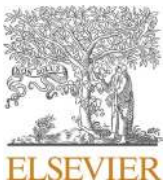
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Insight into the factors of mountain bog and forest development in the Schwarzwald Mts.: Implications for ecological restoration

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ABSTRACT

Peatlands are a significant landscape component in temperate mountain ranges and serve multiple functions. However, many peatlands were damaged, altered, or drained over the past centuries, and knowledge about their development is needed for their protection and sustainable management. In our study, we analysed two peat cores from a bog site located in the Black Forest (Southwest Germany) using high-resolution multi-proxy palaeoecological analysis, including biological indicators (plant macrofossils, pollen, testate amoebae), macro- and micro-charcoal as well as geochemical analyses (peat stoichiometry and stable isotopes ($\delta^{13}C$, $\delta^{15}N$)) supported by radiocarbon dating. We tracked the development of the peatland and forest ecosystem to (i) determine their current ecological state, and to (ii) assess the role of different agents of change at the catchment scale on peatland development. The overall objective was to determine natural reference conditions as a basis for the restoration of degraded mountain bogs in the Black Forest Mountains and other temperate mountain ranges. Our results revealed that: i) the bog developed on mineral bedrock of slight slope through paludification around ca. 10,000 cal. BP; ii) the pristine plant populations dominated by *Sphagnum fuscum* occurring from 6200 cal. BP were replaced by *Sphagnum medium/divinum* and *Eriophorum vaginatum* since ca. 3300 cal. BP, most likely due to hydrological disturbances and possible dust deposition on the bog; iii) peat formation at the study site seems still active despite relatively deep water levels (ca. 22–26 cm below surface) and was active over the last 8000 years also when WTD varied between 12 and 26 cm; iv) the self-recovery of peat formation at this mountain bog is possible; v) the protection and restoration of mountain bog ecosystems should also consider land cover changes in the surrounding catchment, serving as further indicators or drivers of mountain bog development.

1. Introduction

Peatland ecosystems in the mountain ranges in Europe, play an important role in maintaining biodiversity, often being an island among forests or meadows. Many of these peatlands were damaged by human activity, including peat cutting and drainage (Joosten and Clarke, 2002;

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Poschlod et al., 2007). The remaining pristine or semi-pristine sites are often designated as Protected Areas, but knowledge on the long-term development of these sites, which includes their response to past climate change and human activity as well as the impact of past conditions on their current state, is often limited. Understanding the factors that impacted mountain peatland ecosystem development is also important to provide a long-term perspective for peatland restoration (Speranza et al., 2000; Kajukało et al., 2016; Šímová et al., 2019; Jakab et al., 2021). The identification of past species dominance, the resilience of species to disturbance, such as hydrological changes or fires, to name a few examples, can indeed provide valuable information for restoration (Gorham & Rochefort, 2003; Gałka et al., 2019) and help to define baselines for nature conservation planning and protection of those ecosystems (López-Sáez et al., 2014). Moreover, understanding the impact of both allogenic factors such as climate change, drainage, fires, or dust deposition and autogenic factors, such as competition among species and recovery on peatland ecosystems is critical for predicting the future response of ecological communities (Mauquoy and Yeloff. 2008; Mauquoy and van Geel, 2007.

The presence of extensive forests interspersed with peatlands and lakes make the Black Forest of Germany representative for central European, temperate mountain ranges. The first paleobotanical local studies focused on the relationships between climate change and human activity on forest development during the Late Glacial and Holocene (e.g.: Oberdorfer, 1931; Lang, 1954, 1971 and references cited within). Later, more comprehensive paleoecological studies on peat cores provided evidence for local and regional plant succession as well as the presence of lithogenic elements (Ti and Si) in peat due to increased human activity and fire (Hölzer & Schloss, 1981; Hölzer and Hölzer, 1995, 1998, 2002; Rösch, 1989, 2000).

In our study, we applied high-resolution multi-proxy palaeoecological analysis to two peat cores from Moor an der Martinskapelle bog the in Black Forest of southwest Germany. We see the novelty of our approach in i) simultanously conducting biological (plant macrofossils, pollen, testate amoebae, macro-charcoal) and geochemical (XRF, $\delta^{13}C$, $\delta^{15}N$) analyses to link aspects of palaeoecology, peat stoichiometry, and human impact in the region; ii) a detailed palaeobotanical analysis of two peat cores to capture within-site variability; and iii) providing a long-term perspective for peatland restoration. We selected the bog site 'Moor an der Martinskapelle' (hereafter referred to as MK) for two reasons. First, because the bog, despite undergoing some drainage ca. 1980, mostly preserved its natural character and active peat formation, which is rare in this part of Europe. Truly ombrotrophic plant species, including *Sphagnum fuscum, S. rubellum,* and *S. magellanicum*, still occur at the site (Hölzer, 2010), which is a main reason for its current protection status. Second, the size of the bog is relatively small (ca. 2 ha) and the dome is developed; it is assumed that this raised bog ecosystem is sensitive to disturbances associated with allogenic factors and that it preserves a detailed stratigraphic record of those events.

Our aims were to: i) reconstruct peat plant community composition, and explore the relationship among *Sphagnum* assemblages and their respective ecological niches in the past and present; ii) identify the effect of land cover changes in the peatland surrounding on the peatland plant community composition; iii) identify the impact of atmospheric pollution (dust) and fire on the composition and abundance of *Sphagnum* species and vascular plants; iv) to determine the resilience of the main peat froming species to climate and disturbances; v) and finally to define natural reference conditions as the basis for the restoration and evaluation of damaged bogs in the Black Forest Mountains. We hypothesized that besides climate driven factors and direct anthropogenic influence on the peatland, also disturbances in the peatland's surrounding, such as deforestation, fire, and dust deposition, have direct impacts on the development of the peatland and its plant population dynamics. We posited that the impact of such factors on plant populations may be greater than the impact of climatic change.

2. Materials and methods

2.1. Site description

The bog site "Moor an der Martinskapelle" (MK; area ca. 125 × 210 m) is located in the central Black Forest, west of the town of Furtwangen (Fig. 1, 4806'01''N 809'09"E; 1,087 m a.s.l.).

The bedrock mainly consists of gneiss. Mean monthly temperature is −0.5 °C in January and 15.2 °C in July; mean annual temperature is 6.3 °C and total annual precipitation reaches 1746 mm (reference period: 1971–2000, according to Schonach (https://www.dwd.de/DE/leistungen/klimadatendeutschland), Station ID 4556, 904 m a.s.l.). Peatlands in this region developed on minerogenous subsoil on gentle slopes and saddle structures. *Picea abies* (Norway spruce) forests and meadows currently dominate the landscape (Fig. 1). MK bog was drained (ditches approx. 70 cm deep) ca. 1980 CE to dry out a ski trail that ran across the southern part of the bog. The trail was abandoned after two years and led around the bog. Some of drainage channels, although overgrown, are still visible. The water table depths during sampling were >30 cm below the peat surface.

On the bog surface, *Sphagnum magellanicum, S. capillifolium, S. angustifolium, Polytrichum strictum,* and *Eriophorum vaginatum* are the dominant species. Among dwarf shrubs, *Calluna vulgaris* and *Vaccinium uliginosum* dominate. Trees, such as *Pinus sylvestris* and *Picea abies*, occur sparsely.

2.2. Peat core collection

Two peat cores, MKI (492 cm) and MKII (426 cm long), were collected 50 m apart in the central part of the bog surface in autumn 2017 using a 100-cm and 50-cm long Russian type peat corer. Coring locations were characterized by similar plant communities formed by well-developed *Sphagnum* populations (sect. *Acutifolia*), as well as *Polytrichum strictum* and *Calluna vulgaris*. The core segments were individually placed in PVC half-tubes and wrapped in plastic film. The cores were transported to the laboratory and stored at 4 °C until analysis. The cores were then subsampled in 1-cm intervals for the plant macrofossil (MKI and MKII) and macrocharcoal (MKI) analysis, in 4-cm intervals for pollen (MKI), and in 3- or 4-cm for testate amoebae (MKI). For geochemical analysis (MKI), 3-cm thick peat slices were used at 3-cm intervals (0–3, 6–9, 12–15, 18–21 cm, etc.).

2.3. Laboratory procedures and analysis of samples

2.3.1. Peat core chronology

Peat core chronology was constrainted by 19 Accelerator Mass Spectrometry (AMS) radiocarbon dates, eleven on core MKI and eight on core MKII, respectively. Measurements were made on hand-picked plant macrofossils (Table 1).

Radiocarbon dating was undertaken at the Poznań Radiocarbon Laboratory. The age-depth models and date calibration were computed with OxCal (Bronk Ramsey, 2009), using the IntCal20 calibration curve (Reimer et al., 2020) and applying a P_Sequence function with a k parameter of 1 cm^{-1} and 1-cm resolution. The modeled ages are expressed as calendar years (cal. BP).

2.3.2. Plant macrofossils

High-resolution (1-cm peat slices) plant macrofossil analysis was used to reconstruct local plant succession. Plant macrofossils were analyzed in contiguous samples of approximately 10 cm^3 volume. The samples were washed and sieved under a warm water current over 0.20 mm mesh screens. The percentage of individual fossils of vascular plants and brown mosses was estimated, and the fossil carpological remains and vegetative fragments (leaves, rootlets, epidermis) were identified using identification keys (Smith and Smith, 2004; Mauquoy and van Geel, 2007) and compared to recently collected specimens. *Sphagnum*

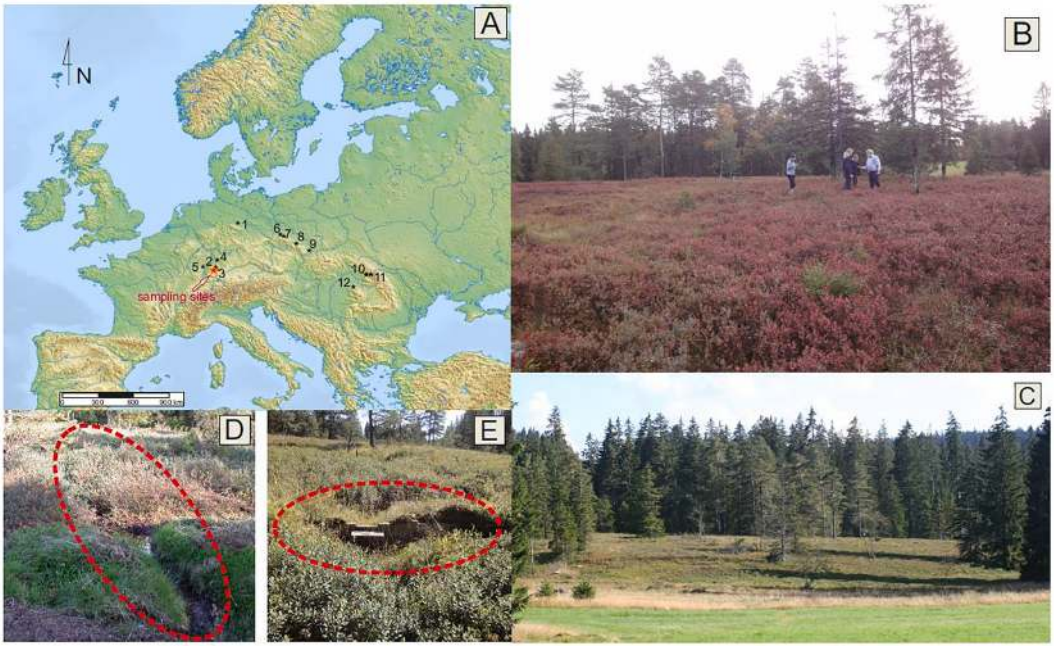


Fig. 1. Map showing locations of studied peatland sites in the Black Forest Mts. region and map and figures showing the study site "Moor an der Martinskapelle" (the bog analyzed in this study). A) Setting within Europe. Sampling site, asterisk; (source: https://mapswire.com/europe/physical-maps/) with the locations of the sites (black triangles) cited in the text: 1) Odersprungmoor (Gałka et al., 2019), 2) Steerenmoos bog (Rösch, 2000), 3) Moor beim Neuhof (Rösch, 1989), 4) Grossen Muhr and Kleinen Muhr bogs (Hölzer & Hölzer, 2002), 5) La Goutte Loiselot bog (Edelman, 1985), 6) Jagnięcy Potok bog (Kajukało et al., 2016), 7) Černá Hora bog (Speranza et al., 2000); 8) Vozka bog (Dudová et al., 2012), 9) Kotelice mire (Šímová et al., 2019), 10) Tăul Muced bog (Gałka et al., 2016), 11) Poiana Stiol bog (Gałka et al., 2017c), 12) Calul de Piatră bog (Jakab et al., 2021);, B and C) View of the study site (September 2017, photo: M. Gałka, and September 2014, photo: A. Hölzer), D) overgrown drainage channel (September 2010, photo: A. Hölzer), E) Remnant (dam) of the restoration works (May 2016, photo: M. Gałka).

capillifolium and *S. rubellum* were grouped together (as *S. capillifolium/rubellum*) due to the difficulty of differentiating them in fossil state, particularly when stem leaves were lacking. Note that both species are typical ombrotrophic mosses that occur together in relatively dry hummocks or lawns (Hölzer, 2010; Laine et al., 2018), with *S. rubellum* preferring moister habitats (Dierßen & Dierßen, 1984; Hölzer, 2010). Similarly, *Sphagnum medium* and *S. divinum* (in the past referred to *Sphagnum magellanicum*, cf. Laine et al., 2018) are expressed as *S. medium/divinum,* because it was impossible to distinguish them based on morphological features.

2.3.2.1. Pollen. A total of 92 samples each 1 cm^3 in volume, were prepared for pollen analysis using standard acetolysis procedures (Berglund & Ralska-Jasiewiczowa, 1986). For taxonomical identification, pollen keys (e.g. Beug, 2004) and a reference collection at the University of Białystok were used. Non-pollen palynomorphs (NPPs) were also counted and identified using the available literature (e.g. van Geel & Aptroot, 2006). Arboreal pollen (AP) and non-arboreal pollen (NAP) were summed and used for percentage calculations. The pollen diagram was stratigraphically ordered and zoned with constrained cluster analysis (CONISS, Grimm, 1987) and divided into local pollen assemblage zones (LPAZ). Summary curves were made for pollen representing human activity indicators, as identified by Behre (1981).

2.3.3. Testate amoebae analysis

A total of 145 samples were analysed for testate amoebae. The samples (1 cm^3) were prepared following standard procedures (Hendon & Charman, 1997). At least 150 testate amoebae shells were counted and identified at each level under a stereomicroscope at 400× magnification. The taxonomic classification followed the available literature (e.g. Mazei & Tsyganov, 2006). The quantitative reconstruction of water table depth (WTD) was obtained using the pan-European transfer function of Amesbury et al. (2016).

2.3.4. Macrocharcoal analysis

A total of 431 subsamples of 2 cm^3 volume each, were analyzed for macrocharcoal in contiguous 1- cm slices between 0 and 370 cm, and 2-cm slices between 370 and 491 cm. The samples were bleached, wet sieved through a 160 μm mesh and separated into charcoal morphological clases under a stereomicroscope following (Feurdean et al., 2017a). The number of charcoal particles counted was expressed as charcoal concentration (particles/cm^3) and charcoal influx (cm^{-2} yr^{-1}) by dividing the charcoal concentration by deposition time (yr cm^{-1}).

2.3.5. Elemental geochemistry and stable isotopic anaylses

In total, 87 subsamples were used for the geochemical analyses. Peat elemental composition and stoichiometry, as well as ^{13}C and ^{15}N stable isotopic composition were determined to derive proxies to reconstruct the local/regional environmental changes (paleohydrology), peat decomposition (using C/N ratios as a proxy), and to reconstruct inputs from atmospheric deposition (e.g. dust), and nutrient contents. Peat total element concentrations of Al, Ba, Br, Ca, Cr, Cu, Fe, K, Mg, Mn, Na, P, Pb, Rb, S, Si, Sr, Ti, and Zn were determined by means of non-destructive XRF (ZSX Primus II wavelength dispersive X-ray fluorescence spectrometer, Rigaku, Tokyo, Japan), calibrated with peat and plant material, and using certified reference materials. Due to material shortage, measurements were performed on 300 and 200 mg pellets, even though the calibration is based on 500 mg pellets. To account for the resulting differences for heavy elements, measured element contents were corrected with the R package elco (Teickner and Knorr 2020) using calibration data where five peat samples from Diaconu et al. (2020) were measured as 500, 300, 250, and 200 mg pellets.

The carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic composition and concentrations of bulk peat were determined using an elemental analyzer (EA 3000, Eurovector, Pavia, Italy) coupled to an IRMS (Nu Horizon, NU Instruments, Wrexham, UK). Peat was freeze-dried and milled to powder. About 4–5 mg of finely ground peat were weighed into tin capsules for analysis. Values of $\delta^{13}C$ are reported vs. V-PDB and $\delta^{15}N$

Table 1
Radiocarbon dates from Moor an der Martinskapelle bog (Black Forest Mts., SW Germany), core MKI and MKII.

Site/ Depth [cm]	Material	Lab. code-number	C14 date [BP]	Age [cal. yr BP] (95.4%)
MKI 23-24	*Sphagnum* stems, *Polytrichum strictum* stems	Poz-103566	55 ± 30 BP	257–31
MK I 27-28	Wood pieces	Poz-108695	280 ± 30 BP	452–155
MKI 43-44	*Sphagnum* stems	Poz-103594	1815 ± 30 BP	1825–1626
MKI 79-80	*Sphagnum* stems	Poz-103595	2080 ± 30 BP	2140–1952
MK I 118-119	*Sphagnum* stems	Poz-103596	2335 ± 30 BP	2456–2311
MK I 180-181	*Sphagnum* stems	Poz-103597	3210 ± 30 BP	3544–3367
MKI 240-241	*Sphagnum* stems	Poz-103599	3930 ± 35 BP	4510–4248
MKI 310-311	*Sphagnum* stems	Poz-103600	4445 ± 35 BP	5284–4480
MKI 381-382	*Sphagnum* stems	Poz-103810	5250 ± 35 BP	6178–5924
MKI 450-451	*Sphagnum* stems	Poz-98092	6510 ± 40 BP	7495–7323
MKI 471-472	*Rubus idaeus* seeds	Poz-103601	8820 ± 50 BP	10155–9686
MKII 23-24	*Sphagnum* stems	Poz-108694	35 ± 30 BP	255–31
MKII 41-42	*Sphagnum* stems	Poz-108773	1890 ± 30 BP	1895–1733
MKII 92-93	*Sphagnum* stems	Poz-108934	2425 ± 30 BP	2698–2352
MKII 155-156	*Sphagnum* stems	Poz-108774	3770 ± 35 BP	4244–3991
MKII 215-216	*Sphagnum* stems	Poz-108775	4410 ± 35 BP	5270–4864
MKII 283-284	*Sphagnum* stems	Poz-108776	4810 ± 35 BP	5605–5470
MKII 330-331	*Sphagnum* stems	Poz-98091	6050 ± 35 BP	6991–6795
MK II 398-399	*Carex rostrata* fruits	Poz-108935	8210 ± 50 BP	9395–9020

values vs. AIR nitrogen, as calibrated using certified reference materials and working standards of known isotopic composition. Carbon and nitrogen concentrations are expressed based on mass-%; C/N ratios are expressed as mass based C to N ratios. The results of the plant macrofossil, testate amoebae, macrocharcoal, and geochemical analyses were presented in the form of diagrams drawn with the C2 graphics program (Juggins, 2003).

3. Results

3.1. Chronology, lithology and peat accumulation rates

The age-depth models (Fig. 2) suggested a fairly constant peat accumulation rate (PAR) at both peat cores between ca. 10,000 cal. BP and ca. 1400 cal. BP (core MKI) and up to ca. 1600 cal. BP (core MKII) with no hiatuses.

From 10,000 to 7500 cal. BP, decomposed peat was formed by vascular plants, whereas between 7500 and 1600 cal. BP of *Sphagnum* species, along with *Eriophorum vaginatum* (especially in core MKII). Apparent peat accumulation rates averaged 0.52 mm/yr in core MKI and 0.45 mm/yr in core MKII between 10,000 and 7500 cal. BP. We observed highly decomposed peat horizons, ca. 1400–250 cal. BP in core MKI; ca. 1600 and ca. 250 cal. BP in core MKII, and hiatuses were identified on results of radiocarbon dating along both cores. The upper portion of both peat profiles was again formed by *Sphagnum* ssp. and *Polytrichum strictum* (ca. 250 and −67 cal yr BP) and PAR reached ca. 0.78 mm/yr.

3.2. Local plant succession

Six zones in the local vegetation development were visually delimited in the macrofossil diagram of core MKI (Fig. 3).

Zone MKI-ma-1 (10,000 – 7500 cal. BP) covers the basal peat layers which were characterized by the presence of herbaceous remains that included Cyperaceae, *Carex rostrata, Juncus* sp., and *Scirpus sylvaticus*. In zone MKI-ma-2 (7500 – 6200 cal. BP), *Sphagnum medium/divinum* and *Eriophorum vaginatum* were dominant species. Zone MKI-ma-3 (6200 – 3300 cal. BP) was dominated by *Sphagnum fuscum*, with *E. vaginatum* found in the lower and upper sections of this zone; Ericaceae rootlets were frequent throughout. Zone MKI-ma-4 (3300 – 1400 cal. BP) was characterized by the predominance of *S. medium/divinum* and *S. fuscum*.

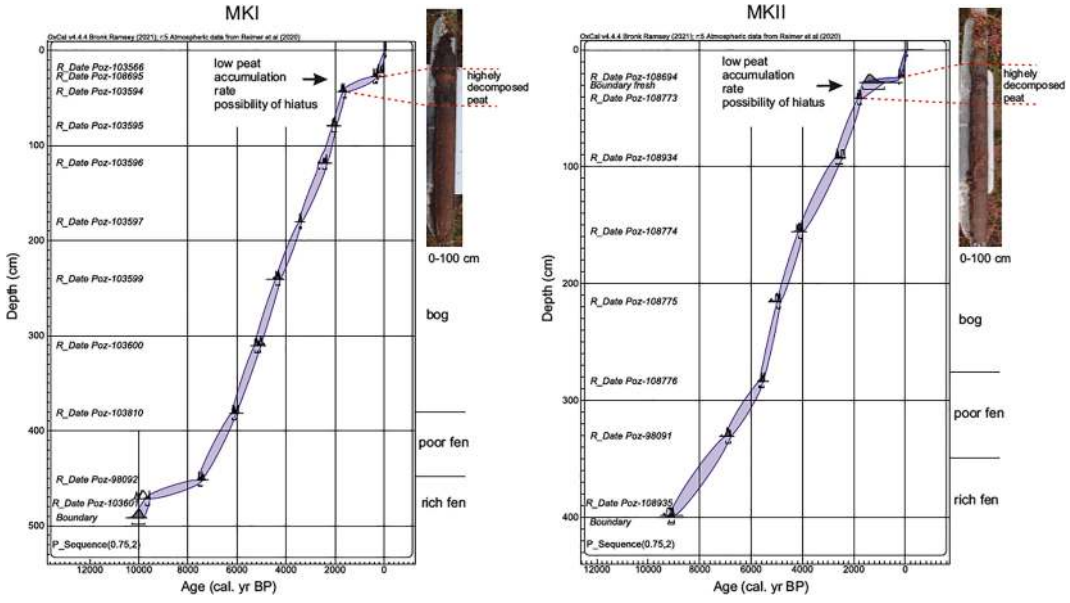


Fig. 2. Age-depth models for the peat profiles from Moor an der Martinskapelle: a) core MKI and b) core MKII.

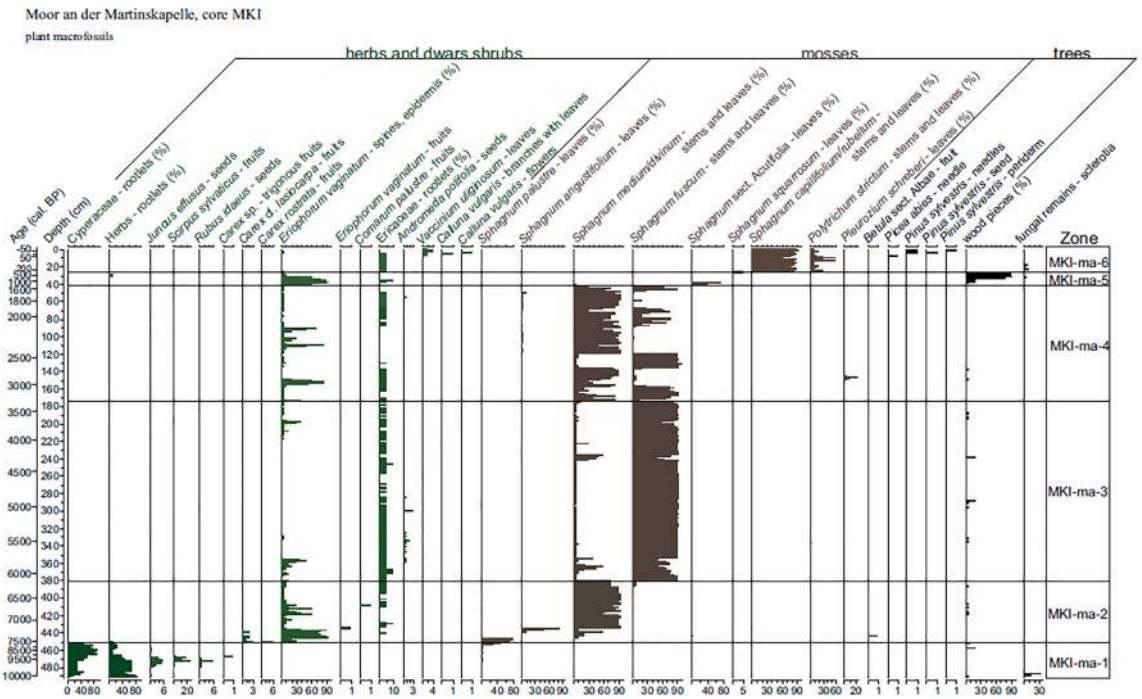


Fig. 3. Plant macrofossil diagram presenting local vegetation development in Moor an der Martinskapelle, Core MKI. Taxa with '%' are estimated volume percentages, the others are counts (note scale differences on the x-axes).

Remains of *E. vaginatum* and *S. angustifolium* were also found. In zone MKI-ma-5 (1400 – 250 cal. BP), mainly *E. vaginatum* and wood pieces were identified. Zone MKI-ma-5 (250 cal. BP – present) was dominated by *S. capillifolium/rubellum* and *Polytrichum strictum*. In the lower section of this zone, sclerotia were found, while in the upper section, *Calluna vulgaris*, *Pinus sylvestris* and *Picea abies* occurred.

Seven zones in local vegetation development were visually delimited in core MKII (Fig. 4).

Zone MKII-ma-1 (10,200 – 9500 cal. BP) was characterized by herbaceous roots, *Juncus* sp., and *S. sylvaticus*. Zone MKII-ma-2 (9500 – 7550 cal. BP) was dominated by herbaceous remains, though wood pieces were abundant in the lower section of this zone, along with *C. rostrata* and *Potentila* sp. Zone MKI-ma-3 (7550 – 5500 cal. BP) was dominated by *E. vaginatum* and *S. medium/divinum*. In zone MKI-ma-4

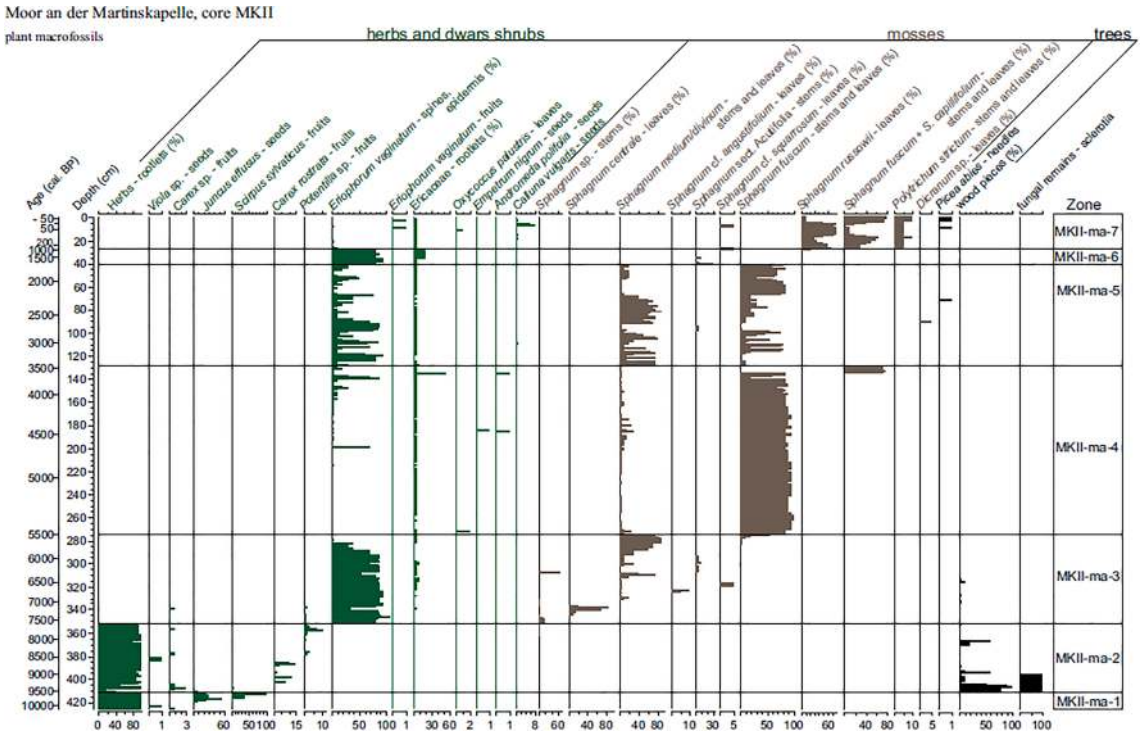


Fig. 4. Plant macrofossil diagram presenting local vegetation development in Moor an der Martinskapelle, Core MKII. Taxa with '%' are estimated volume percentages, the others are counts (note scale differences on the x-axes).

(5500 – 3500 cal. BP), *Sphagnum fuscum* was the dominant species, along with Ericaceae rootlets. Across zone MKII-ma-5 (3500 – 1550 cal. BP), *E. vaginatum, S. medium/divium* and *S. fuscum* dominated the fossil assemblage. *Calluna vulgaris* and *Dicranum* sp. appeared for the first time. In zone MKII-ma-6 (1550 – 250 cal. BP), *E. vaginatum* was predominant. In the uppermost zone MKII-6 (250 cal. BP – present), *S. russowii, S. fuscum,* and *P. strictum* were the dominant species. In the uppermost section of this zone, *C. vulgaris* seeds and *P. abies* needles were documented.

3.3. Pollen based local to regional plant succession

Six pollen zones were delimited with CONISS (Fig. 5). Zone MKI-po-1 (10,000 – 8500 cal. BP) was dominated by *Pinus sylvestris* type (up to 40%), *Betula* (up to 16%), shortly followed by *Corylus avellana* (up to 54%). Other temperate deciduous tree species (*Quercus, Ulmus,* and *Tilia cordata*) had minor contributions.

NAP reached their maximum value (58%) and were dominated by Poaceae and Cyperaceae. In zone MKI-po-2 (8500 – 6100 cal. BP), deciduous trees such as *C. avellana* (up to 60%), *Quercus (*up to 30%), *Ulmus* (up to 6%), and *T. cordata* (up to 10%) were dominant and reached the highest values in the profile. Poaceae dominated the herbaceous assemblages (up to 30%), alongside Ericaceae. Zone MKI-po-3 (6100 – 5200 cal. BP; 154–99 cm) was characterized by an abrupt increase in *Fagus sylvatica* (up to 20%) and *Abies alba* (up to 38%), parelleling the gradual decrease of *C. avellana*, *Quercus, Ulmus,* and *T. cordata*. Notable are scattered pollen grains of cereals and *Plantago lanceolata*. In zone MKI-po-4 (5200 – 3100 cal. BP), *A. alba* (up to 30%) and *F. sylvatica* (up to 43%) were the dominant tree species, but the relative abundance of *Quercus*, *Alnus,* and *Corylus* were also high. Cyperaceae dominated the herbaceous assemblages, and although present with low percentages, the diversity of ruderal plants increased in this zone. Zone MKI-po-5 (3100–700 cal. BP) was characterized by the highest amount of *F. sylvatica* (up to 51%) as well as increases in *Betula* (up to 17%) and *Carpinus betulus* (up to 3%). Notable is the increased abundance of human indicators of both ruderal and cultivated plants. Throughout zone MKI-po-6 (700 – 50 cal. BP), *F. sylvatica* (up to 5.5%) percentages decreased sharply along with an abrupt increase in *P. sylvestris* (up to 30%) and *Picea abies* (up to 19%). The proportion of herbaceous pollen types typical for meadows (Poaceae, Apiaceae), ruderal, cereals, and shrubs (Ericaceae), also increased considerably.

3.4. Macrocharcoal morphologies and microcharcoal-based fire reconstruction

Five macrocharcoal zones were visually delimited based on the fluctuations in the total macrocharcoal influx and charcoal morphotypes (Fig. 6). Zone MKI-mc-1 (10,000–8500 cal. BP) was characterized by high total macrochacrcoal influx (cm^{-2} yr^{-1}) of all morphological types (Poaceae, herbaceous, wood), with charred wood fragments reaching the highest values in the profile (Fig. 6).

In zone MKI-mc-2 (8500–6000 cal. BP), total macro-charcoal influx declined and consistend primarly of the herbaceous morphotype. Zone MKI-mc-3 (6000–4450 cal. BP) was characterized by an increased macrocharcoal influx of all morphotypes, particularly wood. In zone MKI-mc-4 (4450–1800 cal. BP), the total macrocharcoal influx was low, except a peak in herbaceous and wood morphotypes at ca. 3600 cal. BP. Zone MKI-mc-5 (1800 cal. BP - present) was characterized by a high charcoal influx, especially of herbaceous type as well as isolated peaks in charred Poaceae (ca. 1800–1700 cal. BP) and wood (around 1600 cal. BP). However, macrocharcoal influx declined strongly over the past 200 years.

3.5. Testate amoebae succession and corresponding changes in water level

Seven zones of testate amoebae abundance were visually delimited along core MKI (Fig. 7).

Zone MKI-ta-1 (8500 – 6100 cal. BP) was characterized by the dominance of *Assulina muscorum*, *Cryptodifflugia oviformis*, and *Difflugia pulex*, with the reconstructed water table depth (WTD) between 20 and 24 cm below the peat surface. In zone MKI-ta-2 (6100 – 5500 cal. BP), *Arcella flavum* and *D. pulex* dominated; *Heleopera petricola* was recorded for the first time. Derived WTD was increased up to 15.4 cm. In zone MKI-ta-3 (5500–4300 cal. BP), *D. pulex* dominated, though *C. oviformis, Nebela militaris,* and *Trigonopyxis arcula* also occurred in relatively high amounts, and the WTD varied between 16 and 25 cm. Zone MKI-ta-4 (4300 – 3000 cal. BP) was characterized by a high amount of *A. flavum*, a gradual decrease of *D. pulex,* and a gradual increase of *N. militaris.* The WTD increased to 13 cm (ca. 4000 cal. BP) and declined to 19 cm ca. 3300 cal yr BP. Zone MKI-ta-5 (3000 – 2650 cal. BP) was characterized by a decline of *A. flavum,* a peak in *C. oviformis,* and the highest amount of *N. militaris*. Zone MKI-ta-6 (2650 – 1500 cal. BP) was dominated by *A. flavum* and *Hyalosphenia papilio.* The first appearance of *Arcella artocrea* was recorded, whereas the WTD was at ca. 12 cm. In zone MKI-ta-7 (1500 cal. BP – present), the first appearance of *Corythion*

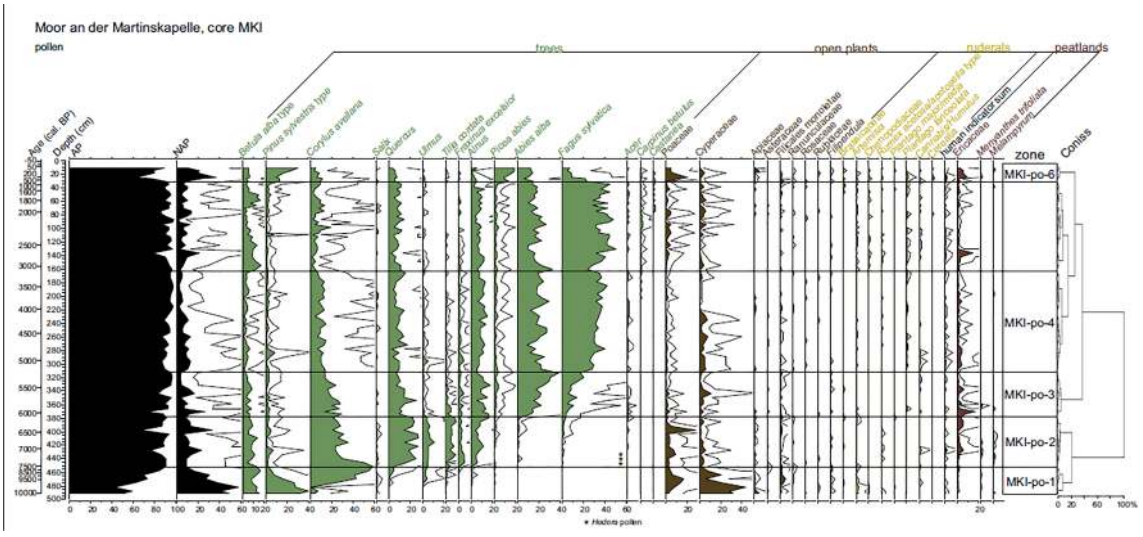


Fig. 5. Pollen, spores and palynomorphs diagram presenting vegetation development in Moor an der Martinskapelle and its vicinity, core MKI. Percentages are shown in black, 5 times exaggeration in grey.

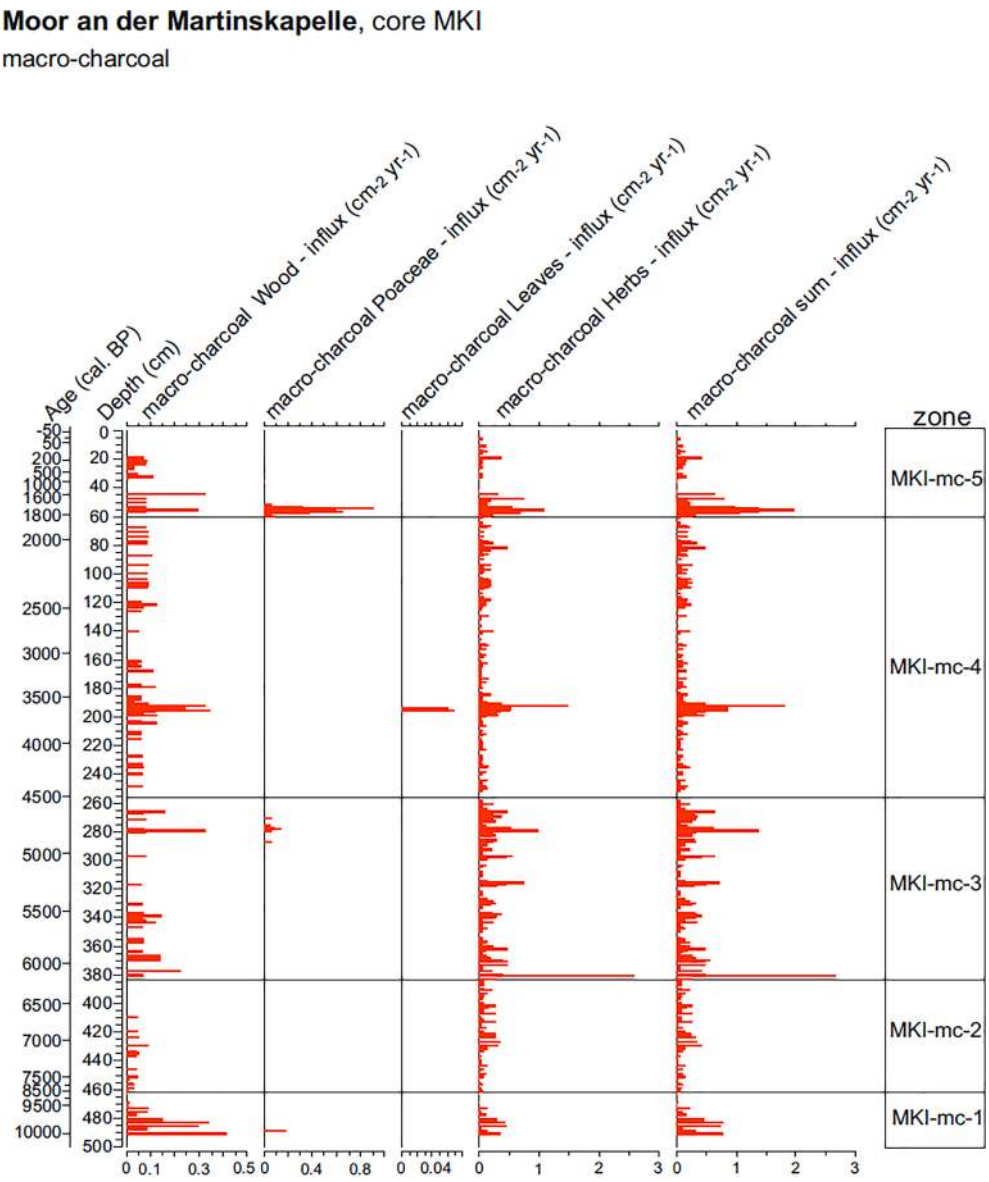


Fig. 6. Fire activity on Moor an der Martinskapelle and its surrounding based on macrocharcoal influx, as derived from peat profile MKI.

dubium and *Euglypha rotunda* was documented, and *Cyclopyxis arcelloides* and *Nebela tincta* reached highest abundances in this zone. The derived WTD declined to ca. 26 cm below the surface in modern time.

3.6. Geochemical records

Six zones were visually delimited based on geochemical analyses (Fig. 8). Zone MKI-ge-1 (10,000 – 7500 cal. BP) was characterized by the highest average contents of Al, Si, and Ti.

The maximum value of N (average +1.41 ‰), highest N concentrations (up to 1.97 %), and lowest C/N and N/P ratios (27.3 and 24.0, respectively) were also observed here. Towards the upper section of this zone, there was a gradual increase of Ca, C/N, N/P and δ^{13}C (-26.19 ‰). Zone MKI-ge-2 (7500–5350 cal. BP) was characterized by low average contents of Na, Al, Si, and Ti, as well as a gradual decrease of C and N, but elevated Ca and Mg. Ratios of C/N sharply increased from 35 to 40 to around 70–80, and N/P ratios varied around 40. Zone MKI-ge-3 (5350 – 4400 cal. BP) was characterized by relatively constant elemental contents and and δ^{13}C stable isotope signatures (on average −3.13 ‰ and −25.28 ‰, respectively), and C/N and N/P ratios (on average 97.9, and 41.0, respectively). In zone MKI-ge-4 (4400–1600 cal. BP), the average content of dust or clay mineral-related elements (Al, Si, Ti) increased again. From ca. 2900 cal. BP on, the average concentration of Zn and Pb increased to 5–12 and 60–80 ppm, respectively, indicating increased human activities. Concentrations of C and N, C/N and N/P ratios, and δ^{13}C signatures varied. In zone MKI-ge-5 (1600 – 100 cal. BP), average contents of elements arising from human activity (Zn, Pb, As, Cu) and dust or deposition-related minerogenic elements reached their maxima (53.7 ppm, 367.9 ppm, and 2.8 ppm, respectively), and decreased again towards MKI-ge-6. Analogous to this, signatures and N and C concentrations increased sharply in the bottom part of the zone and decreased again in the upper part. MKI-ge-5 had again very low C/N ratios (average 36.6), yet comparably high N/P ratios (average 39.0). The uppermost zone MKI-ge-6 (100 cal. BP - present) is characterized by elevated average concentrations of Na, Mg, K, and Ca, while C contents as well as and δ^{13}C signatures all declined. Ratios of N/P decreased sharply (average 21.4), while C/N ratios increased towards the surface compared to the zone MKI-ge-5..

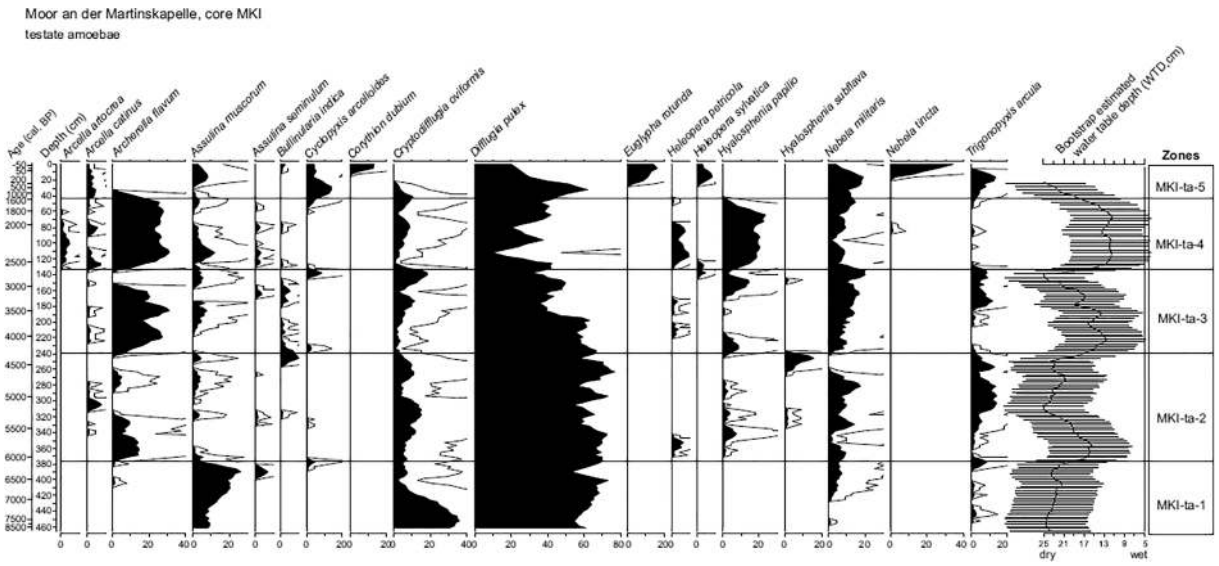


Fig. 7. Testate amoebae relative abundance from Moor an der Martinskapelle, peat profile MKI.

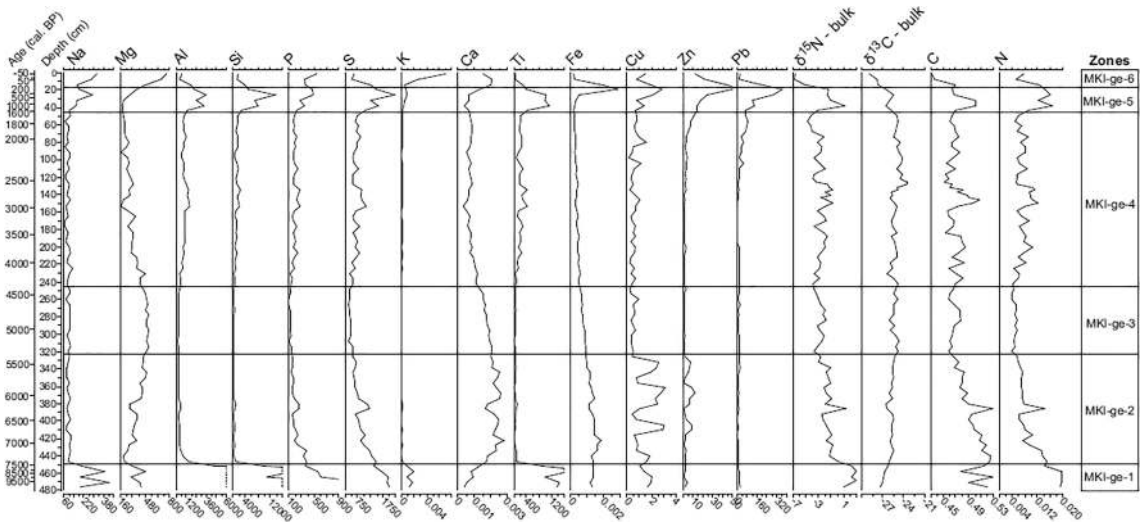


Fig. 8. Selected results of the geochemical analysis of Moor an der Martinskapelle, core MKI. Results for Na, Mg, Al, Si, P, S, Ti, Cu, Zn, and Pb are expressed as ppm (mg/kg), K and Fe are given in mass %, C and N in g/g, and δ^{15}N and δ ^{13}C are given in the common ‰ totation (vs. AIR or V-PDB, respectively).

4. Discussion

4.1. Drivers of the Moor an der Martinskapelle (MK) bog development over the last 10,000 years

The following discussion summarizes our understanding of the development of the MK bog communities and hydrological conditions based on our multiproxy record. We discuss the relationship with past climate, forest changes, and human activity around MK bog as the drivers of its development over the past ca. 10,000 cal. BP. Six common stages were distinguished in the bog and forest ecosystems development (Fig. 9).

4.1.1. Stage A (ca. 10,000 – 8000 cal. BP)

Basal peat dates and age-depth models indicate that the timing for initial peat formation started at ca. 10,000 cal. BP at both coring points. The main peat-forming plants included *Scirpus sylvaticus, Juncus* sp., and *Carex rostrata* (Fig. 4), which, together with C/N ratios that are comparable to those reported for fens and swamp (Wang et al., 2015), likely indicate that a fen developed through paludification. This is contrary to many peatlands in this region, which developed via terrestrialisation (cf. Oberdorfer, 1931; Lotter and Hölzer, 1994; Rösch, 2000). The development of MK bog on a slope is most likely linked to the presence of springs, which are also common in the region today. High average concentrations of Al, Si and Ti during the fen phase (Fig. 9) likely indicate inputs from erosional processes. The development of nutrient-rich wetlands through paludification and the presence of *S. sylvaticus* and *Carex* ssp. in the initial stage were reported for other sites in European mountain ranges, i.e. Eastern Carpathians, Romania (Gałka et al., 2016) and Western Carpathians, Czechia (Šímová et al., 2019). Altough the water table depth (WTD) was probably fluctuating, conditions were generally dry (24 cm below the surface) during the initial stage of bog development (Fig. 9). The prevalence of dry conditions are supported by low δ^{13}C values (Loisel et al., 2010) and C/N and N/P ratios, indicating strong microbial transformation of the herbaceous peat (Kuhry and Vitt, 1996; Krüger et al., 2015) and an enrichment of ^{15}N in the initial fen stage (Drollinger et al., 2019) (Fig. 9). In addition, wood pieces could indicate that the peatland surface was partially covered with shrubs or trees. The pollen record shows that *Pinus sylvestris* and *Betula*, as well as *Corylus avellana, Tilia cordata* and *Ulmus,* were abundant in the vicinity

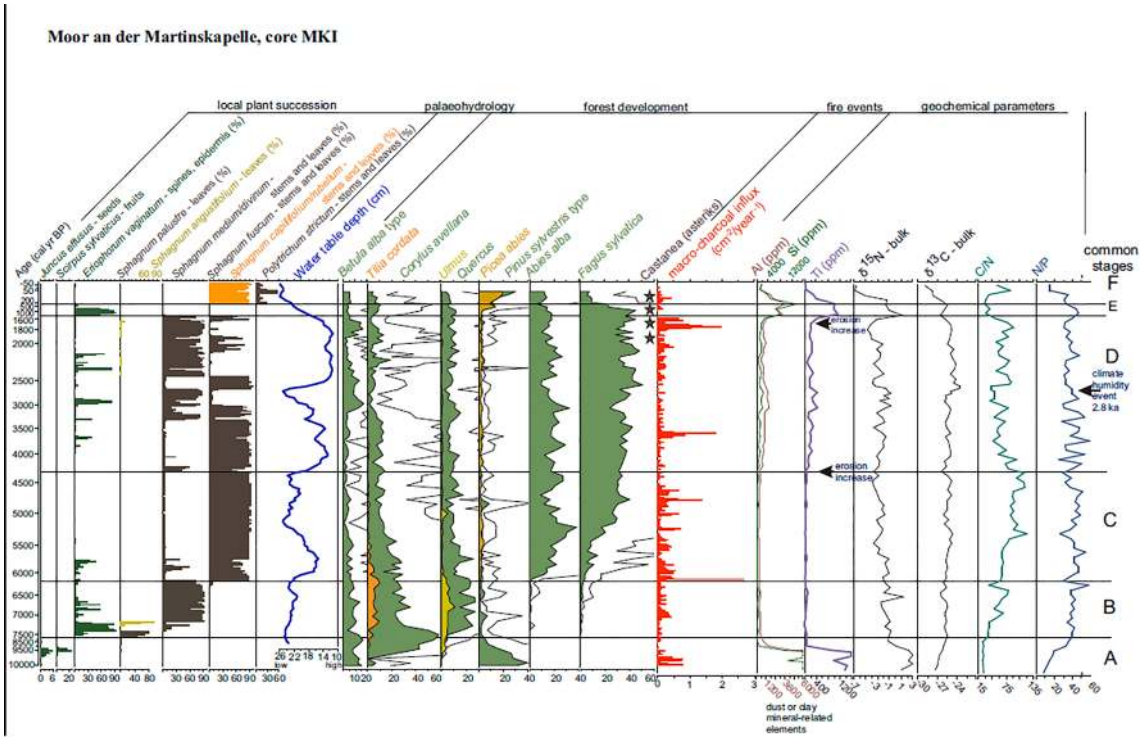


Fig. 9. Comparison of chosen taxa from plant macrofossils and pollen, water table depth (WTD), macro-charcoal, and results of geochemical analysis in the site "Moor an der Martinskapelle". C/N and N/P ratios are mass based ratios from data presented in Fig. 8.

of the MK bog from ca. 9500 cal. BP. This pattern of early Holocene forest succession is consistent with results from other sites in the Black Forest (Lang, 1971; Lotter and Hölzer, 1994; Rösch, 1989; 2000) and also on a wider regional scale in SW Germany and Central Europe (Giesecke et al., 2017; Rösch et al., 2021). The forest dynamic was probably affected by frequent fires, as indicated by abundant macroscopic charcoal particles including wood type, a feature also reported at Steerenmoos bog in the Black Forest (Rösch, 2000) and other sites in SW Germany (Rösch et al., 2021). High fire activity was typical for the early Holocene in CE Europe, a result of warm and dry summer conditions and the dominance of *Pinus* forests (Feurdean et al., 2020).

4.1.2. Stage B (ca. 8000 – 6200 cal yr BP)

Around 8000 cal. BP, populations with *Eriophorum vaginatum* and *Sphagnum* species such as *S. palustre, S. centrale, S. angustifolium* developed and were replaced by *S. medium/divinum* at 7500 cal. BP at both sampling sites. The presence of these species indicates a gradual decrease of the impact of the nutrient-rich groundwater on the local plant populations resulting in the development of a poor-fen habitat mainly fed by rain and snow. This was also reflected in sharp decreases of minerogenic elements such as Al, Si, Ti, Fe, S, and P, yet Ca and Mg were still elevated here and above. The transition from rich to poor fens/bog was documented in peatlands located in various zones around the world (Gorham & Janssens, 1992; Kuhry et al., 1993; Hughes & Barber, 2003; Gałka et al., 2017a, b). The mechanism of the fen-bog transition can be controlled by allogenic or autogenic factors (Loisel & Bunsen, 2020). The MK bog did not experience any abrupt hydrological changes at 7500 cal. BP that could lead to decomposition of peat and consequently initiate the ombrotrophication process (cf. Hughes, 2000; Hughes and Barber, 2003). On the contrary, the reconstructed water table depth was stable (ca. 22–24 cm below surface), and the C/N and N/P ratios increased (Fig. 9), indicating rapid accumulation of nutrient-poor and weakly decomposed peat. Thus, autogenic plant succession may be considered here as a driver for peat plant succession toward an oligotrophic habitat.

During stage B, a highly diverse temperate deciduous forest, that was dominated by *Quercus* and *C. avellana* alongsite *Tilia cordata, Ulmus*, and *Fraxinus*, developed around MK bog. Such a pattern of tree succession is characteristic for this region (cf. Lang, 1971; Edelman, 1985; Rösch, 1989; 2000; de Klerk, 2014) during the Holocene Termal Maximum (Renssen et al., 2009). This period also witnessed the first contiguous presence, albeit in low counts, of two important tree species in the forest around MK bog: *Abies alba* and *Fagus sylvatica*. The presence of *A. alba* and *F. sylvatica* pollen at that time is also visible in the pollen record from a nearby bogs (Rösch, 1989; 2000), where it was linked to Early Neolithic human presence, based on the presence of pollen of *Cereals, Plantago lanceolata*, and increased charcoal and minerogenic content (Rösch, 2000). In our MK record, the first continuous presence of *A. alba* and *F. sylvatica* occurred immediately after a fire event. Except for *Rumex* pollen, we found no other pollen indicators of grazing and cultivation, nor notable changes in lithogenic elements (Al, Si and Ti). Archeological data of Neolithic human settlements in this area are sparse (cf. Winghart, 1986). This is not to preclude the potential impact of humans on the changes in forest tree species composition. But, on the basis of our findings, the recorded changes seem better explained by climate change (a shift towards wetter conditions). Additional multi-proxy and multi-site studies are needed to better assess the role of climate versus humans on forest development at that time in this region.

4.1.3. Stage C (6200 – 4300 cal. BP)

Around 6200 cal. BP the WTD increased slightly, which might have been due to changes towards a wetter climate (Fig. 9). Approx. 6200 cal. BP (and ca. 5700 cal. BP at core MKII), *S. medium/divinum* and *E. vaginatum* were replaced by *S. fuscum* (Figs. 3 and 4). *S. fuscum* is a dominant species in ombrotrophic peatlands, and usually grows on hummocks, which are the driest peatland habitats (Hölzer, 2010; Wojtuń et al., 2013; Laine et al., 2011). Thus, its spread on the bog surface is striking, because at that time WTD on the mire increase from 24 to 16 cm. Further important changes in the peatland and its catchment were a decrease of nutrient contents and minerogenic inputs (low

Al, Si, P, S, and K concentrations) and the beginning of the ombrotrophic phase, i.e highest C/N and N/P ratios, typically observed in ombrotrophic peat (Wang et al., 2015). A sharp transition from *S. medium/divinum* to *S. fuscum* was also reported for Mechacz Wielki bog, NE Poland (Gałka et al., 2017b). The rise in surface moisture conditions likely documents an increase in climate humidity. Regarding the forest composition, there was a rapid spread of *A. alba* and *F. sylvestris* combined with declining contributions of *Tilia, Ulmus*, and *Quercus* at ca. 6200 cal. BP. *A. alba* and *F. sylvestris* demand a moist habitat (cf. Ellenberg, 2009), thus it is most likely that wet conditions triggered such changes in forest composition. Disturbances by fire may have also accelerated this forest change by creating forest gaps and facilitating the establishment of new tree species (Fig. 9). Recent palaeoecological studies in Central European forests are starting to confirm the role of disturbance by fire in the initial establishment of *Fagus* and *Abies* (Tinner et al., 2013; Feurdean et al., 2017b; Kołaczek et al., 2020). However, sustained forest fires near the MK bog have negatively impacted these taxa, especially the proportion of *Abies alba*, as suggested by the decline of fir at times of fire episodes (peaks in charcoal).

4.1.4. Stage D (4300–1400 cal. BP)

The beginning of this stage is indicated by a rise in water table an initial replacement of *S. medium/divinum* with *S. fuscum,* and *E. vaginatum*, a gradual increase of geochemical element contents associated with erosion or dust (Al, Si, and Ti), and a marked decline in C/N ratio (Fig. 9). Changes in local plant populations may be related to increased minerogic /nutrient supply and hydrological fluctuations associated with increased human pressure on the bog and its catchment in this region (Rösch, 2000). The negative role of dust deposition on oligotrophic *Sphagnum* populations was already documented for lowlands and mountain peatlands (van Geel and Middeldorp, 1988; McClymont et al., 2008; Paal et al., 2009; Gałka et al., 2019). A clear relationship between disturbances in the catchment and on bog is visible between 3100 and 2700 cal. BP. The declining proportions of *C. avellana*, *Quercus,* and *A. alba* and increased proportions of *Betula* (17.5%) coincide with a considerable peatland drying and increased peat decomposition (Fig. 9). This may have favored *Betula* spread in the surrounding as well as on the bog. As this change in forest composition parallels an increase in human indicators (higher Al, Si and Ti values), it suggests anthropogenic deforestation, that led to an increase in erosional processes.

The following abrupt increase of water table depth (ca. 12 cm), high δ^{13}C values (up to −23.56), a shift in C/N ratios (70–90), all indicate high peat surface moisture conditions and very weakly decomposed peat around ca. 2700 cal. BP (Fig. 9). Wetter conditions at that time are also well reflected by the increased abundance of *S. medium/divinum* and the appearance of *S. angustifolium*, which usually occupies wetter peatland habitats (between 17 and 4 cm below surface) (Dierssen & Dierssen, 1984; Gałka et al., 2019). Increased moisture conditions around 2800 cal. BP are indicated by higher rates of peat accumulation in many ombrotrophic peatlands in western Europe (van Geel et al., 2014) and rising lake levels in central Europe (Magny, 2004). These wet conditions lasted until 1700 cal. BP at MK bog, and beginning may have coincided with the 2.8 ka cold event (Wanner et al., 2011), which was characterized by climate cooling and increased humidity. *F. sylvatica* became the dominant tree species in the surrouding forests (up to 51%), at 2500 cal BP. This pattern contrasts with the *Fagus* decline reported in the pollen record from Steerenmoos bog, which instead shows a higher proportion of *A. abies* (Rösch, 2000). The distinct pattern of *A. alba* and *F. sylvatica* succession at the two sites most likely reflect different local geomorphological and soil site conditions, typical for the Black Forest (cf. Hölzer and Hölzer, 1995, 2002; Rösch, 1989, 2000).

From ca. 1800 cal. BP, MK bog experienced a drying trend. At that time, marked fire events are documented around MK bog, which may have caused a decline in the proportions of *Fagus* and *Abies* pollen and the expansion of *Betula*. These fires may have been ignited by humans, as supported by the presence of *Plantago lanceolata* (indicator of meadow, cf. Behre, 1981). The permanent human presence in this area is documented since the Middle Ages. The Martinskapelle village near the MK bog was established approx. CE 1122 (Dorer, 1948).

4.1.5. Stage E (1400–250 cal. BP)

During the first part of this stage (1400–250 cal. BP), very low apparent rates of peat accumulation are likely representing a hiatus in the peat sequence, which was recorded at both sampling sites. In contrast to other peatlands in the Black Forest (Hölzer and Hölzer, 1995; Rösch, 2000), we have not identified charcoal pieces or charred plant remains >1 mm at MK, which would indicate burning of the peat layer; but it is possible that the missing peat sequence, identified by differences of radiocarbon age at both nearby peat levels, would have contained local charcoals. Still, abundant macrocharcoal fragments (mainly 150–300 μm) were found, which document fires that took place in the peatland surroundings. Very high contents of Al, Si, and Ti indicate high minerogenic inputs, presumably associated with post-fire erosion initiated by human activity during this time. Greater peat decomposition would further enrich those minerogenic elements (Biester et al., 2014). Drought, linked to dry climate conditions, during the Litle Ice Age (LIA, ca. 1300–1850 CE) might have caused intensified decomposition of previously accumulated peat. This interpretation is supported by relatively low C/N ratios. Many peatlands in Europe experienced such dry conditions (WTD > 20 cm) during the LIA (Marcisz et al., 2020). Overall, this short period was crucial for local plant communities: a quite pristine biodiversity occurred between 7400 cal. BP to 1400 cal BP but was severely altered thereafter.

4.1.6. Stage F (250 cal. BP – present)

Peat formation was re-activated from ca. 250 cal. BP to the present, with the highly decomposed peat getting colonized by *Sphagnum capillifolium, S. fuscum, S. russowii,* and *Polytrichum strictum*. These plants typically occur in dry habitats such as hummocks and cushions in bogs or paludifying forests (Hölzer, 2010; Laine et al., 2011). The appearance and increase in abundance of *S. russowii* over the last centuries has also been reported in peatlands from other mountain ranges in Europe, e.g. Hrubý Jeseník Mountains, Czechia (Dudová et al., 2012) and Rodna Mountains, Romania (Gałka et al., 2016; 2017c). Dudová et al. (2012) suggested that this could be associated with an increase in nitrogen availability in the habitat. Indeed we found an increase in N with *S. russowii* in our cores (Fig. 8). Likewise, we found a strong enrichment of P in the surface layers, presumably a typical phenomenon in ombrotrophic peatlands (Wang et al., 2015), but possibly indicating P (rather than N) limitation for *S. russowii*. Water table depth declined at MK over the past 200 years, a drying trend that is consistent with paleohydrological data suggesting widespread recent drying of peatlands in Europe (Swindles et al., 2019). A decrease of the WTD at MK bog could have enhanced the spreading of *Calluna vulgaris* and *Vaccinium uliginosum* at both sampling sites which are still common at MK bog.

The return of active peat formation may also be associated with warmer climatic conditions after the LIA; similar patterns were observed at Steerenmoos bog (Rösch, 2000) and in other mountain ranges, e.g. La Goutte Loiselot, Vosges (Edelman, 1985), and at Poiana Stiol bog, Eastern Carpathians (Gałka et al., 2017b). While we know that young peat may appear to be accumulating rapidly only because it has not had a chance to decompose and compact (Young et al., 2021), our forest indicators also suggest changing conditions that would support the return of active peat formation. Following the post-LIA period, *F. sylvatica* was almost fully replaced by *Picea abies* and to some extent by *Pinus sylvestris* in the surrounding of MK bog, a pattern consistent with other pollen data from the Black Forest (Hölzer and Hölzer, 1995, 2002; Rösch, 2000). This is in realtively good agreement with modern forest composition, which is formed almost exclusively by *Picea abies*. The gradual dominance of the coniferous species during the last three centuries in this and other European regions (in many cases intensified since

the Medieval Period or earlier, cf. Kaplan et al., 2009) resulted from intensive deforestation for fuel, construction materials, industrial purposes, and sylviculture for the wood industry (Boden et al., 2014). The following widespread plantation of *Picea abies* in the region was at times of moderate moisture conditions. However, extensive die-back of *Picea abies* was observed over the past decades in Central Europe due to a combination of droughts and bark beetle outbreaks (Schafstall et al., 2022), suggesting this species may not be suitable for forestry under projected climate conditions for this region.

4.1.7. Natural reference conditions as the basis for the restoration of degraded bogs

In the area of the Black Forest, extensive efforts are carried out to restore degraded and drained bogs (Eschengrundmoos, Rattay et al., 2016; Hirschbädermoor, von Sengbusch, 2017). We argue that knowledge about past plant assemblages, main peat forming species, their resilience, and factors that impacted the development of MK bog and others in the Black Forest is crucial for a successful restoration, including the return of peat formation. Our results show that the main peat-forming species were *S. medium/S. divinum,* whereas *Sphagnum* sect. Acutifolia (most likely mainly *S. fuscum* and *S. rubellum*). *Sphagnum* sect. Cuspidata (i.e. *S. cuspidatum, S. angustifolium*), played a secondary role. In addition, *E. vaginatum* can also be considered an important peat forming species. Conversely, *S. russowii, S. capillifolium/rubellum,* and *Polytrichum strictum* became part of the community assemblages over the past 400 years at times of excessively dry conditions. Our results on the composition of plant assemblages give support to previous paleobotanical studies (Hölzer and Hölzer, 1995, 2002; Rösch, 2000). In terms of peat hydrology, peat formation at MK bog was active at water tables that varied between 12 and 26 cm below surface and peat formation is currently active, despite relatively deep water table levels (ca. 22–26 cm below surface) (Fig. 9). Hydrological conditions that maintain an active peat layer require water levels deeper than 10 cm below surface. The apparent, current self-recovery process leading to the return of peat accumulation at MK bog indicates a potential for further peat development, which is not clear for all mountain bogs, especially bogs with a well-developed dome. Some mountain bogs, especially small ones, might be close to reaching their growth limit (i.e., maximum peat thickness) due to hydrological reasons (surface drying) and/or the fact that overall decomposition along the peat profile is equal to, or greater than, carbon uptake by surface layers (Belyea and Baird, 2006).

The development of mountain peatlands also depends on local factors such as geohydrological conditions, fires, deforestation, and dust deposition (Speranza et al., 2000; Lamentowicz et al., 2007; Tahvanainen, 2011; Gałka et al., 2021). It is worth considering restoring vegetation in the surrounding catchment to ensure successful restoration of mountain bog ecosystems.

5. Conclusion

Multi-proxy analyses of the Moor an der Martinskapelle peat profiles allowed us to reconstruct Holocene palaeoenvironmental changes in the region of Black Forest Mountains in SW Germany. In sum, the results suggest the following:

1. Moor an der Martinskapelle bog developed on a slightly sloping mineral bedrock through paludification around ca. 10,000 cal. BP.
2. The pristine plant populations dominated by *Sphagnum fuscum* occurring from 6200 cal. BP on were replaced by *Sphagnum medium/divinum* and *Eriophorum vaginatum* since ca. 3300 cal. BP, most likely due to hydrological disturbances and possibly dust deposition on the bog.
3. The observed changes in forest composition ca. 6200 cal. BP (massive spreading of *A. alba* and *Fagus sylvatica*) most likely have primarily been caused by wetter climate conditions. However, we do not preclude the impact of fires and humans on the forest dynamics.
4. The self-recovery of peat formation on the bog is possible. Highly decomposed peat became colonized by *Sphagnum* species during the last ca. 300 years and a fresh layer is accumulating.
5. Reconstructed average water table depths varied between 12 and 26 cm over the last 8000 years, which means that shallow WTDs (<10 cm below the surface) may not be necessary for restoration efforts, especially in bogs where the dome is developed.
6. The protection and restoration of mountain bog ecosystems should also include restoration of vegetation and forest in the surrounding catchment. This is especially important in areas that underwent massive changes in forest types such as the replacement of deciduous tree species by the conifers like in the case of the Black Forest.

CRediT authorship contribution statement

Mariusz Gałka: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Visualization, Writing – original draft. **Adam Hölzer:** Conceptualization, Methodology, Investigation, Writing – original draft. **Angelica Feurdean:** Conceptualization, Methodology, Investigation, Writing – original draft. **Julie Loisel:** Conceptualization, Methodology, Investigation, Writing – original draft. **Henning Teickner:** Methodology, Formal analysis, Investigation, Data curation, Writing – original draft. **Andrei-Cosmin Diaconu:** Methodology, Formal analysis. **Marta Szal:** Methodology, Formal analysis. **Tanja Broder:** Methodology, Investigation, Formal analysis. **Klaus-Holger Knorr:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing – original draft.

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.

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