



A multi-proxy long-term ecological investigation into the development of a late Holocene calcareous spring-fed fen ecosystem (Raganu Mire) and boreal forest at the SE Baltic coast (Latvia)

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ARTICLE INFO

Keywords:

Climate change
Peatland
Plant macrofossils
Mollusc
Fire
Plant succession
Refugia
Biodiversity
Cladium mariscus

ABSTRACT

The calcareous substrate of spring-fed fens makes them unique islands of biodiversity, hosting endangered, vulnerable, and protected vascular plants. Hence, spring-fed fens ecosystems require special conservation attention because many of them are destroyed (e.g. drained, forested) and it is extremely difficult or even impossible to restore the unique hydrogeological and geochemical conditions enabling their function. The long-term perspective of paleoecological studies allows indication of former wetland ecosystem states and provides understanding of their development over millennia. To examine the late Holocene dynamics of a calcareous spring-fed fen (Raganu Mire) ecosystem on the Baltic Sea coast (Latvia) in relation to environmental changes, substrate and human activity, we have undertaken high-resolution analyses of plant macrofossils, pollen, mollusc, stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes combined with radiocarbon dating (AMS) in three coring locations. Our study revealed that peat deposits began accumulating ca. 7000 cal. yr BP and calcareous deposits (tufa) from 1450 cal. yr BP, coinciding with regional hydrological changes. Several fire events occurred between 4000 and 1600 cal. yr BP, which appeared to have had a limited effect on local vegetation. The most significant changes in the forest and peatland ecosystems were at 3200 cal. yr BP associated with a dry climate stage and high fire activity, and then between 1400 and 500 cal. yr BP potentially associated with temperature changes during the Medieval Climate Anomaly (MCA) and Little Ice Age. Hydrological disturbances in the peatland catchment from 1400 cal. yr BP were most likely strengthened by human activity (deforestation) in this region. The relationship between the development of this peatland and changes in its catchment area, such as land cover changes or fluctuations in groundwater levels, suggest that protection and restoration of spring-fed fen ecosystems should also include the surrounding catchment. The presence of calcareous sediments, as well as appropriate temperature and local hydrological conditions appear to be the most crucial factors controlling *Cladium mariscus* populations in our site - currently at the eastern limit of its distribution in Europe.

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¹ Submitted posthumously.

<https://doi.org/10.1016/j.ecolind.2021.107673>

Received 25 June 2020; Received in revised form 19 January 2021; Accepted 29 March 2021

Available online 10 April 2021

1470-160X/© 2021 The Authors.

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1. Introduction

A key characteristic of calcareous spring-fed fen ecosystems is an active supply of groundwater enriched in dissolved carbonates (Succow, 1988; Andrews et al., 1997; Dobrowolski, 2011). The point outflow of the groundwater source typically limits the area of these environments to smaller than ~3 ha. The combination of a calcareous substrate, moist conditions and a relatively small area of calcareous spring-fed fens makes them unique islands of biodiversity - hosting endangered, vulnerable, and protected vascular plants (e.g. *Cladium mariscus*, *Schoenus ferrugineus*, *Epipactis palustris*), brown mosses (e.g. *Helodium blandowii*, *Paludella squarrosa*, *Tomentypnum nitens*), and mollusc species (*Vertigo moulinsiana*, *Vertigo angustior*, *Vertigo geyeri*). These important ecosystems are commonly surrounded by monoculture forests or agricultural fields and meadows (Wolejko et al., 1994; Bedford and Godwin, 2003; Grootjans et al., 2005, 2015). Spring-fed fens require special conservation attention because once they are destroyed (e.g. drained, forested), it is extremely difficult or even impossible to restore the unique hydrogeological and geochemical conditions enabling their function (cf. Grootjans et al., 2006; Lamers et al., 2015). Moreover, many of the species occurring at calcareous spring-fed fens have a stenotopic ecological amplitude limited to this alkaline habitat. They play an important role as bioindicators for various ecological parameters (e.g. water availability, nutrients) of the habitat state (Hájková et al., 2004; Horsák and Hajek, 2003). Decline of the habitat results in loss of this unique fauna and flora. Because the carbonates supplied to the surface of the spring-fed fen originate from leaching of the carbonate bedrock, changes in hydrological conditions resulting from climatic shifts can affect the groundwater supplying the fen and thereby influence the geochemical composition of its sediments (cf. Dobrowolski et al., 2016, 2019; Apolinarska and Gałka, 2017; Gałka et al., 2018). One common geological feature of calcareous spring-fed fens is alternating layers of peat and tufa as a consequence of dry (peat is accumulated) and wet (tufa is accumulated) phases in peatland development, that are often linked to past climate changes on a regional scale (Dobrowolski et al., 2016, 2019; Apolinarska and Gałka, 2017; Gałka et al., 2018; Pietruczuk et al., 2018). Along with the impact of climate changes, human activity such as drainage and deforestation may have played a distinctive role in the development of the spring-fed fens. Such a relationship was observed at some spring-fed fens developed in mountainous areas of the Czech Republic (Rybničková et al., 2005; Hájková et al., 2012a, 2012b). The influence of past climate changes and human pressure on vegetation and mollusc community dynamics can be reconstructed by palaeoecological analysis of the sediments deposited at the spring-fed fens. The results of palaeoecological studies are invaluable in improving understanding of the possible response of these ecosystems to predicted climate change. In temperate climates, where spring-fed fens are located, the future climate is predicted to experience decreased precipitation and higher temperatures (IPCC, 2014). Decreased precipitation is the greatest threat for the existence of the spring-fed fen ecosystems, as they rely on groundwater supply. Therefore, the development of effective management strategies to protect or restore these widely threatened habitats requires knowledge not only of the recent ecological functioning, but also of their long-term history (cf. Osadowski et al., 2018; Blaus et al., 2020).

This study adds to extensive palaeoecological research focusing on the development of rich fen and calcareous spring-fed fen ecosystems in Central Europe that host rare, endangered plant species such as *C. mariscus* (cf. Gałka et al., 2016; 2017a; 2018). Our study area is located at the current eastern limit of *C. mariscus* distribution in Europe, making this species particularly sensitive to changes in climate conditions and therefore fossil occurrence of this species in the sediments should be a promising bioindicator. For our study we selected a unique calcareous spring-fed fen ecosystem surrounded by a forested raised bog called Raganu Mire that has developed near the north-eastern Baltic coast. Since current and fossil plant and mollusc communities at spring-fed fens show high floristic and faunistic diversity, we investigated the

factors that have influenced the past development of these ecosystems, in two different sedimentary cores. Our multi-proxy palaeoecological study of a spring-fed fen ecosystem aims to: i) define the variability in local vegetation and mollusc communities using two parallel peat cores as replicates; ii) reconstruct the history of forest ecosystems and human activity in the surrounding area; iii) determine the influence of drivers (climate changes, fire, deforestation) on ecosystem development; and iv) specifically assess the factors responsible for the presence of *C. mariscus*, which is presently one of the most abundant plants at the study site.

2. Methods

2.1. Study site

The study area of Raganu Mire (56.9682847 N, 23.47946194444444 E) is located on the south-western coast of the Gulf of Riga in the Rigava Plain, characterised by wooded dunes, peatlands, and coastal lagoon lakes (Fig. 1). The upper part of the bedrock is composed of gypsum-bearing Devonian deposits belonging to the Salaspils Formation (Šķinķis, 1997). On a broader scale the study area is in the East European Plain, in the slightly oceanic part of hemiboreal vegetation zone (Ahti et al., 1968). There is maritime climatic influence in our study area. The mean temperature on the western coast of the Riga Gulf is -2 °C in February and 17.2 °C in July. The annual precipitation is 550 mm (Nikodemus, 2018). Raganu Mire is located in the Kemeru National Park and is included in the Natura 2000 network in Latvia (Natura 2000 code LV0200200). It hosts four habitats of the Habitats Directive Annex I, namely 7110* Active raised bogs, 7230 Alkaline fens, 7210* Calcareous fens with *C. mariscus*, and species of the *Caricion davallianae* and 3160 Dystrophic lakes (Council of the European Communities, 1992). Raganu Mire, including the area of calcareous spring-fed fen, is part of a peatland that extends more than 1200 ha. Mean peat depth is 3.6 m. The calcareous fen area includes a mosaic of dense stands of *C. mariscus*, *Sphagnum* hummocks, and shallow open spring water areas over sulphate-rich calcareous mud. Dwarf shrub species *Calluna vulgaris* and *Empetrum nigrum* grow abundantly on *Sphagnum fuscum*, *Sphagnum rubellum*, *Sphagnum medium*, and *Sphagnum angustifolium* hummocks as well as slow-growing *Pinus sylvestris*, *Juniperus communis*, and *Betula pubescens*. Acidophilous species such as *Oxycoccus palustris*, *Andromeda polifolia*, and *Rubus chamaemorus* also occur on *Sphagnum* hummocks. Other plant species, mainly *Schoenus ferrugineus*, *Primula farinosa*, *Pinguicula vulgaris*, and *Triglochin palustre* as well as brown mosses *Scorpidium cossonii* and *Campylium stellatum* occur on the margin of these hummocks close to the water. Common plant species in the *Cladium* stands include *Thelypteris palustris*, *Molinia caerulea*, and *Myrica gale*. The moss layer consists of *Scorpidium scorpioides*, *Scorpidium cossonii*, and *Campylium stellatum*. Small hummocks of *Sphagnum warnstorffii*, *Sphagnum teres*, and *Paludella squarrosa* are occasionally found within *Cladium* stands in the calcareous spring-fed fen. In the open water - *Scirpus tabernaemontani*, *Phragmites australis*, and *Chara aspera* grow.

Raised bog vegetation in the neighbouring area is characterised by low hummocks of *Sphagnum medium*, *S. angustifolium*, *S. fuscum*, and *S. rubellum*, with dense cover of *Calluna vulgaris* and *Ledum palustre*. Common associates are *Eriophorum vaginatum*, *Empetrum nigrum*, *Rubus chamaemorus*, *Oxycoccus palustris*, and *Drosera rotundifolia*. There is a well-developed *Pinus sylvestris* cover in Raganu Mire due to marginal drainage and a road crossing the mire. However, a hummock-hollow complex and bog pools are still present in the central part of Raganu Mire. There was a fire in the 1950s in western part of Raganu Mire, including the calcareous spring-fed fen area.

The first known human evidence in the study area dates from the Middle Neolithic (3000–2000 yr BC; middle Holocene) of hunters and fishermen in the Siliņupe Settlement (Zagorska, 1998; Vasks, 2015). This time corresponds to the Littorina Sea period in the Baltic Sea area. It is assumed that the first intensive land cultivation and live stock keeping in Latvia started in the Bronze Age, ca. 2000 yr BC (Lang, 1999 in Vasks,

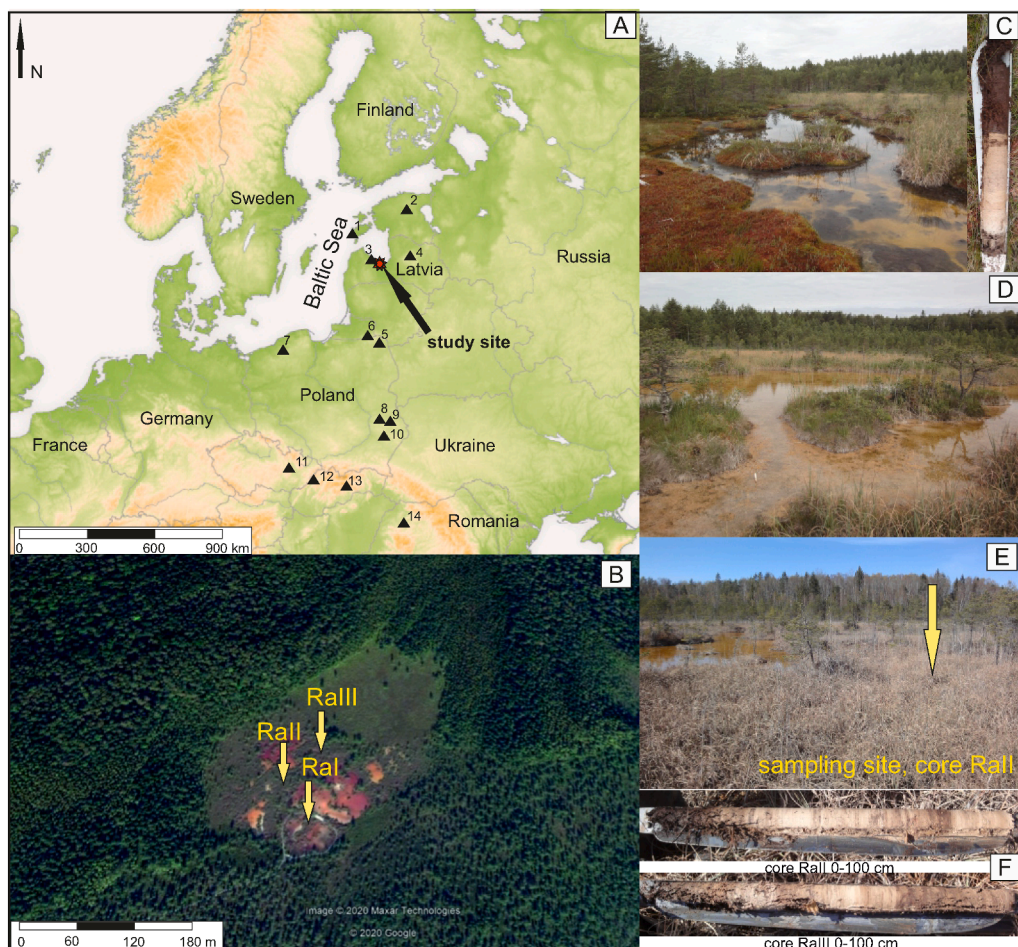


Fig. 1. Site locations across Central Europe (source https://commons.wikimedia.org/wiki/File:Europe_topography_map.png Author: San Jose; modified) with the locations of the sites (black triangles) cited in the text: 1) Kanna fen (Blaus et al., 2020); 1) Männikjärve bog (Sillasoo et al., 2007); 2) Apšuciems Mire (Gaika et al., 2016), 4) Lake Trikāta (Stivrins et al., 2016); 5) Purwin spring-fed fen (Apolinarska and Gaika, 2017), 6) Mechacz Wielki bog (Gaika et al., 2017); 7) Bobolice spring mire (Osadowski et al., 2018); 8) Pawłów spring-fed fen (Pietruczuk et al., 2018); 9) Bagno Serebryskie rich fen (Gaika et al., 2017a), 10) Komarów spring-fed fen (Dobrowolski et al., 2016), 11) Male Bielice (Hájková et al., 2013), 12) Mníchova Lehota (Hájková et al., 2012a), 13) Hozelec (Hájková et al., 2012a); 14) Valea Morii spring-fed fen (Gaika et al., 2018); B) location map of the study site in the Latvia; C-E) view of the Raganu spring-fed fen, please notice *Sphagnum* peat deposited on the tufa, presented on the picture C; F) view of the upper part of the sediments deposited in sampling sites.

Tab 1
Radiocarbon dates. Raganu spring-fed fen.

Site/Depth (cm)	Material	Nr. Lab.	C14 date	Age cal. yr BP (94.5%)	Age CE/BCE (94.5%)
Ra I 109–110	Wing od seed of <i>Picea abies</i> , 2 fruits of <i>Betula</i> sec. Alba, bud scales and periderm of <i>Pinus sylvestris</i>	Poz-64451	1160 ± 30 BP	1177–983	773–968
Ra I 198–199	6 fruits of <i>Carex</i> sp., fragm. needle of <i>Pinus sylvestris</i> , 1 fruit of <i>Betula</i> sect. albae	Poz-67320	3850 ± 35 BP	4408–4155	–2459– –2206
Ra II 21–22	Brown moss stems	Poz-72490	580 ± 30 BP	651–532	1300–1419
Ra II 40–41	3 seeds of <i>Cladium mariscus</i> , 1 fruit of <i>Betula</i> sp. periderm of <i>Pinus sylvestris</i> , flower of <i>Calluna vulgaris</i>	Poz-72491	590 ± 30 BP	652–537	1299–1413
Ra II 64–65	7 seeds of <i>Cladium mariscus</i> , 2 fruits of <i>Betula</i> sp.	Poz-72510	1015 ± 30 BP	979–802	971–1149
Ra II 79–81	7 <i>Cladium mariscus</i> , 2 fruits of <i>Betula</i> sp., 1 bud scales of <i>Pinus sylvestris</i>	Poz-72511	1235 ± 30 BP	1264–1070	686–880
Ra II 104–106	8 fruits of <i>Carex</i> cf. <i>lasiocarpa</i>	Poz-72512	1620 ± 30 BP	1569–1412	382–539
Ra II 136–137	9 fruits of <i>Potentilla erecta</i> , fragments of <i>Pinus sylvestris</i> needle	Poz-72513	2450 ± 30 BP	2703–2360	–754– –411
Ra II 163–164	16 fruits of <i>Potentilla erecta</i>	Poz-70162	3315 ± 35 BP	3632–3458	1683–1509
Ra II 230–231	3 seeds of <i>Rubus idaeus</i>	Poz-70163	5550 ± 40 BP	6407–6287	4458–4338
Ra III 27–28	<i>Pinus sylvestris</i> needle	Poz-72489	455 ± 30 BP	538–478	1413–1473
Ra III 64–65	Brown moss stems	Poz-64453	1230 ± 30 BP	1262–1068	689–882
Ra III 100–101	<i>Sphagnum</i> stems	Poz-64454	1565 ± 30 BP	1532–1391	419–560
Ra III 166–168	17 fruits of <i>Potentilla erecta</i>	Poz-78462	3280 ± 35 BP	3585–3409	–1636– –1460

2015).

2.2. Fieldwork

Three cores located ca. 60 m apart were extracted in 2014 using a Russian-type peat corer (7 cm in diameter and 100 cm in length) from the central part of the mire surface. Selection of the coring sites was determined by the presence of the best-developed populations of *C. mariscus* and mosses. The RaI, RaII, and RaIII cores were 365-cm, 247-cm, and 174-cm long, respectively. At the coring sites, the water-table was ca. 15 cm below the fen surface. The 0.5 m long cores were individually wrapped and stored at 4 °C until subsampling. Two cores (RaII and RaIII) from the central part of peatland were selected for detailed palaeoecological analysis.

2.3. Chronology

To establish the chronology of the two sediment sequences, eight samples from the core RaII, and four from the core RaIII were used for radiocarbon dating. In addition, two dates were analysed from core RaI. AMS (Accelerator Mass Spectrometry) ^{14}C dates were determined at the Poznań Radiocarbon Laboratory (Table 1). The calibration of the radiocarbon dates and the construction of Bayesian age-depth models was performed with OxCal 4.3.2 software (Ramsey and Lee, 2013) using IntCal13 (Reimer et al., 2013) atmospheric curves. The age-depth models were calculated using the *P_Sequence* function (k_0 parameter = 1 cm^{-1} ; interpolation: 1.0-cm resolution, $\log_{10}(k/k_0) = 1$; Fig. 2). The most distinct changes in peat composition determined from plant macrofossil analysis were treated as a signal of changes in peat accumulation rate, and were included in the models using the Boundary command (Fig. 2). For greater readability here, the μ value (mean value of the modelled age) was selected as this reflects the modelled age, which is expressed as cal. yr BP (1950 CE = 0 cal yr BP).

2.4. Plant macrofossils analysis

Plant macrofossils were analysed in contiguous 1-cm slices, totalling 420 samples. Approximately 15 cm^3 of material from each sample interval were washed and sieved under a warm-water spray using a 0.20-

mm mesh sieve. Details of the methods used for the plant macrofossil analysis were provided by Gałka et al. (2016). The volume percentages of the different vegetative remains were estimated to the nearest 5% or presence/absence. Seeds, fruits, and bud scales were counted separately employing a stereoscopic microscope and were expressed as absolute numbers. Macroscopic charcoal pieces ($>1\text{ mm}$) were also counted during routine plant macrofossils analysis. Their presence provides information on past local fire occurrence (Mooney and Tinner, 2011). The ecological requirements of several key plant species (Ellenberg et al., 1991; Zarzycki et al., 2002) were used to distinguish wet and dry phases in peatland development. The nomenclature followed are Gavrilova and Sulcs (1999) for vascular plants, Hill et al. (2006) for mosses, and Hajek et al. (2006) for fen mosses.

2.5. Mollusc analysis

Sediment samples from the RaII and RaIII profiles were examined for mollusc shells at contiguous 1-cm intervals. Complete mollusc shells and recognisable shell fragments were hand-picked and identified under a low-power binocular microscope (Zeiss Stemi 2000-C) using the reference collection of the Institute of Geology AMU in Poznań, as well as keys and atlases (Lożek, 1964; Piechocki, 1979; Welter-Schultes, 2012). The mollusc remains are expressed as absolute numbers (Fig. 5). To better illustrate the response of the mollusc population to palaeohydrological changes, they were divided into two major ecological groups according to their environmental requirements (Alexandrowicz and Alexandrowicz, 2013): terrestrial species (open country, damp, wide ecological tolerance) and aquatic species (very wet, episodic basins, lakes).

2.6. Pollen analysis

Eighty-eight samples from core RaII, each 1 cm^3 in volume, were prepared for pollen analysis using standard preparation procedures (see Berglund and Ralska-Jasiewiczowa, 1986). Due to strongly decomposed peat and low pollen concentrations in the bottom part of the peat core (247–171 cm), the pollen analysis was carried out in 2-cm resolution only at a depth between 0 and 171 cm. Samples were counted until at least 450 tree and herb pollen taxa were reached (mean 461 pollen). Due

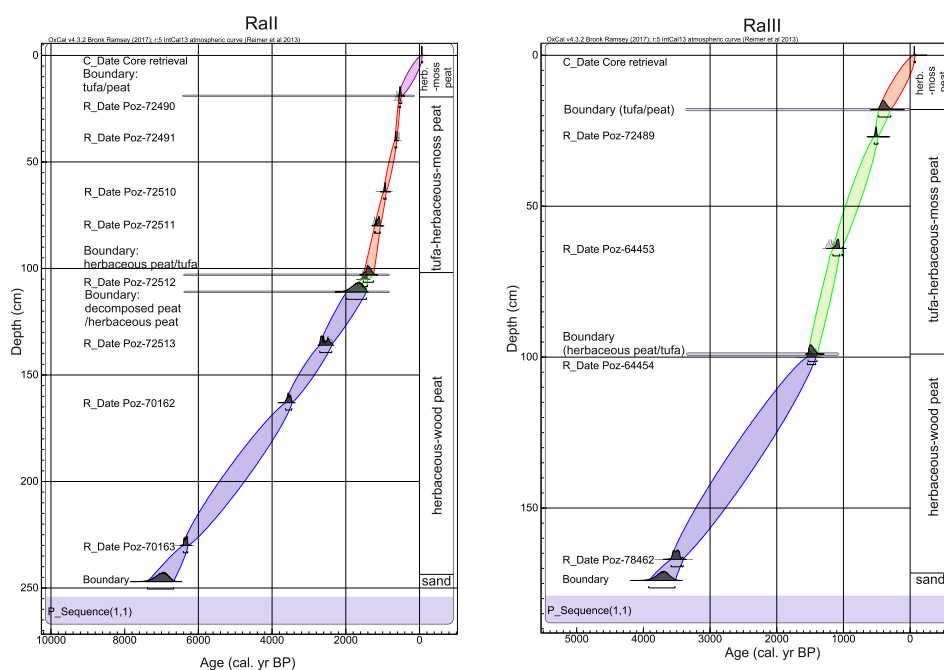


Fig. 2. Age-depth models of the sediment sequences in Raganu spring-fed fen: RaII and RaIII.

to extremely low pollen concentration, this pollen sum was not reached in some samples. Percentage values of terrestrial plants were calculated based on their pollen sum (pollen sum of AP + NAP). Percentages excluded from the terrestrial pollen sum (cryptogams, limnophytes, telmatophytes, and Cyperaceae) were calculated as a proportion of their own sum added to the terrestrial pollen sum. The pollen taxa were

identified with the assistance of the modern pollen slide collection of the Department of Biogeography and Paleocology, Adam Mickiewicz University in Poznań as well as relevant keys and atlases (e.g. Moore et al., 1991; Beug, 2004).

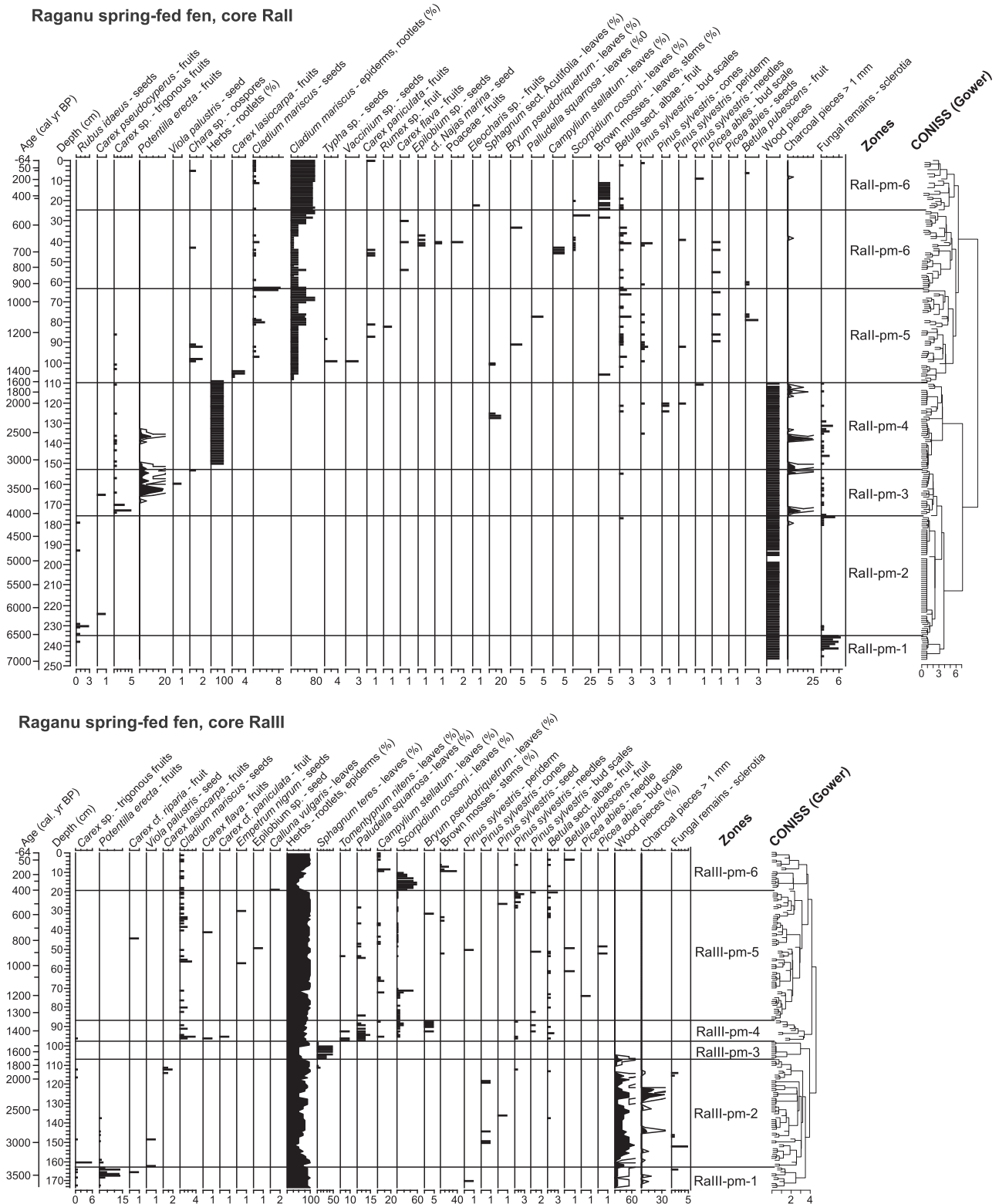


Fig. 3. Local plant succession in Raganu spring-fed fen based on plant macrofossils: A) Core Rall; B) Core RallI. Taxa with (%) are estimated volume percentages and all others are counts (with X-axis scale labels; note scale differences).

2.7. Stable isotope analysis

Stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopic compositions were measured in the carbonate tufa occurring in the RaII sediment sequence at a depth between 23 and 99 cm. Samples for the isotope analysis (1 cm³ each) were taken at 2-cm intervals. After drying at 50 °C, the samples were sieved through a 0.5-mm mesh to eliminate mollusc shells and ground to a fine powder in an agate mortar. Stable isotope compositions of the carbonates were analysed using a Kiel IV online carbonate preparation line connected to a Thermo Finnigan Delta + mass spectrometer. Calcites were dissolved using 100% phosphoric acid (density 1.9) at 75 °C. All values are reported as δ values, where $\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, in per mil relative to V-PDB by assigning a $\delta^{13}\text{C}$ value of 1.95‰ and a $\delta^{18}\text{O}$ value of -2.20‰ to NBS19. Reproducibility was checked based on the long-term repeatability of NBS19 analysis and was better than ± 0.03 and 0.07% , for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively.

2.8. Numerical analysis and data presentation

The results of the plant macrofossil, charcoal, pollen, mollusc, and stable isotope analyses (Figs. 3–5) and the summary figure (Fig. 7) were presented as diagrams drawn with the C2 graphics program (Juggins, 2003). The results of pollen analysis are presented as diagrams, divided into zones cross validated by the CONISS method, drawn with the Tilia graphics program (Grimm, 1992). Principal component analysis (PCA) was performed on the pollen record to determine the relationships between past vegetation composition. The resulting eigenvalues were tested for significance using a broken stick model (Birks, 2012). The PCA was constructed based on the correlation matrix using the PAST software (Hammer et al., 2020). Ordination of principle coordinates (CAP) analysis was undertaken to investigate the relationship between corresponding isotope ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) and species data with depth for pollen, molluscs, and plant macrofossils respectively in the RaII core (23–99 cm). Mollusc and plant macrofossil species with <5 occurrences were removed to reduced clustering and pollen species with a maximum abundance <5% or <5 occurrences were removed. Owing to the mixture of count and percentage abundance data in the plant macrofossil dataset, we used the “capscale” function in the R package vegan (Oksanen et al., 2019), a variant of CAP (Anderson and Willis, 2003) alongside Gower (1971) dissimilarity (see Birks, 2014).

3. Results

3.1. Lithostratigraphy, chronology and sediment accumulation rate

Results of the radiocarbon dating of all cores are presented in Table 1 and the age-depth models of RaII and Ra III are shown in Fig. 2. In RaII the peat has accumulated since ca. 7000 cal. yr BP and in RaIII since ca. 3700 cal yr BP. The lowermost sections of both profiles 244–108 cm (ca. 7000–1600 cal. yr BP) in RaII and 174–106 cm (ca. 3700–1650 cal. yr BP) in RaIII, respectively, contain highly decomposed herbaceous-wood peat deposited on sand. Peat composed mainly of *Sphagnum* remains was recorded at the depth of 106–100 cm (1650–1500 cal. yr BP) in core RaII. Tufa with herb roots and brown mosses was accumulated between 108 and 19 cm (ca. 1600–500 cal. yr BP) in core RaII and between 100 and 18 cm (1500–400 cal. yr BP) in core RaIII. The uppermost sections, between 19 and 0 cm (500 to -64 cal. yr BP) in RaII and between 18 and 0 cm (400 to -64 cal. yr BP) in RaIII, consist of decomposed peat with brown moss remains and *Cladium mariscus* roots. The RaI sediment sequence comprises decomposed peat between 345 and 125 cm, herbaceous-moss peat between 125 and 109 cm, tufa between 109 and 22 cm, and herbaceous-moss peat between 22 and 0 cm. Tufa began accumulating ca. 1100 cal. yr BP (radiocarbon date 1177–983 cal. yr BP, cf. Table 1). The age-depth models (Fig. 2) show that the sedimentation rate (SR) averaged 0.34 mm/year in RaII and 0.46 mm/year in RaIII.

The highest SR was observed between 1600 and 500 cal. yr BP in RaII (1.11 mm/year) and between 1500 and 400 cal. yr BP in core RaIII (1.34 mm/yr), coinciding with the carbonate tufa sediments.

3.2. Plant macrofossils

Core RaII. Seven zones in the local vegetation development were determined based on a visual inspection and CONISS for the core RaII (Fig. 3). Zone RaII-pm-1 (7000–6500 cal. yr BP; 247–235 cm) is macrofossil poor, characterised by the abundant presence of fungal remains and *Rubus idaeus* seeds. Zone RaII-pm-2 (6500–4050 cal. yr BP; 235–176 cm) is composed of wood pieces and *R. idaeus* seeds. A single charcoal piece is also present. During RaII-pm-3 (4050–3200 cal. yr BP; 176–152 cm) numerous fossils of *Potentilla erecta* appear with *Carex* sp. and charcoal pieces are present throughout the zone. In zone RaII-pm-4 (3200–1600 cal. yr BP; 152–110 cm), the presence of *P. erecta* and *Carex* sp. continues, while *Sphagnum* sect. *Acutifolia* and *Pinus sylvestris* macrofossils are recorded for the first time. Charcoal pieces and fungal remains are quite common during this zone. Zone RaII-pm-5 (1600–950 cal yr BP; 152–63 cm) is characterised by the increase of species diversity. In this zone numerous and diverse remains of trees (*Betula* sect. *albae*, *P. sylvestris* and *Picea abies*), the appearance of brown mosses (*Bryum pseudotriquetrum* and *Paludella squarrosa*), *Cladium mariscus* and *Carex lasiocarpa* are also documented. In RaII-pm-6 (950–550 cal. yr BP; 63–25 cm), *Campylium stellatum*, *Scorpidium cossonii* (both brown mosses), and *Carex flava* are recorded for the first time. *C. mariscus* and the remains of *P. sylvestris* and *Betula* sp. trees are quite common. Zone RaII-pm-7 (550–64 cal. yr BP; 25–0 cm) is dominated by *C. mariscus* and brown moss remains.

Core RaIII. Six zones in the local vegetation development, confirmed by CONISS (Gower), were determined for the core RaIII (Fig. 3). Zone RaIII-pm-1 (3700–3350 cal. yr BP; 174–163 cm) is composed of *P. erecta*, *Carex* sp., and fragments of unidentified wood. Charcoal pieces are also present. In RaIII-pm-2 (3350–1700 cal. yr BP; 163–106 cm) wood and charcoal pieces are dominant. *P. erecta* and *Carex* sp. are still present, alongside *P. sylvestris* and fungal remains. Zone RaIII-pm-3 (1700–1450 cal. yr BP; 106–97 cm) is characterised by the dominance of *Sphagnum teres*. In zone RaIII-pm-4 (1450–1350 cal. yr BP; 97–87 cm), the presence of *Cladium mariscus* and numerous brown mosses, e.g. *Tomentypnum nitens*, *Bryum pseudotriquetrum*, and *Paludella squarrosa* are recorded for the first time. Zone RaIII-pm-5 (1350–400 cal. yr BP; 87–19 cm) is characterised by numerous *C. mariscus* seeds, herbs roots, *Scorpidium cossonii* leaves, as well as the presence of *Empetrum nigrum* seeds. This zone also shows abundant and diverse remains of trees. In RaIII-pm-6 (400–64; 19–0 cm), herb roots and *S. cossonii* leaves dominate the record, with limited *P. sylvestris* and *Betula* sp. remains. *C. mariscus* seeds are present almost continuously.

3.3. Molluscs

Core RaII. Five mollusc zones, confirmed by CONISS (Gower), were distinguished in the core RaII (Fig. 4). Zone RaII-mo-1 (1600–1320 cal yr BP; 109–97 cm) is characterised by low diversity and abundance of the mollusc assemblage. The first species, *Carychium tridentatum* and *Omphiscola glabra*, appear ca. 1600 cal. yr BP. At ca. 1370 cal yr BP the first occurrence of *Galba truncatula*, and *Planorbis planorbis* is recorded. In Ra-mo-2 (1320–1100 cal. yr BP; 97–88 cm) *G. truncatula* and *P. planorbis* are dominant species. Before the end of this zone, ca. 1120 cal. yr BP, *Bathymophalus contortus* appears. Zone Ra-mo-3 is dominated by *Stagnicola palustris*, *G. truncatula*, and *P. planorbis*. The abundant species among Lymnaeidae are comprised of juvenile shells, most probably indistinguishable at the early stage of growth between *S. palustris* and *G. truncatula*. During zone Ra-mo-4 (1100–400; 88–18 cm) *S. palustris*, *G. truncatula*, and species among Lymnaeidae are dominant and reach their highest abundance. *Radix labiata* appears ca. 670 cal. yr BP. Two terrestrial species, *Vallonia pulchella* and

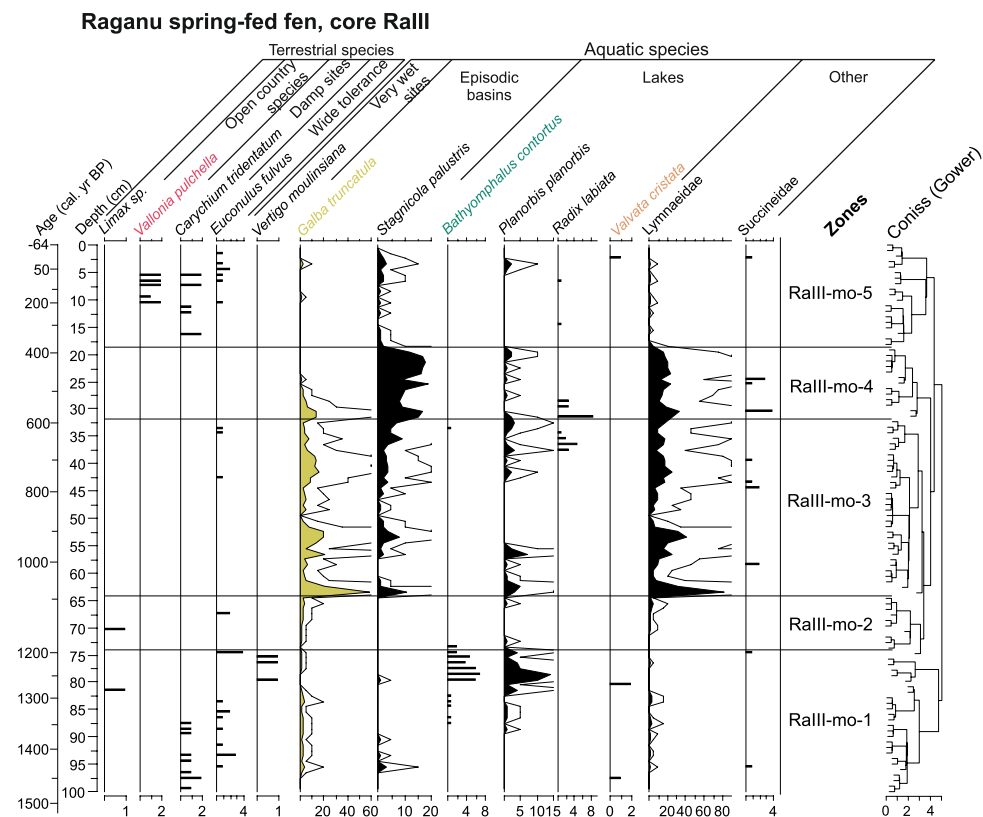
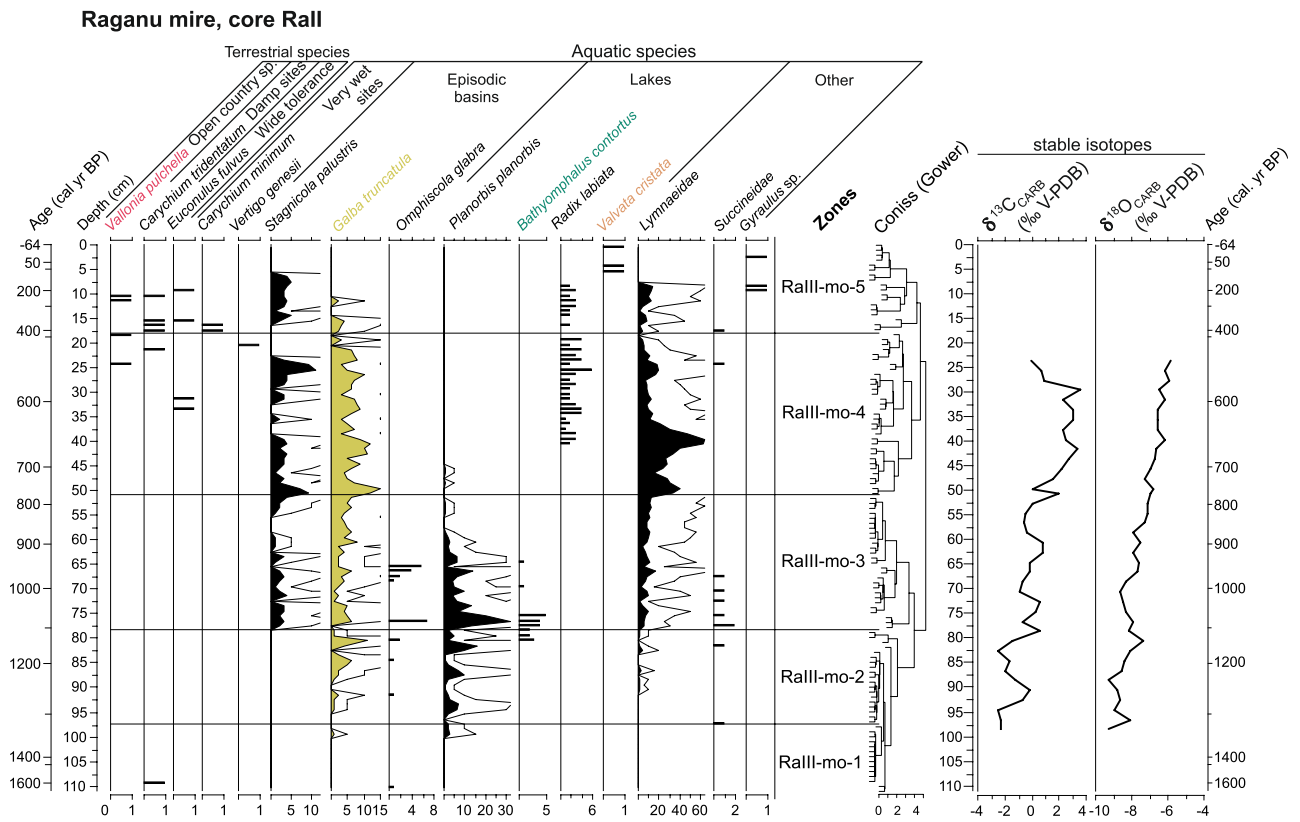


Fig. 4. Local mollusc succession in Raganu spring-fed fen: A) Core Rall; B) Core Ralll and stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopic compositions.

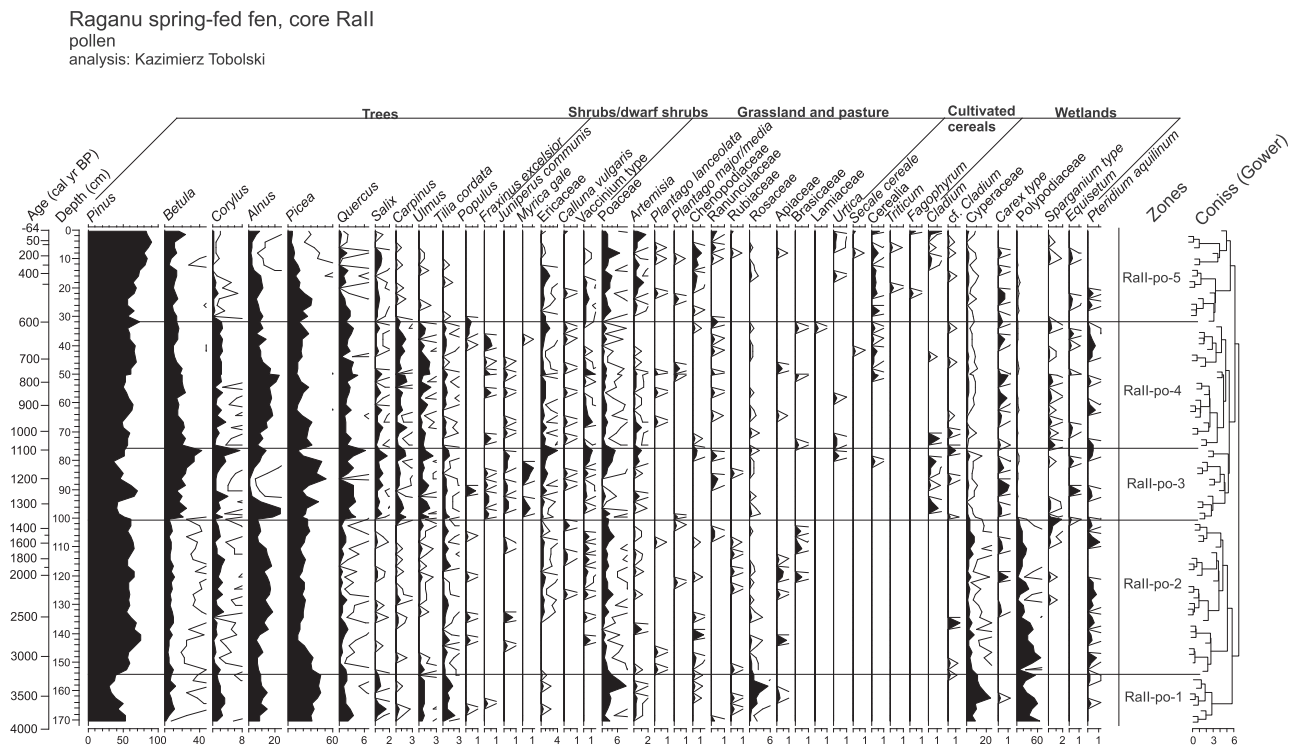


Fig. 5. Regional and local plant succession in Raganu spring-fed fen based on selected taxa of pollen and spores in core RaII. Percentages are shown in black; 5 times exaggeration in grey.

C. tridentatum, occur in the upper part of this zone. Zone RaII-mo-5 (400–64; 18–0 cm) is characterised by the highest species variability in the sediment sequence. *Carychium minimum*, *Valvata cristata*, and *Gyrulus* sp. are recorded only during this zone.

Core RaIII. Five mollusc zones, confirmed by CONISS (Gower), were determined for the core RaIII (Fig. 4). Zone RaIII-mo-1 (1470–1200 cal yr BP; 100–74 cm) is composed of terrestrial (*Carychium tridentatum*, *Euconulus fulvus*) and aquatic species (*Galba truncatula*, *Bathymorphalus contortus*, *Planorbis planorbis*). Zone RaIII-ma-2 (1200–1100 cal. yr BP; 74–64 cm) is characterised by the lowest abundance of the shells in the profile. However, *E. fulvus*, *G. truncatula*, and *P. planorbis* are still the dominant species. In the zone RaIII-mo-3 (1100–600 cal. yr BP; 64–32 cm) numerous occurrences of aquatic species such as *G. truncatula*, *Stagnicola palustris*, and *P. planorbis* are recorded. Abundant shells of Lymnaeidae and the appearance of *Radix labiata* is also characteristic for this zone. During zone RaIII-mo-4 (600–380 cal. yr BP; 32–18 cm) *S. palustris* reaches its maximum abundance, whereas ca. 370 cal. yr BP *G. truncatula* disappears. During zone Ra-mo-5 (370–64 cal. yr BP; 18–0 cm) terrestrial snails (*Vallonia pulchella*, *C. tridentatum*, *E. fulvus*) reappear. Among aquatic species *S. palustris* is present, but in low numbers.

3.4. Isotopes

There is a clear increasing trend in the carbon and oxygen stable isotope values measured in the carbonate tufa in the RaII core (Fig. 4). $\delta^{13}\text{C}$ values increase from -2.5 to 3.6‰ and $\delta^{18}\text{O}$ values increase from -9.3 to -5.8‰ between ca. 1350 cal. yr BP and ca. 580 cal yr BP. The overall enrichment in the heavy carbon (^{13}C) and oxygen (^{18}O) isotopes is interspersed with slight variation from the general trend, particularly in the carbon stable isotope record (amplitude of up to 2.3‰).

3.5. Pollen

Five pollen zones, confirmed by CONISS (Gower), were determined in RaII (Fig. 5). The samples below 171 cm (older than 3900 cal yr. BP)

were devoid of pollen, which hampered a vegetation reconstruction prior to this time. In terms of coniferous trees, the zone RaII-po-1 (3900–3200 cal. yr BP; 171–154 cm) is dominated by *Pinus* (up to 50%) and *Picea* (up to 40%). Among deciduous tree species, the cold adapted *Betula* and *Alnus* dominate, whereas temperate species (*Quercus*, *Ulmus*, and *Tilia*) have a minor contribution. Poaceae and Rosaceae reach the highest values in the RaII-po-1. The zone RaII-po-2 (3200–1370 cal. yr BP; 154–99 cm) is characterised by an increased pollen percentage of *Pinus* (ca. 55%, with one peak up to 70% ca. 2800 cal. yr BP). In contrast, the pollen abundance of *Betula* (ca. 10%), *Picea* (mean value ca. 18%), and temperate deciduous trees decreased. Pollen of natural grasslands (Poaceae) and pastures (*Plantago* spp.) is also common. Relatively high values of Cyperaceae and Polypodiaceae are also recorded.

The third zone RaII-po-3 (1370–1100 cal. yr BP; 99–78 cm) shows an increase in *Picea* (up to 40%), cold deciduous species, e.g. *Betula* (up to 40%, ca. 1100 cal. yr BP), and temperate deciduous species, e.g. *Quercus* (up to 3%), *Ulmus*, *Tilia*, *Salix* and *Fraxinus* trees. A peak of *Alnus* (up to 20%) followed by a sudden decrease (to 0.8%) is observed at the beginning of this zone. *Myrica*, *Cladium*, and *Cerealia* appear for the first time. In the zone RaII-po-4 (1100–600 cal. yr BP; 78–32 cm) the proportion between conifer and deciduous trees percentages remains relatively stable. From ca. 790 cal. yr BP, an almost constant presence of *Cerealia* is recorded. *Sparganium* pollen is relatively common during this zone. The zone RaII-po-5 (600–64 cal. yr BP; 32–0 cm) starts first with a sharp decline in the proportion of temperate deciduous trees, including *Carpinus*, *Ulmus*, *Tilia*, followed by a decrease in *Quercus* (from ca. 550 cal. yr BP) and *Alnus* (from ca. 400 cal. yr BP). Among conifer species, the proportion of *Pinus sylvestris* increases while that of *Picea abies* declines. The proportion and diversity of grassland and pasture pollen types (including Poaceae, *Artemisia*, Chenopodiaceae) and in cultivated cereals increase. *Cladium* appears in the uppermost part of the sediment sequence.

3.6. Numerical analysis (Fig. 6)

Relationship between local vegetation and mollusc species, isotopic values in core RaII.

3.6.1. Constrained ordination of principle coordinates (CAP)

In RaII (23–99 cm) ordination analysis (CAP) revealed a very weak association between plant macrofossil data and isotope values ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$), with 9.43% and 1.67% inertia (squared Gower distance) in the data explained by axis 1 (CAP1) and axis 2 (CAP2) respectively (Fig. 6a). There is a very slight association of *Cladium mariscus* rootlets and increasing isotope values and this could in fact be an artefact, as younger roots may have penetrated into older peat layers. Mollusc data with depth had a stronger relationship with $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ concentrations, here axis 1 (CAP1) explains 34.67% inertia in the data and 1.31% in axis 2 (CAP2; Fig. 6b). Isotope concentrations appear to be driving axis 1 and there is a clear association between Lymnaeidae and higher isotope concentrations. There is slight association of *Galba truncatula* and *Stagnicola palustris* and increased isotope values, while *Planorbis planorbis* is linked to lower values. For pollen data and isotope values with depth, axis 1 (CAP1; 15.85% of inertia) appears to be largely driven by isotope concentrations and axis 2 (CAP2) explains 2.68% of inertia in the data (Fig. 6c). *Pinus sylvestris* shows an association with higher isotope values and decreased sample depth, while *Picea abies* and *Betula* spp. appear to

be associated with lower $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ concentrations and increased sample depth.

3.6.2. Principle components analysis (PCA)

The first significant PCA axis explains 13% of the variance on the pollen record and separates *Pinus*, *Betula*, dry pastures, and meadows from *Picea abies*, deciduous tree species and wetlands shrubs and herbs, thus appearing to capture a change in hydrological gradient. The second significant axis explains 12% of the variance and separates all forest taxa, except of *Pinus* from non-arboreal taxa (pastures, grasslands, and crops, including *Cladium*), thus likely capturing the degree of vegetation openness.

4. Discussion

4.1. Heterogeneity or homogeneity of vegetation and mollusc communities at two sites

Due to lateral diversity of vegetation and mollusc assemblages typically observed in modern spring-fed fen ecosystems (cf. Galka et al., 2018), differences were also expected in the local succession of plant and mollusc records between the two cores at the Raganu Mire. However, the plant successions in RaII and RaIII show more similarities than differences. Between 3700 and 1600 cal. yr BP peat was accumulated in the

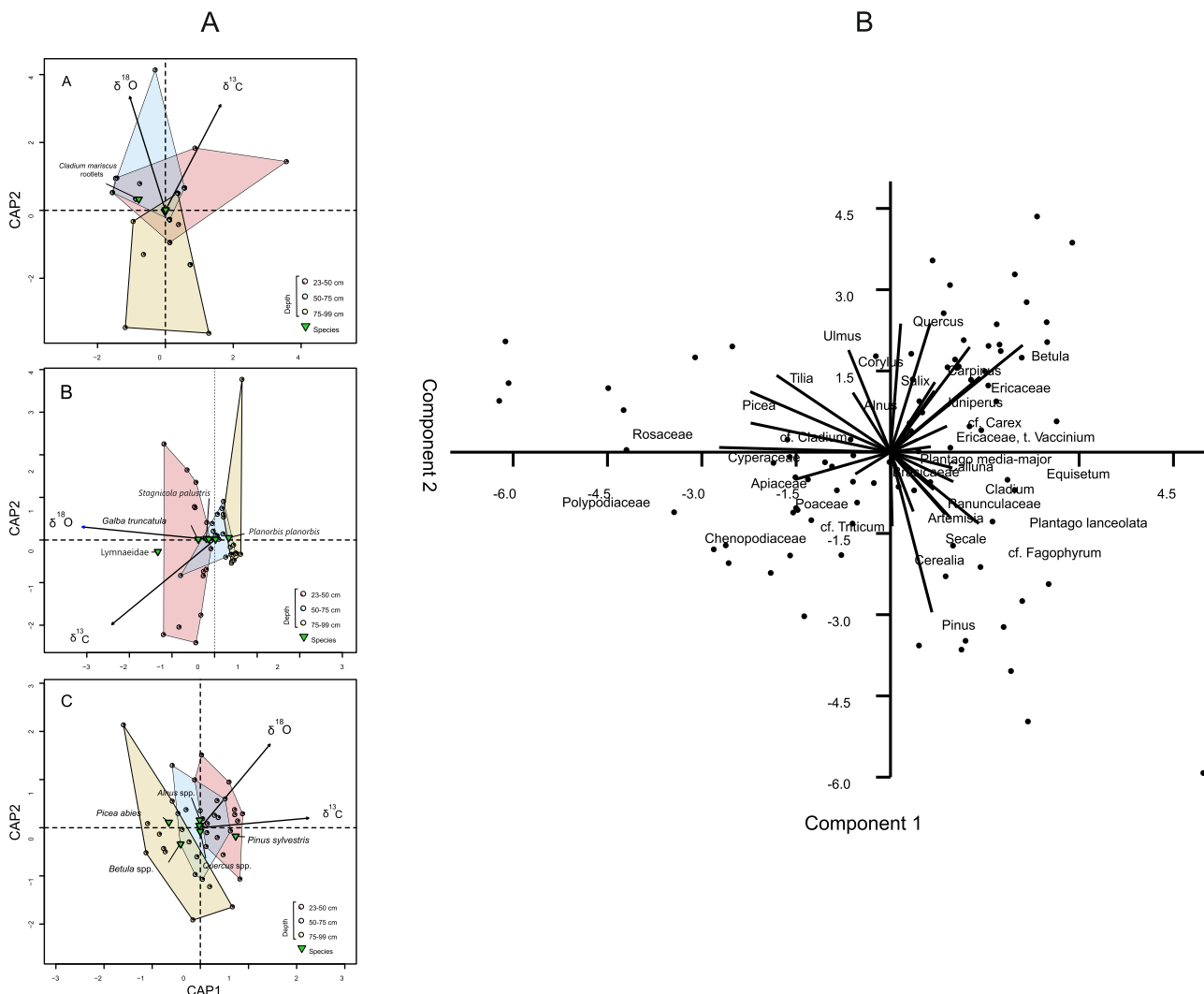


Fig. 6. A: Constrained analysis of principle coordinates (CAP) species-depth bi-plot of isotope concentrations ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) and corresponding a) plant macrofossil, b) mollusc and c) pollen data in core RaII; B: PCA scatterplot and species scores for RaII.

same dry hydrological conditions at both sites. *Potentilla erecta* and *Carex* sp. are common species in the plant communities between 3700 and 2500 cal. yr BP (Fig. 7). The next interval also recoded similarities in plant composition e.g., occurrence of *Cladium mariscus* from ca. 1300 cal. yr BP to the present in both cores. There is also a similarity in the composition of brown mosses (*Campyllum stellatum*, *Paludella squarrosa*, *Scorpidium cossonii*), although the timing of their appearance is different - this may be due to morphology of the spring-fed fens. Presently brown mosses and *Sphagnum* spp. hummocks develop among *C. mariscus* and their development may be impacted by an ecological gradients such as the availability of nutrients and water-table depth (cf. Slack et al., 1980; Andersen et al., 2011 and references quoted there) and autogenous factors, such as the competition between the species (Craine and Dybzinski, 2013).

The composition of mollusc assemblages in the two cores also shows comparable trends in the development of local communities (Fig. 4). In both profiles, the mollusc record begins and ends with terrestrial species and those inhabiting damp and very wet sites. The first terrestrial species at the fen were noted ca. 1600 cal. yr BP (RaII) and 1500 cal. yr BP (RaIII), whereas molluscs preferring standing water occurred about 1370 cal. yr BP (RaII) and 1440 cal. yr BP (RaIII). *Bathomphalus contortus* is a species typical of shallow freshwater ponds and is present in the lower part of both records ca. 1130–950 cal. yr BP in RaII and ca. 1350–1190 cal. yr BP in RaIII. This is followed by *Radix labiata*, 660–200 cal. yr BP in RaII and 680–100 cal. yr BP in RaIII. Finally, there is a common occurrence of *Vallonia pulchella*, a species indicative of the open terrestrial environments, between 550 and 200 cal. yr BP (RaII) and 200–50 cal. yr BP (RaIII). The small differences in the composition of mollusc assemblages and the timing of the species occurrence at the two sites may have resulted from the specific character of the spring-fed fen environment (Fig. 1B-D). Pools occurring in the calcareous spring-fed fen are scattered on the fen surface. Their presence is controlled by the effectiveness of the groundwater outflow, distance from the outflow, succession of vegetation (i.e. overgrowing), and peat thickness (cf. Foster and Fritz, 1987; White and Payette, 2016).

4.2. History of forest ecosystems and human activity in the surrounding area of the calcareous spring-fed fen

Between 3700 and 3200 cal. yr BP, *Picea abies* and *Pinus sylvestris*

played a dominant role in the forests composition surrounding Raganu Mire (Fig. 7). These forests contained a sizeable proportion of cold deciduous tree species (*Alnus* and *Betula*), as well as temperate deciduous taxa (*Quercus*, *Carpinus*, *Tilia*). The composition of forests resulted from climate cooling from ca. 4500 cal. yr BP that promoted a massive spread of conifer species (particularly spruce) and a decline in temperate deciduous forests through Baltic countries and NE Poland (Seppä and Poska, 2004; Galka et al., 2014; Stivrins et al., 2014; Feurdean et al., 2020). However, from ca. 3200 cal. yr BP *Pinus* abundance abruptly increased from 39% to 75% (ca. 2800 cal. yr BP), along with a minor increase in *Alnus* (alder), and a simultaneous decline in *Picea* and temperate deciduous taxa (Fig. 7). Such a pattern of coniferous trees composition from Raganu calcareous spring-fed fen is in accordance with pollen data from two other Latvian sites: Lake Lielais Svētiņu and Mazais Svētiņu bog (Stivrins et al., 2014). A distinctive change in forest composition (especially coniferous taxa) documented in several sites in the region suggests that it has been triggered by a common driver, likely a drier climate. An increase in *Pinus* pollen percentage at this time may be connected to a lower fen water-table, allowing *Pinus* to colonise peatland areas. In addition, the presence of macrocharcoal pieces in peat, indicates that the surface peatland was sufficiently dry to burn. A similar increase in macrocharcoal influx and therefore of fire activity is documented at this time at Lake Lielais Svētiņu (Feurdean et al., 2017), which strengthens the inference of dry climatic conditions, at least during the summer when most natural fires occurred.

The period between 1400 and 400 cal. yr BP is distinguished by a significant compositional change in the forest taxa expressed by increasing values in *Betula* and *Picea* and decline of *Pinus* (Fig. 7, stage 3). The abundance of temperate deciduous tree taxa, *Quercus*, *Tilia*, *Ulmus*, and *Carpinus*, increased in particular between 1400 and 1100 cal. yr BP. Such fluctuations were most likely caused by the hydrological changes in the peatland catchment (see Stage C below) and reflect the climate changes during MCA (Medieval Climate Anomaly) and LIA (Little Ice Age) (Büntgen et al., 2011, 2013; Wanner et al., 2011; PAGES 2k Consortium, 2013; Luterbacher et al., 2016). Between 1300 and 1150 cal. yr BP a dramatic decline in *Alnus* pollen (from 18 to 0.8%) was observed, which is concurrent with its abrupt decrease in the Baltic countries and Scandinavia during the medieval centuries (cf. Sarmaja-Korjonen, 2003; Saarse et al., 2010; Stivrins et al., 2017). Three reasons for *Alnus* decline are suggested: human activity, drier climate

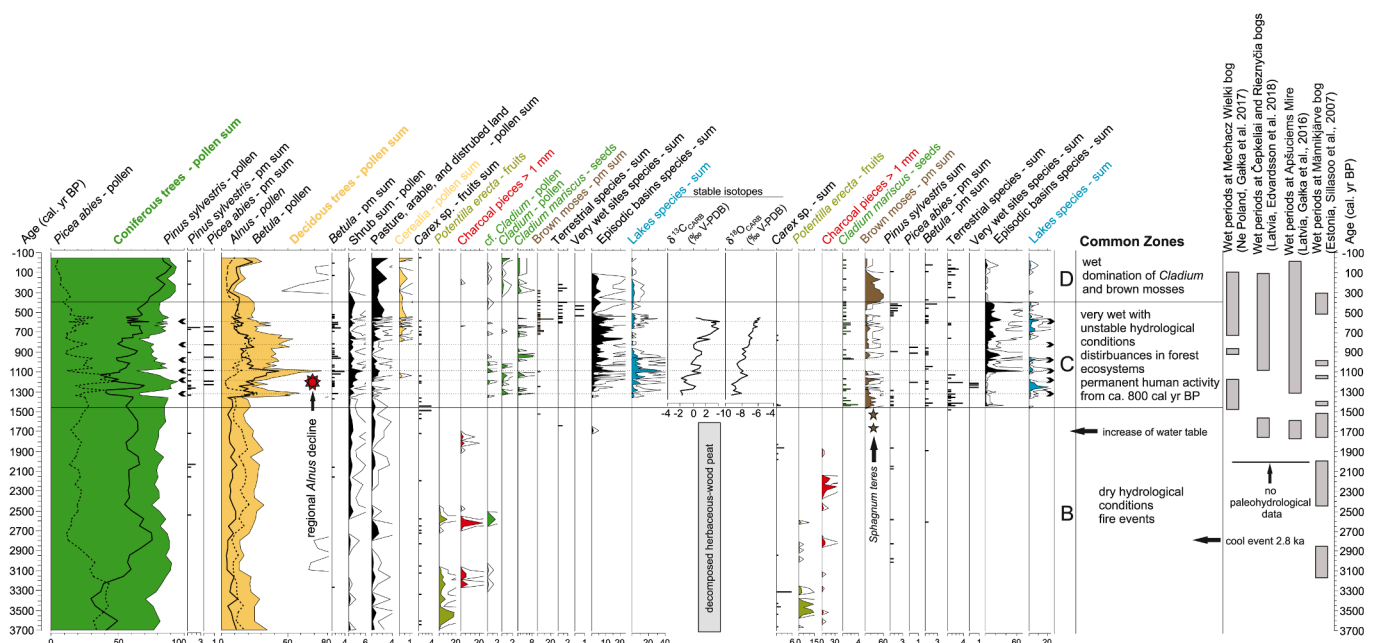


Fig. 7. Selected palaeoecological data from Raganu spring-fed fen compared to known climatic events in NE Europe.

conditions, and pathogen outbreak, but no single factor can be considered as a definite explanation for this event at the present stage of knowledge (cf. Stivrins et al., 2017). Here *Alnus* decline was preceded by a peak in its abundance (from 6.5 to 20.1%) that was coincident with tufa deposition and an increase of groundwater level, perhaps favouring *Alnus* forest development. *Alnus* typically grows in wet habitats such as river valleys, lake shores, and peatlands. However, after 50 years we documented a dramatic *Alnus* decline, likely only surviving in isolated patches. The reason for *Alnus* decline at that time is still unknown, although it is worth mentioning that such a dramatic alder decline is not documented everywhere in this region during medieval times, e.g. Apšuciems Mire (Gaika et al., 2016). Similarly, the various patterns of *Alnus* at that time were documented in NE Poland (Suwalski Landscape Park) (Gaika et al., submitted), suggesting that some local hydrogeological conditions might have also played a role in alder decline. The heterogeneity of alder populations in neighboring sites may indicate that *Alnus* presence has experienced selective cutting and survived in less accessible habitats.

Human activity in the region is recorded since ca. 1150 cal. yr BP, yet a permanent human presence from ca. 800 cal. yr BP is evidenced by the record of cultivated plants such as Cereal pollen. This record of anthropogenic impact is in accordance with other data from the region studied and linked to colonisation following the crusades (cf. Stivrins et al., 2016 and papers quoted there). Transformations of more fertile soil into fields ca. 600 cal. yr BP is suggested by a decrease of temperate deciduous taxa such as *Corylus*, *Carpinus*, *Tilia*, and *Ulmus*. The preference for fast growing conifers by the wood industry (cf. Boden et al., 2014) caused *P. sylvestris* to become the dominant tree component in north-east Europe during the last 300 years (Stivrins et al., 2016; Edvardsson et al., 2018; Gaika et al., 2017b). This transformation of forest composition is also recorded at the Raganu spring-fed fen.

4.3. Drivers of the Raganu calcareous spring-fed fen development over the last 7000 years

The following discussion deals with the development of the Raganu calcareous spring-fed fen based on plant macrofossil, mollusc, pollen, macrocharcoal (pieces >1 mm), and stable isotope records for oxygen and carbon. The relationship with past climate as the driver of the spring-fed fen development and changes in local hydrological conditions between ca. 7000 and –65 cal. yr BP are discussed. We distinguish four hydro-climatic stages in the sediment sequences studied (Fig. 7).

4.3.1. Stage A (ca. 7000–3700 cal. yr BP)

The deposition of organic sediments (highly decomposed peat) on sandy bedrock at Raganu calcareous spring-fed fen began ca. 7000 cal. yr BP (Figs. 3, 7). However, the possibility of earlier deposition of peat at this part of peatland cannot be excluded, because the studied spring-fed fen is only a small part of the large ombrotrophic peatland complex (ca. 1200 ha). Accumulation of peat at ca. 7000 cal. yr BP may be linked to an increase in the water level due to the Littorina Sea transgression, documented in other parts of Latvian Baltic Sea Coast (cf. Kalnina et al., 2012; Gaika et al., 2016). Unfortunately, the strong decomposition of the peat and poor preservation of plant macrofossils and pollen between ca. 7000 and 3700 cal. yr BP, allows for only a limited palaeo-environmental reconstruction. Only single remains of *Rubus idaeus*, *Carex* sp., *Carex pseudocyperus*, and *Betula* cf. *albae* along with numerous fungal remains (especially between 6800 and 6500 cal. yr BP) were found in the peat, suggesting dry hydrological conditions between 7000 and 3700 cal. yr BP. Charcoal pieces deposited ca. 4200 and 3900 cal. yr BP document local fire episodes, that could have initiated some changes/transformations in the peatland. *R. idaeus* is a pioneer species after fire in dry mixed forests, typically in the boreal zone (Gilliam, 2014). The decomposed peat and presence of a hiatus covering the second half of the middle Holocene records was documented at the Apšuciems Mire located at the area ca. 15 km away from Raganu Mire

(Gaika et al., 2016). This poorly preserved peat sequence indicates a low water level at the Raganu calcareous spring-fed fen and is well associated with the Holocene thermal maximum (HTM). In NE Europe the HTM was characterised by warm and dry climatic conditions accompanied with reduced groundwater and lake levels (Heikkilä and Seppä, 2010; Stivrins et al., 2014 and papers quoted there).

4.3.2. Stage B (3700–1450 cal. yr BP)

Between 3700 and 1400 cal. yr BP peat was most likely accumulated in similar dry hydrological conditions to stage A, evidenced by fungal remains (sclerotia) that are common in both cores at that time (Fig. 7). Sclerotia commonly appear in decomposed peat indicating a decrease in the water level and aerobic conditions (cf. Gaika et al., 2020 and papers quoted there). Indirect evidence of episodic dry hydrological conditions during stage B comes from the occurrence of macrocharcoal - indicative of the fire events - at both coring points, roughly ca. 3200–3100, 2850–2150, 2700 and 1900–1700 cal. yr BP. High fire activity was also documented between 3000 and 1500 cal. yr BP by the increased macrocharcoal influx at Lake Lielais Svētiņū (Feurdean et al., 2017). Some incompatibility in the timing of the fire events documented between the two cores studied has previously been reported in other spring-fed fens (Valae Morri; Gaika et al., 2018), as well as the rich fen ecosystems (Apšuciems Mire; Gaika et al., 2016 and Bagno Serebryskie; Gaika et al., 2017a). This difference may be associated with: i) morphology of the peatland and its local peat moisture, that resulted in patchy burning of the mire surface; or ii) charcoal pieces might have originated from fire events occurring outside of peatland. Given that *Cladium* pollen was only noted in layers where charcoal pieces were also found, fire could have positively influenced the spreading of the *Cladium mariscus* (pollen recognised as cf. *Cladium*) population, during stage B ca. 3250–3100 and 2600 cal. yr BP (core RaII). The positive effect of fire on *Cladium* populations has been documented in SE Poland (Buczek, 2005). However, Vaughan (2012) reports that severe fire during dry conditions can damage *Cladium* rhizomes.

Increases in the water level at the Raganu calcareous spring-fed fen is evidenced ca. 1600 cal. yr BP, by the appearance in RaII of the snail species *Carychium tridentatum* and *Omphiscola glabra* (Fig. 7), characteristic of very wet sites and periodic water basins. The occurrence of snail shells in the sediments indicates that the ecological conditions at the fen were supporting the development of mollusc population, as generally only a few species are adapted to the acidic conditions and low levels of calcium characteristic of peat bogs (Horsák and Cernohorsky, 2008). Although tufa had not yet been deposited in the RaII core ca. 1600 cal. yr BP, hydrological conditions are likely to have already changed with the groundwater enriched in the dissolved carbonates and Ca^{2+} ions favourable both for development of mollusc population and preservation of the shells (Ložek, 2000). It is also possible that the mollusc populations inhabiting the fen before 1600 cal. yr BP escaped the fossilisation process because in low pH environments, snail shells are readily dissolved after the mollusc death (Cernohorsky et al., 2010). The occurrence of mollusc shells in RaII at ca. 1600 cal. yr BP is concurrent with the presence of well-preserved *Sphagnum teres* in RaIII (Fig. 7), one of the most minerotrophic, calcitolerant *Sphagnum* species, commonly occurring in wet open fens and floating-mats surrounding the lake shores and ponds (Hajek et al., 2006; Hölzer, 2010). Furthermore, *S. teres* in fossil records often coincides with the initial stage of peatland development, preceding a shift to ombrotrophic conditions (cf. Lamentowicz et al., 2015; Gaika et al., 2017b; 2020). The increase of water level from ca. 1600 cal. yr BP may be associated with climate cooling and wetting documented in many European sites during the Migration Period (Büntgen et al., 2011; Luterbacher et al., 2016; Gaika et al., 2017a, b; Edvardsson et al., 2018).

4.3.3. Stage C (1450–400 cal. yr BP)

Calcareous deposits began to accumulate ca. 1450 cal. yr BP in core RaIII, at ca. 1350 cal. yr BP in core RaII, and at ca. 1100 cal. yr BP in core

RaI. An increase in the humidity of the climate may have led to the increase in the groundwater level that supported the sustained outflow of the groundwater enriched in dissolved carbonates at the fen surface and enabled tufa deposition at the sampling site. Differences in the timing of when tufa started to accumulate at the three coring points could be caused by the lateral development of the spring-fed fen. Errors associated to the radiocarbon dating are also possible given the small age difference between the cores. The presence of numerous mollusc species could be explained by either the highly alkaline habitat that was rapidly colonised by molluscs, or that the terrestrial species that potentially occurred at the fen previously were now being preserved in the sediments. The presence of small pools of standing water at the fen is reflected in the high occurrence of very wet habitat and open water body mollusc species including *Planorbis planorbis* and *Bathyomphalus contortus* and of *Chara* sp. oospores (cf. Fig. 1C–E). *Chara* sp. usually occurs as a submerged macroalgae (Forsberg, 1965) and its fossils are often found in the Holocene deposits at spring-fed fens (Hájková et al., 2013; Gałka et al., 2018). The profound change in the chemistry of the substrate also triggered restructuring of the plant communities. *Cladium mariscus* - that most likely grew on the edge of pools - became the dominant vascular species from ca. 1450 at the core RaIII and ca. 1300 cal. yr BP at the core RaII. Populations of alkaline brown mosses such as *Scorpidium cossonii*, *Tomentypnum nitens*, *Paludella squarrosa*, and *Campyllum stellatum* also developed. These mosses are typical of the calcareous fen habitats (cf. Hajek et al., 2006) and were commonly documented from the Holocene deposits of the spring-fed fen ecosystems at lowlands (Pietruczuk et al., 2018; Dobrowolski et al., 2019) and in the mountains (Hájková et al., 2013, 2015; Gałka et al., 2018). The timing of the above-discussed changes in the environmental conditions at the Raganu Mire is concurrent with the increased water level recorded at Apšuciems Mire at ca. 1200 cal. yr BP and supported by the presence of *Chara* sp. and *C. mariscus* communities that likely colonised the small pools in fen (Gałka et al., 2016).

From 1350 to 500 cal. yr BP the mollusc assemblages at the RaII site changed from species characteristic of permanent water reservoirs (*Planorbis planorbis*, *Bathyomphalus contortus*, *Radix labiata*), to species preferring episodic basins (*Galba truncatula*, *Stagnicola palustris*) (Fig. 7). The tufa isotope record shows a 3.5‰ increase in $\delta^{18}\text{O}$ of the water between ca. 1350 and 500 cal. yr BP. This is equivalent to about a 9 °C increase in air temperature, assuming 0.4‰ change in $\delta^{18}\text{O}$ values of carbonates precipitated from water per 1 °C increase in the air temperature (Ralska-Jasiewiczowa et al., 2003; Apolinarska and Hammarlund, 2009). However, this shift may be linked with gradually decreasing water flow at the fen, associated with decreased water supply to the fen surface, longer water residence time in the pools and growing importance of evaporation on $\delta^{18}\text{O}$ composition of the water. Composition of $\delta^{13}\text{C}$ in the groundwater emerging at the surface is modified by the plants occurring in pools. During photosynthesis molecules with lighter ^{12}C isotope are preferentially incorporated by plants leaving the ambient DIC ^{13}C enriched (Leng and Marshall, 2004). As the water level at the fen lowered, $\delta^{13}\text{C}$ values of DIC, and therefore also carbonates, were affected by photosynthesis to a greater extent. The decreased supply of water with time likely resulted from either decreased moisture availability or changes in local hydrological conditions at the Raganu Mire. Because the start of wet conditions at the fen is concurrent with a change in the forest composition (mainly increase in *Betula* and decline in *Pinus*), it is probable that changes in forest composition caused the hydrological fluctuations at the fen. The overall increasing $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values between 1300 and 500 cal. yr BP are interspersed with short-term decreases ca. 1320, 1230–1150, 1020–950, 860–820, and 600 cal. yr BP, that coincide well with changes in forest composition, especially *Pinus* decrease and *Betula* increase (Fig. 7). It was shown in other peatland ecosystems that disturbance in the catchment, e.g. changes in forest composition or deforestation, can trigger hydrologic disturbances (Tahvanainen, 2011; Woodward et al., 2014).

The fossil mollusc assemblage at the Raganu Mire was comprised of

two species of land snails typical of calcareous mires of soligenous type i. e. *Vertigo moulinsiana* (1300–1200 cal yr BP, RaIII) and *Vertigo genesii* (ca. 500 cal. yr BP, RaII) (Welter-Schultes, 2012). *V. genesii* was characteristic of the full glacial and Late glacial and today has an arctic-alpine distribution (Ložek, 1964; Gedda, 2006), whereas *V. moulinsiana* is a relic from the early Holocene (Horsák et al., 2007). Because of the scattered character of their occurrence both are threatened and legally protected species (Horsák et al., 2007; Welter-Schultes, 2012). Nowadays both species are very rare in Latvia, less than ten sites for each species are known (<https://natura2000.eea.europa.eu/#>). *Vertigo moulinsiana* is mainly found in *Alnus glutinosa* forests, as well as in poor fens, calcareous fens and in floodplains, but *V. genesii* is restricted to calcareous fens and extremely rich fens in Latvia (Pilāte, 2018). However, they have not been recorded in Kemeru National Park area so far.

4.3.4. Stage D (400–64 cal. Yr BP)

The uppermost sediments (<20 cm) are comprised of decomposed peat, perhaps because the development of the spring-fed fen is strictly connected with the water level of pools (supply of ascensive waters to the fen surface) and above this level peat cannot form. The spread of the brown mosses *Scorpidium cossonii* and *Campyllum stellatum* as well as *Sphagnum* species could indicate that the open pools are gradually being terrestrialised by peatland plants (cf. Weber, 1902; Soudzilovskaia et al., 2010). Moreover, lateral expansion of the oligotrophic plant communities, dominated by *Sphagnum* species (Fig. 1, photos C–D), may have led to a reduced area of the spring-fed fen. We assume that recent terrestrialisation was likely aided by local human impact – drainage next to the spring area, which took place at the beginning of 20th century or maybe even earlier according to old maps. Terrestrial snails occurred already ca. 600 cal. yr BP in core RaII, but became more numerous and diversified ca. 400 cal. yr BP in cores RaII and RaIII, further indicating a change in the character of the habitat (Fig. 4). However, the concurrent presence of species requiring temporal or permanent standing water (*S. palustris*, *G. truncatula*, *R. labiata*, *V. cristata*, *P. planorbis*) indicates that water pools remained present at the fen. The peatland habitat since ca. 400 cal. yr BP was likely open and similar to the modern habitat (Fig. 1B–D), as indicated by species *Vallonia pulchella* characteristic of open environment.

4.4. The factors responsible for the presence of *Cladium mariscus* and its current and future threats

Botanical (von Post, 1925; Salmina, 2004; Buczek, 2005) and palaeoecological studies (Pott, 1995; Gałka and Tobolski, 2012; Hájková et al., 2013; Gałka et al., 2018) conducted in Europe have shown that *C. mariscus* has a wide ecological amplitude to soil and water parameters. However, climatic and hydrological conditions, as well as the presence of the carbonate sediments, are considered to be the most important factors controlling the occurrence of this species (cf. Gałka and Tobolski, 2012). At mountainous spring-fed fen ecosystems in Western Carpathians, *C. mariscus* has persisted for ca. 14,000 years (Pokorný et al., 2010; Hájková et al., 2013). Unfortunately, in recent centuries human pressure, mainly drainage of peatlands has led to a decreased range expansion of *C. mariscus* in Central Europe (Hegi, 1980; Salmina, 2004; Pokorný et al., 2010; Buczek, 2005).

In Raganu Mire continuous local presence of *C. mariscus* (seeds) is documented from ca. 1450 cal. yr BP in core RaIII and ca. 1300 cal. yr BP (Fig. 3) and is connected with the onset of tufa deposition at the time of increased temperatures of the MCA (Figs. 3 and 7). *C. mariscus* may have occurred at this site or near the coring sites, earlier as recognised by the first pollen of cf. *Cladium*, ca. 3200 cal. yr BP. However, difficulties in distinguishing of *Cladium* pollen from other Cyperaceae (cf. Beug, 2004) make this archive insufficiently precise to prove the local presence of this species from the pollen. Nonetheless, the simultaneous appearance of *C. mariscus* seeds and the onset of tufa deposition at both cores is

strong evidence that the presence of carbonate sediments is crucial for *C. mariscus* occurrence at this peatland. Geobotanical studies on the distribution of *C. mariscus* in Latvia, at the current eastern range limit of this species in Europe, show that warmer climate conditions determine its recent distribution (Salmina, 2004). However, *C. mariscus* can also persist in cooler climate conditions provided that warmer microclimate and enriched hydrological conditions prevail. It is known that water provides insulation to *C. mariscus* frost-sensitive meristems (Conway, 1938) and pristine mires can mitigate temperature extremes (Kiselev et al., 2019; Baisheva et al., 2020). In the easternmost sites in Eurasia, e.g. in south of Arkhangelsk Oblastj (the Russian Federation) and in the Southern Urals, *C. mariscus* grows in pools in extremely rich fens or in calcareous spring-fed fens (Baisheva et al., 2020), while in the eastern part of Latvia *C. mariscus* grows mainly in lakes (Salmina, 2004), thus proving the importance of local conditions in long-term persistence of this species at eastern limit of its distribution area. The impact of a warmer climate during the MCA on local *C. mariscus* population was also documented in Eastern Carpathians at Valae Morii calcareous spring-fed fen, where its presence (seed) was recorded ca. 1300 cal. yr BP, although calcareous sediments accumulated from at least 4000 cal. yr BP (Galka et al., 2018). Furthermore, the spread of *C. mariscus* ca. 1300 cal. yr BP was also recorded at Bagno Serebryskie rich fen in SE Poland, where carbonate sediments are present (Galka et al., 2017a). Evidence from Raganu Mire combined with those from other records from Central Europe appears to point that the warm climate during MCA favoured the spread of *C. mariscus*. Nevertheless, *C. mariscus* survived the recurring phases of cold climate and changes in humidity during Little Ice Age (LIA) due to favourable local site conditions i.e., a calcareous habitat.

The pollen record and PCA analysis (Figs. 5 and 6) indicate that population of *C. mariscus* continued to develop under increased human impact in this region visible from ca. 800 cal. yr BP. However, extensive deforestations most probably took place on more fertile soil occupied by deciduous forests located further inland. Macrocharcoal pieces evidencing on-site fire occurrence, were found only sporadically (ca. 630 and 200 cal. yr BP in RaII) at the time of local presence of macroremains of *C. mariscus*, suggesting no or little fire on the mire during this time (Fig. 7). The picture of no direct human pressure on *C. mariscus* existence at the study site persisted until 20th century. According to topographic maps e.g. 1914–1919, 1920–1940, 1947, marginal drainage north of *C. mariscus* stands was performed after World War II. Until the 1950s, there was a winter road next to *C. mariscus* stands leading from the road crossing Raganu Mire to Lake Dūņieris and further to the seacoast, which also may have had a negative effect on site hydrology. Despite these massive modifications in the catchment, it seems that they did not affect spring discharge and *C. mariscus* population in Raganu Mire.

In summary, evidence from Raganu Mire supports previous suggestions that the presence of carbonate substrate and favourable local hydrological conditions are likely the most important factors controlling the existence of *C. mariscus* populations at the current eastern limit of its distribution in Europe. Moreover, the spread of this species within the wetland and in surrounding area was additionally supported by the warm climate conditions during the MCA and recent warm period. However, *C. mariscus* populations occurring in calcareous spring-fed fen were resilient to colder temperatures and general human pressure in the coastal area in Baltic countries. There are many current *C. mariscus* sites in Kemer National Park and the largest is in Lake Kanjieris. At present, the lateral expansion of oligotrophic *Sphagnum* communities poses a minimum potential threat to well-established *C. mariscus* population in Raganu Mire, because tufa depositions prevents acidification (Grootjans et al., 2006). However, *Sphagnum* populations, that recently occupied small hummocks among dense *Cladium* populations, may expand during dry periods. Additionally, our study shows that protection as well as potential restoration of the spring-fed fen ecosystems should also include the catchment area. This is because changes in its catchment area, such as land cover changes or fluctuations in groundwater levels

can lead to hydrological disturbances and changes in plant and mollusc populations on the fen. Nevertheless, the prospects of calcareous spring-fed fen related to site hydrology are promising at Raganu Mire as lowering of mire water level is prohibited in this Kemer National Park.

5. Conclusions

We draw the following conclusions from our analysis:

1. The most evident palaeoenvironmental events for Raganu calcareous spring-fed fen development are: i) deposition of organic sediment accumulated since ca. 7000 cal. yr BP; ii) fire events, documented by numerous macrocharcoal pieces, occurring between 3800 and 1600 cal yr BP; iii) deposition of the carbonate sediments since ca. 1500 cal. yr BP is corroborated by the development of plant and mollusc populations characteristic of wet habitat and coincides with well-known increased humidity recorded at this time in Central Europe.

2. The most significant changes in the forest and peatland ecosystems noted between 1400 and 500 cal. yr BP, were potentially associated with temperature changes during the Medieval Climate Anomaly (warm) and Little Ice Age (cold). Hydrological disturbances in the peatland catchment from 1400 cal. yr BP most likely were also strengthened by human activity (deforestation) in this region.

3. Changes in forest composition since ca. 1400 cal. yr BP (increase *Betula*; decline *Picea* abundance) were triggered by hydrological disturbances in peatland ecosystem and lead to distinctive shifts in mollusc populations. Hence, protection and restoration of the spring-fed fen ecosystems should also include the catchment area.

4. We confirm our previous suggestion that carbonate sediment substrate and good hydrological conditions are most likely the most important factors for existing *C. mariscus* populations at the current eastern range limit of its distribution in Europe under cooler climate conditions.

5. Based on the reaction of Raganu spring fen to the past climatic conditions, predicted future warmer temperature and lower precipitation could threaten this ecosystem only if the active supply of groundwater enriched in dissolved carbonations is reduced.

Funding

Research funded by the National Science Centre, grant no UMO-2013/09/B/ST10/01589 (2014–2016).

CRediT authorship contribution statement

Mariusz Galka: Conceptualization, Data curation, Funding acquisition, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Angelica Feurdean:** Conceptualization, Data curation, Writing - review & editing. **Thomas G. Sim:** Methodology, Formal analysis, Visualization, Writing - review & editing. **Kazimierz Tobolski:** Conceptualization, Data curation, Methodology, Formal analysis. **Liene Aunina:** Conceptualization, Data curation, Writing - review & editing. **Karina Apolinarska:** Conceptualization, Data curation, Methodology, Formal analysis, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We express our gratitude to Marcin Sznal for assistance in the field and sediment sampling and to Małgorzata Suchorska for her help during laboratory work (pollen sample preparation). We greatly appreciate

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