functions. Though, it was often the case in the investigated lakes, that bank vegetation was distinctly different from the vegetation, surrounding the basin. Typically, in such cases results were less precise.

Also, it should be noted, that surface lake sediments represent last 100-200 years, while vegetation dataset represents situation in 2006-2007. Even though in most cases changes over last two centuries were probably minor, in cases when vegetation in the area changed significantly, higher errors should be expected.

Nevertheless, in most cases pollen-vegetation relationship models proved to be sufficiently reliable as the source of quantitative information. More sophisticated models provided more precise results, except BM and LM case. Even though LM is more sophisticated, it‘s errors are slightly higher than those of BM simulations. Essentialy BM and LM are versions of the same pollen-vegetaton relationship function. BM models pollen, deposited on the surface of the basin, and therefore considered suitable for bogs, while LM also evaluates turbulence in the basin and therefore recommended to be used in lakes. Simulations didn‘t show that LM gives better results in lakes than BM. However, simulation dataset was too small to deny LM effectiveness in lakes. Therefore, both models were selected for reconstruction of past vegetation in Lithuania following recommendations: LM for lakes, and BM – for bogs and forest openings.

Isopollen maps

Isopollen maps (Fig. 6-9) show spatial distribution of pollen for a certain time-window. Since these maps are created by interpolating pollen spectra between investigated sites, and in reality pollen spectra can differ significantly even over hundreds of meters, the maps are not ment to predict pollen percentage values between the interpolation points. They rather show main trends of spatial pollen distribution.

Isopollen maps do not represent past vegetation either, since they do not take into account such factors as pollen productivity, basin size, etc. However, these maps can be successfully used for vegetation reconstruction (Ralska-Jasiewiczewa et al., 2004). As palaeovegetation maps are created in this study as well, conclusions on past vegetation are based on the latter. Isopollen maps were used to compare pollen data to other investigations, because in vast majority of other studies only pollen percentages are operated, not the vegetation perscentages, achieved by quantitative reconstruction.

156 isopollen maps were created in total (for 13 most abundant tree and shrub taxa in Lithuania, at 12 time-windows of the Late Glacial and Holocene). More abundant taxa are represented with 10 per cent interval color palette, less abundant taxa – with 1 per cent palette. Investigated sites with percentages are shown on maps as well. Interpolation took place only in the area, bounded by the investigated sites. Therefore, isopollen signal along the borders of investigated area was not determined.

Isopollen maps were compared to similar studies in the neighbouring countries, and they seem to correlate well with other researchers data.

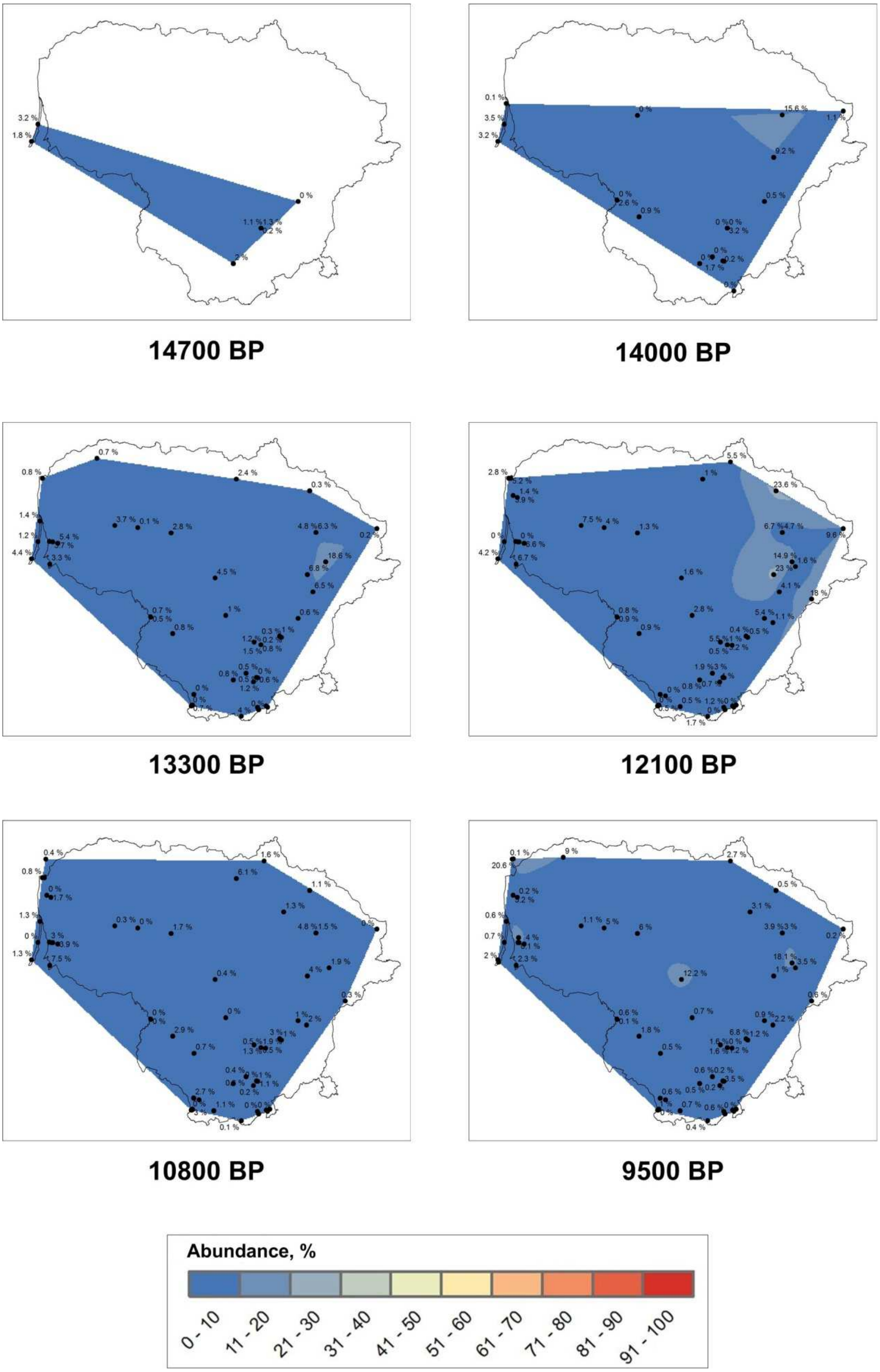


Fig. 6. *Isopollen maps of Picea 14 700 BP, 12 100 BP, 10 800 BP and 9 500 BP.*

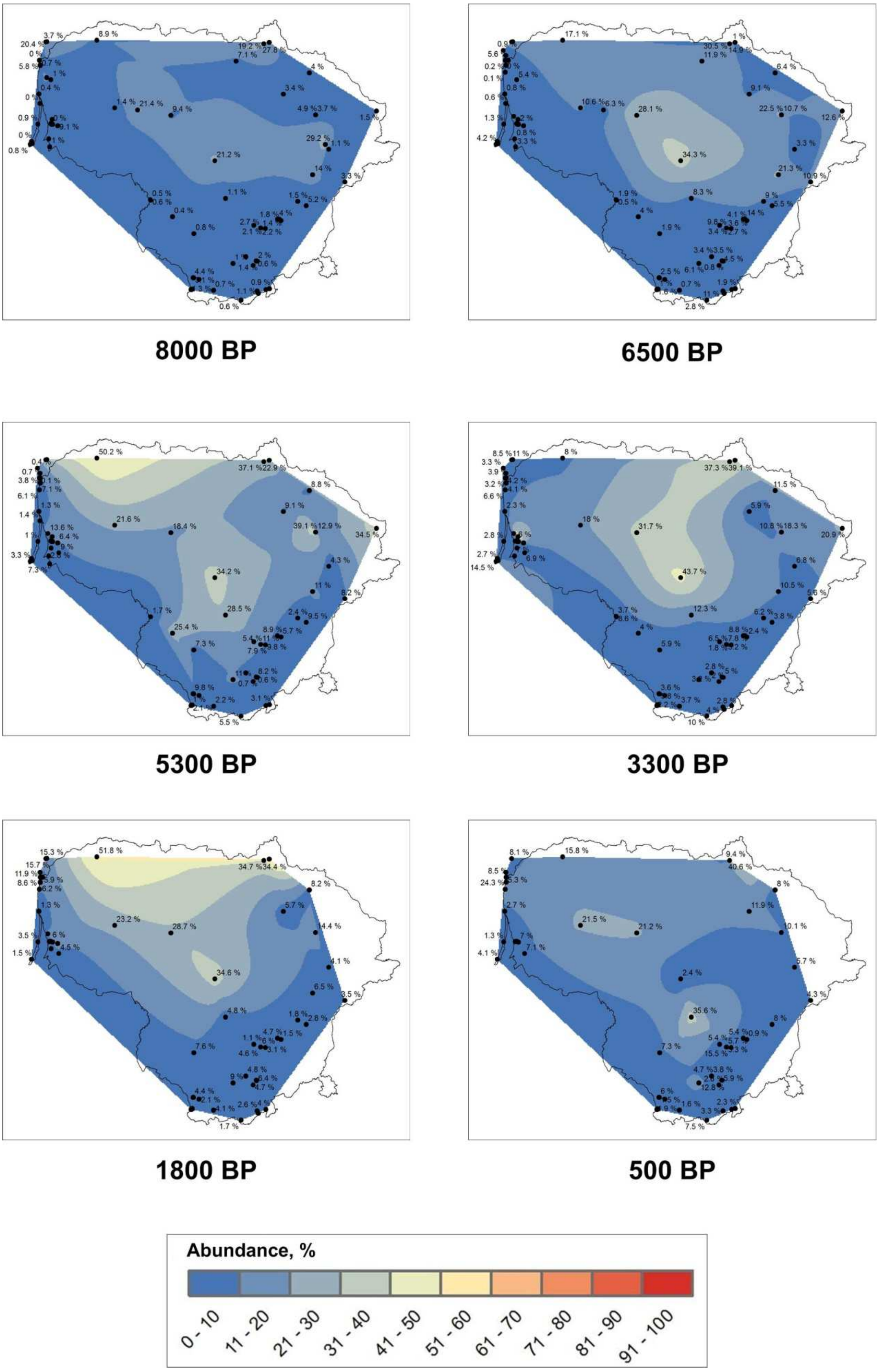


Fig. 7. *Isopollen maps of Picea 8 000 BP, 6 500 BP, 5 300 BP, 3 300 BP, 1 800 BP and 500 BP.*

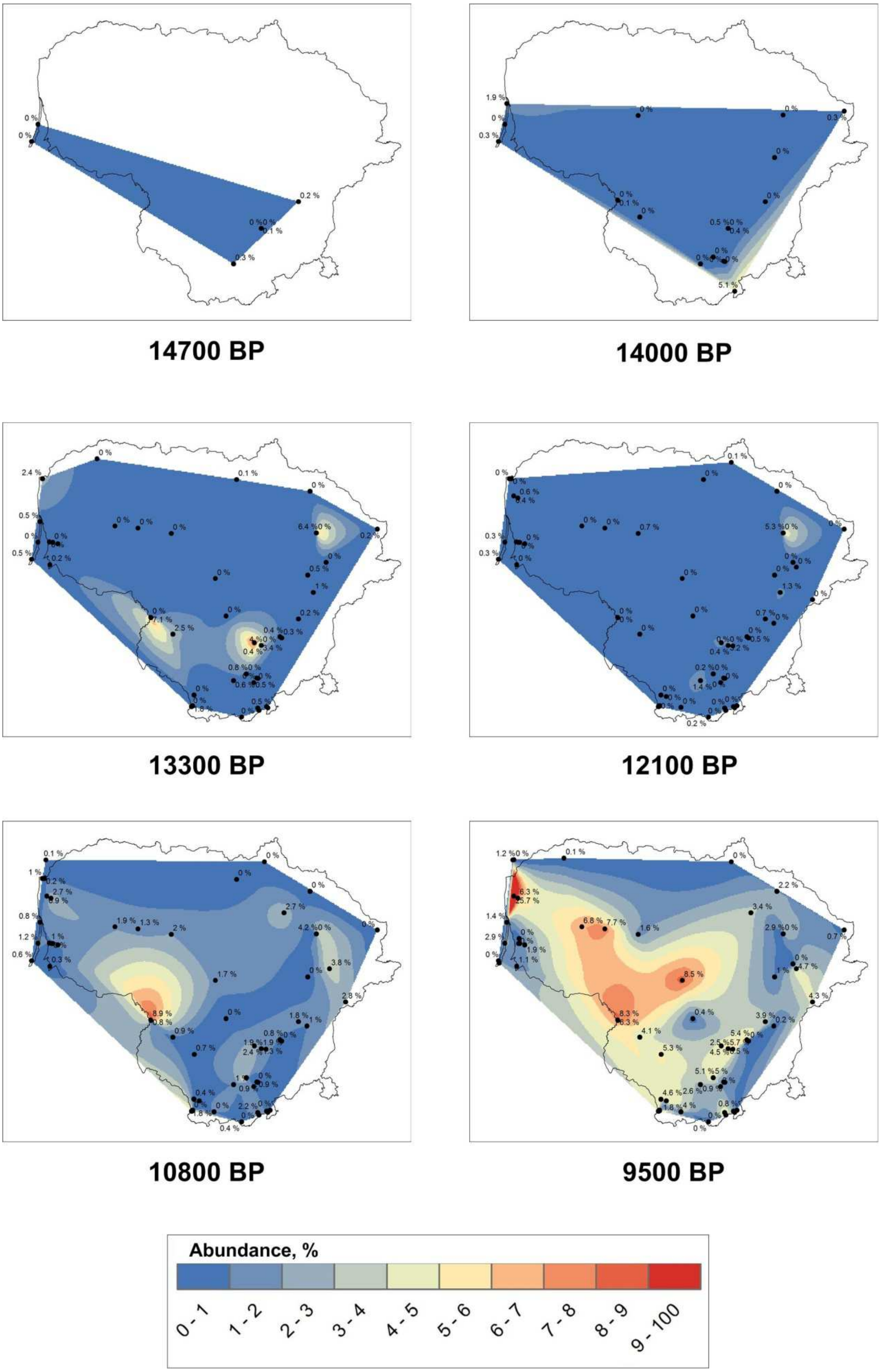
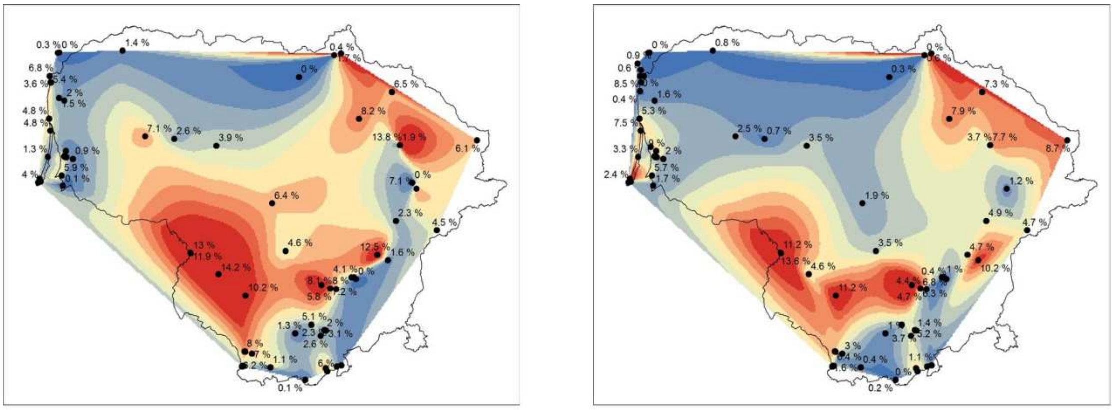
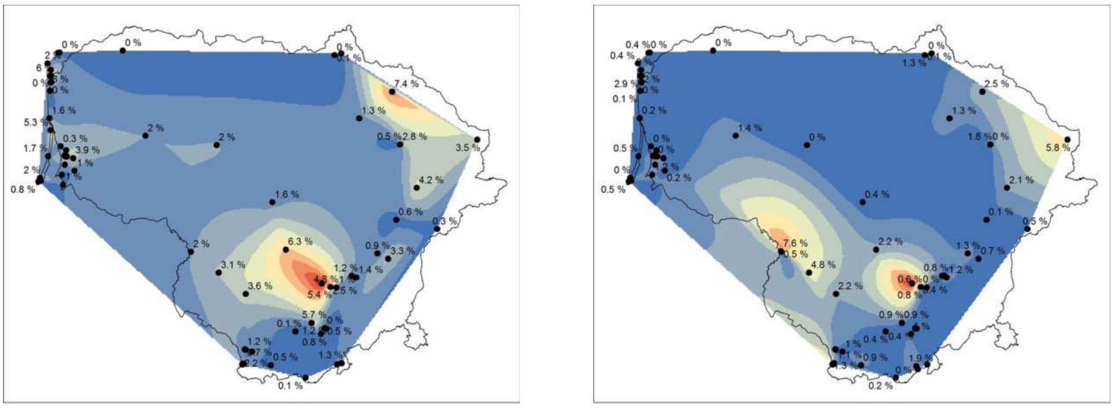


Fig. 8. *Isopollen maps of Ulmus 14 700 BP, 12 100 BP, 10 800 BP and 9 500 BP.*



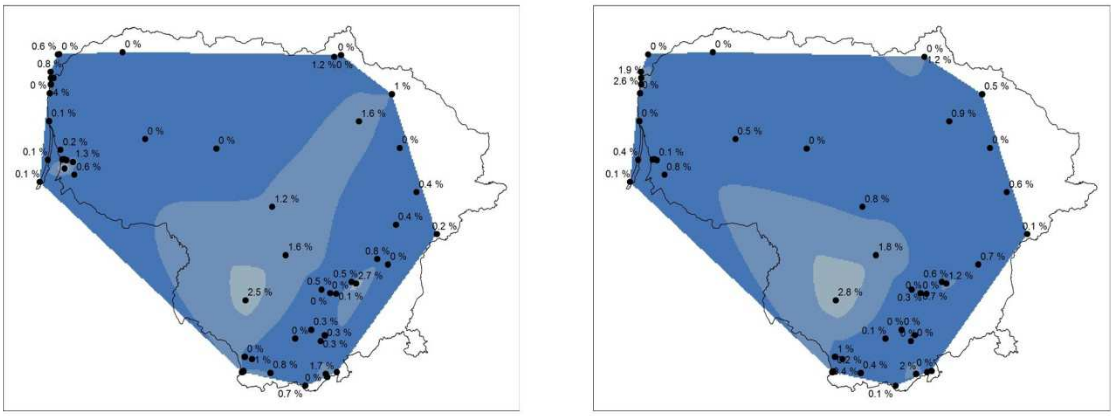
8000 BP

6500 BP



5300 BP

3300 BP



1800 BP

500 BP

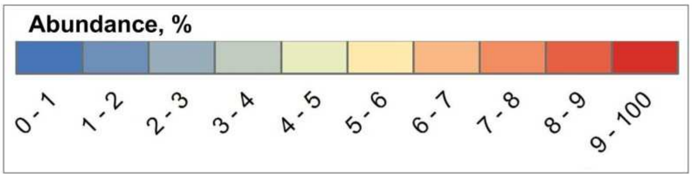


Fig. 9. *Isopollen maps of Ulmus 8 000 BP, 6 500 BP, 5 300 BP, 3 300 BP, 1 800 BP and 500 BP.*

Palaeovegetation maps

Unlike isopollen maps, palaeovegetation maps (Fig. 10-14) show distribution of past vegetation, determined by quantitative vegetation reconstruction. One of the possible sources of errors in such maps are errors of vegetation reconstruction (e.g. data or model imperfections). Furthermore, these maps are created by interpolation between points, therefore, the bigger ir distance to the nearest point, the more likely are errors in the area. These sources of errors should be carefully evaluated when interpreting palaeovegetation maps. After evaluation and elimination of errors, palaeovegetation maps can be used as reliable sources of information on past vegetation.

143 palaeovegetation maps were created in total (for 13 most common tree taxa in Lithuania, at 11 time-windows of the Late Glacial and Holocene). More abundant taxa are represented with 10 per cent interval color palette, less abundant taxa – with 1 per cent palette. Investigated sites with percentages are shown on maps as well. Interpolation took place only in the area, bounded by investigated sites, therefore, palaeovegetation signal along the borders of investigated area was not determined.

Palaeovegetation maps provided more detail knowledge of vegetation distribution in Lithuania, as well as quantitative estimates of past vegetation.

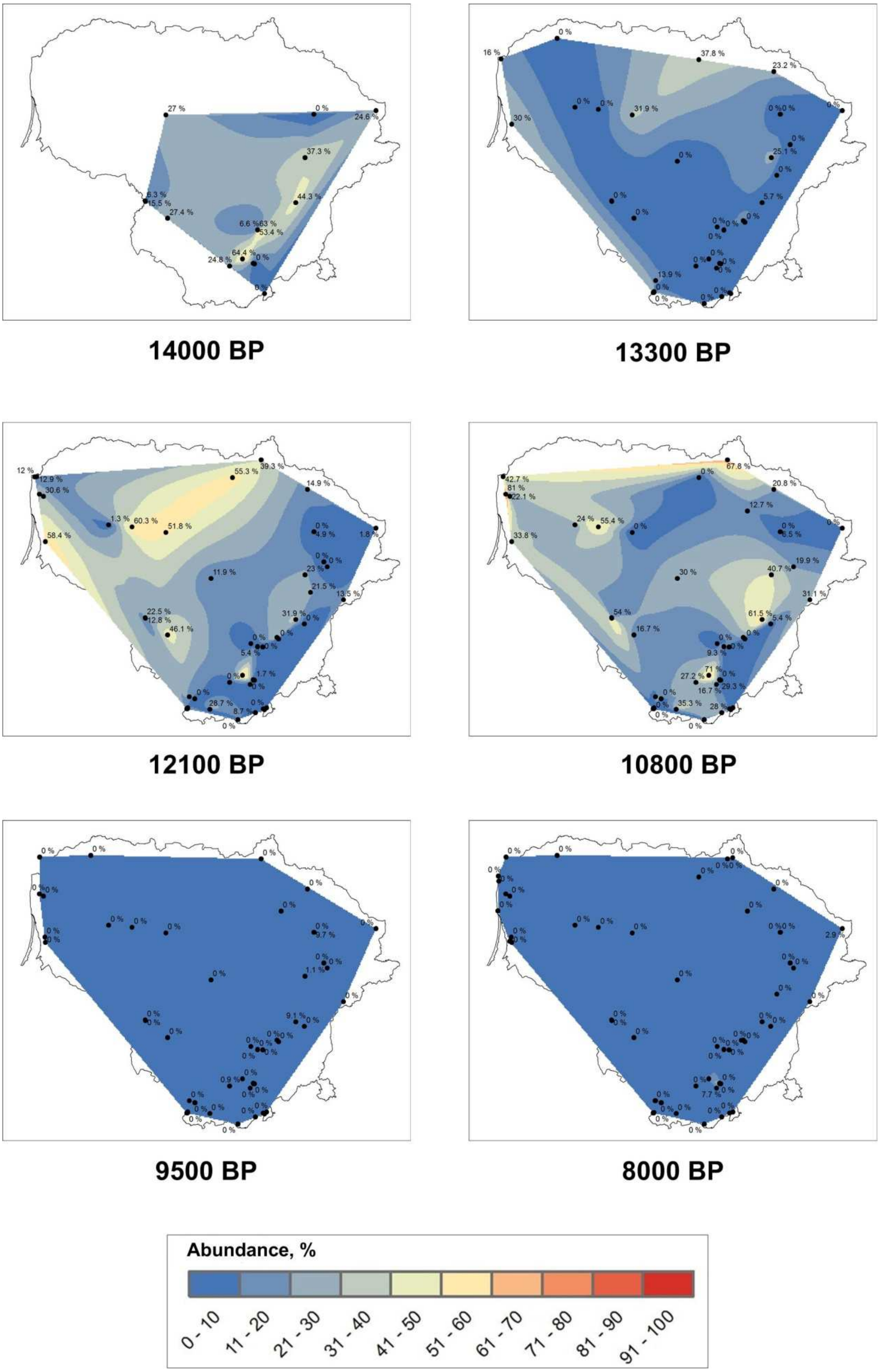
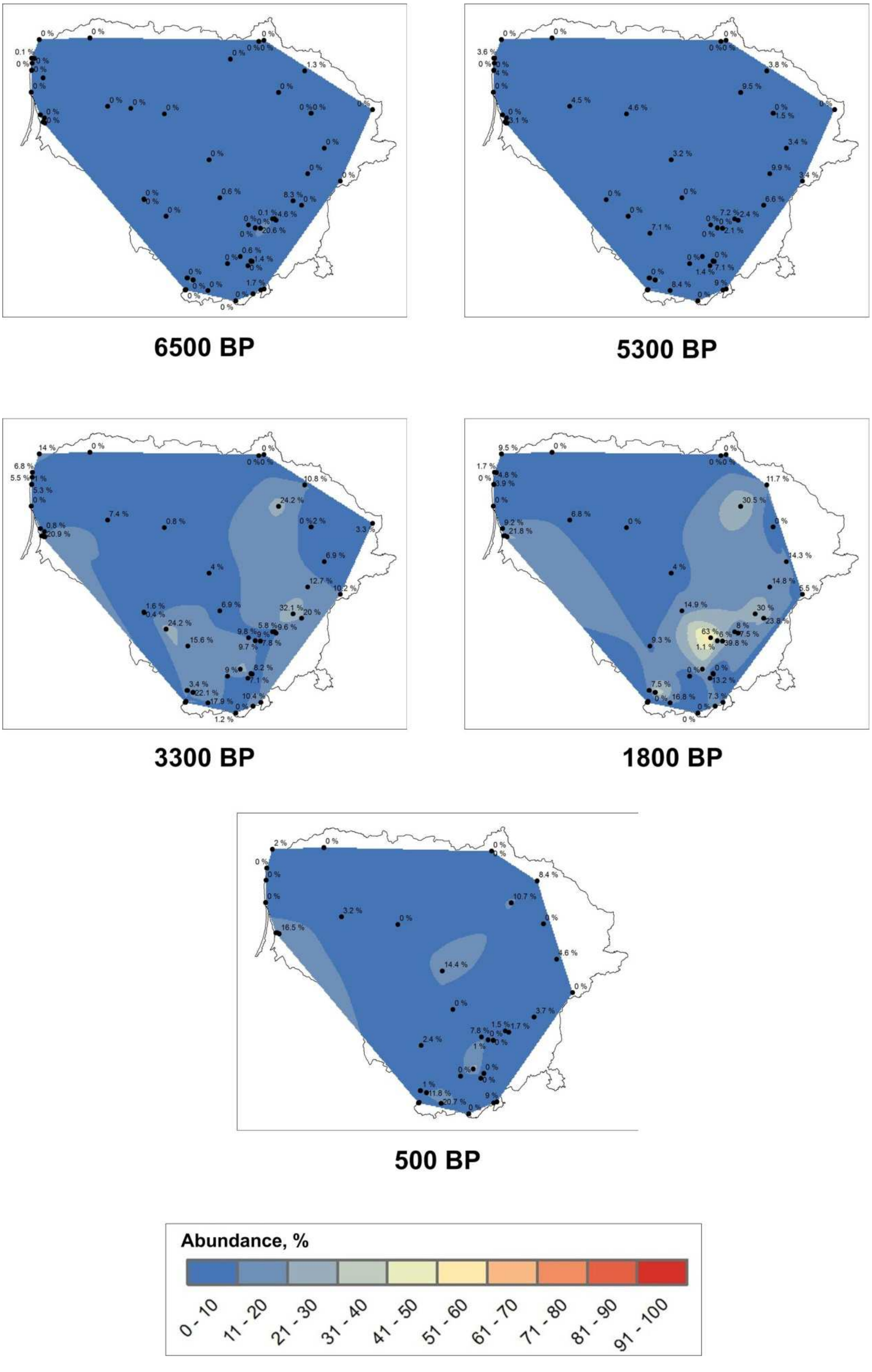


Fig. 10. *Palaeovegetation maps of Betula 14 000 - 12 100 BP, 10 800 BP, 9 500 BP and 8000 BP.*



6500 BP

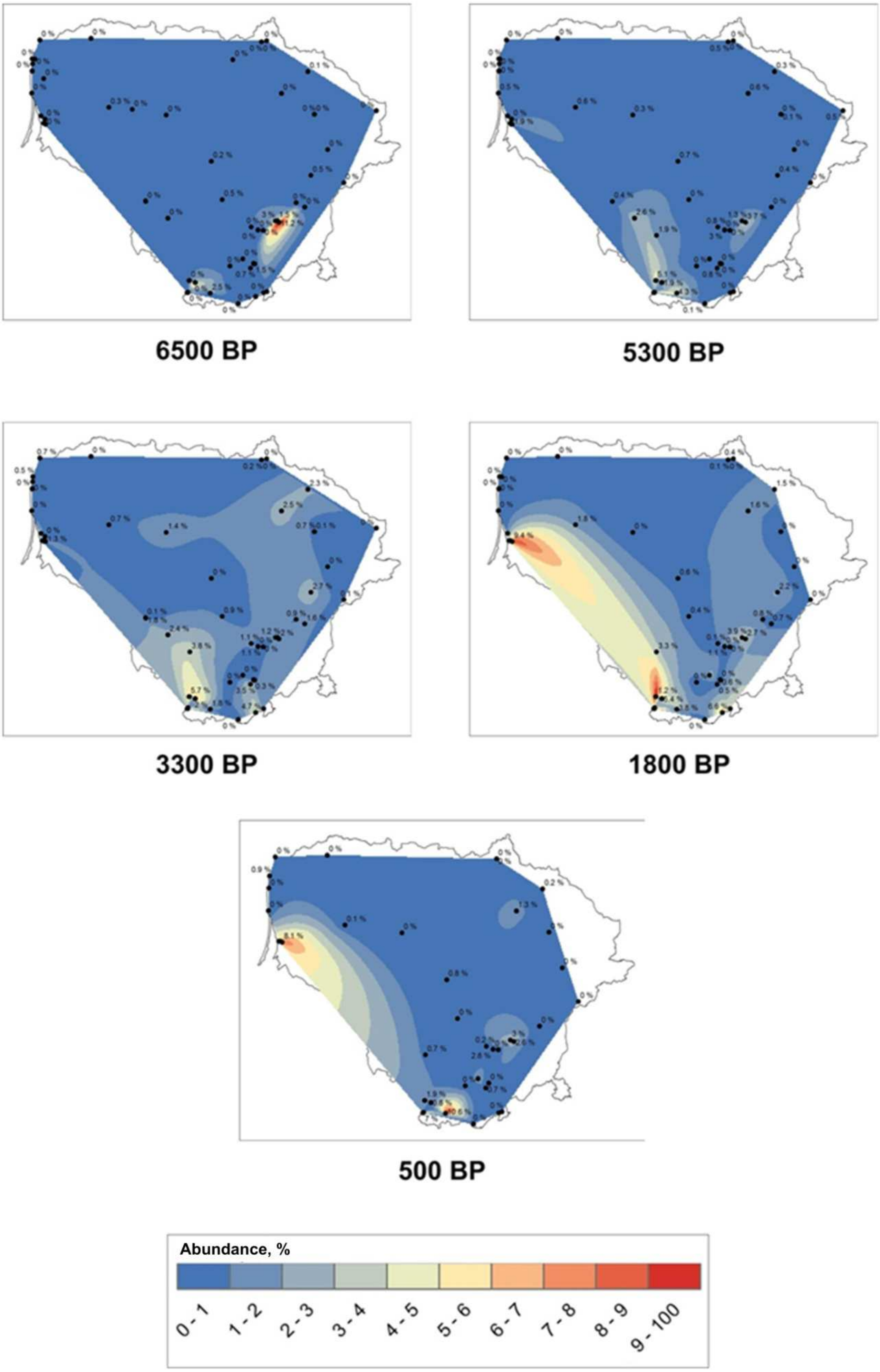
5300 BP

3300 BP

1800 BP

500 BP

Fig. 11. *Palaeovegetation maps of Betula 6 500 BP, 5 300 BP, 3 300 BP, 1 800 BP and 500 BP.*



6500 BP

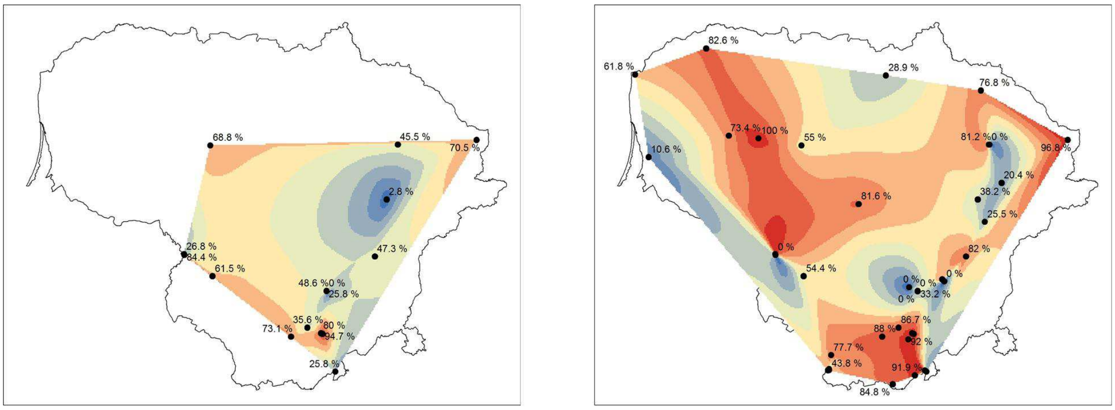
5300 BP

3300 BP

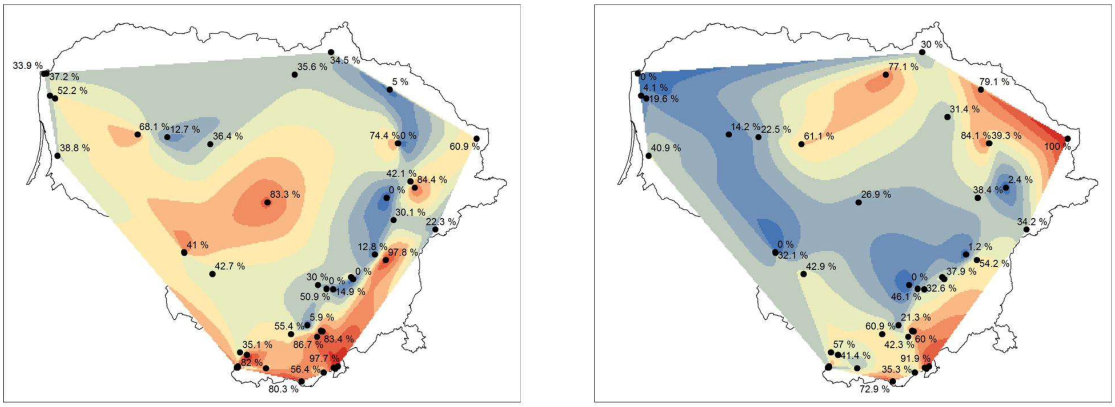
1800 BP

500 BP

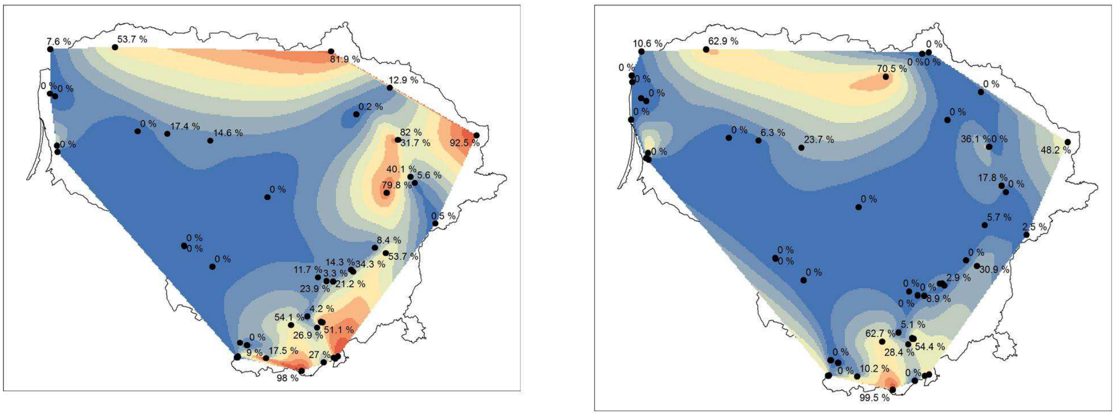
Fig 12. *Palaeovegetation maps of Carpinus 6 500 BP, 5 300 BP, 3 300 BP, 1 800 BP and 500 BP.*



14000 BP **13300 BP**



12100 BP **10800 BP**



9500 BP **8000 BP**

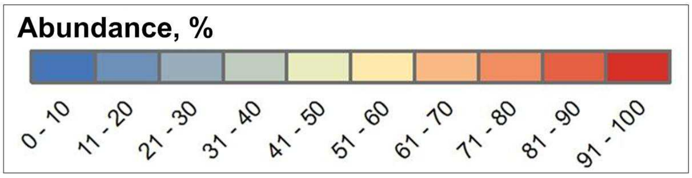
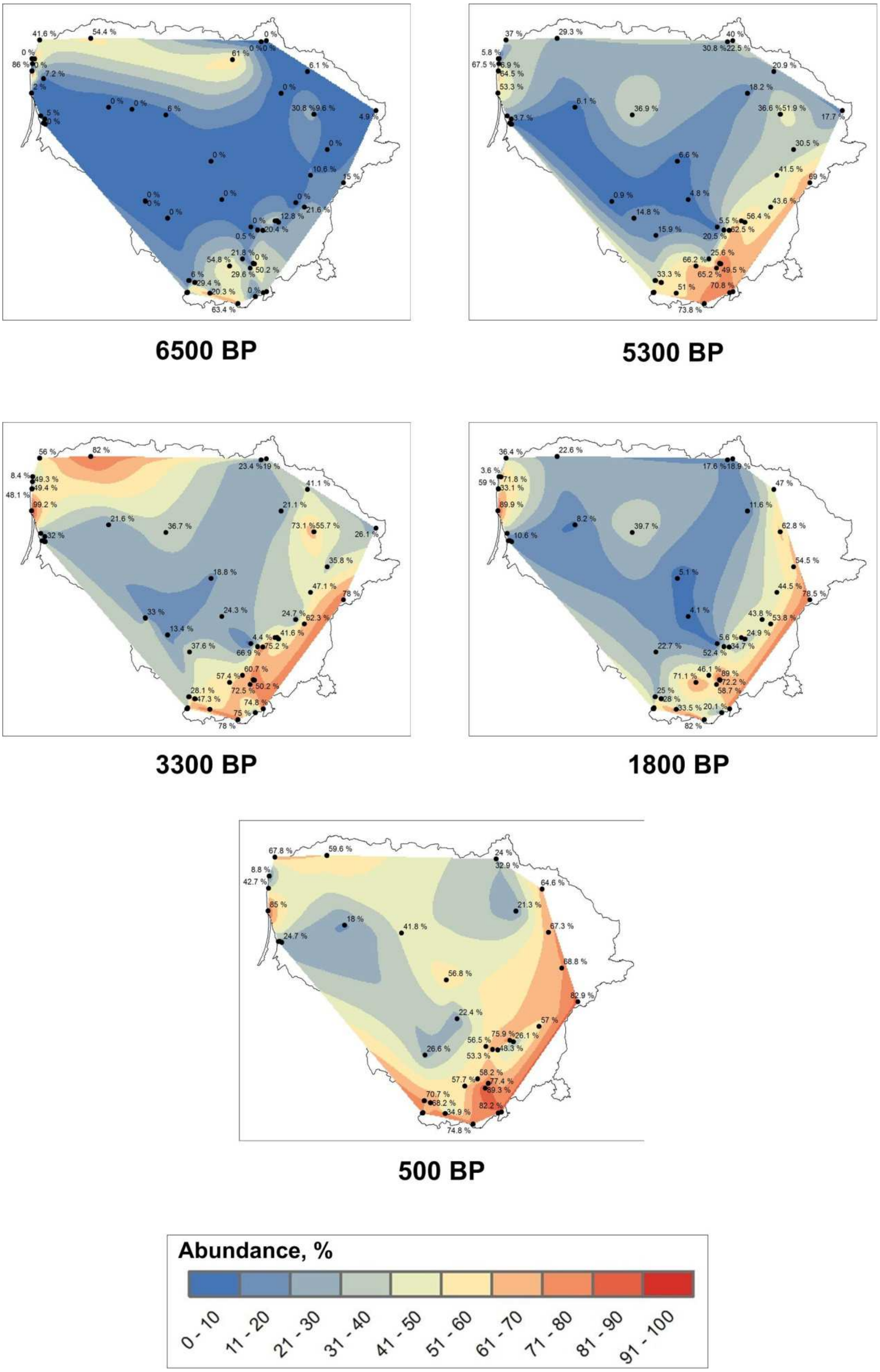


Fig 13. *Palaeovegetation maps of Pinus 14 000 - 12 100 BP, 10 800 BP, 9 500 BP and 8000 BP.*



6500 BP

5300 BP

3300 BP

1800 BP

500 BP

Fig 14. *Palaeovegetation maps of Pinus 6 500 BP, 5 300 BP, 3 300 BP, 1 800 BP and 500 BP.*

4. LATE GLACIAL AND HOLOCENE FOREST HISTORY IN LITHUANIA, ACCORDING TO LRA MODELLING, AND IT‘S COMPARISSON TO THE RESULTS OF OTHER INVESTIGATIONS

Comparison of the reconstructed vegetation to the results of earlier investigations

In comparison with earlier quantitative vegetation reconstructions in Lithuania, present study provides considerably higher spatial resolution. By ealier investigations, vegetation was reconstructed for five regions on Lithuania (Кабайлене, 1973). In the present study, vegetation is reconstructed at 1 km^2 resolution. In order to compare both studies, palaeovegetation maps were generalized into five regions, identical to those used by M. Kabailienė (Кабайлене, 1973).

Even though main trends of vegetation change in both studies are similar, LRA application generally resulted in higher pine (Fig. 15) and spruce values. EPM, in turn, presents higher amounts of birch (Fig. 16) and alder. Higher hazel values were determined by LRA in the beginning of the Holocene, while in the end of Holocene, higher values were reconstructed with EPM. Absolute differences in other taxa are considerably lower, since these taxa is less abundant. However, relative differences are significant. Higher values of elm and lime were achieved with LRA, higher oak – with EPM.

After comparison of both modelling results in the latest time-window (500 BP; Late Subatlantic) with modern vegetation (determined using FCIIS data), it is evident that pine percentages, reconstructed by LRA, match modern vegetation percentages well (Fig. 17). Highest differences (12.1 %) are observed in North-Western Lithuania, while in Western and South-Eastern Lithuania differences do not exceed 0.8-2 %. At the same time EPM result differs from modern vegetation by 23.9 % in South-Eastern Lithuania, and average discrepancy in Lithuania equals 11.1 %.

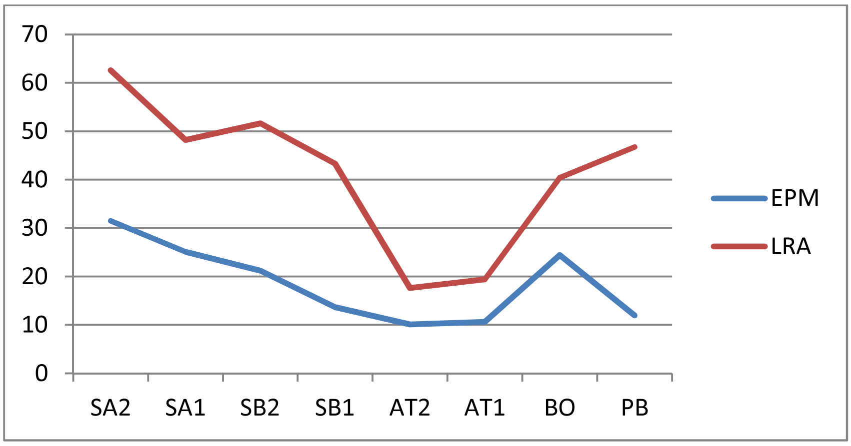


Fig. 15. *Pine percentages, determined in South-Eastern Lithuania, according to EPM and LRA models.*

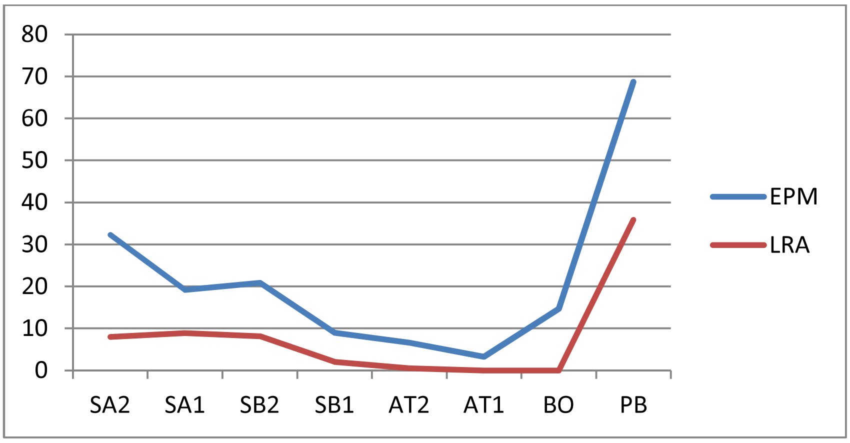


Fig. 16. *Birch percentages, determined in Western Lithuania, according to EPM and LRA models.*

Spruce percentages, determined by LRA differ from modern vegetation by 2.4-13.1 % in different regions of Lithuania. EPM results in differences of 10.3-22 %. Birch percentages, achieved with LRA are in average 20.4 % lower than in modern vegetation, EPM percentages – higher by 8.3 %. Alder percentages were underestimated by 12 % with LRA, and overestimated by 11.8 % with EPM. Oak values were underestimated with both models by 3.2-3.3 %. Elm values by LRA are 2 % higher, EPM values – 0.2 % lower than modern. Lime percentages differ by 0.1-0.2 % with both models.

When comparing reconstruction results for the last millenium to modern vegetation, it should be taken into account that vegetation could change during this time, mostly because of human acticity (Kabailienė et al., 2001). However, on the assumption that vegetation did not change considerably, more precise results were achieved with LRA modelling.

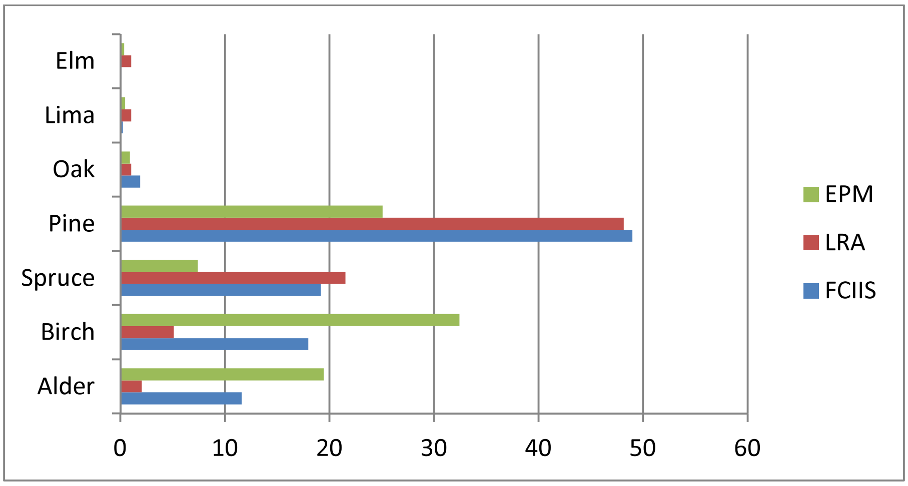


Fig. 17. *Comparison of EPM and LRA reconstructed percentages with FCIIS modern vegetation percentages in South-East Lithuania.*

Late Glacial and Holocene forest vegetation history in Lithuania, according to LRA modelling

17 000 – 15 850 cal BP

This time-window is represented only by few sequences in pollen database. Because of low number of sites, isopollen and palaeovegetation maps have not been created for this time-window. However, it is known from other investigations (Gaigalas et al., 2001; Rinterknecht et al., 2008) that a considerable part of Lithuania was still covered by glacier ar that time. In the rest part of Lithuania, soils and vegetation only started to form. In such conditions, only occasional trees could grow, and dwarf-shrubs, e.g. *Betula nana* and *Salix polaris* could be present in considerable quantities (Iversen, 1973; Ralska-Jasiewiczowa et al., 2004; Kabailienė, 2006b). Most of *Pinus*, *Betula*, *Alnus* and *Picea*, as well as broadleaf taxa that was found in these sediments was most probably redeposited (Кабайлене, 1973; Kabailienė, 2006a).

15 850-14 600 cal BP

This time-window also contains low number of sequences and pollen samples. Climate became warmer, especially towards the end of this period (Björck et al., 1998; Rasmussen et al., 2006), though part of Lithuanian territory was still covered by permafrost (Gaigalas et al., 2001; Rinterknecht et al., 2008), and in the rest part temperatures were still low (Kabailienė, 1990).

Macrofossils of tree birch were found in Lithuania (Stančikaitė et al., 2008) and neighbouring territories (Wasilykowa, 1964). Dwarf birch (*Betula nana*) was also significant (Wacnik, 2003). Another significant species during this time-window could be *Salix*. Even though, significant numbers of pine and other tree pollen are observed in pollen assemblages of this period, and occasional conifer trees could grow in Lithuania at that time, their significant spread is extremely unlikely (Кабайлене, 1973).

14 600 – 13 600 cal BP

21 pollen sequence reach sediments of this period. Open landscape still dominated in the investigated area (Kabailienė, 2006a), therefore, palaeovegetation maps of tree distribution are difficult to interpret. *Betula*, *Salix* and *Juniperus* could have grown in significant numbers in Lithuania during this time (Kabailienė, 2006a; Stančikaitė et al., 2008). Pine and spruce macrofossils were indentified, mostly in the eastern part of Lithuania and neighbouring territories (Makhnach et al., 2004; Stančikaitė et al., 2008; Heikkilä et al., 2009), which shows that these taxa could have been significant in some limited areas. Other tree taxa, found in pollen spectra of this period are probably redeposited.

13 600 – 12 800 cal BP

Forested landscape started to prevail during this time in Lithuania (Kabailienė, 2006a). Therefore, palaeovegetation maps of this period are much easier to interpret. *Pinus* dominated in most territory of Lithuania (Fig. 18), though *Betula* was significant as well, and even dominated in limited areas in the North and West of

Lithuania. According to earlier investigations (Stančikaitė et al., 2004; Kabailienė, 2006a), birch has spread from the South as climate became warmer. Then, relatively quickly pine trees followed. This is confirmed by the created palaeovegetation maps – *Betula* tends to be more significant in the north, *Pinus* – in the south. *Picea* is rather significant in the North-East Lithuania, though it is not among the dominant taxa. Other investigations in Lithuania and neighbouring territories (Stančikaitė et al., 1998; Heikkilä et al., 2009) also showed that *Picea* could be significant, especially in the South-East of Lithuania.

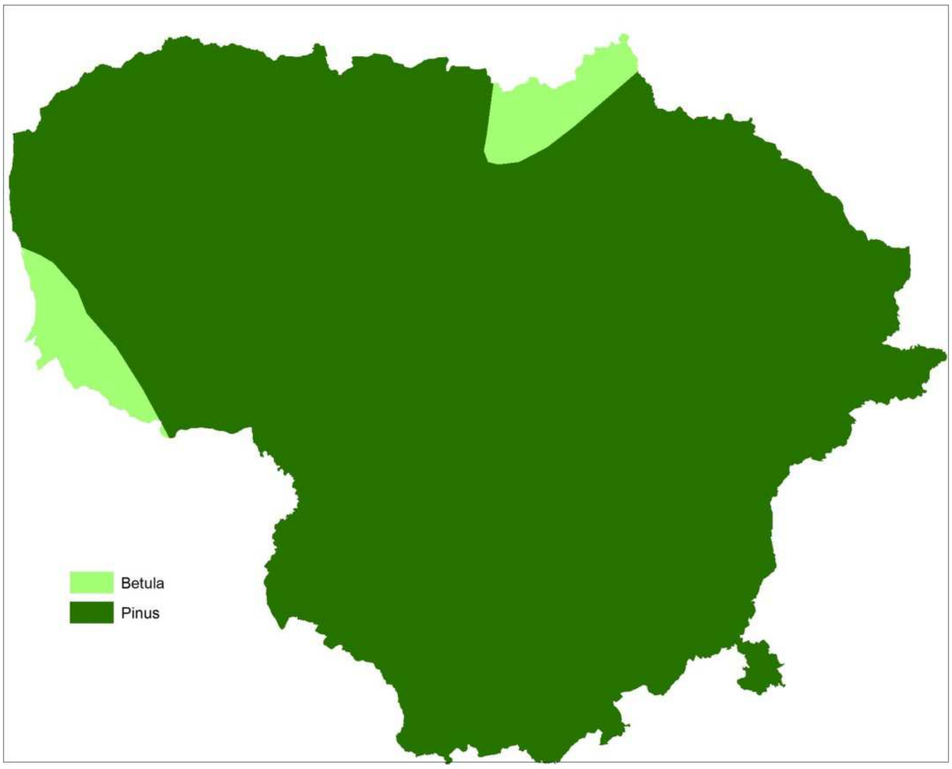


Fig. 18. *Prevailing tree taxa in Lithuania 13 600 – 12 800 cal BP, according to LRA modelling.*

12 800 – 11 500 cal BP

In the end of the Late Glacial, forestation decreased again, and herb vegetation prevailed (Kabailienė, 2006a). Interpretation of palaeovegetation maps is not straightforward because of the open landscape, however, it is noticeable that birch was more abundant in the Northern part of Lithuania, while pine was more abundant in the South. *Picea* was significant in the North-East of Lithuania, and probably even dominated in some limited areas. Most of *Alnus* pollen, found in Lithuanian pollen spectra of this period, is redeposited or deposited due to long-distance transport. Although, *Alnus* macrofossils, found in Northern Poland (Środoń, 1981; Latałowa, Borówka, 2006) and Lithuania (Stančikaitė et al., 2008), show that occasional *Alnus* trees could possibly grow in Lithuania.

11 500 – 10 200 cal BP

In the beginning of the holocene *Betula* spreads relatively quickly from the South, and *Pinus* follows (Kabailienė, 1990; 1998; Stančikaitė et al., 2002; 2003). This is also seen in palaeovegetation maps (Fig. 19). *Picea* percentages in the North-East significantly decrease, though, they remain significant. *Corylus* and *Ulmus* are starting to spread from West or North-West. These migrations match conclusions of other investigators (Ralska-Jasiewiczowa et al., 2004; Gaidamavičius et al., 2011). Some authors (Ralska-Jasiewiczowa, 1999; Saarse, 2004; Heikkilä et al., 2009) identify *Populus* pollen in sediments of this period. *Populus* pollen is not well-preserved, and it should be noted that it could possibly make a significant of vegetation, but this can not be observed in palaeovegetation maps.

10 200 – 8 600 cal BP

During this period birch-dominated forests shift northwards, while in Lithuania it virtually dissapears (Fig. 20). Retreat of birch from Lithuania is dated 10 050 cal BP (Stančikaitė et al., 2006), i.e. in the end of the previous time-window. *Pinus* is increasing further. *Corylus* and *Ulmus* are also spreading. *Corylus* now dominates in vast part of Lithuania, except sandy South-Western part, and Northern Lithuania, where unfavourable Quaternary deposits are spread for *Corylus* and *Ulmus*. Spruce spreads in Lithuania from North-West, and even prevails in limited areas of the coast. Alder forests appear in the western part of Lithuania, where damp conditions and low altitudes prevail. Low amounts of lime and oak appear in the South of Lithuania.

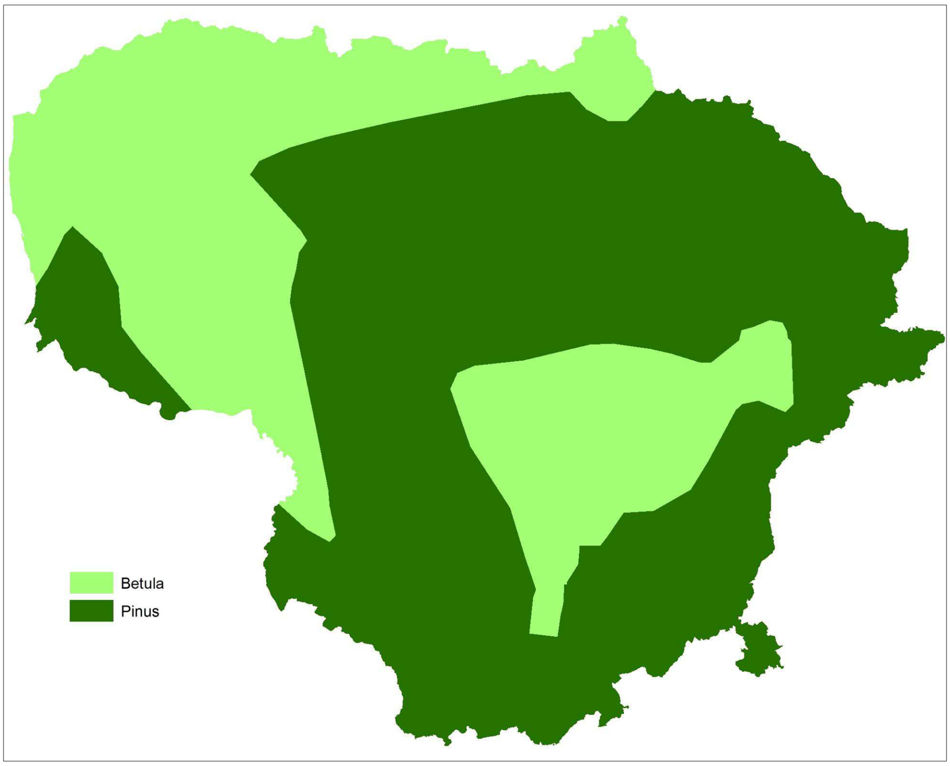


Fig 19. *Prevailing tree taxa in Lithuania 11 500 – 10 200 cal. BP, according to LRA modelling.*

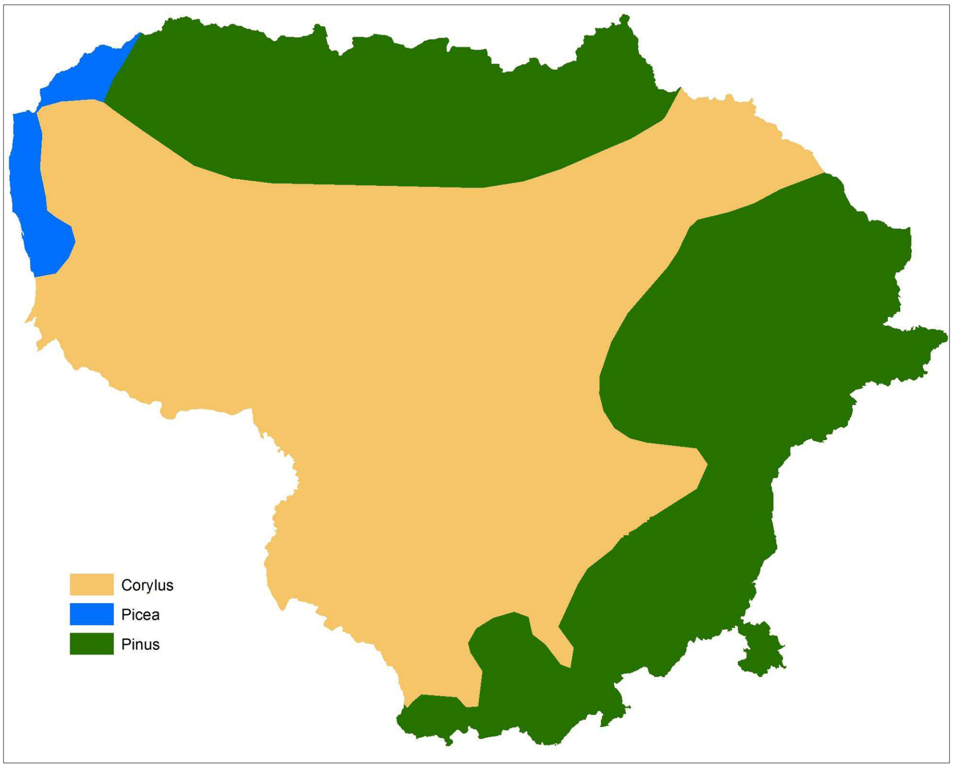


Fig. 20. *Prevailing tree taxa in Lithuania 10 200 – 8 600 cal. BP, according to LRA modelling.*

8 600 – 7 400 cal BP

Pine forests decrease, spruce and broadleaf forests spread even more (Fig. 21). Oak, lime and ash spread in all Lithuania and make significant quantities. However, they do not become dominant in any part of Lithuania.

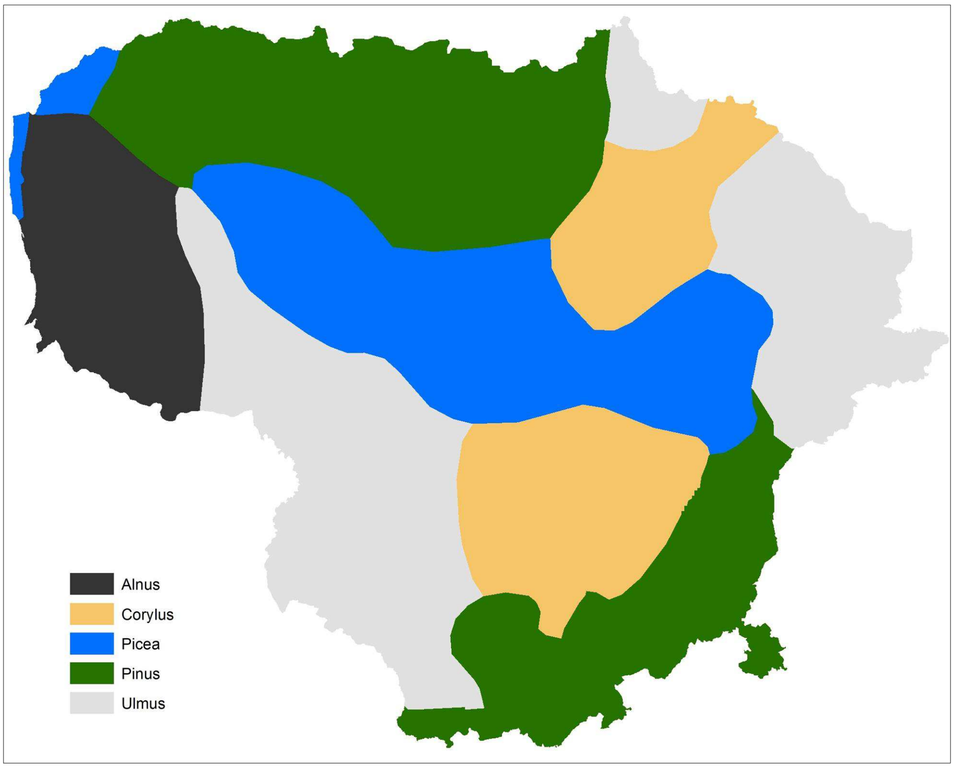


Fig. 21. *Prevailing tree taxa in Lithuania 8 600 – 7 400 cal. BP, according to LRA modelling.*

7 400 – 5 700 cal BP

This is the warmest period throughout the Holocene (Kabailienė, 1990). Areas, dominated by pine shrink to infertile, sandy regions in the north and south of Lithuania (Fig. 22). *Picea* dominates in central Lithuania, *Ulmus* – in the North-East, *Corylus* and *Alnus* – in the South-West. Lime and oak are very abundant throughout Lithuania.

5 700 – 4 000 cal BP

Climate becomes colder during this period (Kabailienė, 1990; Seppä, Birks, 2002; Davis et al., 2003), importance of broadleaf trees decreases (Fig. 23), confiers and birch take their place. Spruce becomes dominant in most territory of Lithuania. According to other researchers (Stančikaitė et al., 2002), intensive spread of spruce to the south started ca. 5 400 – 5200 cal BP. Small quantities (up to 5 %) of *Carpinus* appear in the South of Lithuania. It was determined that hornbeam appeared in the territory of Lithuania right before the onset of this period (Кабайлене, 1965; Stančikaitė, 2000) – 5 800 cal BP.

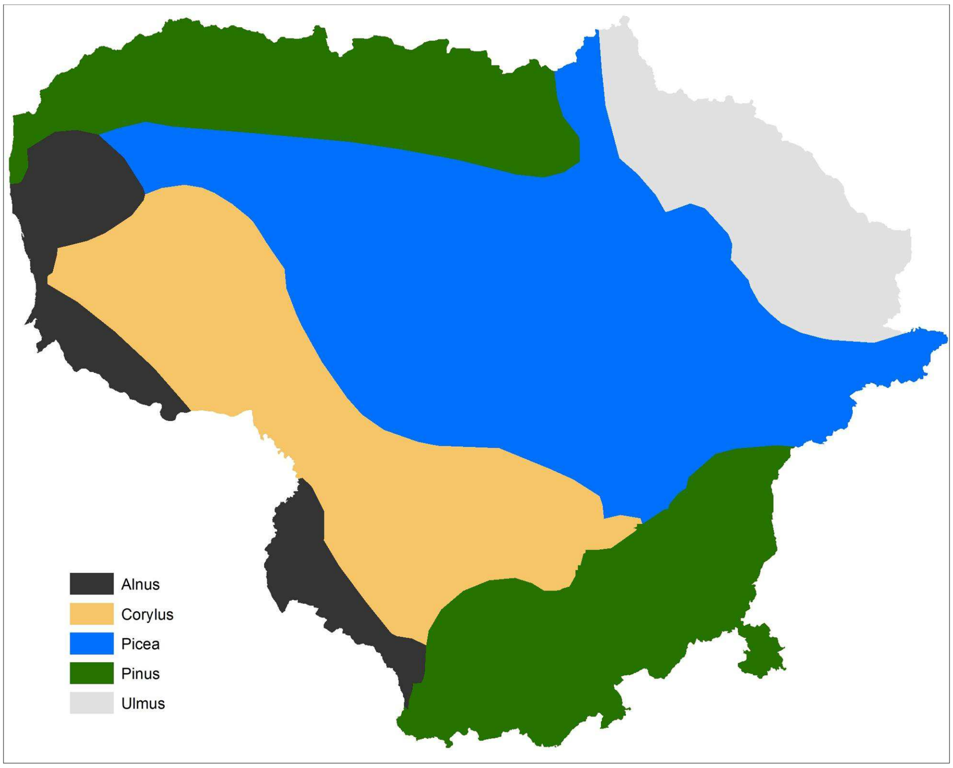


Fig. 22. *Prevailing tree taxa in Lithuania 8 600 – 7 400 cal. BP, according to LRA modelling.*

4 000 – 2 600 cal BP

Pine forests increase, spruce forests shrink (Fig. 24). Lowering of spruce percentages is also observed in neighbouring countries from 2 800 - 3 000 cal BP (Obidowicz et al., 2004; Kupryjanowicz, 2007; Niinemets, Saarse, 2007; 2009; Arslanov et al., 2011). Birch forests increase as well, especially in South-East Lithuania, where they make up to 10-20 %.

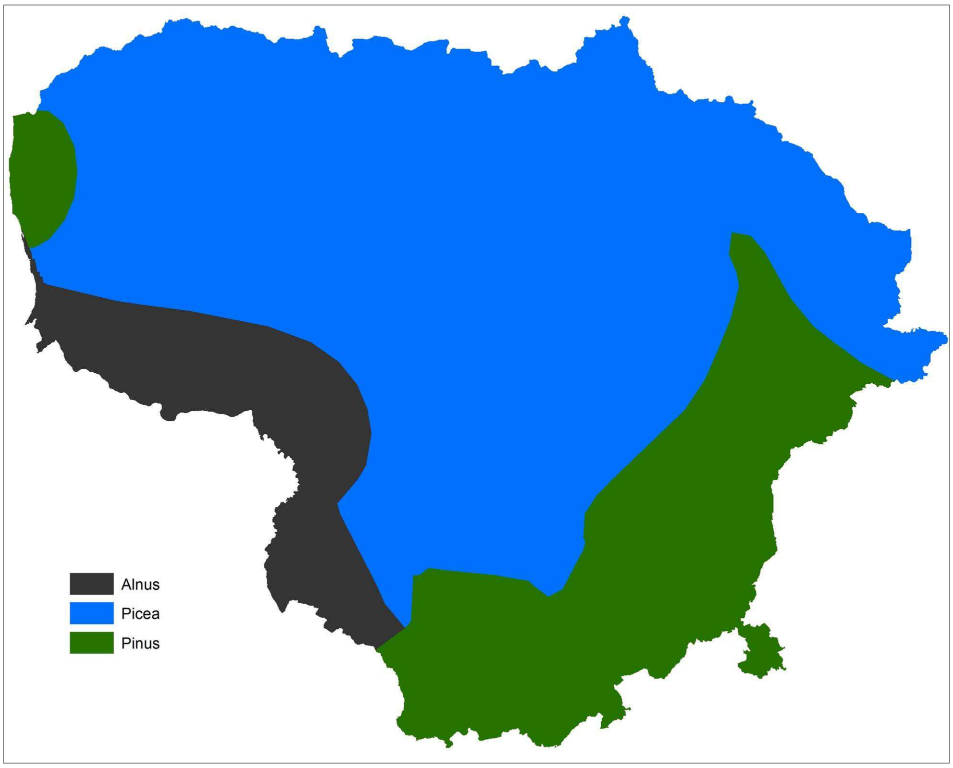


Fig. 23. *Prevailing tree taxa in Lithuania 5 700 – 4 000 cal BP, according to LRA modelling.*

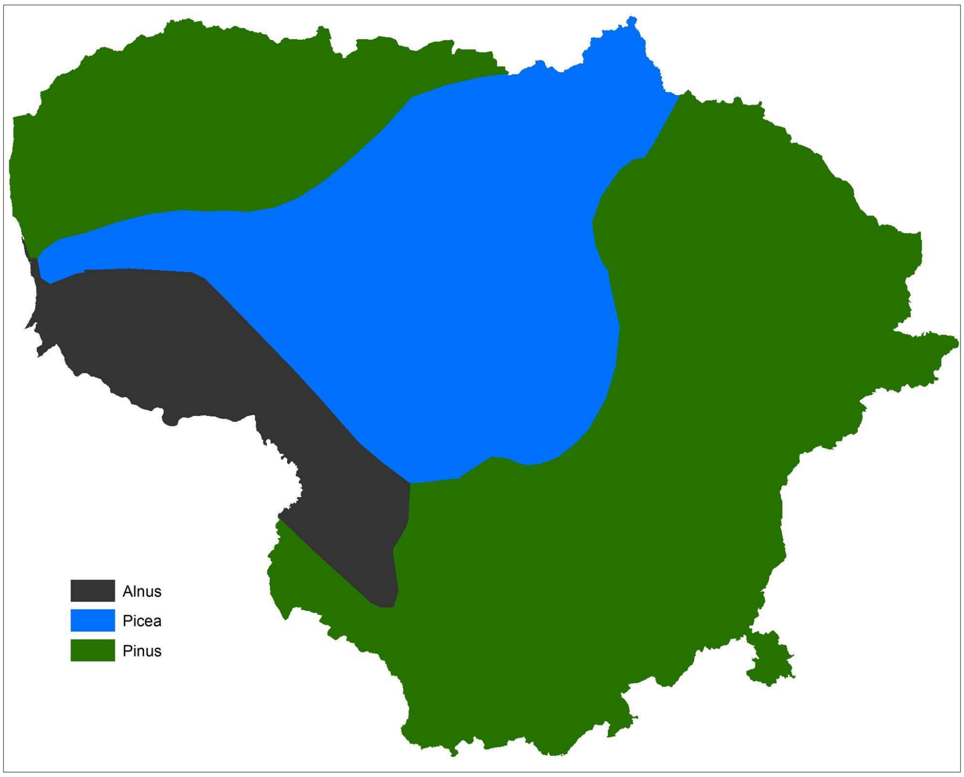


Fig. 24. *Prevailing tree taxa in Lithuania 4 000 – 2 600 cal BP, according to LRA modelling.*

2 600 – 1 000 cal BP

Territory, dominated by pine increase again (Fig. 25), which also matches conclusions of other investigators (Kabailienė, 1993). Birch increases as well, however, pine still prevails in sandy South-Eastern part of Lithuania. *Carpinus* decreases slightly, though, makes up to 10 % in the South-West.

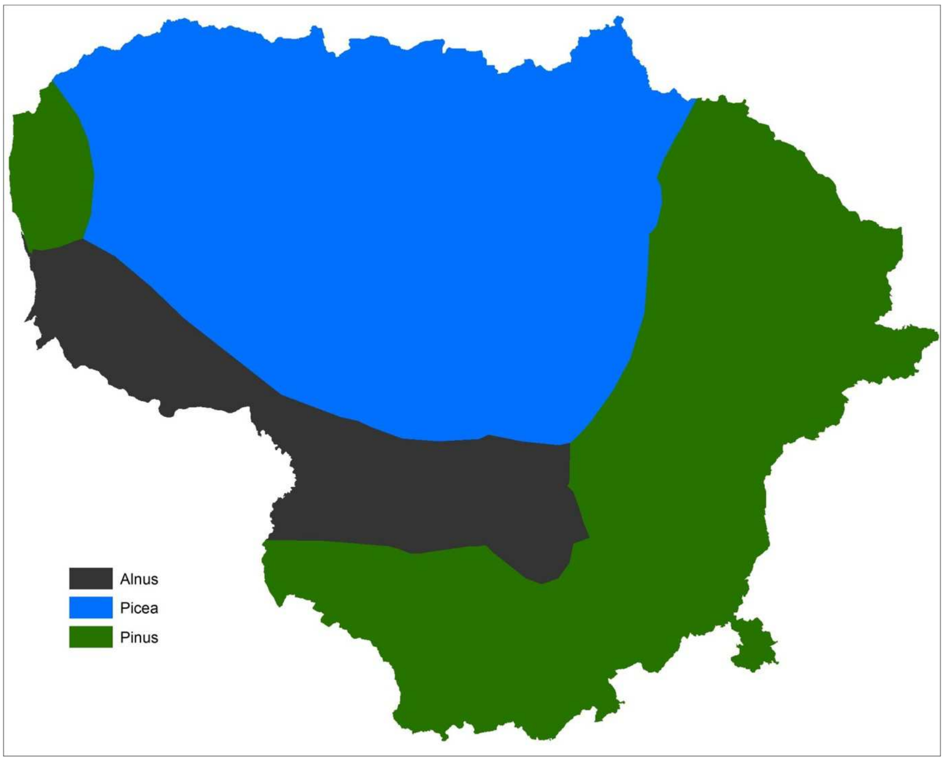


Fig. 25. *Prevailing tree taxa in Lithuania 2 600 – 1 000 cal BP, according to LRA modelling.*

1000 - 0 cal BP

Variety of prevailging taxa is lowest throughout the Holocene during this period (Fig. 26). Pine prevails almost in all Lithuania, except limited areas in the North and West, where spruce is the most abundant. However, spruce is significant in all territory of Lithuania and in many parts it is second most abundant after pine. Birch rarely makes more than 10 %. Ash spreads relatively significantly (up to 3-12 %) in the south, oak and lime forests make up to a few per cent in the south of Lithuania, but are less frequent in the Northern part. Alder and hornbeam forests decline dramatically, though they remain significant in Nemumas delta (Western Lithuania). Willow is relatively significant in the West.

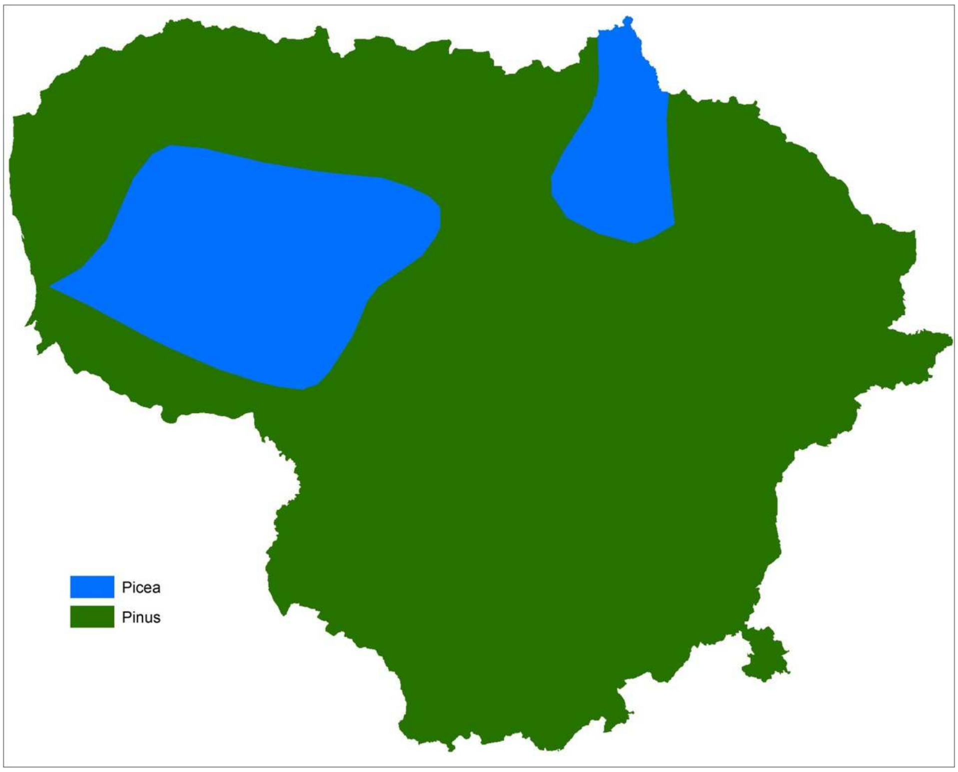


Fig. 26. Prevailing tree taxa in Lithuania 1 000 – 0 cal BP, according to LRA modelling.

Dependency of vegetation composition on the lithology of Quaternary sediments

In order to compare relationship of the past vegetation to underlying sediment lithology, palaeovegetation maps were intersected with the map of Quaternary deposits, provided by Geological Survey of Lithuania. Vegetation percentages were averaged for every sediment type. As palaeovegetation maps present smooth, interpolated data, while spatial patchiness of lithological types is relatively high, differences in vegetation percentages between different sediment types should be expected to be smoothened. Therefore, even small changes of average vegetation percentages between different sediment types can show significant dependency.

From curves of different lithological types, it is evident that pine has been more common in sandy and peaty deposits, and less common in territories, dominated by gyttja, clay or silt. Differences in birch percentages are less pronounced (Fig. 27). Birch was slighty more common in gyttja deposits (especially in the beginning of the Holocene and during the last 4 000 years) and tills. Spruce (Fig. 28) is more characteristic for till and silt, less common in gyttja. Alder is the most abundant in gyttja, clay or silt. Differences of hazel, elm and lime percentages in different sediment types are relatively low.

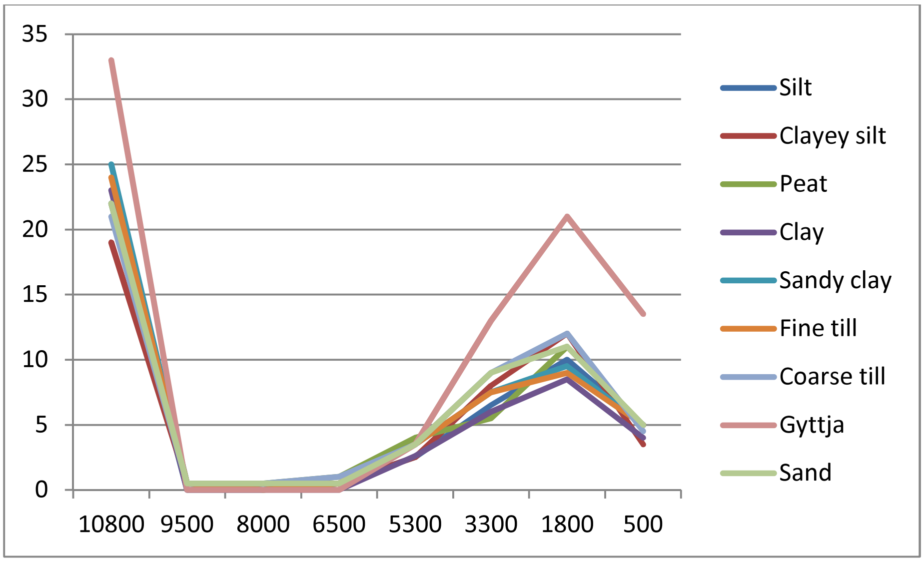


Fig. 27. *Reconstructed birch percentages during the Holocene in different lithological sediment types.*

It is evident from the analysis of dependency, that alder, spruce and pine are the most dependant on sediment types. Distribution of other taxa is considerably more even. During the first half of the Holocene, differences between sediment types are generally higher. This suggests that sediment lithology was more significant to distribution of vegetation. In the second half of the Holocene, significance of lithology decreases, since vegetation becomes increasingly affected by human activity.

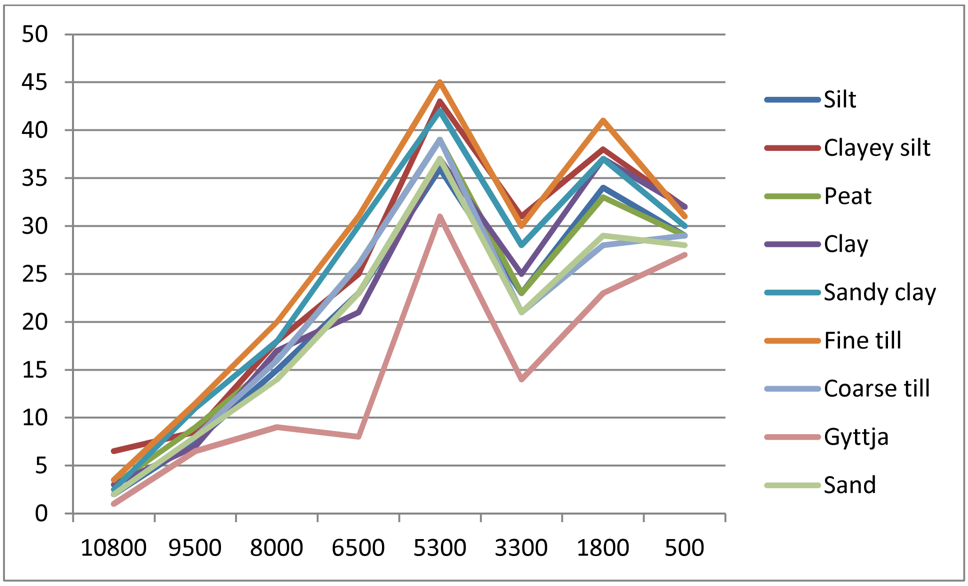


Fig. 28. *Reconstructed spruce percentages during the Holocene in different lithological sediment types.*

CONCLUSIONS

1. Using spatial pollen data in combination with automated GIS analysis and pollen-vegetation relationship functions enables detail reconstruction of past vegetation.
2. Simulation according to different pollen-vegetation relationship functions in the environment of Lithuania showed that best results were achieved using models developed by I. C. Prentice (1985, 1988) and S. Sugita (1993, 1994). As these models comprise LRA model (Sugita, 2007a; 2007b), the latter is best suited for past vegetation reconstruction in Lithuania.
3. Created isopollen maps correlate with similar studies in the neigbouring coutries, and therefore are suitable for vegetation modelling.
4. During the Late Glacial (17 000 – 11 500 cal BP) open landscape dominated in Lithuania, and almost no trees were present, except warmer period of 13 600 – 12 800 cal BP.
5. During the first slight warming of the Late Glacial (15 850-14 600 cal BP), dwarf birch (*Betula nana*) and polar willow (*Salix polaris*) were significant in the territory of Lithuania. Tree *Betula* started to grow at the same period.
6. During the warming of 13 600 – 12 800 cal BP, *Pinus* dominated in forests of Lithuania (in some territories making up to 90-100 %), as well as *Betula*. In the North-East Lithuania significant numbers of *Picea* were present.
7. Forested landscape started to prevail in the study area since 11 500 – 10 200 cal BP. During the first centuries of this period, *Betula* has spread throughout territory of Lithuania, then it was replaced by *Pinus*. *Corylus* and *Ulmus* were spreading from West or South-West. These taxa were making up to 10-20 % from total tree vegetation. *Picea* quantities decreased significantly.
8. 10 200 – 8 500 cal BP *Pinus* and *Betula* started to retreat, in large part of Lithuania *Corylus* became most abundant. *Pinus* still dominated in south-east because of sandy soils, that are wide-spread in this area. *Alnus* started to migrate to Lithuania from south-west.

9. During the warmest period of the Holocene (8 500 – 5 700 cal BP), *Picea* has spread from North to South. *Pinus* and *Betula* decreased. *Corylus* dominated in South-West and Central Lithuania, *Ulmus* – in North-East, *Alnus* – around Nemunas delta in Western Lithuania.
10. Starting with 5 700 cal BP, broadleaf trees dramatically decline in Lithuania and conifers prevail. *Picea* dominated in most of Lithuania, except South-West and South-East, where *Alnus* and *Pinus* were most abundant (respectively). Small amounts of *Carpinus* are recorded during this period in the South.
11. 4 000 – 2 600 cal BP *Picea* slightly retreats northwards, and returns at 2 600 – 1 000 cal BP.
12. Vegetation of the last millenium is similar to nowadays – pine prevails in most of the territory, maiking uo to 60-90 % in South-East. Spruce is more significant in the West.
13. The acquired results of vegetation reconstruction by their trends are similar to the results of earlier investigations, though, quantitative values differ significantly. Comparison of the reconstructed vegetation of the latest time-window to modern vegetation, suggests that results presented in this study are more precise.
14. Data, gathered in pollen database shows relatively low human impact (mostly – forest burning) in Mesolithic. During the Neolithic, cattle breeding becomes prevaling human activity. Arable farming becomes most important activity only during historical times.
15. Distribution of alder, spruce and pine was being determined mostly by the sediment lithology. Distribution of other taxa was more even.
16. In the first half of the Holocene, distribution of vegetation was mostly influenced by lithology of Quaternary sediments and climate change. In the second half of the Holocene, anthropogenic factor became increasingly significant, and eventually it became major factor, determining distribution of vegetation.

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