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IM. ADAMA MICKIEWICZA
W POZNANIU

ZABURZENIA TORFOWISK MSZARNYCH W ŚRODKOWO-WSCHODNIEJ EUROPIE

DISTURBANCES OF *SPHAGNUM* PEATLANDS IN CENTRAL-EASTERN EUROPE

Rozprawa doktorska
Doctoral thesis

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Rozprawa doktorska napisana pod kierunkiem

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,,Nigdy nie dostrzega się tego, co zostało zrobione,
widzi się tylko to, co pozostaje do zrobienia"

Maria Skłodowska-Curie

Torfowisko Hara w Estonii (listopad, 2018)

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LISTA ORYGINALNYCH ARTYKUŁÓW NAUKOWYCH SKŁADAJĄCYCH SIĘ NA ROZPRAWĘ DOKTORSKĄ

Rozprawa doktorska składa się z trzech oryginalnych artykułów naukowych opublikowanych w międzynarodowych czasopismach naukowych posiadających współczynnik Impact Factor (IF). Artykułom została przypisana numeracja, do której odnoszono się w dalszej części rozprawy doktorskiej.

1. **Łuców, D.,** Lamentowicz, M., Kołaczek, P., Łokas, E., Marcisz, K., Obremska, M., Theuerkauf, M., Tyszkowski, S., and Słowiński, M. (2021). Pine forest management and disturbance in Northern Poland: combining high-resolution 100-year-old paleoecological and remote sensing data. Frontiers in Ecology and Evolution (IF: 4.171), 9:747976, doi 10.3389/fevo.2021.747976

2. **Łuców, D.,** Lamentowicz, M., Obremska, M., Arkhipova, M., Kittel, P., Łokas, E., Mazurkevich, A., Mróz, T., Tjallingii, R., and Słowiński, M. (2020). Disturbance and resilience of a *Sphagnum* peatland in western Russia (Western Dvina Lakeland) during the last 300 years: a multiproxy, high-resolution study. The Holocene (IF: 2.769), 30 (11), 1552-1566, doi.org/10.1177/0959683620941064

3. **Łuców, D.,** Küttim, M., Słowiński, M., Kołaczek, P., Karpińska-Kołaczek, M., Küttim, L., Salme, M., and Lamentowicz, M. (2022). Searching for an ecological baseline: Long-term ecology of a post-extraction restored bog in Northern Estonia. Quaternary International (IF: 2.130), 607, s. 65-78, doi.org/10.1016/j.quaint.2021.08.017

STRESZCZENIE

Minimalizowanie skutków zmian klimatu wskazuje na potrzebę ochrony torfowisk, a także przywracanie zaburzonym i zdegradowanym ekosystemom zdolności akumulacji węgla i odpowiednich warunków hydrologicznych. Dlatego celem rozprawy doktorskiej była próba oceny odporności torfowisk mszarnych na zaburzenia w ciągu ostatnich 300 lat z wykorzystaniem metod paleoekologicznych. W pracy przeanalizowano trzy główne lokalne rodzaje zaburzeń torfowisk o różnym stopniu intensywności: 1) zmiany użytkowania ziemi, 2) odwodnienie oraz 3) eksploatacje torfu wraz z efektem restytucji. Do badań wybrano trzy obiekty torfowiskowe zlokalizowane na obszarze Polski, Rosji oraz Estonii. Wykorzystano wysokorozdzielcze, wielowskaźnikowe analizy paleoekologiczne rdzeni torfowych wsparte danymi teledetekcyjnymi, monitoringowymi, historycznymi, badaniami prób powierzchniowych oraz chronologią opartą na datowaniu radiowęglowym i ołowiowym. W pierwszym artykule zbadano zmiany użytkowania ziemi wywołane działalnością człowieka oraz procesami naturalnymi (zręby zupełne oraz wycinki uszkodzonego drzewostanu po gradacji owadów i tornadzie). Z wykorzystaniem torfu zrekonstruowano pierwszy raz w Polsce paleoekologiczny zapis zniszczeń lasu spowodowanych przez tornado. Drugi artykuł ukazuje 300 letnią historię torfowiska oraz wpływ działalności człowieka na użytkowanie ziemi i meliorację torfowiska na terenie dzisiejszej zachodniej Rosji. Natomiast trzecia publikacja dotyka problematyki przemysłowej eksploatacji torfu wraz z etapem restytucji ekologicznej i jej wpływem na regenerację torfowiska.

Słowa kluczowe:

zaburzenia torfowisk, badania wielowskaźnikowe, paleoekologia, odtwarzanie torfowisk, wylesienia

ABSTRACT

Minimizing the effects of climate change indicates the need to protect peatlands, as well as restore disturbed and degraded ecosystems to the ability to accumulate carbon and appropriate hydrological conditions. Therefore, the aim of the PhD thesis was to attempt to assess the resistance of peatland to disturbances during the last 300 years using the palaeoecological methods. The study considers three main local types of disturbances of peatlands of varying intensity: 1) land use changes, 2) drainage, and 3) exploitation of peat with the effect of restoration. Three peatlands located in Poland, Russia and Estonia were selected for the study. High-resolution multi-proxy palaeoecological analyzes of peat cores were used, supported by remote sensing, monitoring and historical data, surface samples as well as chronology based on AMS^{14}C and ^{210}Pb dating. The first article studies changes in land use caused by human activity and natural drivers (clear-cutting, cutting of damaged stands after insect gradation and tornado). The first in Poland palaeoecological record of damage caused by a tornado in peat sediments was documented. The second article presents the 300-year history of the bog and the impact of human activity on the use of the landscape and drainage of the peatland in Western Russia. The third publication present the industrial exploitation of peat along with the stage of ecological restoration and its impact on the regeneration of the peatland.

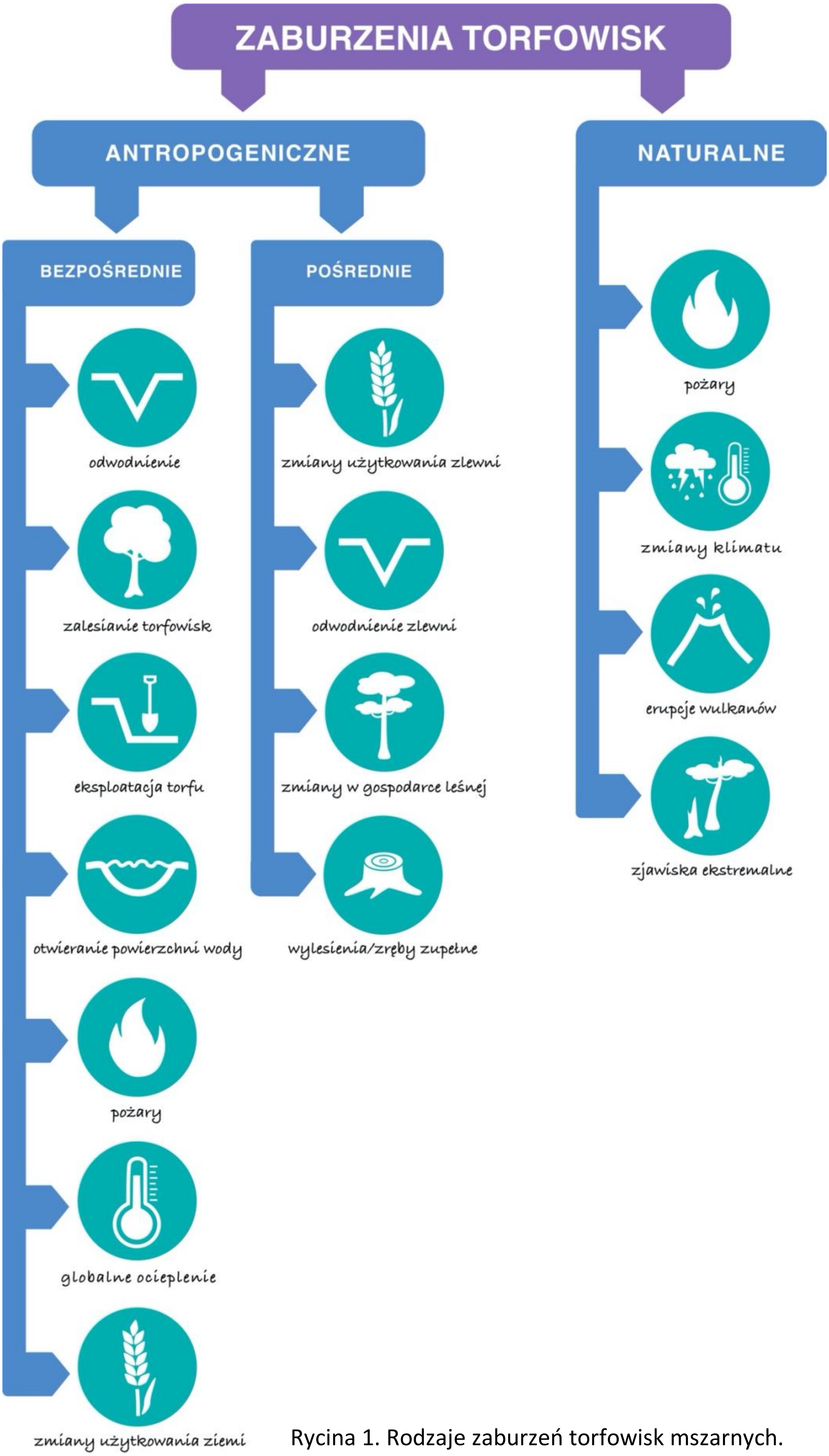
Keywords:

peatland disturbances, multi-proxy studies, palaeoecology, peatland restoration, deforestation

WSTĘP

Ze względu na zdolność do akumulowania materii organicznej, dwutlenku węgla (CO_2), magazynowania dużych ilości wody, zachowania różnorodności biologicznej oraz łagodzenia skutków zmian klimatu, torfowiska należą do najcenniejszych ekosystemów Europy (Charman, 2002; Tobolski, 2003; Gorham, 1991; Turunen i inni, 2002). Są one jednak bardzo wrażliwe na zmiany zachodzące w środowisku i współcześnie podlegają intensywnym zaburzeniom, które w różnym stopniu wpływają na ich hydrologię, strukturę, roślinność, mikroorganizmy oraz akumulacje węgla (Rydin i inni, 2006; Słowiński i inni, 2016; Lamentowicz i inni, 2019; Jassey i inni, 2015; Amesbury i inni, 2019; Loisel i inni, 2021; Loisel i inni, 2014, Tanneberger I inni, 2021; Hugelius i inni, 2020). Torfowiska należą do najbardziej zagrożonych ekosystemów w Europie.

Connolly and Holdem (2013) definiuje zaburzenie torfowiska jako „każdy naturalny lub antropogeniczny proces, który przerywa naturalną trajektorię wzrostu torfowiska". Zaburzenia torfowisk mogą mieć charakter antropogeniczny bądź naturalny (Rycina 1), jednak często procesy te nakładają się na siebie. Antropogeniczne zaburzenia torfowisk - spowodowane dzielnością człowieka, mogą mieć charakter bezpośredni jak i pośredni (Ilnicki, 2002; Connolly and Holdem, 2013). Zaburzenia bezpośrednie mają miejsce na obszarze ekosystemu. Należą do nich wszelkiego rodzaju odwodnienia (melioracje), zmiany użytkowania ziemi, zalesienia torfowisk, pożary torfowisk, otwarcie powierzchni wody (przekształcanie torfowisk w zbiorniki retencyjne), eksploatacja torfu czy globalne ocieplenie. Zaburzenia pośrednie obejmują zmiany w zlewni torfowiska i jego bliskim sąsiedztwie. Są to między innymi zmiany użytkowania zlewni, odwodnienie zlewni, zmiany w gospodarce leśnej czy wylesienia/zręby zupełne. Z kolei naturalne zaburzenia torfowisk mogą być wywołane przez pożary, zmiany klimatu, erupcje wulkanów czy zjawiska ekstremalne - należą do nich między innymi: topnienie wiecznej zmarzliny, pożary przesuszonych torfowisk, odlesienia czy zniszczenia drzewostanu zlewni torfowisk spowodowane przez naturalne pożary, burze, silne wiatry czy tornada.



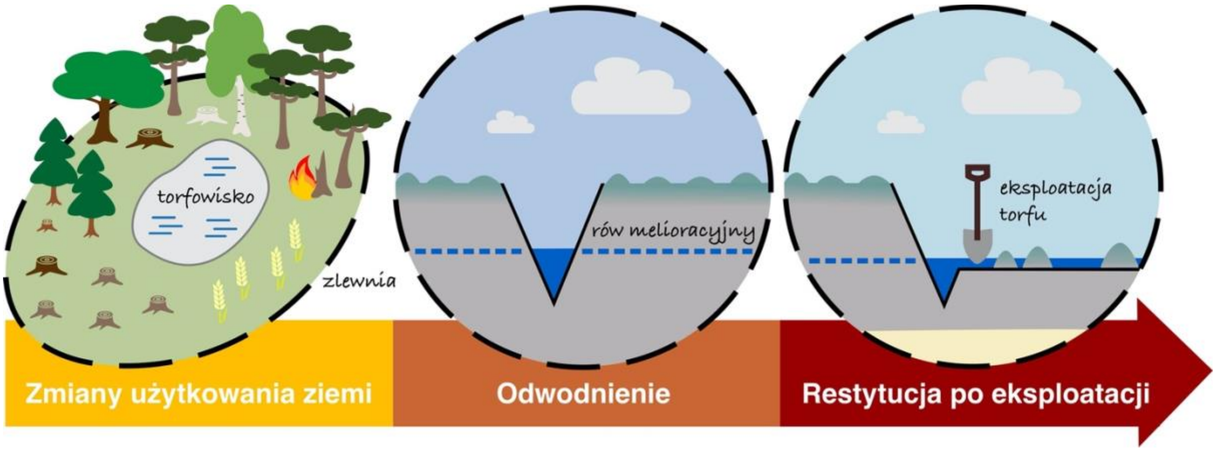
Rycina 1. Rodzaje zaburzeń torfowisk mszarnych.

Europejskie torfowiska znajdują się pod olbrzymią presją ze strony człowieka oraz zmian klimatu (Charman, 2002). Ogromna ich część bezpowrotnie znikła z powierzchni Europy na skutek osuszania torfowisk i przekształceniu ich w łąki, pastwiska czy pola uprawne (Tobolski, 2012, Tobolski, 2003, Joosten i inni, 2017). Nieodwracalne zmiany w środowisku wyrządziła także przemysłowa eksploatacja torfu, która doprowadziła do jego utraty wraz z lokalną pulą gatunków torfotwórczych. Znaczna część torfowisk została pocięta rowami melioracyjnymi i regularnie jest odwadniana. Zaburzenia te destrukcyjnie wpłynęły na funkcje ekosystemów torfowiskowych w Europie (Jasnowski, 1972; Rydin i inni, 2013; Joosten, 1997; Parish i inni, 2008). Torfowiska w strukturze krajobrazu niżu europejskiego stanowią system płatów i korytarzy ekologicznych (Richling i Solon, 1998) ściśle powiązanych z ekosystemami przyległymi. Dlatego też obiekty torfowiskowe są bardzo podatne nie tylko na zaburzania związane z samymi torfowiskami (wyżej wymienione), ale i zagrażają im także zmiany użytkowania ziemi w obrębie ich zlewni. W ostatnim czasie zaobserwowano wzrost zniszczeń lasów spowodowanych przez wiatry w Europie, a w najbliższej przyszłości spodziewany jest ich dalszy wzrost (Seidl, 2014), co niewątpliwie może wpłynąć na rozwój śródleśnych torfowisk. Co więcej, europejskie torfowiska wysychają od 300 lat (Swindles i inni, 2019), co zwiększa ryzyko ich pożarów i emisji dwutlenku węgla do atmosfery. Minimalizowanie skutków zmian klimatu wskazuje na potrzebę ochrony torfowisk, zachowania ich jak w najlepszym stanie oraz przywracanie zaburzonym i zdegradowanym ekosystemom potencjału akumulacji torfu, bioróżnorodności i odpowiednich warunków hydrologicznych, tak by w dalszym ciągu były one dla nas ważnymi magazynami węgla, oazami bioróżnorodności i zbiornikami wody.

Rozpoznanie zaburzeń powodujących zmiany zachodzące w ekosystemie torfowisk i jego otoczeniu w przeszłości oraz ustalenie przyczyny tych zmian wymaga odpowiedniego, kompleksowego podejścia oraz wykorzystania wysokorozdzielczych (high-resolution), wielowskaźnikowych (multi proxy) badań paleoekologicznych (Lamentowicz i inni, 2015, Gałka i inni, 2017; Forysiak i inni, 2008; Van der Knaap i inni, 2011; Dobrowolski i inni, 2019; Sillasoo i inni, 2007). Szczególnie ważne jest odróżnienie zmian spowodowanych działalnością człowieka od zmian klimatycznych. W XXI wieku nastąpił wyraźny wzrost badań paleoekologicznych oraz monitoringowych, dostarczając to coraz bardziej cenniejszych, dokładniejszych, interdyscyplinarnych i wielowymiarowych badać na temat stanu, historii i rozwoju torfowisk na całym świecie. Co więcej, osady torfowe stały się docenianym źródłem informacji o zmieniającym się środowisku i klimacie, dlatego też zostały uwzględnione w raporcie IPCC (Intergovernmental Panel on Climate Change) (Zhongming i inni, 2021). Badania paleoekologiczne i monitoringowe mogą wspierać ochronę i odbudowę torfowisk. Z tej perspektywy istotne jest poznanie odporności torfowisk na różnego rodzaje zaburzenia oraz poznanie zarówno jego przeszłości jak i aktualnego stanu.

CELE I METODY BADAŃ

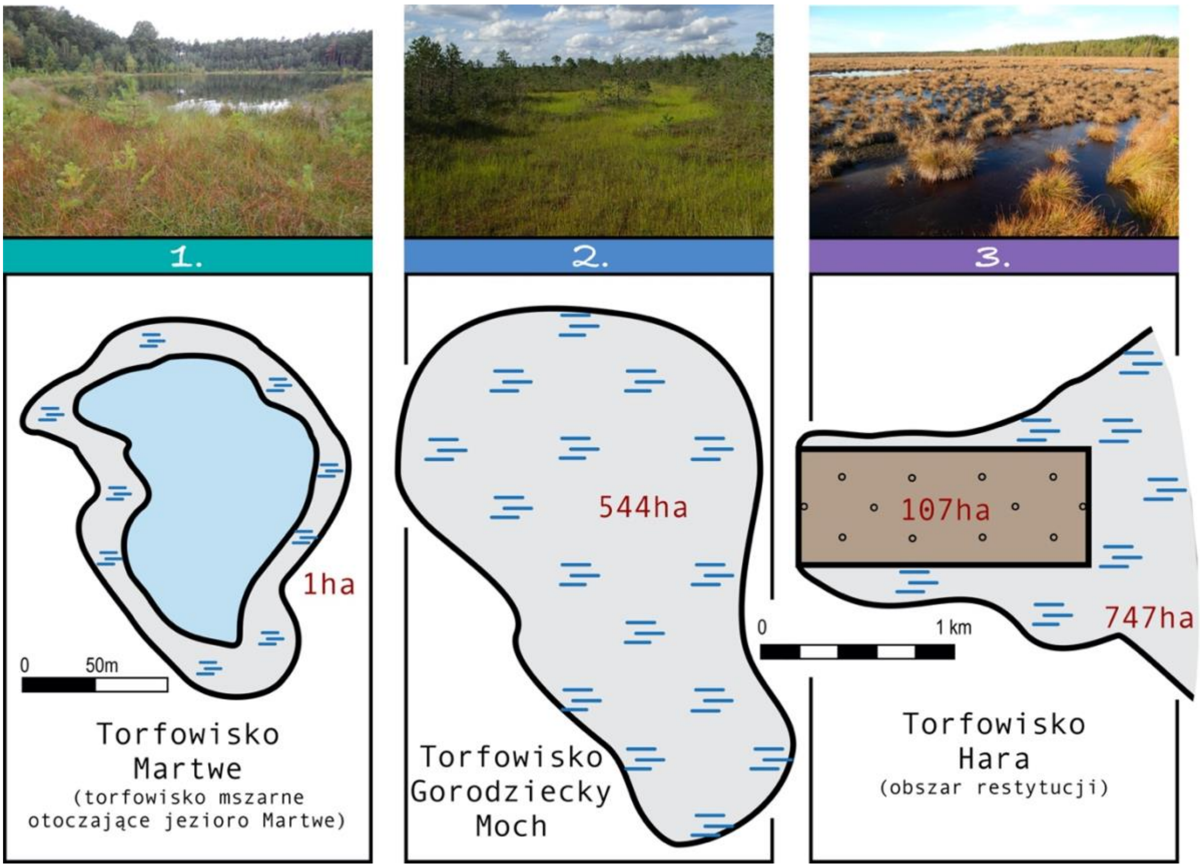
Głównym celem rozprawy doktorskiej jest ocena odporności torfowisk mszarnych na zaburzenia w ciągu ostatnich 300 lat z wykorzystaniem metod paleoekologicznych. W pracy rozpatrzono trzy główne, lokalne rodzaje zaburzeń europejskich torfowisk mszarnych charakteryzujące się różnym stopniem intensywności. Należą do nich: zmiany użytkowania ziemi, odwodnienie oraz eksploatacja torfu wraz z procesem restytucji (Rycina 2). Badania przeprowadzono na trzech torfowiskach zlokalizowanych na obszarze środkowo-wschodniej Europy, które w przeszłości uległy presji antropogenicznej.



Rycina 2. Rodzaje zaburzeń torfowisk mszarnych rozpatrywane w rozprawie doktorskiej wraz ze skalą ich intensywności.

Do badań wybrano (Rycina 3):

1) Torfowisko Martwe (torfowisko mszarne otaczające jezioro Martwe, powierzchnia: 1,06 ha) położone na obszarze Borów Tucholskich w środkowo-północnej Polsce, którego otaczający drzewostan w przeszłości został przekształcony w monokulturę sosnową oraz w dużej części został zniszczony przez tornado w 2012 roku,
2) Torfowisko Gorodziecky Moch (torfowisko ombrotroficzne, powierzchnia: 544 ha) zlokalizowane w Obwodzie Pskowskim w zachodniej Rosji, odwodnione w przeszłości na skutek wykopania rowu melioracyjnego,
3) Obszar wydobycia torfu torfowiska Hara (powierzchnia: 107.66 ha) podlegający restytucji (część torfowiska ombrotroficznego, powierzchnia: 747 ha) położony w zachodniej części Parku Narodowego Lahemaa w Północnej Estonii.



Rycina 3. Różnorodność stanowisk badawczych (Fot. D. Łuców, 2019; M. Słowiński, 2016; D. Łuców, 2018).

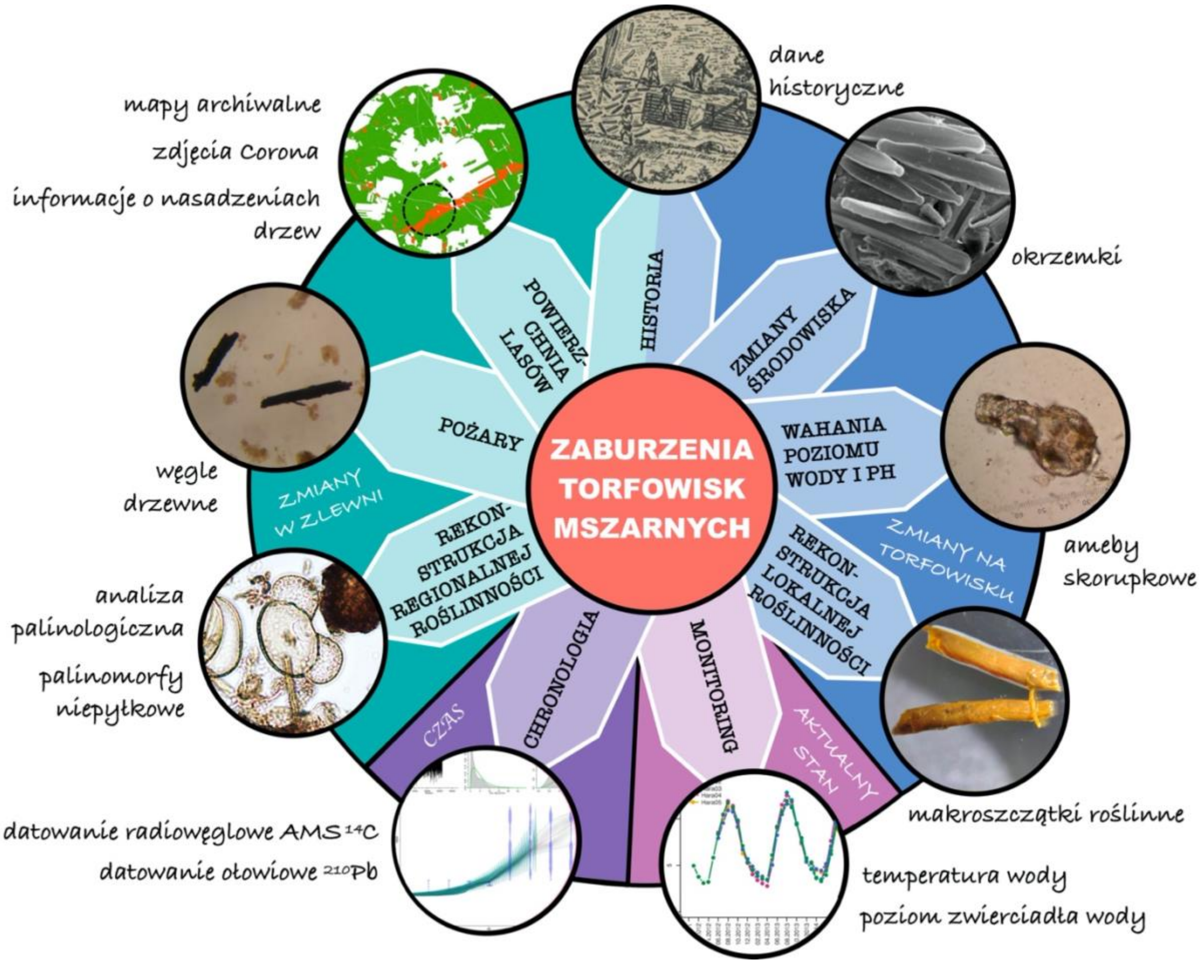
W trakcie badania wykorzystano archiwa torfowe, które poddano analizom paleoekologicznym przeprowadzonych z wysoką rozdzielczością (Rycina 4). Chronologię wydarzeń oparto o szczegółowe modele wiek-głębokość zbudowane w oparciu o wyniki modelowania datowań radiowęglowych i ołowiowych. W przedstawianych artykułach wykorzystano szeroką gamę analiz paleoekologicznych. Należą do nich analizy: ameb skorupkowych, makroszczątków roślinnych, palinologiczna z uwzględnieniem modelu REVEALS, palinomorf niepyłkowych, właściwości torfu (np. gęstość, straty na prażeniu), węgli drzewnych oraz okrzemek. W zależności od rozpatrywanego problemu i przyjętego podejścia analizy paleoekologiczne wspierane były przez dane teledetekcyjne (w tym dane na temat wielkości i lokalizacji nasadzeń drzew), dane historyczne, dane monitoringowe czy badania prób powierzchniowych (Rycina 5). Podejście wielowskaźnikowe do badań torfowisk przeprowadzone w wysokiej rozdzielczości pozwoliło rozpoznać rodzaj zaburzenie oraz prześledzić jego czas trwania oraz reakcje torfowiska.

Rycina 4. Schemat postępowania badawczego.

W pierwszym artykule zbadano oryginalny zapis paleoekologiczny uszkodzeń spowodowanych przez tornado z obszaru plantacji sosny na tle dotychczasowej gospodarki leśnej (zręby zupełne, wycinki drzew po ogniskach gradacji owadów). Zapis ten został udokumentowany w oparciu o rekonstrukcję roślinności 100-letniego rdzenia z torfowiska Martwe przy użyciu analizy palinologicznej wraz z modelem REVEALS oraz danych teledetekcyjnych i historycznych.

Drugi artykuł dotyka problematyki wpływu lokalnych zakłóceń (odwodnień), pożarów i zmian użytkowania ziemi (otwarcie krajobrazu i intensywność rolnictwa) na rozwój torfowiska Gorodetsky Moch w ciągu ostatnich 300 lat. Badania te przeprowadzono przy użyciu analiz paleoekologicznych oraz map historycznych.

W trzecim artykule zbadano reakcje obszaru wydobycia torfu torfowiska Hara na zabiegi restytucji ekologicznej w oparciu o analizy paleoekologiczne, badania prób powierzchniowych oraz dane z monitoringu środowiska przyrodniczego. Zapis ten został powiązany z początkowym, niezaburzonym etapem rozwoju torfowiska oraz działaniami ochronnymi i celami odtworzenia zdegradowanego ekosystemu.



Rycina 5. Metody badań.

WYNIKI BADAŃ

Artykuł nr 1

W pierwszym artykule zbadano przeszłe zmiany użytkowania ziemi otaczającego krajobrazu torfowiska Martwe, położonego na obszarze Borów Tucholskich w Północnej Polsce na przestrzeni ostatniego stulecia. Badanie oparte na danych palinologicznych rdzenia torfowego z torfowiska Martwe, teledetekcyjnych (w tym danych na temat wielkości i lokalizacji nasadzeń drzew) oraz historycznych wskazują na zmiany użytkowania ziemi w otaczającym krajobrazie torfowiska Martwe, które były spowodowane gospodarka leśną związaną z wycinką plantacji sosnowych (zręby zupełne), gradacją owadów oraz zniszczeniami spowodowanymi przez tornado.

Badania wykazały, że spadek procentowego udziału w powierzchni lasu w zapisie torfowym w pierwszej połowie XX wieku był najprawdopodobniej związany ze zrębami zupełnymi i usuwaniem uszkodzonego drzewostanu po gradacjach owadów. Wskazują na to również duże ilości późniejszych nasadzeń (najprawdopodobniej świadczące o wycince drzewostanów poprzedzających nasadzenia) oraz spadek procentowego udziału w powierzchni świerka (*Picea*), który obok sosny zwyczajnej (*Pinus sylvestris)* był najbardziej narażony na gradacje owadów. Wyniki badań pokazały, że zapis tornada z 2012 roku w osadach torfowych związany jest ze zmniejszeniem procentowego udziału w powierzchni sosny zwyczajnej (*Pinus sylvestris)* i wzrostem procentowego udziału w powierzchni brzozy (*Betula* spec.). Spadek procentowego udziału w powierzchni sosny zwyczajnej (*Pinus sylvestris)* jest rezultatem usuwania uszkodzonego przez tornado drzewostanu. Zarejestrowano związek między spadkiem procentowego udziału w powierzchni sosny zwyczajnej (*Pinus sylvestris)* w zapisie palinologicznym a wzorcami nasadzeń lasu po tornadzie. Rekonstrukcja roślinności sugeruje także ekspansję brzozy (*Betula* spec.) w drugiej połowie XX wieku przy rzeczywistym niskim udziale tego gatunku w drzewostanie Borów Tuchoskich i pobliskiego Nadleśnictwie Trzebciny. Wzrost ten mógł być spowodowany rozwojem brzozy na torfowisku, zmniejszeniem wypasu czy zaprzestaniu usuwania brzozy jako ,,chwastu leśnego".

Rekonstrukcja struktury przestrzennej roślinności na podstawie analizy palinologicznej i modelu REVEALS wraz z danymi teledetekcyjnymi opisana w artykule pokazała podobieństwa w zapisie, ale także różnice, co wskazuje na ograniczenia obu analiz. Przykładem jest wzrost lesistości do około 1950 roku w rekonstrukcji procentowego pokrycia roślinności REVEALS, podczas gdy dane archiwalne wskazują na stabilny udział lasu w tym czasie.

Badania opisane w pierwszym artykule wskazują słabą odporność plantacji sosnowych w otoczeniu torfowiska Martwe na silne wiatry i gradacje owadów w ciągu ostatniego stulecia. Na przestrzeni wieku monokultury sosnowe szybko zastępowały zniszczone drzewostany, co pozwalało na utrzymanie plantacji sosny i nie spowodowało zmian w gospodarowaniu lasu. Dopiero w ostatnich dwóch dekadach zaobserwowano zmianę sposobu gospodarowania i wprowadzanie do monokultur sosnowych większej ilości nasadzeń drzew liściastych. Zmiany użytkowania ziemi w zlewni i bliskim otoczeniu torfowiska Martwe przejawiające się przede wszystkim poprzez wycinki drzewostanu niewątpliwie miały wpływ na rozwój i aktualny stan zachowania torfowiska Martwe.

Artykuł nr 2

Druga praca dotyczy problematyki wpływu odwodnienia na rozwój torfowiska Gorodetsky Moch zlokalizowanego w Obwodzie Pskowskim na terenie zachodniej Rosji, jego odbudowę po stresie związanym z odwodnieniem oraz przeszłe zmiany użytkowania ziemi na przestrzeni ostatnich 300 lat w jego otaczającym krajobrazie.

Wpływ zaburzeń na funkcjonowanie tego ekosystemu przeprowadzono w oparciu o analizy ameb skorupkowych i makroszczątków roślinnych rdzenia torfowego. Badania wykazały, że torfowisko zostało najprawdopodobniej odwodnione na skutek wykopania rowu melioracyjnego na torfowisku w latach 60 XX wieku. Stres hydrologiczny spowodował zmianę składu roślinności torfowiskowej, doprowadzając do spadku udziału mchów torfowców (*Sphagnum* spp.) i wzrostu obfitości roślin naczyniowych. Spowodował on także zmianę w zespołach ameb skorupkowych, doprowadzając do tąpnięcia w populacji miksotroficznych ameb skorupkowych, zaniku liczebności ameb skorupkowych preferujących wilgotne warunki siedliska (*Archerella flavum* i *Hyalosphenia papilio*) oraz wzrostu udziału gatunków preferujących suchsze warunki (*Alabasta militaris*, *Cryptodifflugia oviformis*, *Assulina muscorum* i *Difflugia pulex*). Odwodnienie torfowiska spowodowało niestabilność hydrologiczną w ekosystemie i wygenerowało nowe warunki o dużych wahaniach sezonowych, co spowodowało wysoką różnorodność gatunkową ameb skorupkowych z dużą liczebnością *Galeripora discoides* (*Arcella discoides*). Wyniki te potwierdzają dotychczasowe badania (Hendon i Charman, 1997; Lamentowicz i Mitchell, 2005; Marcisz i inni 2015), że *Galeripora discoides* (*Arcella discoides*) może być wskaźnikiem niestabilności hydrologicznej. Torfowisko Gorodetsky Moch wykazało się silną odpornością i odbudowało się hydrologicznie po około 40 latach, pokazując, że umiarkowanie zaburzone (wg klasyfikacji Charman, 2002) torfowisko wysokie w Europie potrafi się odbudować. Efektem regeneracji torfowiska był wzrost liczebność mchów torfowców (*Sphagnum* spp.) wraz z liczebnością miksotroficznych ameb skorupkowych preferujących wilgotne warunki (*Archerella flavum* i *Hyalosphenia papilio*). Badania te wspierają założenie o dużej bioindykacyjnej wartości miksotroficznych ameb skorupkowych dostarczającego wczesnego sygnału ostrzegawczego zaburzenia mszarnego torfowiska, a ich odbudowę obiecującym sygnałem efektywnego odtwarzania ekosystemu (Jassey i inni, 2015).

W niniejszym artykule wpływ przeszłych zmian użytkowania ziemi na rozwój torfowiska zbadano w oparciu o analizy palinologiczną, mikroskopowych i makroskopowych węgli drzewnych rdzenia torfowego oraz map historycznych i obrazów Corona (obrazów satelitarnych programu CORONA). Największe zmiany w otaczającym krajobrazie (wylesienia, intensywność rolnictwa) związane były głównie z intensywnym rozwojem działalności człowieka w pierwszej połowie XX wieku w efekcie czego, kosztem powierzchni leśnych wrosła powierzchnia gruntów rolnych i osad. Warunki wilgotnościowe na torfowisku były wówczas względnie stabilne. Jednak zmiany w użytkowaniu ziemi obserwowane w dłuższej perspektywie czasu, w tym postępujące wylesienia na przestrzeni ostatnich stuleci, mogły najprawdopodobniej przyczynić się do spadkowego trendu poziomu wód gruntowych, co w rezultacie prawdopodobnie doprowadziło do spadku liczebności miksotroficznych gatunków ameb skorupkowych. Nie stwierdzono jednak istotnych wyraźnych związków między roślinnością regionalną (wylesienia) a zmianami hydrologicznymi na torfowiska w tym czasie.

Artykuł nr 3

W trzecim artykule zbadano wpływ eksploatacji torfu oraz restytucji ekologicznej na poprzednio eksploatowane torfowisko Hara, zlokalizowane w Parku Narodowym Lahema w Północnej Estonii. Wpływ zaburzeń na funkcjonowanie tego ekosystemu przeprowadzono w oparciu o analizy ameb skorupkowych, okrzemek, makroszczątków roślinnych, palinologicznej, palinomorf nie pyłkowych, właściwości torfu, badań monitoringowych (średnia miesięczna temperatura wody, głębokość zwierciadła wody, roczna suma opadów) oraz analizy ameb skorupkowych, makroszczątków roślinnych i okrzemek z prób powierzchniowych.

Badania wykazały, że w wyniku przemysłowej eksploatacji torfu prowadzonej w drugiej połowie XX wieku doszło do degradacji torfowiska i utraty torfu, który akumulował się na przestrzeni ostatnich ok. 1900 lat. Zabiegi restytucji stworzyły nowe, bardzo dynamiczne środowisko, z dużymi wahania poziomu wody (od -90 do +30 cm), które przyczyniły się do rozwoju kęp wełnianki pochwowatej (*Eriphorum vaginatum*) na odsłoniętej, pozbawionej roślinności powierzchni torfu, zielenic (*Chlorophyt*a) oraz zespołu ameb skorupowych silnie zdominowanych przez *Galeripora discoides* (*Arcella discoides*). Wyniki te potwierdzają dotychczasowe przypuszczenia (Lamentowicz i inni, 2019; Lamentowicz i inni, 2009), że obecność *Galeripora discoides* (*Arcella discoides*) może być związana z okresowymi zalewami i wysychaniem eksploatowanych powierzchni torfowisk, a także, że może być pionierskim taksonem w niestabilnych, nowych siedliskach. W artykule zwrócono także uwagę na zielenice jako potencjalne źródło pożywienia, które może również wpływać na skład gatunkowy ameb skorupkowych i może być powiązany ze wzrostem *Galeripora discoides* (*Arcella discoides*). Obiecującą przesłanką regeneracji torfowiska Hara jest zwiększona obfitość miksotroficznych gatunków ameb skorupkowych.

Zapis regeneracji torfowiska porównano z początkowym, niezaburzonym etapem rozwoju torfowiska (około 2 tysięcy lat temu). Wyniki ujawniły uderzający kontrast ekologiczny pod względem lokalnej roślinności i zespołów ameb skorupkowych. Około 2 tysięcy lat temu torfowisko Hara było wilgotnym i stabilnym ekosystemem, na co wskazuje dominacja torfowca brunatnego/czerwonawego (*Sphagnum fuscum/rubellum*) i *Archerella flavum*. Główną różnicą między porównywanymi zapisami jest mała obfitość mchów torfowców

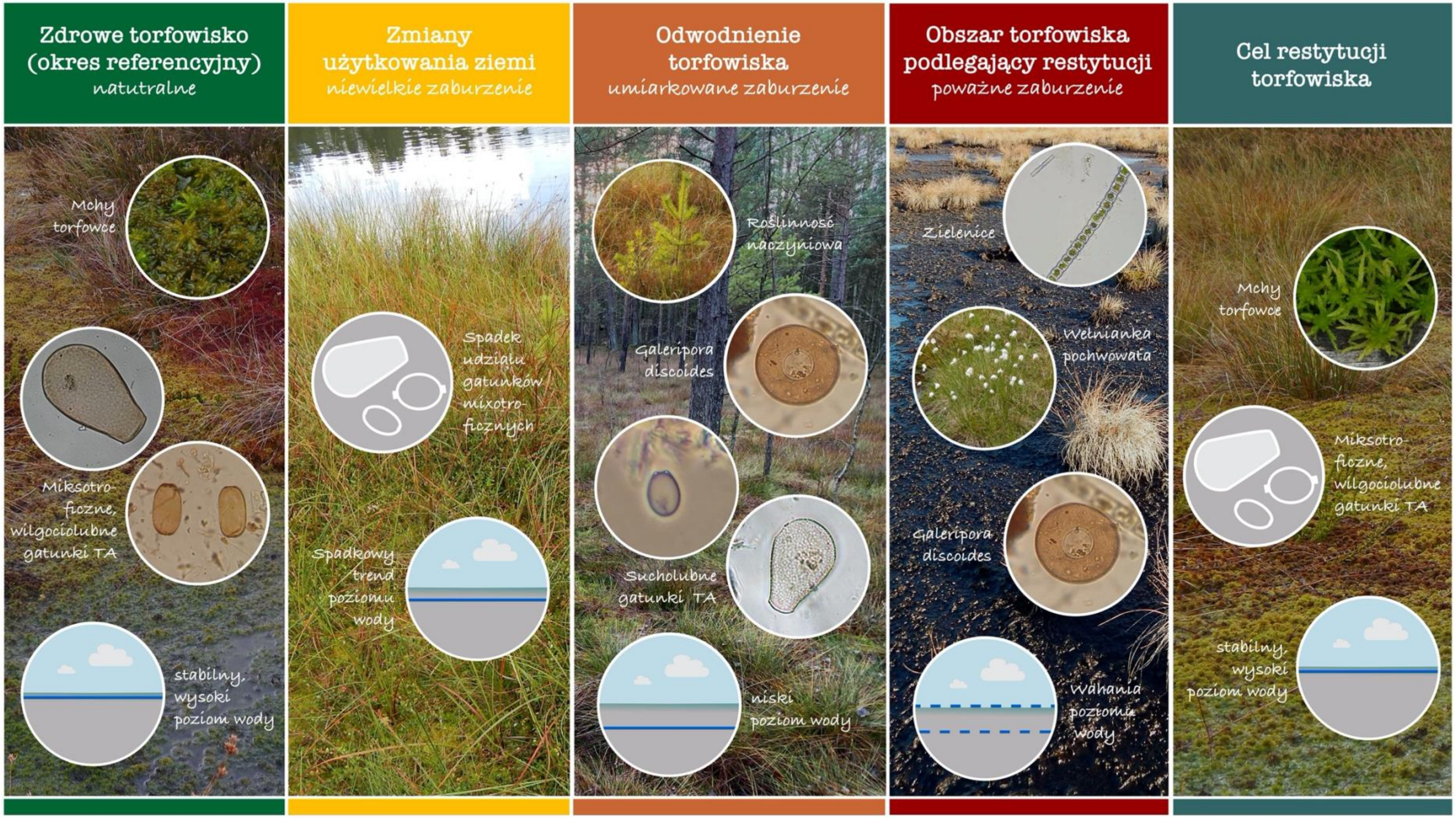
(*Sphagnum* spp.) oraz niska liczebność miksotroficznych ameb skorupkowych w współczesnym zapisie regenerującego się torfowiska. Mając na względzie perspektywę długoterminową starano się ocenić postęp procesu regeneracji obszaru wydobycia torfu torfowisko Hara, który jest jeszcze w początkowej fazie procesu odtwarzania. Na podstawie syntezy danych paleoekologicznych oraz współczesnych zespołów ameb skorupkowych i okrzemek, stwierdzono, że zdrowe torfowisko wysokie powinno posiadać określony zestaw złożony z miksotroficznych gatunków ameb skorupkowych. Są one wskaźnikami odpowiedniego stanu hydrologicznego torfowiska mszarnego, nawet jeśli skład gatunkowy mchów torfowców różni się od zrekonstruowanych warunków referencyjnych.

PODSUMOWANIE I WNIOSKI

Głównym celem prezentowanej rozprawy doktorskiej było dokonanie charakterystyki, analizy a następnie interpretacji zapisu zaburzeń w archiwach torfowych (tj. zmian użytkowania terenu, odwodnienia, przemysłowej eksploatacji torfu wraz z etapem restytucji) oraz próby określenia odporności i możliwości regeneracji torfowisk po badanych zaburzeniach. Badania te dostarczyły nowych, wysokorozdzielczych i wielowskaźnikowych paleoekologicznych danych ilościowych i jakościowych, które przybliżają nas do lepszego zrozumienia wpływu zaburzeń na ekosystemy torfowisk mszarnych. Zwracają one szczególną uwagę na niezwykle istotną w obecnym czasie potrzebę ochrony torfowisk oraz przywracanie zniszczonym i zdegradowanym ekosystemom zdolności akumulacji węgla, bioróżnorodności i odpowiednich warunków hydrologicznych wynikające z potrzeby minimalizowanie skutków globalnego ocieplenia. Wyniki badań omówione w rozprawie doktorskiej wzmacniają istotność lepszego zrozumienia odporności torfowisk na różnego rodzaju zaburzenia w różnorodnych skalach czasowych i przestrzennych oraz poznania zarówno jego przeszłości jak i aktualnego stanu. Co więcej, potwierdzają one znaczenie badań paleoekologicznych we wspieraniu restytucji zaburzonych i zdegradowanych torfowisk oraz w wyznaczaniu celów ochrony tych cennych ekosystemów.

Konsekwencje zaburzeń dla funkcjonowania torfowisk mszarnych oraz odporność tych ekosystemów w rozprawie doktorskiej rozpatrywano na różnych poziomach zaburzeń torfowisk: niewielkie, umiarkowane oraz poważne zaburzenie (wg. klasyfikacji Charman, 2002) (Rycina 6). W pierwszym oraz drugim artykule przedstawiono analizy przestrzenne przeszłych zmian użytkowania ziemi (artykuł pierwszy: zręby zupełne, wycinki uszkodzonego drzewostanu po gradacji owadów i tornada; artykuł drugi: otwarcie krajobrazu, intensywność rolnictwa, pożary) w oparciu o porównanie wyników analizy palinologicznej ze zmianami pokrycia terenu przy użyciu danych teledetekcyjnych (w tym danych na temat wielkości i lokalizacji nasadzeń drzew) w artykule pierwszym oraz map historycznych, obrazów Corona i węgli drzewnych w artykule drugim. W pierwszym artykule udokumentowano pierwszy w Polsce paleoekologiczny zapis zniszczeń spowodowanych przez tornado, potwierdzając tym samym nieliczne do tej pory badania (Du i inni, 2019), że zapis tornada w osadach torfowych jest możliwy. Zwrócono szczególną uwagę na syntezę danych paleoekologicznych, teledetekcyjnych i historycznych, które mogą być pomocne w określeniu dynamiki zaburzeń, takich jak zręby zupełne, gradacje owadów, wiatr oraz wpływ tych zmian na postrzeganie lasów przez lokalną społeczność.

W kolejnych artykułach opisano wpływ działalności człowieka t.j. otwarcie krajobrazu oraz odwodnienia (wykopanie rowu melioracyjnego) w artykule drugim oraz przemysłowej eksploatacji torfu wraz z etapem restytucji w artykule trzecim na rozwój torfowiska w oparciu o analizy ameb skorupkowych, makroszczątków roślinnych, a także analizy okrzemek i palinomorf niepyłkowych wspieranych badaniami monitoringowymi w artykule trzecim. Pomimo względnie stabilnych warunków hydrologicznych na torfowisku Gorodziecky Moch, zmiany w użytkowaniu ziemi w tym postępujące wylesienia na przestrzeni ostatnich stuleci (niewielkie zaburzenie wg. klasyfikacji Charman, 2002), najprawdopodobniej przyczyniły się do spadku liczebności miksotroficznych gatunków ameb skorupkowych poprzez spadek poziomu wód gruntowych. Z kolei, późniejszy stres hydrologiczny na skutek melioracji odwadniających doprowadził do poważnych zmian w ekosystemie, który wykazał tendencję ku regeneracji. Badania opisane w artykule, pokazują, że umiarkowanie zaburzone (wg. klasyfikacji Charman, 2002) torfowiska wysokie w Europie po silnym stresie, takim jak osuszenie posiadają potencjał do samodzielnej regeneracji. Z odmienną sytuacją mamy do czynienia w przypadku zabiegów restytucji zdegradowanego obszaru wydobycia torfu torfowiska Hara (poważne zaburzenie wg. klasyfikacji Charman, 2002), które spowodowało stworzenie dynamicznego siedliska z dużymi wahania poziomu wody. W rezultacie doszło do rozwoju kęp wełnianki pochwowatej (*Eriophorum vaginatum*) na odsłoniętej, pozbawionej roślinności powierzchni torfu, zielenic (*Chlorophyta*) oraz zespołów ameb skorupowych zdominowanych przez *Galeripora discoides* (*Arcella discoides*). Wyniki badań opisane w publikacji drugiej i trzeciej wspierają dotychczasowe wyniki dotyczące gatunku *Galeripora discoides* (*Arcella discoides*) jako indykatora niestabilności hydrologicznej torfowiska, a także gatunku pionierskiego migrującego na nowe siedliska. Co więcej, dostarczają kolejnych przykładów wysokiej wartości bioindykacyjnej miksotroficznych gatunków ameb skorupkowych. W pracy pokazano, że gatunki te są wartościowymi indykatorami stabilnie uwodnionego torfowiska mszarnego, a spadek ich liczebności można traktować jako wczesny sygnał ostrzegawczy zaburzenia, a ich odbudowa jest obiecującym sygnałem odporności i regeneracji ekosystemu.



Rycina 6. Podsumowanie wyników badań. Zaburzenia torfowisk mszarnych i ich efekty z uwzględnieniem klasyfikacji opracowanej przez Charman (2002) - porównanie ze zdrowym ekosystemem oraz celem restytucji torfowiska (Fot. D. Łuców, 2016, 2019; M. Lamentowicz, 2019; D. Łuców, 2018, 2016). Skrót ,,TA” na rycinie oznacza ameby skorupkowe.

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Pine Forest Management and Disturbance in Northern Poland: Combining High-Resolution 100-Year-Old Paleoecological and Remote Sensing Data

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Global warming has compelled to strengthen the resilience of European forests. Due to repeated droughts and heatwaves, weakened trees become vulnerable to insect outbreaks, pathogen invasions, and strong winds. This study combines high-resolution analysis of a 100-year-old high-resolution peat archive synthesized from the Martwe peatland in Poland with remote sensing data. We present the first REVEALS based vegetation reconstruction in a tornado-hit area from Poland on the background of previous forest management in monocultural even-aged stands – Tuchola Pinewoods. During the 20th century, the pine monocultures surrounding the peatland were affected by clear-cutting and insect outbreaks. In 2012, a tornado, destroyed ca. 550 ha of pine forest around the peatland. The palynological record reflects these major events of the past 100 years as well as changes in forest practices. Our study showed the strong relationships between the decrease of *Pinus sylvestris* (Scots pine) in palynological record as well as planting patterns after the tornado. Moreover, past forestry practices [such as domination of *Pinus sylvestris*, the collapse of *Picea abies* (Norway spruce), low share of *Betula* spec. (birch) due to *Pinus sylvestris* promotion and probable also to a lesser by removal of *Betula* as a “forest weed,” and low plant coverage of tree species due to clear-cutting and cutting after insect outbreaks] were well identified in the proxy record. In monocultures managed over decades, the reconstruction of vegetation may be challenging due to changes in the age composition of the *Pinus sylvestris* stands. We found that through historical, remote sensing, and paleoecological data, the dynamics of disturbances such as insect outbreaks and tornadoes, as well as the changing perceptions of local society about forests, can be determined.

Keywords: tornado, peatland, paleoecology, pollen analysis - REVEALS, monocultures, insect outbreaks

INTRODUCTION

Forest disturbance by storms, including tornadoes, is a rare but important problem that needs to be considered in the development of forest management strategies (Dobrowolska, 2015; Szmyt and Dobrowolska, 2016). Over the past decades, the frequency of extreme events such as storms and tornadoes has increased across Europe (Seidl et al., 2014) and is forecasted to increase further in the future (Senf and Seidl, 2021). Atmospheric phenomena that can damage forests, such as strong winds and tornadoes, are difficult to predict. However, it is important to understand the complex interactions between the damage caused by extreme events, the resilience of forest communities, climate change, and forest management due to the increased extent of forest destruction by the wind in recent years in Europe (Gardiner et al., 2010; Seidl et al., 2014; Gregow et al., 2017). Moreover, observations from the last decades indicate that the future will witness more extreme events that will not just affect the forests. These events include heatwaves, which will increase the possibility of fires (Ummenhofer and Meehl, 2017; Brando et al., 2019). The European monocultures are expected to be more sensitive to drought, and hence, the exposure of forests to pathogens, insect outbreaks, and strong winds (Leuschner and Ellenberg, 2017; Seidl et al., 2017, 2020).

Wind disturbances were more frequent in the European forests in the last decades (Seidl et al., 2017). During 1950–2010, more than 130 separate storms occurred, causing significant damage to forests (Gardiner et al., 2010). Huge economic losses resulted from cyclone Gudrun in 2005 and extratropical cyclones in Sweden in 1969 (wood loss of 42.2 mln m^3), Lothar and Martin storm in 15 European states in 1990 (more than 240 mln m^3), and cyclone Klaus in France, Spain, Portugal, and Italy in 2009 (43.1 mln m^3) (Jantz, 1971; Gardiner et al., 2010). Furthermore, tornadoes of F2 or higher intensity can harm and uproot trees (Fujita, 1971). Across Europe, 9,529 tornadoes have been recorded between 1800 and 2014 CE (Groenemeijer and Kühne, 2014; European Severe Weather Database, 2020), with the actual number predicted to be higher (Shikhov and Chernokulsky, 2018).

Our study is focused on the Tuchola Pinewoods, which are one of the largest forest complexes in Poland. The current forest composition includes pine monocultures (plantations) in even-aged stands, introduced in the second half of the 18th century by Prussian forestry (Gietkowski, 2009). At present, *Pinus sylvestris* (Scots pine) is the dominant species, occupying more than 95% of the forest area, and is accompanied by other species such as *Betula* (birch) (1.8%), *Quercus* (oak) (1.1%), *Alnus glutinosa* (black alder) (1.0%), and *Picea abies* (Norway spruce) (0.5%) (State Forests data, 2020).

Studies report that forests have been affected by fires, insect outbreaks, strong winds, and tornados in the last 100 years (Karasiewicz, 1926; Koziński, 2007; Gietkowski, 2009; Słowiński et al., 2019). The Tuchola Pinewoods showed markedly low resistance to insect outbreaks. The most severe outbreak in this forest and Poland, in general, was that of *Panolis flammea* (pine beauty) in 1922–1924 (Mokrzecki, 1928; Broda, 2000, 2010). Due to the outbreak, most of the Notecka Forest and the Tuchola Pinewoods were cut down (Koehler, 1974; Ankudo-Jankowska, 2003; Broda, 2003). During 1978–1985, weather anomalies with cold winters and changes in water conditions triggered the outbreak of *Lymantria monacha* (black arches), which was the largest recorded in the history of the Polish State Forests (since its founding in 1924) (Sliwa, 1989; Jablonski, 2015). This outbreak affected the northern and western parts of Poland, including the Tuchola Pinewoods.

On 14 July 2012, the Tuchola Pinewoods have been hit by one of the most destructive tornadoes in Poland, which had an intensity of F3 (Taszarek et al., 2016). The tornado caused one fatality and 10 injuries, and within minutes, around 550 ha of the Tuchola Pinewoods in the Trzebciny District and 105 buildings were damaged. The track of the tornado was 20-km long and 800-m wide at maximum. On 11/12 August 2017, a hurricane hit the Tuchola Pinewoods. It destroyed forests up to an area of ca. 80,000 ha (9.8 mln m^3) in 60 forest districts in northwestern Poland (Trębski, 2019).

In Poland, about 350 tornadoes have occurred between 2000 and 2019 (European Severe Weather Database, 2020). Moreover, 37 deadly tornadoes were known from earlier periods, for example, in Turzyn (1829), Tuchola (1871), Rowiska (1926), and Rawa Mazowiecka (1958) (Taszarek, 2016; Taszarek and Gromadzki, 2017). Each year, an average of 8–14 tornadoes hits Poland. The country is also affected by tornadoes of very high intensity (F4 on the Fujita scale) once every one or two decades (Taszarek, 2016).

Martwe peatland, located within the area deforested by the July 2012 tornado, offers the rare opportunity to study the imprint of a tornado in the paleoecological (pollen) record. We moreover use this archive to study the representation of other forest changes during the past 100 years, including further catastrophic events such as large-scale disasters and clear-cutting. To this end we attempt quantitative interpretation of the pollen record using the REVEALS model and compare the results with archival data from the area 4 km radius around the lake.

Here, we used a *Sphagnum* peatland as a natural archive that is often used to reconstruct long-term environmental and climate changes of the past based on paleoecological research (Tobolski, 2000; Charman, 2007; Słowiński et al., 2014). Paleoecological archives, such as peat, provide information about the past landscape changes, regional and local vegetation, climate, fires, and human history (Booth et al., 2004; Mitchell et al., 2007; Lamentowicz et al., 2015; Payne et al., 2015). In particular, pollen analysis serves as a proxy to reconstruct local- and regional-scale vegetation (van Geel, 1978; Słowiński et al., 2015; Kołaczek et al., 2018) and infer the history of forest management (Słowiński et al., 2019; Lamentowicz et al., 2020; Schafstall et al., 2020). Pollen percentage values do not perfectly represent past vegetation composition because pollen production and dispersal differ among plant taxa so strong pollen producers are over-represented while weak pollen producers are under-represented. We applied the REVEALS model (Sugita, 2007) to reduce this bias in the pollen data.

Furthermore, peatlands have been used extensively as archives of the past direct and indirect disturbances such as deforestation, clear-cutting, drainage, land use, pollution, fragmentation, fire, floods, or storms (Ireland and Booth, 2012; Ireland et al., 2012; Marcisz et al., 2019; Swindles et al., 2019; Łuców et al., 2020). However, they have never been used so far to explore past tornado events. Therefore, the aim of this study, is to present the first tornado-related paleoecological record from a monoculture in Poland on the background of previous forest management (clear-cutting, cutting after insect outbreaks), through vegetation reconstruction of a 100-year-old peat core, based on pollen analysis and the REVEALS model (Sugita, 2007) as well as on remote sensing data. We used the pollen analysis for the better understanding disturbances recorded in pine dominated forests in periods that devoid of historical data.

MATERIALS AND METHODS

Study Site

The study site is the Martwe peatland in NW Poland (a partly floating mat on the Martwe lake) and its neighboring area within a radius of 4 km (**Figure 1B**). The peatland, which is located in the middle of a Pine monoculture forest, surrounds a small dystrophic lake. This lake is overgrown by *Sphagnum* floating mat (Martwe peatland) (**Figure 1C**), from which the peat core was obtained. The forest in this area has existed continuously for centuries, however, since after the first partition of Poland (1772 CE), a large-scale transformation of forests to pine monocultures by Prussian forestry was recorded. It was exactly connected with the introduction of the decree "On the management of the Tuchola Forest" issued by King Frederick of Prussia in 1782 (Jaszczak, 2008; Jaździewski, 2008). As a result, eight administrative areas were created in the forested area of Tuchola Forest, whose first purpose was to make a detailed map of the forest area in order to estimate the potential for timber harvesting. The study site is located in Trzebciny Forest District in the southern part of the Tuchola Pinewoods (53°37′07.0′′N, 18°12′09.0′′E, 109.4 m a.s.l.; **Figure 1**). It is situated in the outwash plain of the Wda River, which developed during the Pomeranian phase of the

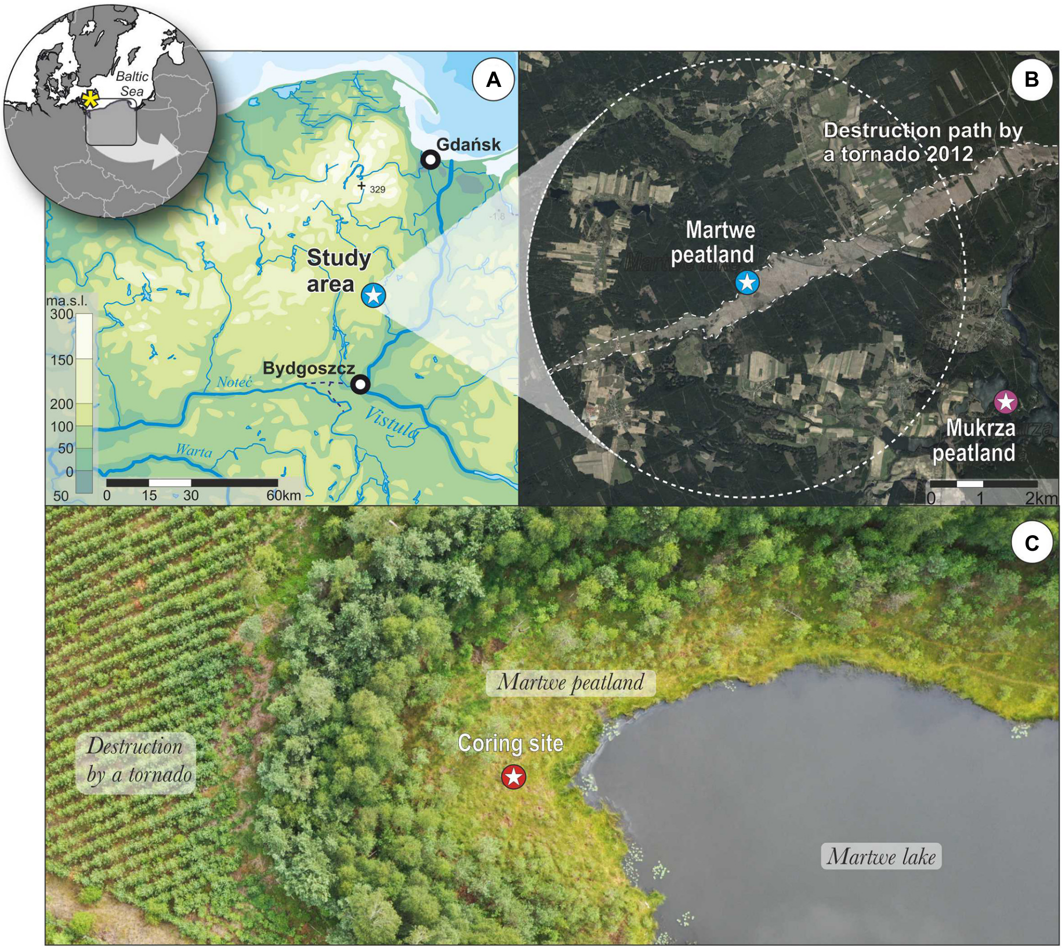


FIGURE 1 | Setting of the study site. **(A)** Location on the Europe and Poland maps. **(B)** Location of the tornado path from 2012 in the southern part of the Tuchola Pinewoods. The Martwe peatland is in the center of map. Its neighboring area within the 4-km radius is marked in a white circle. The Martwe peatland is indicated by blue color, and Mukrza peatland (the nearest well-dated paleoecological site) by magenta color. **(C)** Coring site from the Martwe peatland (*Sphagnum* floating mat on the Martwe lake) and drone picture from July 2020.

Vistulian glaciation (Błaszkiewicz et al., 2015). The Martwe lake was formed by the melting of a buried ice block (Kordowski et al., 2010; Słowiński, 2010; Słowiński et al., 2015). The entire peatland as well as the lake (3.56 ha) is protected at the national level as Nature Reserve. It is assumed that acidification of the lake and the development of floating mat have been triggered by the cultivation of *Pinus sylvestris* monoculture about 200 years ago (Gietkowski, 2009; Kordowski et al., 2010). The maximum depth of the lake in the central part is about 3 m, while the peat layer has a thickness of 20–100 cm (Kordowski et al., 2010). The climate data from the meteorological station in Chojnice (about 45 km from the study site) obtained for the years 1951–2017 reveal that the warmest month is July with a temperature of 17.1°C and the coldest is January with −2.5°C (Institute of Meteorology and Water Management - National Research Institute, 2019). The average annual temperature of the study site is 7.3°C, and the average annual precipitation ranges between 550 and 600 mm.

Current Forest Composition and Potential Vegetation

In the study area, the forests are currently dominated by *Pinus sylvestris* forests (**Figures 2A,C**). The map of potential natural vegetation suggests a greater variety of trees species (**Figure 2B**; Matuszkiewicz et al., 1995), with mixed oak-pine forests being dominant (*Querco-Pinetum*), accompanied by oak-lime-hornbeam forests (*Tilio-Carpinetum*, poor) and swampy ash-alder wood forests (*Frazino-Alnetum* [*Circaeo-Alnetum*]). *Leucobryo-Pinetum*, *Peucedano-Pinetum*, and *Carici elongate-Alnetum* associations occupy a small area of the forests.

Peat Record

Four peat monoliths were extracted from the Martwe peatland in spring 2016 using a Wardenaar sampler (chamber dimension: 10 cm × 10 cm × 100 cm) (Wardenaar, 1987). The most representative peat core was selected for this study. For reconstruction covering the last 100 years, we analyzed a 47-cm-long part of one peat monolith (MAR1, 67 cm) from the southern part of the Martwe peatland, which was affected by a tornado from 2012. Pollen analysis was performed to reconstruct changes in the composition of forests over the last 100 years. Pollen samples (1 cm^3) were collected continuously at 0.5-cm intervals (from 4 to 11 cm) and 1-cm intervals (1–3 and 12–47 cm), and prepared using standard laboratory procedures for palynological analysis (Berglund and Ralska-Jasiewiczowa, 1986). Pollen grains were identified using atlases (Moore et al., 1991; Beug, 2004) under a microscope at 400× and 1,000× magnifications. The figure of the simplified percentage pollen diagram was prepared using the Tilia program (version 2.0.41) (Grimm, 1992; **Supplementary Figure 1**). The pollen records from the Martwe peatland was compared with pollen record from Mukrza peatland, which is ca. 5 km southeast of the Martwe peatland. Original data come from the doctoral dissertation of Milena Obremska (Obremska, 2006; Lamentowicz and Obremska, 2010).

To extract past vegetation cover from pollen data we applied REVEALS using the REVEALSinR function from the discover R package (Theuerkauf et al., 2016). REVEALS is a correction factor approach, i.e., bias in pollen data is removed by dividing pollen counts by two corrections factors, i.e., pollen productivity estimates (PPEs) to account for differential pollen production and

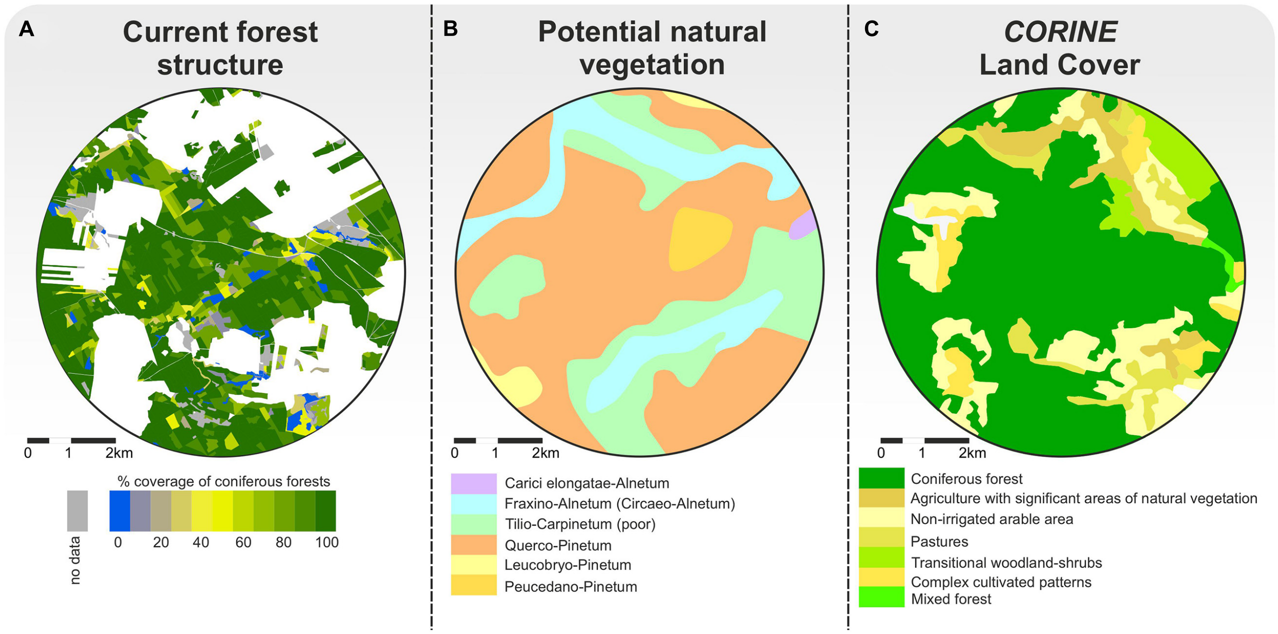


FIGURE 2 | Maps of the area within the 4-km radius from the Martwe peatland (*Sphagnum* floating mat on the Martwe lake). **(A)** Current forest structure. The map was developed for the year 2020. **(B)** Differentiation of potential natural vegetation (Matuszkiewicz et al., 1995). **(C)** CORINE Land Cover. The map was developed for the year 2018. The Martwe peatland is located in the center of each map.

the dispersal-deposition factor K which accounts for differential pollen dispersals. We selected the Lagrangian-stochastic model to calculated K factors. As yet no PPEs are available from Poland, we used a preliminary PPE data set, which is based on the application of the ROPES model on a number of lake pollen records from northern Poland and Germany (**Supplementary Table 1**; Theuerkauf and Couwenberg, 2018). ROPES is a quantitative method for translating single pollen records into past vegetation composition without PPEs as an input parameter. The method requires pollen counts and pollen accumulation rate data. Besides reconstructed vegetation composition, ROPES also estimates PPEs. Stratigraphic diagrams were prepared using C2 (Juggins, 2003).

Chronology

The six samples of *Sphagnum* stems were dated using ^{14}C AMS method in Poznań Radiocarbon Laboratory (laboratory code: Poz; **Table 1**). The Bayesian age-depth model based on these dates was constructed to determine the absolute chronology the age-depth model was constructed using OxCal 4.3 software (Bronk Ramsey, 1995, 2006), by applying the *P_Sequence* function, assuming $k_0 = 0.9$, $\log_{10}(k/k_0) = 1$, and interpolation = 0.5 cm (Bronk Ramsey, 2008; Ramsey and Lee, 2013). IntCal20 (Reimer et al., 2020) and BombNH1 (Hua et al., 2013) ^{14}C atmospheric curves were used as the calibration sets. For better readability, μ (mean) values are used to reflect the modeled age derived from the age-depth model.

The topmost peat profile (53 cm) was dated using the ^{210}Pb method. A samples for the analysis were processed at the Institute of Nuclear Physics, Polish Academy of Sciences, in Kraków. The activity of ^{210}Pb was determined as the activity of its daughter radionuclide ^{210}Po (half-life 138 days), which is in radioactive equilibrium with ^{210}Pb. A total of 52 peat samples, weighing 0.35–0.63 g, were spiked with ^{208}Po as a yield tracer and digested using a concentrated mixture of HNO_3, HCl, and H_2O_2. Then, the solution was treated with 0.5 M HCl. Finally, a thin alpha-spectrometric Po source was prepared by spontaneous electrodeposition onto a silver plate after reduction of Fe^{3+} with ascorbic acid (Flynn, 1968; Fernández et al., 2012; Lee et al., 2014). The ^{210}Po activities were measured using Alpha Duo spectrometer with Ortec detectors.

Excess ^{210}Pb (unsupported) was calculated as the difference between the total activity concentration and supported activity concentration of ^{210}Pb. The supported activity was calculated from the mean ^{210}Pb activity concentration for the bottom layers (56 ± 5 Bq/kg). The age–depth relationships in a part of the peat core were estimated using two alternative dating models: Constant Rate of Supply (CRS) and Constant Flux Constant Sedimentation (CF/CS) (Sanchez-Cabeza and Ruiz-Fernández, 2012). The total unsupported inventory of ^{210}Pb was calculated to be 2,800 ± 350 Bq/m^2. The value was then corrected based on the extrapolation of the exponential equation to eliminate a systematic deviation of CRS dates toward erroneously old ages—the so-called "old-date error" (Binford, 1990; Tylmann et al., 2016).

Remote Sensing Methods

The land-use changes in the study area (neighboring area within a radius of 4 km) were reconstructed using archival material and the following maps: (1) German topographic maps—Messtischblatt (Meßtischblätter) in the scale of 1:25,000 [sheet: Lonsk (2375) from 1932 CE]; (2) Topographic Map of the Military Geographical Institute—Tactical Map of Poland in the scale of 1:100,000 (sheet P34 S26 Tuchola, released in 1933 CE, based on a photo from 1928 CE); (3) postwar topographic maps in the scale of 1:25,000 published in the 1980s CE; (4) overview map of the stands of the Osie Forest District, Szarłata area, in the scale of 1:20,000 (state on 1975); and (5) potential natural vegetation map of Poland in the scale of 1:300,000 (sheet A2) (Matuszkiewicz et al., 1995). All historic maps used for the analysis were calibrated and geo-referenced. Their spatial accuracy was ca. 30 m or better. The current state of the forest was determined using aerial orthophotomaps. Information layers with age, type, and tree species were obtained from the Forest

TABLE 1 | ^{14}C dating results from the Martwe peatland with the calibration and description of the dated plant macrofossils.

Laboratory code - number	Depth (cm)	^{14}C date (14C BP)	Calibrated dates [cal. CE] (2σ - 95.4%)	Dated material
Poz-88711	12.5	107.15 ± 0.35 pMC	1956–1957 (2.7%) 2002–2006 (92.8%)	*Sphagnum* stems
Poz-88710	20.5	115.36 ± 0.36 pMC	1957–1958 (12.8%) 1989–1992 (82.6%)	*Sphagnum* stems
Poz-88709	30.5	132.62 ± 0.4 pMC	1977–1979 (95.4%)	*Sphagnum* stems
Poz-88714	40.5	101.78 ± 0.43 pMC	1955–1956 (95.4%)	*Sphagnum* stems
Poz-88713	50.5	255 ± 30	1520–1587 (22.4%) 1622–1677 (54.4%) 1742–1751 (0.9%) 1764–1800 (17.8%)	*Sphagnum* stems
Poz-88708	56	230 ± 30	1530–1539 (1.2%) 1635–1686 (44.9%) 1732–1805 (44.1%) 1927–undefined limit (5.2%)	*Sphagnum* stems

pMC—the percentage of modern carbon; this unit is applied to modern dates (i.e., after 1950 CE).

Data Bank of the Polish State Forests (pl. Bank Danych o Lasach – Lasy Państwowe), which is part of the Numerical Forest Map. The Forest Data Bank provides detailed information about the modern forest. Data about open land were obtained from CORINE Land Cover, topographic maps in the scale of 1:10,000, and aerial photographs. Private forests were not included in the study. At present, their share in the total forest area is insignificant but it was considerable in the past in Tuchola Pinewoods (Pączewski, 1924). All maps were prepared using ArcGIS software.

RESULTS AND INTERPRETATION

Chronology

The age-depth model revealed that the model agreement (A_{model}) was 59%, which is almost equal to the recommended minimum (60%) (Bronk Ramsey, 2008). As most of the dates showed an individual agreement of >30% and all dates represented the period after the year 1945, we decided to accept the model (**Figure 3** and **Table 1**). The fragment of the profile that was studied (0–47 cm) spanned a period of ca. 1892–2016. For the period after 1945, the maximum error of modeled age reached 4.3 years, whereas for the period between ca. 1891 and 1945 the age uncertainty ranged between 10.6 and 30 years.

The results showed that ^{210}Pb and ^{14}C chronologies were inconsistent for the lower part of the profile after applying the two models (CF/CS and CRS) and correcting for the lower part of the ^{210}Pb date profile (**Supplementary Files**). For the section between 35.5 and 25.5 cm, the chronologies did not overlap even when maximum uncertainties were taken into account and both models differed from each other by ca. 15–20 years. Finally, we chose the absolute chronology based on ^{14}C dates as it spans a longer time interval. However, it must be mentioned that the chronology for the period before the year 1945 (below 41 cm) should be treated with caution as it is encumbered by relatively high uncertainty.

Forest Composition Over the Last Century

The results of the pollen analysis of the 47-cm peat core and descriptions of the maps of plantings in 1900–2016 CE within the 4-km radius of the Martwe peatland are presented together for common zones (A–D) (**Figures 4**, **5**). Zonation was based on changes in regional vegetation between ca. 1900 CE and 2016, data on planting areas (km^2) within the 4-km radius of the peatland, and historical events such as a tornado that occurred on 14 July 2012 in Tuchola Pinewoods and local outbreaks of *Panolis flammea* during 1922–1924 CE and *Lymantria monacha* during 1979–1982 (Mokrzecki, 1928; Sliwa, 1989; Broda, 2000).

For the interval between ca. 1900 and 1922 CE (zone A, 47–44 cm), the pollen-based reconstruction suggested that the forest covered on average ca. 52% of the surroundings of the Martwe peatland (**Figure 4**). *Pinus sylvestris* was found to be the most abundant taxon (ca. 29.7–34.9%), while *Betula* spec. was rarer (ca. 3.8–10.8%). *Picea abies* had covered more than 10% at the beginning of zone A but then its abundance declined to almost zero. *Secale cereale* (11.4–19.7%) and other cereals (5.8–12.8%) were the most abundant open land taxa, followed by *Rumex acetosa/acetosella* (ca. 7.1–12.6%), Poaceae (grasses) (ca. 3.5–5.6%), *Artemisia* (ca. 4.6–5.5%), and *Plantago lanceolata* (ca. 2.2–4.2%). The lower forest cover (pollen data) in the peat core accompanied with an increase in the planting area (**Figure 5A**). The pollen data reflected high openness with simultaneous afforestation, which might be interpreted by the lag between tree planting and the onset of pollen production. Historical map data showed that ca. 5.6 km^2 of the surface area within the 4-km radius of the peatland (i.e., ca. 10% of the area) was afforested between 1900 and 1922 CE (**Figure 5A**). Most plantings were made beyond 1 km from the peatland, and the plantations included ca. 90.2% coniferous, ca. 9.1% deciduous, and ca. 0.7% unidentified trees. The plantings probably suggests previous clear cutting within these areas (assuming the forest has been continuously maintained over the last 100 years in the area) and/or afforestation of new areas (for example, agricultural fields) (Koziński, 2007). Tuchola Forest became the largest center of wood production at the end of the 19th century. Therefore, in the planting area, there may have been felling of trees for industrial purposes in the earlier period and/or afforestation after clear-cutting for war (Broda, 2010).

The reconstructed plant abundances are roughly similar in zone B (1922–1955 CE, 44–40 cm). The forest cover remained at an average of ca. 47% (**Figure 4**), with *Pinus sylvestris* covering ca. 31% and *Betula* spec. covering ca. 6–9% on average. *Picea abies* clearly recovered from the decline in zone A, covering ca. 5% in zone B. The reconstructed cover of *Secale cereale* is ca. 15–22%, that of other cereals ca. 9–16%, that of Poaceae ca. 5%. Between 1922 and 1955 CE, trees were newly planted on ca. 13.3 km^2 (ca. 26.5% of the study area), mainly as large plantations and also in the vicinity of the Martwe lake (**Figure 4B**). Again, more than 93.1% of the trees planted were coniferous, mainly Pinus sylvestris, maintaining pine monocultures (ca. 6.1% deciduous and ca. 0.8% unidentified trees). Much of the plantations likely compensated for clear-cutting following World War II, and especially disturbances caused by insect outbreaks from the beginning of the 20th century (1922–1924 CE) (Stieber and Bartz, 1923; Bartz and Ziółkowski, 1924; Mokrzecki, 1928; Ziółkowski and Bartz, 1928; Andrzejewski and Bartz, 1929; Broda, 2010; Słowiński et al., 2019). Widespread large-scale clear-cutting in the Tuchola Pinewoods was interspersed with insect outbreaks in these times (Fudała, 1985; Sukovata and Kolk, 2000), resulting in high economic losses. Between 1922 and 1925 CE, the influence of the insect outbreaks was the strongest, and the outbreaks mainly included that of *Panolis flammea* (moth and its caterpillars feed on *Pinus* needles), and to a lesser extent *Lymantria monacha*, which affected the Trzebciny Forest District (forest district in which the lake is located) (Mokrzecki, 1928; Fudała, 1985; Broda, 2000; Załoga, 2014). In this case, an increase in plantings was noted (**Figure 5B**). The clear-cutting caused by insect outbreaks led to the removal of trees and reforestation, mainly of *Pinus sylvestris*, in very large areas of Trzebciny Forest District (**Figure 5B**).

In the period 1955 to 1980 CE (zone C, 40–28.5 cm), the reconstructed forest cover increases from ca. 50% to ca. 80%,

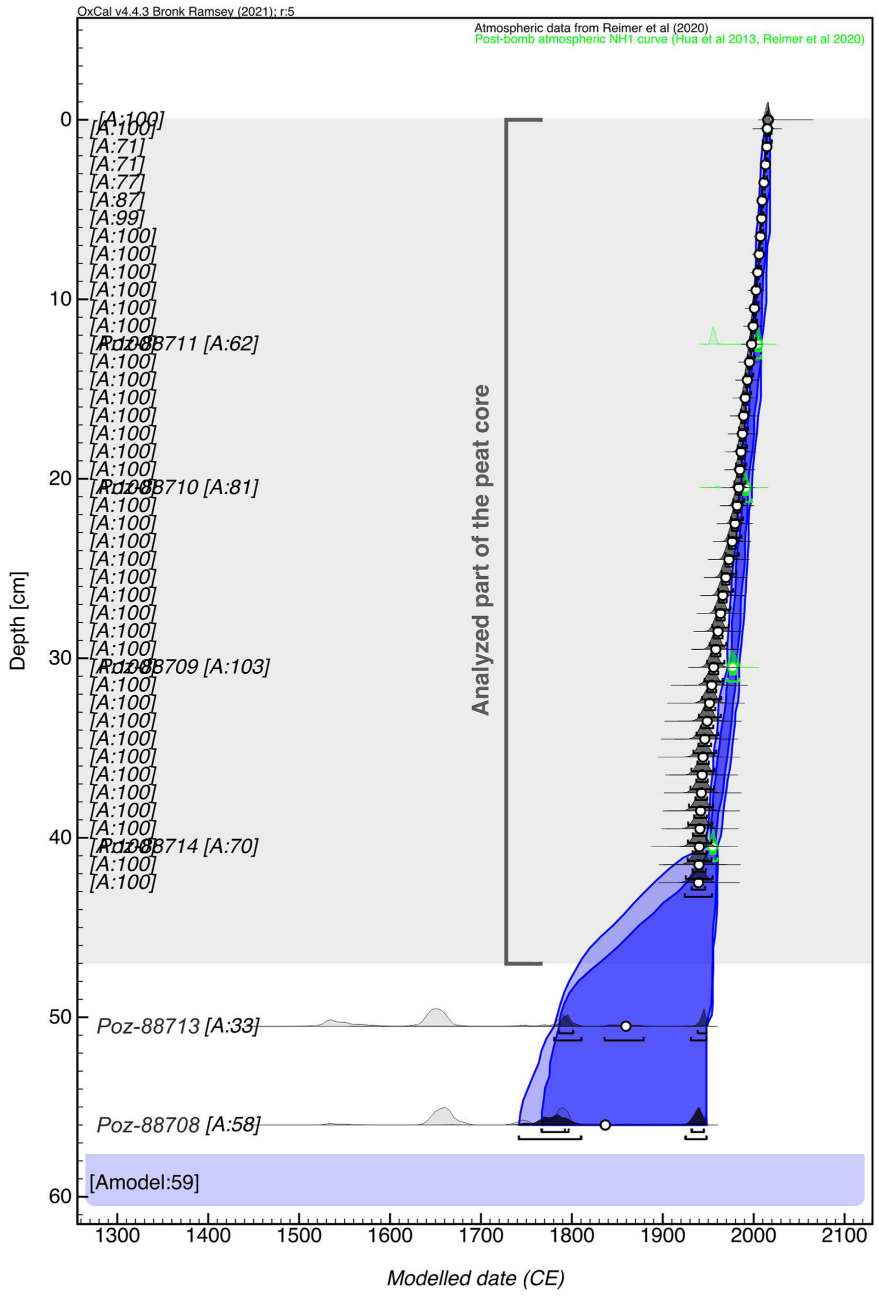


FIGURE 3 | Age–depth model of the peat core (MAR1) from the Martwe peatland.

mainly because of an increase in the cover of *Betula* spec. from ca. 5% to ca. 22%, particularly after 1965 CE (**Figure 4**). The cover of *Pinus sylvestris* remains at about ca. 33%. The reconstructed cover of *Picea abies* shows large variations from ca. 1.4% to ca. 17.4%, and at least periodic higher values than before. For most herbal taxa, including *Secale cereale* and other cereals, the reconstructed cover in zone C is somewhat lower that before. Only the cover of Poaceae is somewhat higher than before, arriving at ca. 4.7% to ca. 8.6%. Between 1955 and 1980 CE, ca. 5 km^2 of the area was afforested, i.e., significantly less than during previous periods (**Figure 5C**). As before, most planted trees have been coniferous (ca. 90%), mainly pine (**Figure 5A**). Although archival data do not indicate prominent changes in forest cover, our pollen-based reconstruction still suggests an increase in forest cover, i.e., particularly a higher cover of *Betula* spec. and *Picea abies*. We consider two likely explanations for this mismatch. First, *Betula* spec. may have truly expanded within existing, pine dominated forests, e.g., due to changes in forest management or nutrient availability. Secondly, *Betul*a spec. may have expanded in the vicinity of the sample site. In this case,

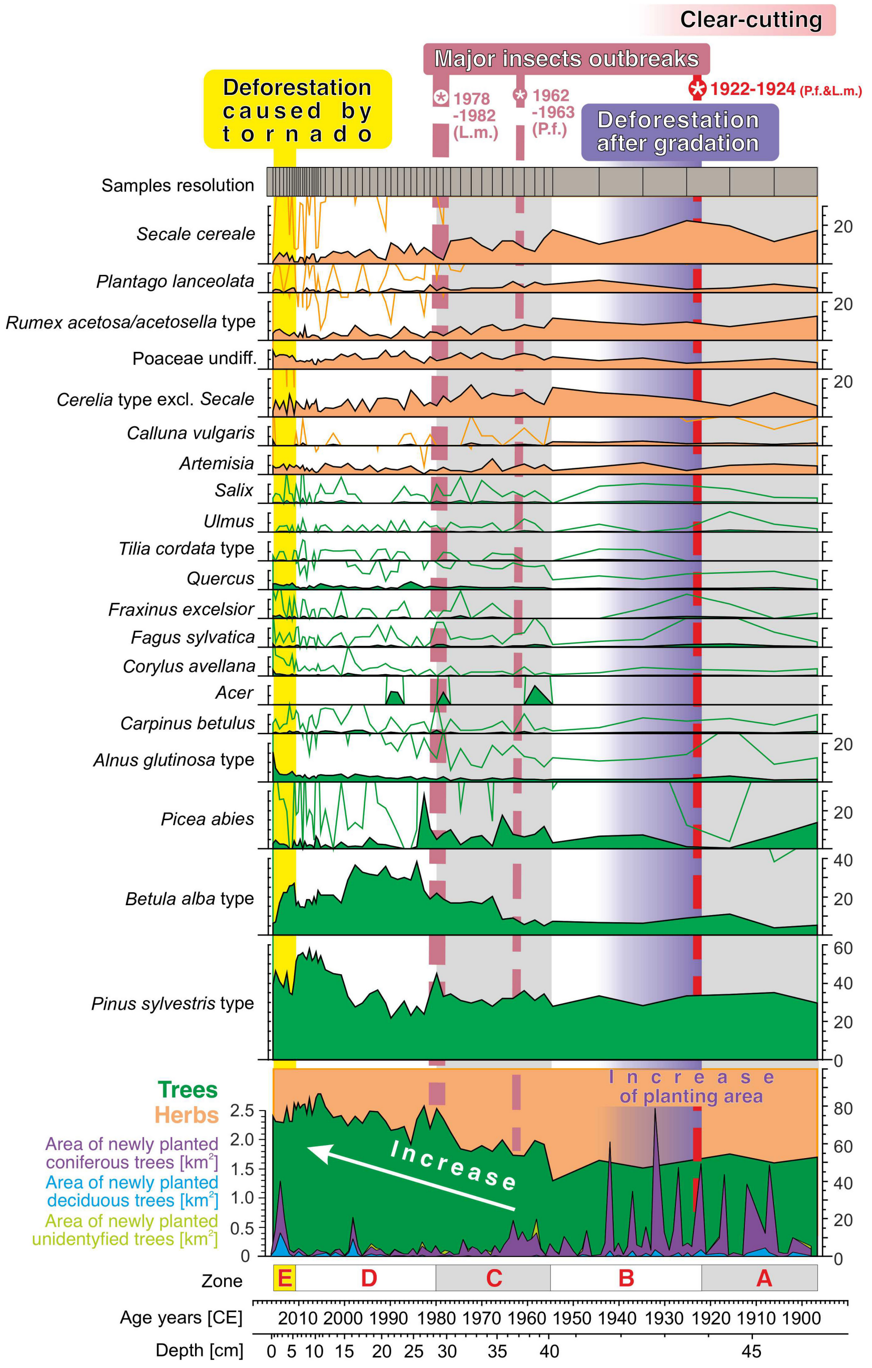


FIGURE 4 | REVEALS-reconstructed abundance of major plant taxa in the surroundings of the Martwe peatland (*Sphagnum* floating mat on the Martwe lake) (×10 magnification). The figure also includes the area of newly planted (km^2) coniferous, deciduous, and unidentified trees within the 4-km radius from the peatland, major local outbreak events (*Lymantria monacha*—L.m.; *Panolis flammea*—P.f.), and a description of the main stages.

higher pollen deposition of *Betula* spec. a is result of high (extra) local pollen deposition.

Zone D (28.5–5.5 cm, 1980 and 2012 CE ± 2 years) is characterized by the highest reconstructed forest cover (ca. 67.2–86.7%, **Figure 4**). Within the zone, the cover of *Betula* spec. is highest between 1980 and 2000 CE (ca. 30%) while the cover of *Pinus sylvestris* is highest between 2000 and 2012 CE (ca. 50%). Moreover, at the beginning of zone D, a peak in the cover of *Picea abies* (ca. 28%) is observed. After ca. 1980, the reconstructed cover remains much lower. This decline likely represents the outbreak of *Lymantria monacha* between 1979 and 1982 in the Trzebciny District (Sliwa, 1989; Załoga, 2014; Jablonski, 2015).

Our reconstruction also suggested some expansion in *Alnus glutinosa* to ca. 2.6% on average. Other deciduous taxa showed only slight changes. The cover of open taxa and, including Cerealia type excl. Secale, *Secale cereale*, *Plantago lanceolota*, and *Rumex acetosa/acetosella*, is lower than before. Between 1980 and 2012 CE, an area of ca. 3.6 km^2 has been afforested within 4 km distance from lake Martwe, i.e., a smaller area than before (**Figure 5C**). Among the newly planted trees, the proportion of deciduous trees is higher than before (>30%) whereas the proportion of coniferous trees is lower (>60%) (**Figure 5A**).

Our reconstruction suggests a prominent role of *Betula* spec. in the forests of the study area at least between 1980 and 2000 CE. Currently the forests in the Trzebciny District are clearly dominated by *Pinus sylvestris* (ca. 91%) whereas *Betula* spec. plays only a minor role (ca. 3%) (Kasprzyk, 2021). The literature/maps indicate that the cover of *Betula* spec. was not substantially higher between 1980 and 2000. The higher reconstructed cover may be an artifact of high (extra)local pollen deposition, i.e., pollen deposition from *Betula* spec. trees growing at or close to the core location. We cannot evaluate whether the increase in the reconstructed cover of *Betula* spec. since 1965 is fully attributable to such effect, or whether it represents some true regional expansion of *Betula* spec. Such expansion may have been triggered by changes in forest management and grazing intensity. *Betula* could be actively removed as a "forest weed" until the mid-20th century (our results) (Grus, 1891, 1897; Dec, 1945). Also, in the past *Betula* was limited by intense grazing (**Supplementary Figures 2, 3**; Mokrzecki, 1928; Broda, 2000) and insect outbreaks. In previous centuries, the forest was used more by humans (**Supplementary Figures 2, 3**).

Finally, our reconstruction indicates very recent changes in forest composition (zone E, 2012 ±1 year to 2016 CE, 5.5–1 cm, **Figure 4**). The cover of *Pinus sylvestris* is somewhat lower (40%), which can be mainly related to forest tornado damage in 2012 CE (**Figure 1**; Taszarek et al., 2016; Kaleta, 2017). For *Betula* spec., a short increase to ca. 26% was observed, followed by a steady decline to ca. 6%. For *Alnus glutinosa*, a distinct increase to ca. 16% is indicated after 2014 CE. Other tree taxa showed no prominent changes. Both the high cover of *Betula* spec. around 2012 CE and the high cover of *Alnus glutinosa* in recent years are unrealistically high, forest inventories show much lower cover. Hence, the high values likely are an artifact of (extra) local pollen deposition at the coring site. Among the herbs, some increase was noted particularly for the grasses, compared to the end of zone D. Between 2012 and 2016 CE, ca. 2.6% of the area within 4 km from the study site was afforested (**Figure 5E**), with ca. 67.3% coniferous and ca. 32.7% deciduous trees (**Figure 2A**). The afforested areas included those bordering the peatland to the south and east. Most trees were newly planted following the tornado in 2012 in the devastated areas (**Figures 1**, **4D**; Stopiński, 2012; Taszarek et al., 2016). The tornado had mostly destroyed ca. 80-year-old *Pinus sylvestris* trees planted after an outbreak of *Panolis flammea* from 1922 and 1924 (**Figure 4**; Mokrzecki, 1928; Broda, 2003).

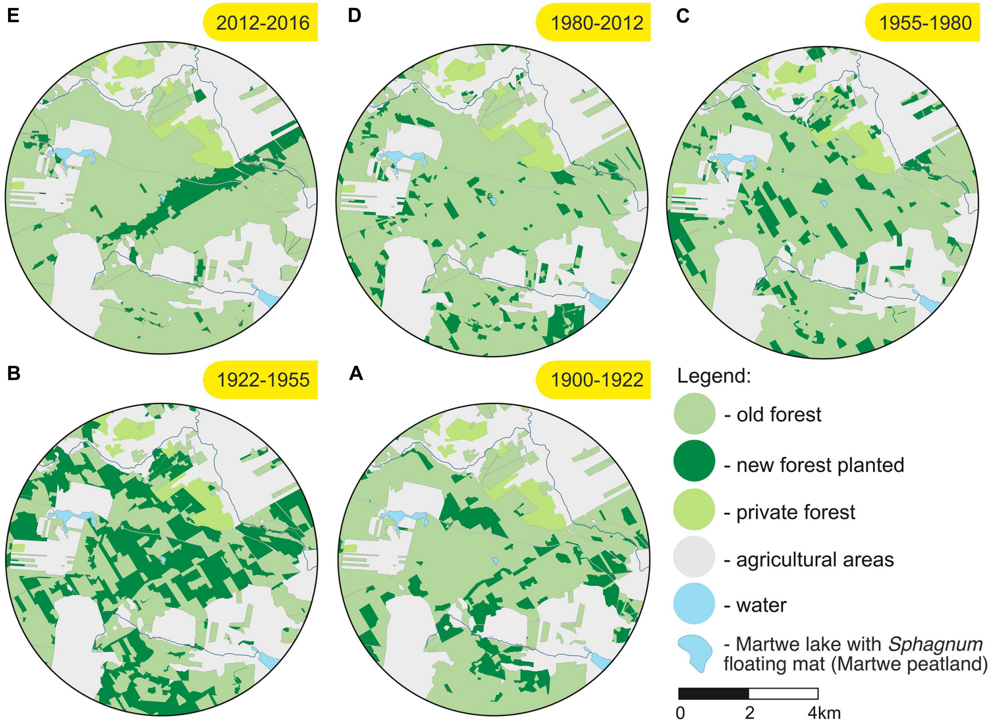


FIGURE 5 | Maps of the subsequent plantings in 1900–2018 CE within the 4-km radius from the Martwe peatland (*Sphagnum* floating mat on the Martwe lake). The peatland is located in the center of each map. The letters **(A–E)** correspond to the palynological zones. The term "old forest" in the map refers to an already wooded area.

DISCUSSION

Legacy of Forest Management

The forests of the study area (**Figures 4**, **5**) are mainly pine monocultures introduced by humans for timber harvesting (Mokrzecki, 1928; Gietkowski, 2009). The current vegetation clearly differs from the potential natural vegetation, which is richer in deciduous tree taxa (**Figure 5**). Human impact on the vegetation in the Tuchola region is well recognizable since the beginning of the Middle Ages (Milecka and Szeroczyńska, 2005; Noryśkiewicz, 2006), whereas the origin of the *Pinus sylvestris* monocultures dates back to the Prussian Partition (Gietkowski, 2009; **Figure 6**). Large-scale transformation of forests was started by Prussia soon after the first partition of Poland in 1772 CE (Gietkowski, 2009; Słowiński et al., 2019). Some effects of this transformation were clear-cutting and introduction of pine monocultures on poor soils developed on Wda and Brda sandy outwash plains (Dysarz, 1998; Gietkowski, 2009; **Supplementary Figure 1**). Paleoecological studies conducted on the lakes and peatlands in the Tuchola forest have confirmed strong human-induced changes in the composition of the forest over the last 300 years (Lamentowicz et al., 2007, 2013; Dietze et al., 2019; Słowiński et al., 2019).

The forest management, as well as the perception of the forest by managers and local communities, has changed through time. This is most clearly visible in the species composition of the forests that were managed before the last centuries in the entire Tuchola Pinewoods (Broda, 2000). Due to changes in the management and transformation of forests into a pine monoculture, the perception of local people and foresters toward pine monoculture and particular tree species has also been affected (Karasiewicz, 1922, 1926; Mokrzecki, 1928; **Supplementary Figures 1, 2**). The most prominent example is *Betula* spec. which has been considered a forest pest (Grus, 1897) and hence was simply removed from the undergrowth (Grus, 1897; Dec, 1945). Correspondingly, our reconstruction showed a low cover of *Betula* spec. until World War II. After the war, *Betula* spec. became more abundant because *Betula* strips were introduced as a so-called green belt surrounding pine monocultures to better control forest fires (Forest Fire Protection Manual). Moreover, in the past, local communities were allowed to use the forest for the grazing of sheep and cows and to collect needles and cones (Mokrzecki, 1928; Broda, 2000). These activities largely removed the forest undergrowth, including *Betula*, and prevented ground fires. However, these activities also removed nutrients, and as a result, caused degradation of forests and increased their susceptibility to insect attacks (Broda, 2000).

Methodological Implications – Archival Materials Meet Paleoecology

The present comparison of a pollen-based land-cover reconstruction with archival data shows similarities but also differences, which points at limitations of either approach. Most importantly, the land-cover reconstruction suggests an increase in forest cover since about 1950 CE, while archival data show a stable pattern of forest and open land. The primary cause for that mismatch may be the changing age structure of pine plantations. Our pollen-based reconstruction assumes that pollen productivity of all taxa is a constant. In reality, however, pollen productivity is variable and influenced, e.g., by the age of a forest stand. Before 1950 CE, the area of newly planted pine forests was high, following large scale harvesting and insect outbreaks. Hence, the area of young pine forests, which still produce low or little pollen was high. After 1950 CE, the situation was more stable and the proportion of older forests with high pollen production likely increased. Besides age, pollen production may also be influenced by nutrient availability. Until the mid 20th century, forest grazing and the removal of organic matter probably has reduced nutrient availability, which may have reduced tree growth and pollen productivity. Moreover, over the past decades, atmospheric fertilization has enabled accelerated tree growth (Pretzsch et al., 2014), and may have also affected pollen production.

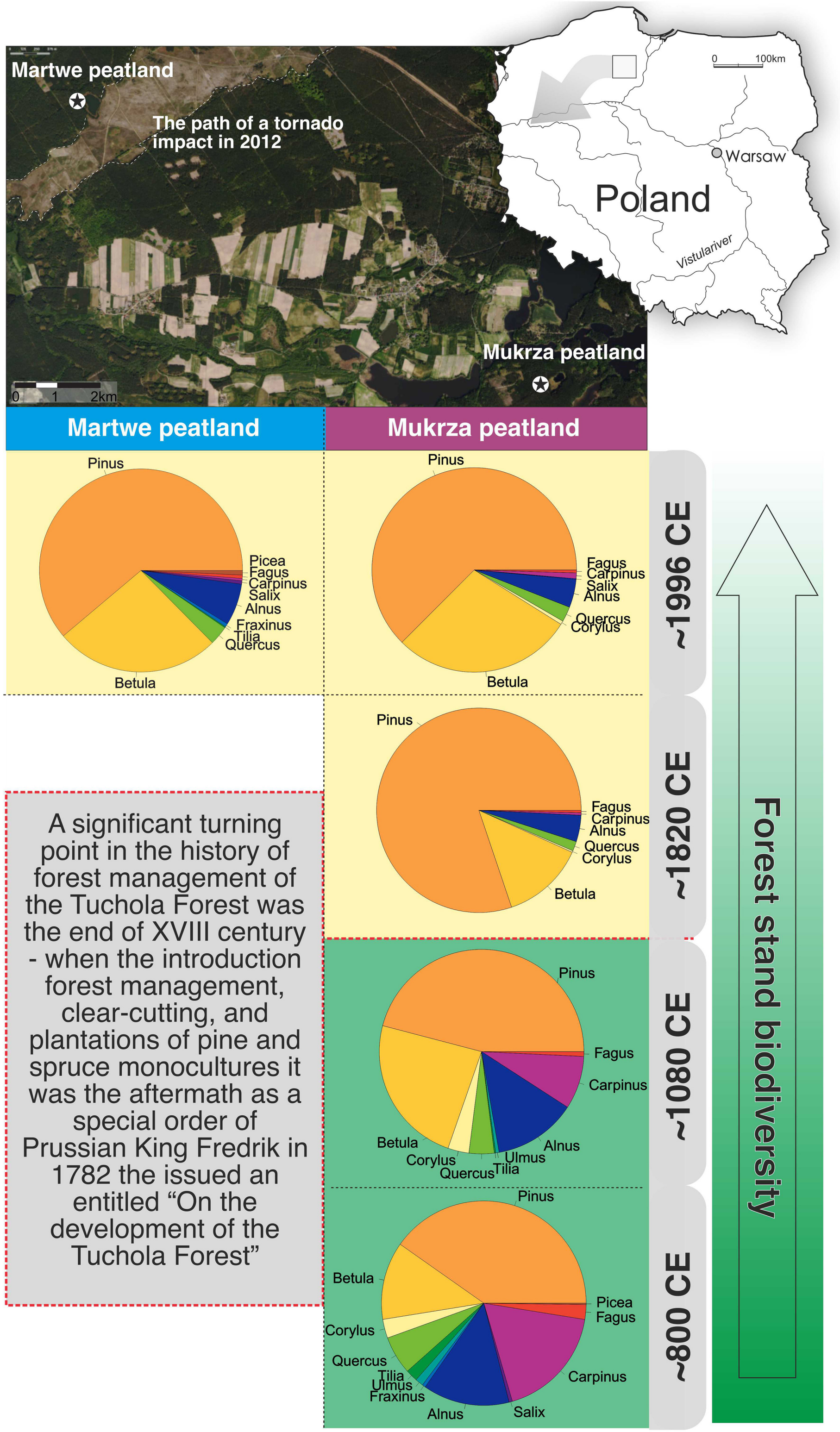
Our reconstruction suggests widespread expansion of *Betula* spec. during the second half of the 20th century, likely because forest grazing ended and more nutrients were available. *Betula* spec. did not expand in previously open areas but obviously in the existing pine forests, as understory element and/or along forest margins. The forests would hence produce, besides *Pinus sylvestris* pollen, an increasing amount of *Betula* spec. pollen. In other words, the pollen deposition of tree taxa, mainly *Pinus sylvestris* and *Betula* spec., increases, although the forest cover is unchanged. Hence, a second cause for the mismatch between the pollen-based forest cover and archival pollen cover may be the expansion of *Betula* spec. in *Pinus sylvestris* forests.

Alternatively, the possibly too high reconstructed cover of *Betula* spec. particularly between 1980 and 2000, may be attributable to (extra) local pollen deposition. The REVEALS approach is suited for pollen records from large lakes, which well represents regional vegetation composition. Pollen deposition in small lakes and peatlands, like lake Martwe, may instead be much influenced by (extra) local pollen deposition from nearby vegetation and hence represent a mixture of regional and local scale vegetation composition. Application of more suited local scale methods, such as LOVE or Marco Polo, was impossible because of a missing regional reference site (Sugita, 2007; Mrotzek et al., 2017).

Overall, our results underline that interpretation of pollen records from the recent past is far from simple, mainly because the pollen production of trees and herbs is variable due to changes in land management, atmospheric fertilization and also the climate. Further comparisons of archival and pollen-based reconstructions would be helpful to better understand the effects. To this end, records of pollen accumulation rates, e.g., from varved lakes, would be particularly useful because they avoid the mutual interdependence of pollen percentage data.

Long-Term Environmental Consequences of the Forest Plantations – Archival Materials Meet Paleoecology

The pollen signal from the Martwe peat core (MAR1), along with the remote sensing data, clearly show the land-use changes that were caused by the clear-cutting of pine monocultures and insect



A significant turning point in the history of forest management of the Tuchola Forest was the end of XVIII century - when the introduction forest management, forest management, clear-cutting, and plantations of pine and spruce monocultures it was the aftermath as a special order of Prussian King Fredrik in 1782 the issued an entitled "On the development of the Tuchola Forest"

FIGURE 6 | Relative abundance of arboreal pollen (AP, standard and untransformed pollen values) in the past based on a pollen record from the Mukrza peatland and comparison of records from the Martwe peatland. The figure present four phases of forest transformation by human activities in the Tuchola Pinewoods: (a) around 800 CE, before the end of the Migration Period, seminatural vegetation forest composition; (b) early Medieval Period, beginning of the 12th century, low human activity; (c) beginning of the 19th century, the period after the introduction of pine monoculture; and (d) current forest vegetation composition, end of the 20th century. The zones are based on a study of the Mukrza peatland by Obremska (2006).

outbreaks in the 20th century as well as a recent disaster—the tornado in 2012 (**Figures 4**, **5**). Especially, a good correspondence was observed between the changes in *Pinus sylvestris* pollen signals with archival materials and the cartographic data of the tornado event. The last dramatic event (and other massive wind throws that occurred in the region) and historical events like insect outbreaks during the last 100 years in Tuchola Pinewoods confirm the high vulnerability of these types of ecosystems to various disturbances like winds, pathogens, and fires (Mokrzecki, 1928; Seidl et al., 2017). Similar changes were observed in the forest composition during the last 100 years in the Mukrza peatland (**Figures 1**, **6**). The pollen records of both peatland are compared in **Figure 6**. It can be noticed that the relative abundance of arboreal pollen was similar—90.8% in Martwe and 87.5 in Mukrza peat—in ca. 1996 CE (standard and untransformed pollen values). The relative abundance of *Pinus sylvestris* was ca. 55.9% and ca. 54.7%, respectively (**Figure 6**). Studies of forest plantations in various regions of the world show that forest homogenization increases the vulnerability of the emerging novel ecosystem (Słowiński et al., 2019; Matusick et al., 2020). Monocultures of *Pinus sylvestris* cause acidification and depletion of soils, which not only results in reduced productivity (Bialy, 1999; Baltodano, 2000; Rutkowska, 2019; Steckel et al., 2020), but also has a negative impact on the biodiversity of forests (Gustafsson et al., 2012; Fedrowitz et al., 2014) and leads to acidification of wetlands (Lamentowicz and Mitchell, 2007). Furthermore, the long-term process of restoration influences soil biodiversity (Fedrowitz et al., 2014) and, as a consequence, the resistance of Scots pine in Tuchola Pinewoods. Due to the transformation of mixed-forest (mainly removal of hornbeam, oak, ash, and alder forests) into pure *Pinus sylvestris* monoculture (**Figure 6**; Miotk-Szpiganowicz, 1990; Boiński, 1993), the Tuchola Pinewoods are more vulnerable to disturbances such as insect outbreaks, fires, or winds (Słowiński et al., 2019).

Across Poland, pine forest monocultures have usually been established on sandy soils (Matuszkiewicz, 1999). The susceptibility of pine forest in our study area represents a climate-related hazard. Due to maintaining pine monocultures, the management of Tuchola Pinewoods is not focused on the natural regeneration of forests (**Figure 6**). The current challenge is to find optimal solutions for forest regeneration and adapt its species composition to changing habitat (Tomaś and Jagodziński, 2019). As a consequence of delay in the adaptation of tree composition to new conditions caused by climate changes due to the long-life cycle of trees (Jagodziński, 2020), *Picea abies* and *Betula* forests die out in many regions of Poland (Boczoń et al., 2018; Skrzecz and Perlińska, 2018). Although the European forest policy and management widely promote the shift from coniferous monocultures to mixed stands of coniferous and broadleaved species, these suggestions are either not introduced in most of the forested areas or not applied appropriately (**Figure 7**; Zerbe, 2002; Kint et al., 2006; Knoke et al., 2008; Zhang et al., 2012; Thurm et al., 2016; del Río et al., 2017). In the last decade, several studies confirmed that the replacement of monocultures by mixed forests increases their resistance to sudden climate shifts (Thurm et al., 2016; Leuschner and Ellenberg, 2017) and disturbances such as insect outbreaks, fires, and pathogen invasion. Nevertheless, it has been highlighted that natural recovery leads to higher biodiversity as well as a more resilient and productive ecosystem (Liang et al., 2016; Leuschner and Ellenberg, 2017). Based on the forecasts of threats to individual tree species in Europe, Dyderski et al. (2018) clearly emphasized that the so-called pioneering tree species like *Betula pendula*, *Larix decidua*, *Picea*

FIGURE 7 | Drone pictures of the forest planted after forest tornado damage from 2012 with characteristic *Betula pendula* islands and *Betula pendula* trees along the roads. In the background – Martwe lake with *Sphagnum* floating matt (Martwe peatland).

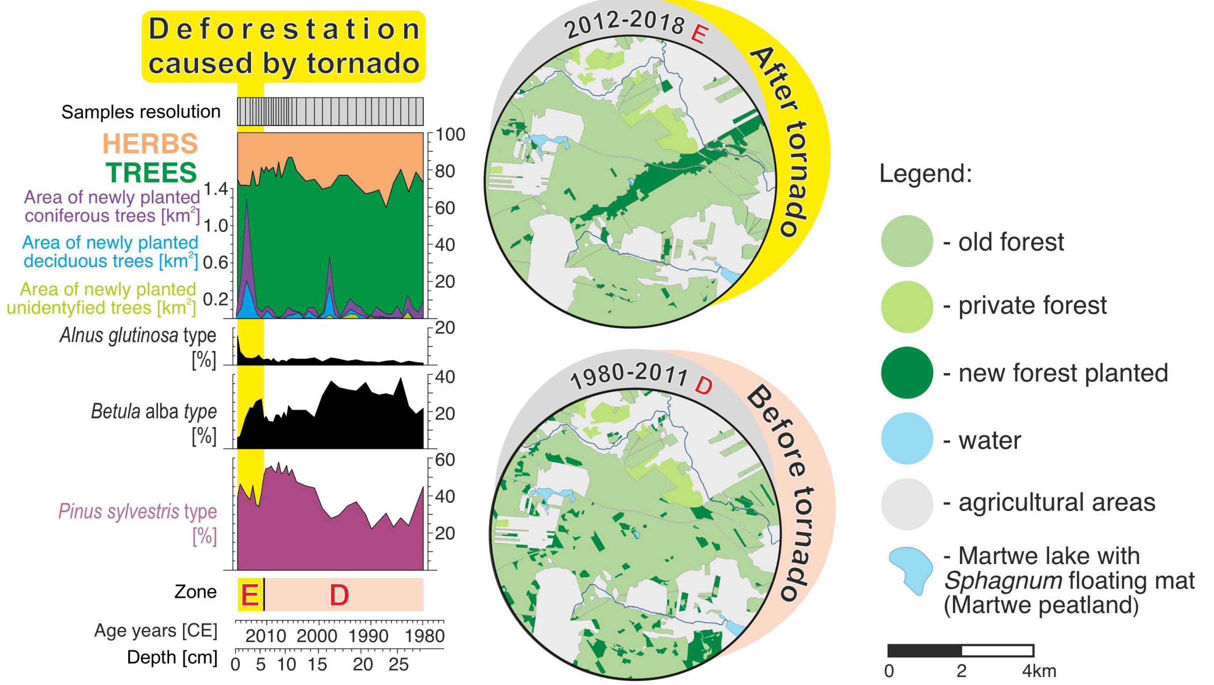


FIGURE 8 | Summary diagram of REVEALS-reconstructed plant abundances and remote sensing data after and before the tornado event from 2012. Maps of the area within the 4-km radius from the Martwe peatland (*Sphagnum* floating mat on the Martwe lake).

abies, and *Pinus sylvestris* will be increasingly affected by climate change-related issues such as increases in disturbances and insect outbreaks (Seidl et al., 2014). The authors underline that this constitutes a serious threat to both forest management and nature conservation due to the fact that *Pinus sylvestris* occupies about 67% of the forest area of the country (Dyderski et al., 2018). The cultivation of *Picea* abies and *Pinus sylvestris* forest was adequate in the past two centuries; however, with progressive global warming, the measurable benefits might be difficult to achieve. Droughts cause permanent changes in forest composition and conditions (Jagodziński, 2020), and thus contribute to the weakening of trees in the forests. Our study documented an increased abundance of deciduous forests (**Figure 4**) in the last two decades. During that time, the planting of deciduous forest accounted for a high percentage, which was not observed earlier (**Figure 4**). However, there is still a large difference in relation to the species composition from the Medieval Period (**Figure 6**; Obremska and Lamentowicz, 2006).

The changes in the structure and composition of the forest during the last 100 years were compared using pollen records and archive maps. The results (**Figures 4**, **5**) showed that the size and location of tree plantings in the last 100 years allowed the reconstruction of considerable land-use changes. We recorded a strong relationship between the pollen spectra of *Pinus sylvestris* and the planting process, and consequently, forest tornado damage by the tornado in 2012 (**Figures 4**, **5**, **8**). Data combination proves that paleoecology with archival materials and cartographic data complement each other well, especially in the case of heavily economically exploited monoculture leading to critical transitions. The pollen pattern of *Pinus sylvestris*, along with the archival materials and cartographic data between 1900 and 1943 CE, indicates clear cutting on a wide scale. Moreover, the location and size of plantings and later clear-cutting suggest dynamic changes in land use until 1965 CE, especially in the first half of the 20th century, while the period between 1965 and 2012 CE was characterized by a clear slowdown in changes. We have planned to use precise data about the location and size of plantings in further paleoecological research to study the impact of deforestation and clear-cutting on the functioning of wetland ecosystems (Słowiński et al., 2017; Łuców et al., 2018).

CONCLUSION

We present the first tornado-related paleoecological record from a monoculture in Poland on the background of previous forest management (clear-cutting, cutting after insect outbreaks), through vegetation reconstruction of a 100-year-old peat core, based on pollen analysis and the REVEALS model as well as on remote sensing data. Results of this study confirm that an event such as a tornado (forest tornado damage) may be recorded in a peat core. The forest tornado damage from 2012 was characterized by a decrease in *Pinus sylvestris* cover as a result of the destruction of the forest by a tornado and the increase of *Betula* spec. cover. The combination of paleoecological and remote sensing data allowed us to present the forest management practices during the last 100 years. The past forestry practices (like clear-cutting and cutting after insect outbreaks, also to a lesser extent an active removal of *Betula* as a "forest weed") are well identified in the proxy record. Our study shows that the observed monocultural stands lacked resistance to strong winds, but they were weakened most possibly also by droughts, and susceptible to insect outbreaks. Although the monocultures quickly replaced the disturbed stands, they did not result in any change in management, and as a result, only *Pinus sylvestris* was newly planted repeatedly. It is only in the last two decades that a change occurred in management and deciduous species such as oak and hornbeam were introduced into monocultures. This trend should be maintained to achieve the species composition and percentage share as that of 300 years ago to make the forest less sensitive to wind and better adapted to climate change.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MS contributed to the conception and design of the study. MS, ML, KM, and DŁ collected the peat core. DŁ wrote the first draft of the manuscript. PK performed the pollen analyses. ST performed the maps analysis. MT performed the REVEALS analysis. PK, ML, EŁ, and MS contributed to the chronology. DŁ, MS, and ST contributed to the figures and tables. All authors contributed to edit and revision of the manuscript and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.747976/full#supplementary-material

Supplementary Figure 1 | Simplified percentage pollen diagram from the Martwe peatland (×10 magnification).

Supplementary Figure 2 | A postcard from around 1900 CE showing the life of the inhabitants of Tuchola Pinewoods and their integration with the forest (from the collection of the Muzeum Pomorza, www.muzeumpomorza.pl) and wood run-off down the Wda River.

Supplementary Figure 3 | A postcard from around 1900 CE showing the life of the inhabitants of Tuchola Pinewoods and their integration with the forest (from the collection of the Muzeum Pomorza, www.muzeumpomorza.pl) as well as the life of the inhabitants of pine monocultures.

Supplementary Table 1 | Parameters (fall speed, PPE, and PPE error) of pollen used to prepare REVEALS reconstruction.

Supplementary Files | Absolute chronologies derived from 14C and 210Pb dates from the Martwe peat profile (MAR-1).

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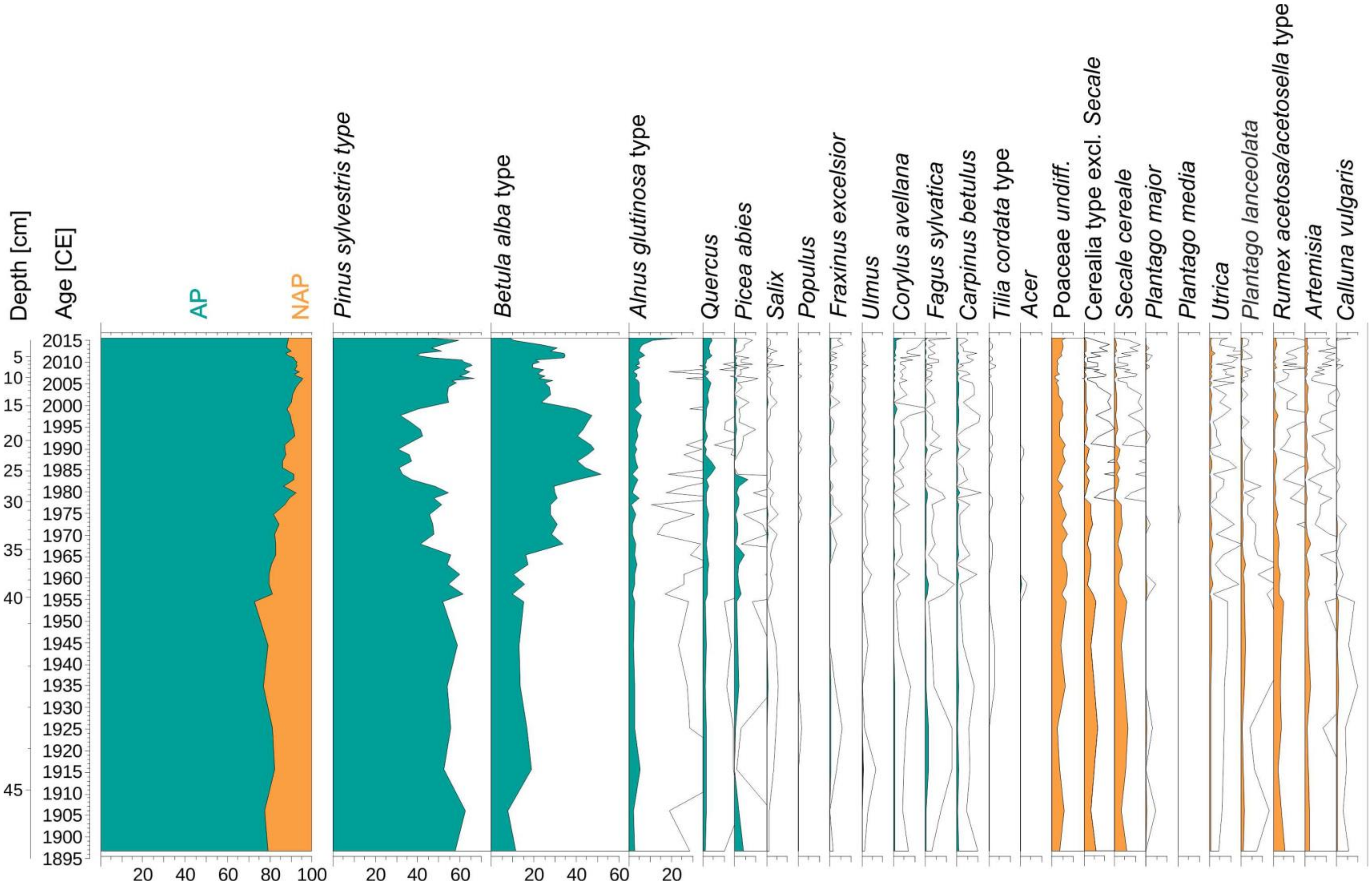
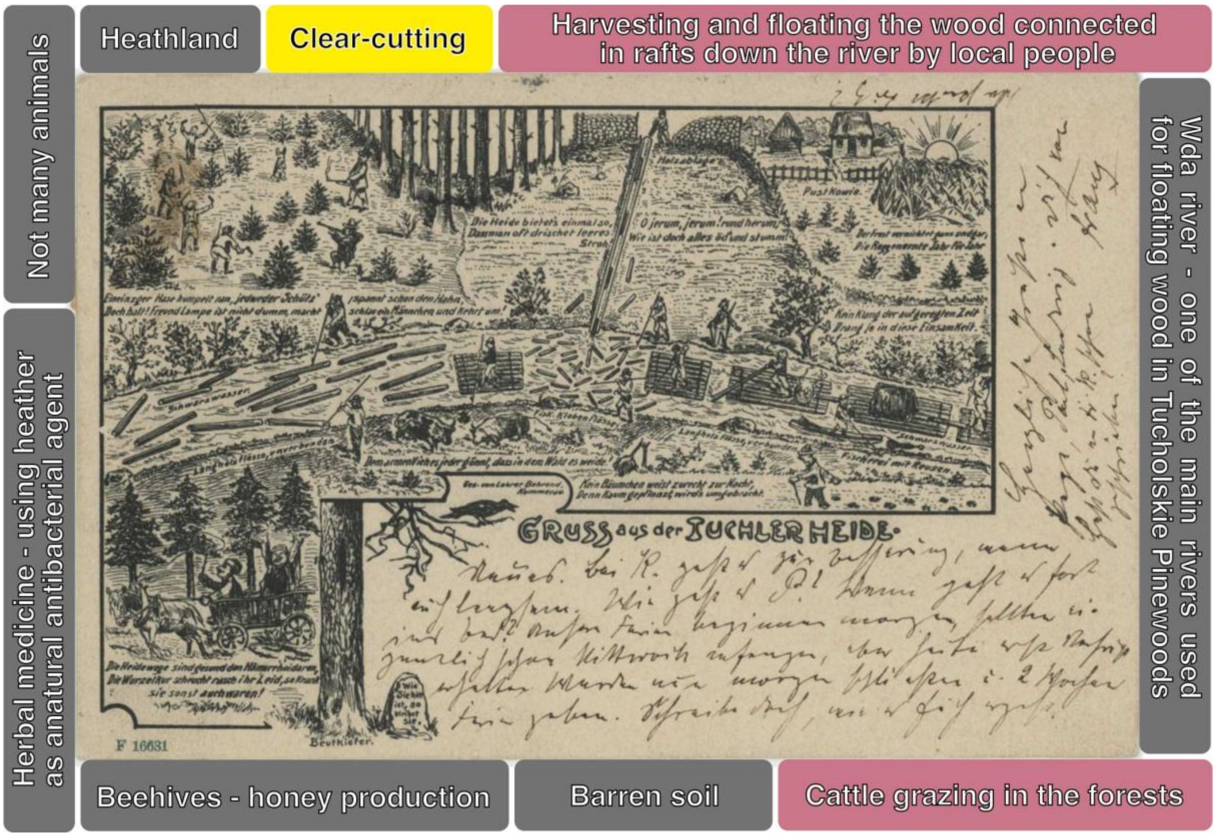
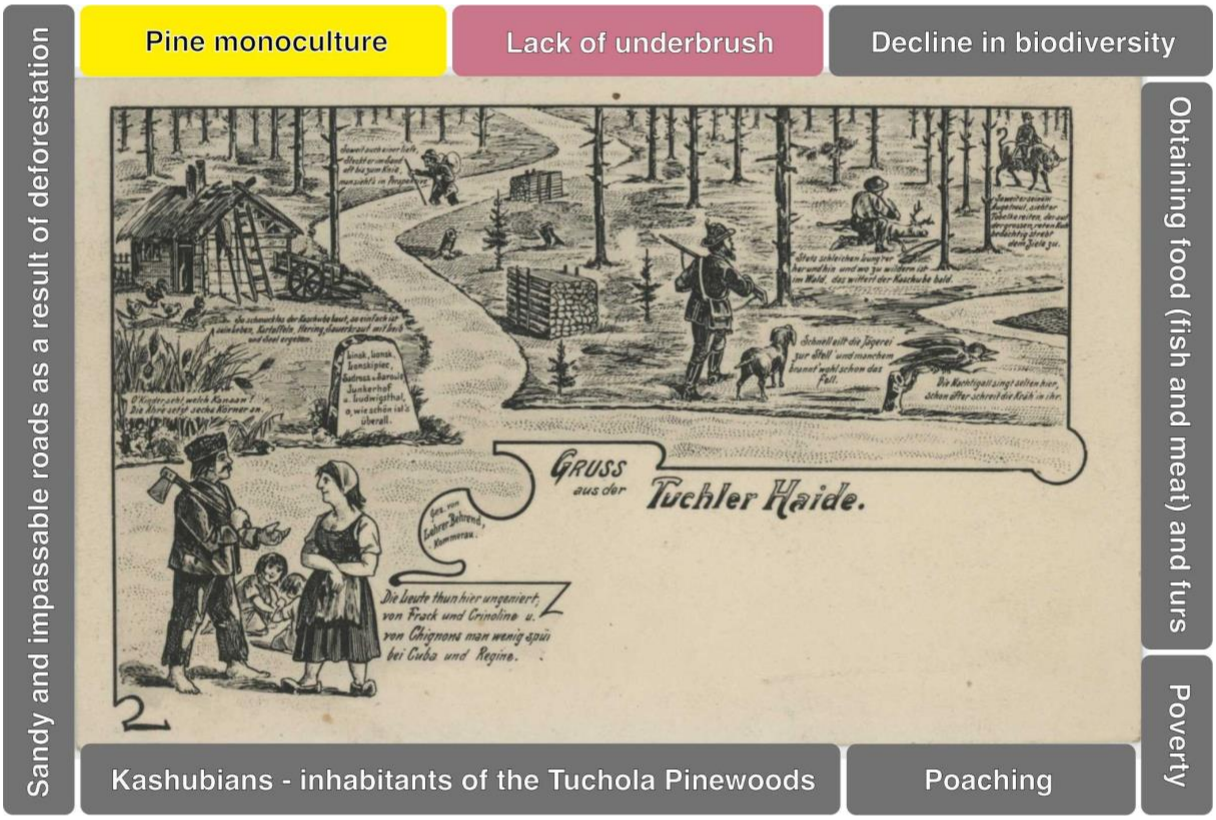
Supplementary Figure 1 | Simplified percentage pollen diagram from the Martwe peatland (×10 magnification).



Supplementary Figure 2 | A postcard from around 1900 CE showing the life of the inhabitants of Tuchola Pinewoods and their integration with the forest (from the collection of the Muzeum Pomorza, www.muzeumpomorza.pl) and wood run-off down the Wda River.



Supplementary Figure 3 | A postcard from around 1900 CE showing the life of the inhabitants of Tuchola Pinewoods and their integration with the forest (from the collection of the Muzeum Pomorza, www.muzeumpomorza.pl) as well as the life of the inhabitants of pine monocultures.



Supplementary Table 1 | Parameters (fall speed, PPE, and PPE error) of pollen used to prepare REVEALS reconstruction.

No.	**Taxon/species**	**Fallspeed m s-1**	**PPE**	**PPE error**
1	*Acer*	0,056	0,03	0,003
2	*Alnus glutinosa* type	0,021	2,228	0,223
3	*Betula alba* type	0,024	2,081	0,208
4	*Carpinus betulus*	0,042	0,965	0,096
5	*Corylus avellana*	0,025	1,801	0,180
6	*Fagus sylvatica*	0,057	0,925	0,093
7	*Fraxinus excelsior*	0,022	0,500	0,050
8	*Picea abies*	0,056	0,262	0,026
9	*Pinus sylvestris* type	0,031	1,833	0,183
10	*Quercus*	0,035	1,900	0,190
11	*Tilia cordata* type	0,032	0,457	0,046
12	*Ulmus*	0,032	0,730	0,073
13	*Salix*	0,022	0,500	0,050
14	*Artemisia*	0,025	0,422	0,042
15	*Calluna vulgaris*	0,038	0,365	0,036
16	Cerealia type excl. *Secale*	0,06	0,165	0,016
17	Cyperaceae	0,035	0,419	0,042
18	Poaceae	0,035	1,000	0,100
19	*Plantago lanceolata*	0,029	0,325	0,032
20	*Rumex acetosa/acetosella* type	0,018	0,436	0,044
21	*Secale cereale*	0,06	0,318	0,032

Supplementary Files | Absolute chronologies derived from 14C and 210Pb dates from the Martwe peat profile (MAR-1).

	Absolute chronology derived from 14C age depth-model		Chronology derived from 210Pb measurements			
Depth [cm]	Calendar date [CE]	Sigma error [years]	Calendar date [CE]	Uncertainty [years]	Activity concnetration of 210Pb unsupported (Bq/kg)	Uncertainty (Bq/kg)
0,5	2016	1	2016	0.205107548342522	251.66305416416	16.8483740269826
1,5	2015	1	2015	0.5280661118334	222.057795904585	13.9818951052029
2,5	2014	2	2013	0.81618292207264	346.765362486269	19.7549031434899
3,5	2013	3	2011	1.07213574671841	238.050210711409	13.688326567007
4,5	2012	3	2010	1.29707937189393	223.936389430437	13.2227020134408
5,5	2011	2	2009	1.48176227618232	200.337119313903	11.8881085679844
6,5	2010	2	2008	1.66929006388075	184.125998347421	12.003262101745
7,5	2009	3	2006	1.89875442698695	198.494706261491	12.0063123981247
8,5	2008	3	2005	2.15890153549611	204.029033319688	11.7114851006934
9,5	2007	3	2003	2.47566457025347	187.154789201888	10.8419056397284
10,5	2006	2	2001	2.77853249640366	158.990985755459	10.3985999046235
11,5	2005	2	1999	3.02356149723605	163.786058964017	13.2997946467442
12,5	2004	2	1998	3.3141024159614	187.96635297395	13.7392401467285
13,5	2003	3	1995	3.70295720366985	211.251290904081	11.7688797680685
14,5	2001	3	1993	4.1401404146074	181.104676347499	12.2026539840228
15,5	1999	3	1991	4.58548671283352	176.399936570363	10.4594039946056
16,5	1998	3	1989	4.9265709713066	82.0066159252444	7.82095261881072
17,5	1996	3	1988	5.18393356689336	97.5757192417648	9.43138220590874
18,5	1995	3	1986	5.47542682473548	102.206237195775	9.33224024000226
19,5	1993	3	1985	5.71181569718348	62.9981763762617	6.75357926596181
20,5	1991	2	1984	5.92691323308004	72.8426034124735	8.57853779516515
21,5	1990	2	1982	6.25345063436389	96.5768626120212	7.59084362781963
22,5	1989	3	1980	6.64924506187533	87.5652283753764	7.51586233993798
23,5	1987	3	1976	7.21775499798395	123.441564455777	10.1808508892519
24,5	1986	3	1973	7.89176803271494	99.8268052086794	11.2633039003882
25,5	1984	3	1969	8.58216800543837	115.709280956632	11.7893566574647
26,5	1983	3	1966	9.28711137840724	92.5137767571033	5.9356668603277
27,5	1981	3	1964	9.84912760345018	75.8593076560684	6.60725902687385
28,5	1980	3	1961	10.4305550594526	83.6747146656893	7.91768074696078
29,5	1979	4	1958	11.0048149624092	66.9259448709402	8.27678599494786
30,5	1977	4	1956	11.4396332361724	56.4957456017308	9.21293649579341

31,5	1975	4	1954	11.7877514483289	51.521103758645	6.85690806622227
32,5	1972	4	1952	12.1689268537926	58.1985458257708	6.5454338767788
33,5	1970	4	1949	12.5195920357952	50.7055670920767	5.67190971586847
34,5	1968	4	1946	12.5970649178327	44.2460021435222	6.15603959028672
35,5	1966	4	1944	12.0672707746528	16.0584128502588	5.46620023769959
36,5	1963	4	1943	11.0285371152379	12.5355082973004	6.34758187609128
37,5	1961	4	1942	9.9508578520752	20.3347473886947	5.77932556245851
38,5	1959	3	1942	9.24652086858586	11.1094630523532	5.5970260030623
39,5	1956	3	1941	8.91881770473349	30.395190726143	6.44410260744379
40,5	1955	2	1940	8.26432727929973	7.68180099102685	5.13039779453514
41,5	1944	11	1940	7.03888662586579	7.80257431959955	4.87184818723198
42,5	1935	15	1939	5.18068034873982	9.23217474493174	6.24499796535022
43,5	1925	19				
44,5	1916	23				
45,5	1906	26				
46,5	1897	29				
47,5	1887	31				
48,5	1878	34				
49,5	1868	37				
50,5	1859	39				
51,5	1852	38				
52,5	1846	36				
53,5	1839	35				
54,5	1833	34				
55,5	1826	33				

	intcal20_t	intcal20_dt	z	mu	sed	from_68_3	to_68_3	from_95_4	to_95_4
0.5	2015.7	0.5	0.5	2015	NaN	2014	2017	2012	2017
1.5	2015.1	1.4	1.5	2015	1.03	2013	2018	2009	2018
2.5	2014.2	2.2	2.5	2014	1.03	2012	2018	2008	2018
3.5	2013.0	2.5	3.5	2013	1.03	2010	2018	2007	2018
4.5	2011.8	2.5	4.5	2011	1.03	2008	2015	2006	2018
5.5	2010.8	2.2	5.5	2010	1.03	2007	2014	2005	2018
6.5	2009.9	2.3	6.5	2009	1.03	2007	2013	2003	2017
7.5	2009.0	2.5	7.5	2009	1.03	2006	2012	2002	2014
8.5	2008.0	2.6	8.5	2008	1.03	2005	2010	2002	2014
9.5	2006.9	2.5	9.5	2006	1.03	2003	2010	2001	2014
10.5	2006.0	2.2	10.5	2006	1.03	2003	2009	2000	2013
11.5	2005.2	2.0	11.5	2005	1.03	2002	2008	1998	2011
12.5	2004.3	2.2	12.5	2004	0.779	2002	2008	1998	2008
13.5	2002.5	2.7	13.5	2002	0.626	1999	2008	1996	2008
14.5	2000.8	2.7	14.5	2000	0.626	1996	2005	1994	2008
15.5	1999.3	2.8	15.5	1999	0.626	1995	2003	1991	2008
16.5	1997.7	2.9	16.5	1997	0.626	1994	2000	1991	2005
17.5	1996.1	2.8	17.5	1996	0.627	1991	2000	1989	2003
18.5	1994.5	2.7	18.5	1994	0.626	1991	1998	1986	2001
19.5	1992.8	2.6	19.5	1992	0.626	1989	1995	1987	1999
20.5	1991.0	1.7	20.5	1991	0.661	1988	1993	1986	1998
21.5	1989.9	2.1	21.5	1989	0.700	1987	1993	1982	1996
22.5	1988.5	2.7	22.5	1988	0.700	1986	1992	1982	1994
23.5	1987.0	3.0	23.5	1987	0.700	1983	1990	1980	1994
24.5	1985.6	3.1	24.5	1985	0.700	1981	1990	1978	1994
25.5	1984.2	3.2	25.5	1984	0.699	1980	1988	1976	1992
26.5	1982.7	3.3	26.5	1982	0.700	1979	1986	1974	1990
27.5	1981.3	3.3	27.5	1981	0.700	1977	1985	1973	1990
28.5	1979.9	3.3	28.5	1979	0.700	1976	1984	1971	1988
29.5	1978.5	3.5	29.5	1978	0.700	1976	1982	1971	1986
30.5	1976.9	3.6	30.5	1976	0.535	1973	1980	1971	1984
31.5	1974.7	3.8	31.5	1974	0.433	1970	1979	1963	1984
32.5	1972.4	4.1	32.5	1972	0.433	1969	1977	1961	1982
33.5	1970.1	4.2	33.5	1970	0.433	1965	1975	1960	1979
34.5	1967.8	4.3	34.5	1967	0.433	1963	1973	1958	1977
35.5	1965.5	4.3	35.5	1965	0.433	1960	1970	1955	1975
36.5	1963.2	4.1	36.5	1963	0.433	1958	1967	1954	1972

37.5	1960.8	3.9	37.5	1960	0.433	1956	1965	1952	1969
38.5	1958.5	3.4	38.5	1958	0.433	1954	1961	1951	1966
39.5	1956.4	2.5	39.5	1956	0.433	1953	1959	1949	1964
40.5	1954.5	2.0	40.5	1954	0.169	1952	1958	1948	1960
41.5	1944.4	10.6	41.5	1944	0.105	1939	1956	1920	1959
42.5	1934.8	15.3	42.5	1934	0.105	1929	1953	1901	1957
43.5	1925.3	19.1	43.5	1925	0.105	1916	1949	1883	1954
44.5	1915.8	22.5	44.5	1915	0.105	1904	1943	1867	1952
45.5	1906.2	25.6	45.5	1906	0.105	1891	1939	1848	1949
46.5	1896.7	28.6	46.5	1896	0.105	1880	1936	1832	1946
47.5	1887.2	31.4	47.5	1887	0.105	1870	1937	1818	1942
48.5	1877.6	34.1	48.5	1877	0.105	1863	1936	1799	1939
49.5	1868.1	36.8	49.5	1868	0.105	1796	1916	1789	1939
50.5	1858.5	39.4	50.5	1858	0.125	1788	1884	1783	1934
51.5	1852.0	37.9	51.5	1852	0.154	1786	1879	1777	1928
52.5	1845.5	36.4	52.5	1845	0.154	1782	1875	1770	1916
53.5	1839.0	35.1	53.5	1839	0.154	1782	1870	1766	1898
54.5	1832.5	33.9	54.5	1832	0.154	1781	1863	1757	1883
55.5	1826.1	33.0	55.5	1826	NaN	1781	NaN	1749	NaN

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Disturbance and resilience of a *Sphagnum* peatland in western Russia (Western Dvina Lakeland) during the last 300 years: A multiproxy, high-resolution study

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Abstract

This paper presents the results of multiproxy research (pollen, charcoal, plant macrofossil and testate amoebae) on the biogenic deposits core from Gorodetsky Moch, an ombrotrophic peatland in western Russia (Western Dvina Lakeland). We reconstructed the impact of disturbance on peatland development in the last 300 years by using chronology of the records based on ^{14}C and ^{210}Pb data set. The multiproxy reconstruction was compared with changes in the land cover using historical maps and Corona images, which provides a unique spatial analysis of past ecological and land-use changes. We aimed to determine the effect of local disturbances (drainage) and land-use changes (landscape openness) on the development of the peatland during the last 300 years. Our study suggests that human activity had a crucial impact on the development of the peatland in the last centuries. The analysis of testate amoebae and plant macrofossils revealed a clear disturbed layer in the second half of the 20th century CE. Most probably, the drainage of the peatland triggered changes in the community of testate amoebae and plants, thereby causing a functional shift in *Sphagnum* peatland ecosystem. The hydrological stress and vegetation composition shift led to the collapse of mixotrophic testate amoebae. However, the peatland showed strong resilience and recovered toward the end of the 20th century CE and the beginning of the 21st century CE, despite the lower water table. Our study shows an example of the peatland ecosystem that experienced a considerable stress but finally sustained the former function.

Keywords

Ombrotrophic peatland, human impact, drainage, land-use, wetland, Eastern Europe, functional traits, multiproxy, western Russia (Western Dvina Lakeland)

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Introduction

Peatlands are particularly sensitive to environmental disturbances resulting from human activities (Dise, 2009). Throughout Europe, many peatlands have been disturbed due to agricultural intensification and forestry practices in the last centuries (Joosten and Clarke, 2002; Tobolski, 2003; Swindles et al., 2019). Loss of wetlands in the 19th and 20th centuries CE was related mostly with mire drainage and peat exploitation (Chambers et al., 2013; Kołaczek et al., 2018b; Swindles et al., 2016). The development of many of these ecosystems has also been disturbed owing to the effects of deforestation (Lamentowicz et al., 2007; Słowiński et al., 2016; Woodward et al., 2014), fire (Florescu et al., 2018; Marcisz et al., 2015; Tinner et al., 2005), and pollution (Fialkiewicz-Koziel et al., 2016). Therefore, there is a need to understand the effects of disturbances caused by human activity to peatland ecosystem. Especially important in this context are high-resolution studies based on several proxies and detailed chronology (Lamentowicz et al., 2009, 2013; van der Knaap et al., 2011) from ombrotrophic peatlands. They are unique repository of high-quality information about environmental changes because receive water and nutrients through a single source (i.e., rainfall).

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The simultaneous application of pollen, plant macrofossil, and testate amoeba analyses has been particularly emphasized in the palaeoecology of peatlands in the last two decades. Multiproxy studies have been conducted mostly in Western and Central Europe (Blundell and Barber, 2005; Gałka et al., 2013) and North America (Booth and Jackson, 2003; Booth et al., 2004); however, palaeoecological studies from the European continental peatlands are very rare (Novenko et al., 2017; Payne et al., 2015; Tsyganov et al., 2019). Eastern Europe is affected by the continental climate conditions; therefore, ombrotrophic bogs that possess a flat surface profile and were classified by Kulczyński (1949) as continental-raised bogs in contrast to Atlantic or Baltic raised bogs of the Northern and Western Europe. Past human impact on these ecosystems that cover large areas in this studied region (Lappalainen, 1996) is also insufficiently recognized. To date, multiproxy research on peatlands in the East European Plain was focused primarily on the Holocene climate and vegetation history including long temporal scales. Their relatively low sampling resolution did not allow for a detailed analysis of short-term events. Studies on peatland in the East European Plain (including pollen, macrofossil, testate amoebae, pollen, humification, and isotope analyses) have been performed in Estonia (Sillasoo et al., 2007), European Russia (Novenko et al., 2015, 2016; Payne et al., 2015; Tsyganov et al., 2019), Ukraine (Kołaczek et al., 2018a) and Poland (Gałka et al., 2015, 2017; Karpińska-Kołaczek et al., 2018).

Droughts that we currently observe, and predictions inspire to study disturbances and resilience of ecosystems. The long-term ecosystem monitoring (Bartczak et al., 2019; Lamentowicz et al., 2016; Marcisz et al., 2014; Słowińska et al., 2010) or experiment (Jassey et al., 2018; Rastogi et al., 2019; Reczuga et al., 2018; Samson et al., 2018) provide a short temporal look at a disturbance. In contrast, palaeoecological multiproxy studies provide a long-term perspective (Marcisz et al., 2016; Zawisza et al., 2019). Reconstructions provide information about the ecosystem state before and after disturbances (Fialkiewicz-Koziel et al., 2016; Lamentowicz et al., 2007), but also give reference conditions (Moore et al., 1999). Such knowledge is important for nature conservation (Hamilton, 2018; Marcisz et al., 2018; Słowiński et al., 2019).

The present study aim to determine the effect of local disturbance (drainage), fires and land-use changes (e.g., opening of the landscape and agriculture intensity in the peatland vicinity) on the development of Gorodetsky Moch peatland (western Russia, Western Dvina Lakeland) in the last 300 years. We hypothesized that the drainage of the bog affected taxonomic composition and functional diversity of testate amoeba as well as changes in vegetation structure causing water table deficit in the peatland ecosystem. Furthermore, we aimed to explore a possible self-regeneration process of the bog and its resilience on a long temporal scale (300 years). In this study, we used a several proxies: testate amoebae, which are very sensitive to environmental changes, were used to reconstruct pH and hydrological variability on peatland ecosystem in the past (Charman, 2001; Mitchell et al., 2007a); pollen and plant macrofossils were used for the reconstruction of the local and regional vegetation cover changes, and human impact (Birks and Birks, 1980; Poska et al., 2004); and charcoal was used for the reconstruction of fire history (Conedera et al., 2009). The palaeoecological results were compared with data on land cover changes developed using cartographic materials (analysis of historical maps and Corona images), which provides a unique spatial analysis of past ecological and land-use changes (Ott et al., 2018; Veski et al., 2005). Moreover, a detailed chronology of the records was based on ^{14}C and ^{210}Pb dating.

Materials and methods

Study site

Gorodetsky Moch (local name: Городецкий мох), an ombrotrophic peatland covering an area of 544 ha, is located in western Russia in Pskov Oblast, close to the Smolensk Oblast border, in the basin of the Western Dvina River and around 16 km NE of Velizh city (Figure 1). The coordinates for the central part of the peatland are 55°44’23.2”N and 31°18’02.8”E. The land relief of the peatland neighborhood was formed during the Valdai Glaciation (Weichselian Glaciation in Northern, Western and Central Europe) (Velichko et al., 2011). The average altitude in the peatland vicinity is between 170 and 180 m a.s.l. Presently, the peatland is surrounded mainly by coniferous forests (*Pinus sylvestris*, *Picea abies*) with small-leaved forests (*Populus tremula*, *Betula pendula* and *Alnus incana*), fields, and other wetlands. A drainage ditch is situated in its northern part. The Gorodetsky Moch peatland was drained at unknown time for unknown purposes. Currently, despite the presence of a drainage ditch, the peatland is wet and still retains its original characteristic of a raised bog. The present vegetation of the peatland are dominated by hummocks formed by *Sphagnum fuscum* and *Sphagnum magellanicum*, and the hollows is dominated by *Sphagnum cuspidatum* with *Eriophorum angustifolium* and *Eriophorum vaginatum*, *Andromeda polifolia*, *Rhynchospora alba*, and *Carex limosa*. The climate of the area is continental with warm summer (Köppen climate classification Dfb) (Kottek et al., 2006) with a mean annual air temperature of 5.4°C; the warmest month is July with a temperature of 17.8°C and the coldest month is February with a temperature of -6.4°C, with annual precipitation of 738 mm (Weather and climate, 2016).

Coring and subsampling

The peat core (dimensions measuring 89 × 10 × 10 cm) was extracted from the central-east part of the peatland in summer 2016. The peat monolith was subsampled every 1 cm (except for the 0- to 2-cm sample) in the laboratory. In total, 47 samples were analyzed for pollen, 44 for testate amoeba, and 89 for plant macrofossils and charcoal.

Chronology

The chronology of the core is based on ^{14}C and ^{210}Pb data set. Nine samples were selected for AMS radiocarbon dating (Table 1). *Sphagnum* stems of 1-cm thickness and 5 cm^{3} volume were carefully collected from the samples and treated in Poznań Radiocarbon Laboratory in 2017, and sixty-two 1-cm-thick samples were used for ^{210}Pb measurements at the Institute of Nuclear Physics PAS in Kraków. The activity of ^{210}Pb was determined from the alpha activity of its daughter radionuclide ^{210}Po (half-life 138 days). Secular equilibrium between those radionuclides was assumed because one year had elapsed between the sampling and analyses. Peat samples were spiked with ^{208}Po yield tracer and digested with concentrated acids. Po isotopes were deposited on an Ag disk, and their activity was measured by alpha spectrometry using Ortec silicon detectors. The ^{210}Pb chronologies were established using the constant rate of supply model (*CRS* model). An age-depth model was calculated using the rbacon in R statistical packages (Blaauw and Christen, 2011) (Figure 2).

Pollen analysis

Pollen samples were prepared following the procedure described in a previous study (Berglund and Ralska-Jasiewiczowa, 1986). Every second sample between 2 cm and 46 cm, and the next samples at depths: 48, 49, 50, 52, 54, 56, 58, 60, 62, 64, 66, 67, 68, 70, 72, 74, 76, 77, 78,79, 82, 84, 86, 88, 89 cm (in 1-cm resolution) of volume 1 cm^{3} were analyzed. The pollen was analyzed using a microscope at 400× and 1000× magnifications. A minimum of 500 arboreal pollens was counted in each sample using a procedure described in the literature (Beug, 2004; Moore et al., 1991). The sums of particular taxa were used to assess the human impact and changes in land-use (Supplementary Table 1) (Behre, 1981; Poska et al., 2004).

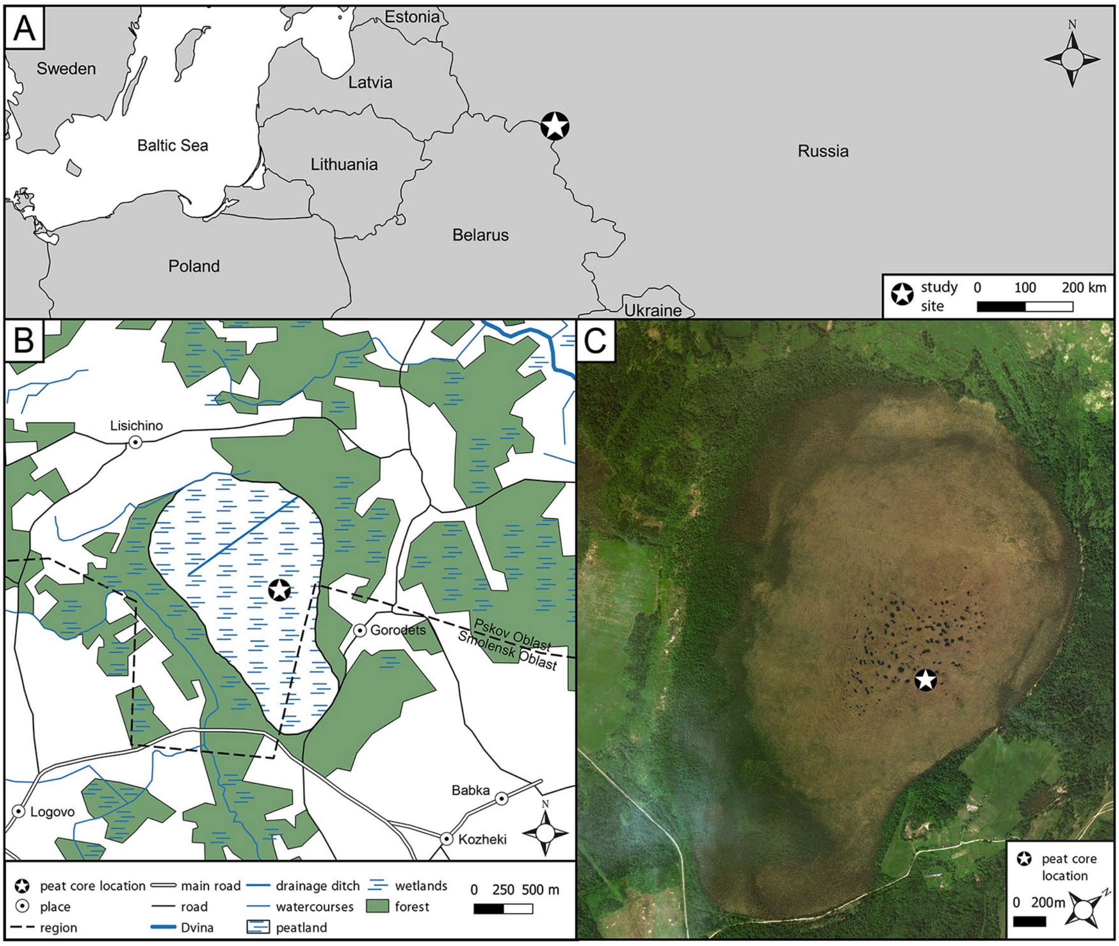

Figure 1. Setting of the study site.

Charcoal

Microscopic charcoal (10–100 µm) was analyzed to reconstruct past regional fire activity (Gardner and Whitlock, 2001; Tinner et al., 1998), whereas macroscopic charcoal (>100 µm) was analyzed to reconstruct local fire activity (Clark, 1988; Clark et al., 1998). Microscopic charcoal was counted on the pollen slides until the sum of 200 was reached using a microscope at 400× magnification (Finsinger and Tinner, 2005). Macroscopic charcoal was analyzed in the peat samples of 2 cm^3 volume with 1-cm resolution following the procedure described in a previous study (Whitlock and Larsen, 2002), and it was then counted using a stereoscopic microscope at 200× and 400× magnifications in two fractions: 100–500 µm and above 500 µm. Microscopic and macroscopic charcoal influx (particles/cm^2/year) was calculated using the charcoal concentration and the peat accumulation rate.

Plant macrofossil analysis

Sediment samples of 5 cm^3 volume with 1-cm resolution were washed under running water and sieved through a 0.2-mm-mesh sieve to estimate the values of *Sphagnum* and vascular plant remains. The macrofossils were identified under a stereoscopic microscope at 200× magnification using identification guides (Grosse-Brauckmann, 1974; Mauquoy and van Geel, 2007; Tobolski, 2000).

Testate amoebae

Testate amoebae samples were analyzed in every second sample (in 1-cm resolution) of volume 2 cm^3 following the procedure described in a previous study (Booth et al., 2010). The samples were shaken in distilled water and then washed through a sieve with a mesh of 300 µm. The testate amoebae were analyzed using a microscope at 200× and 400× magnifications. A minimum of 100 tests of testate amoebae were counted in each sample (Payne and Mitchell, 2008). Identification guides were used to recognize testate amoebae taxa (Mazei and Tsyganov, 2006; Siemensma, 2019). On the basis of the construction of tests, the testate amoebae taxa were divided into four categories (idiosomes, idiosomes + organic, protein + calcium, and xenosomes) according to a previous study (Mitchell et al., 2008). Furthermore, three groups were separated: wet indicators (dominant species: *Archerella flavum*, *Hyalosphenia papilio*, and *Amphitrema wrightianum*), dry indicators (dominant species: *Cryptodifflugia oviformis*, *Assulina muscorum*, *Alabasta militaris*, and *Difflugia pulex*), and indicator of hydrological instability—*Arcella discoides* (Hendon and Charman, 1997; Lamentowicz and Mitchell, 2005a; Marcisz et al., 2015).

Historical maps and Corona images

Archival maps and Corona images were georeferenced in ArcGIS program. Types of land-use were digitized from the following cartography and photogrammetry archive: (1) Plans of the Russian Empire land survey - Scale: 2 versts in inch (1: 84000) (Period of reflect for Velig region 1750–1780, accessed on 05.2019), (2) Corona images (resolution 2-7 meterdate 1971 July, accessed on 05.2019), (3) Image Landsat ETM (resolution 30 meter, date 2000 May, accessed on 05.2019), (4) Image Sentinel2 (resolution 10 meter, date 2015 May, accessed on 05.2019), (5) Three-verst military topographic map of

Table 1. Radiocarbon dates with calibration results from Gorodetsky Moch. Dates were calibrated in the OxCal program (Ramsey and Lee, 2013).

Lab.no.	Depth [cm]	Conv. Age [BP]	Error	Calibrated ages [cal. BP] (2σ 95.4%)	Dated material
Poz88118	10,5	105.13	0.39 pMC	1959 (5.5%) 1957calCE 2006calCE (89.9%)	*Sphagnum* stems
Poz88704	20,5	110.66	0.34 pMC	1957 (1.4%) 1957calCE 1995 (94.0%) 1999calCE	*Sphagnum* stems
Poz88703	30,5	128.93	0.39 pMC	1959 (3.4%) 1959calCE 1961 (11.1%) 1962calCE 1979 (80.9%) 1980calCE	*Sphagnum* stems
Poz88117	40,5	133.1	0.45 pMC	1976 (95.4%) 1978calCE	*Sphagnum* stems
Poz88116	50,5	110	30	1681 (27.1%) 1739calCE 1745 (2.8%) 1763calCE 1802 (65.5%) 1938calCE	*Sphagnum* stems
Poz86530	60,5	145	30	1668 (16.3%) 1710calCE 1717 (29.2%) 1782calCE 1797 (33.5%) 1891calCE 1909 (16.4%) 1948calCE	*Sphagnum* stems
Poz88707	70,5	100	30	1682 (27.1%) 1736calCE 1805 (68.3%) 1935calCE	*Sphagnum* stems
Poz86528	80,5	90	30	1685 (26.3%) 1733calCE 1807 (69.1%) 1928calCE	*Sphagnum* stems
Poz86529	88,5	120	30	1679 (32.8%) 1765calCE 1800 (62.8%) 1940calCE	*Sphagnum* stems

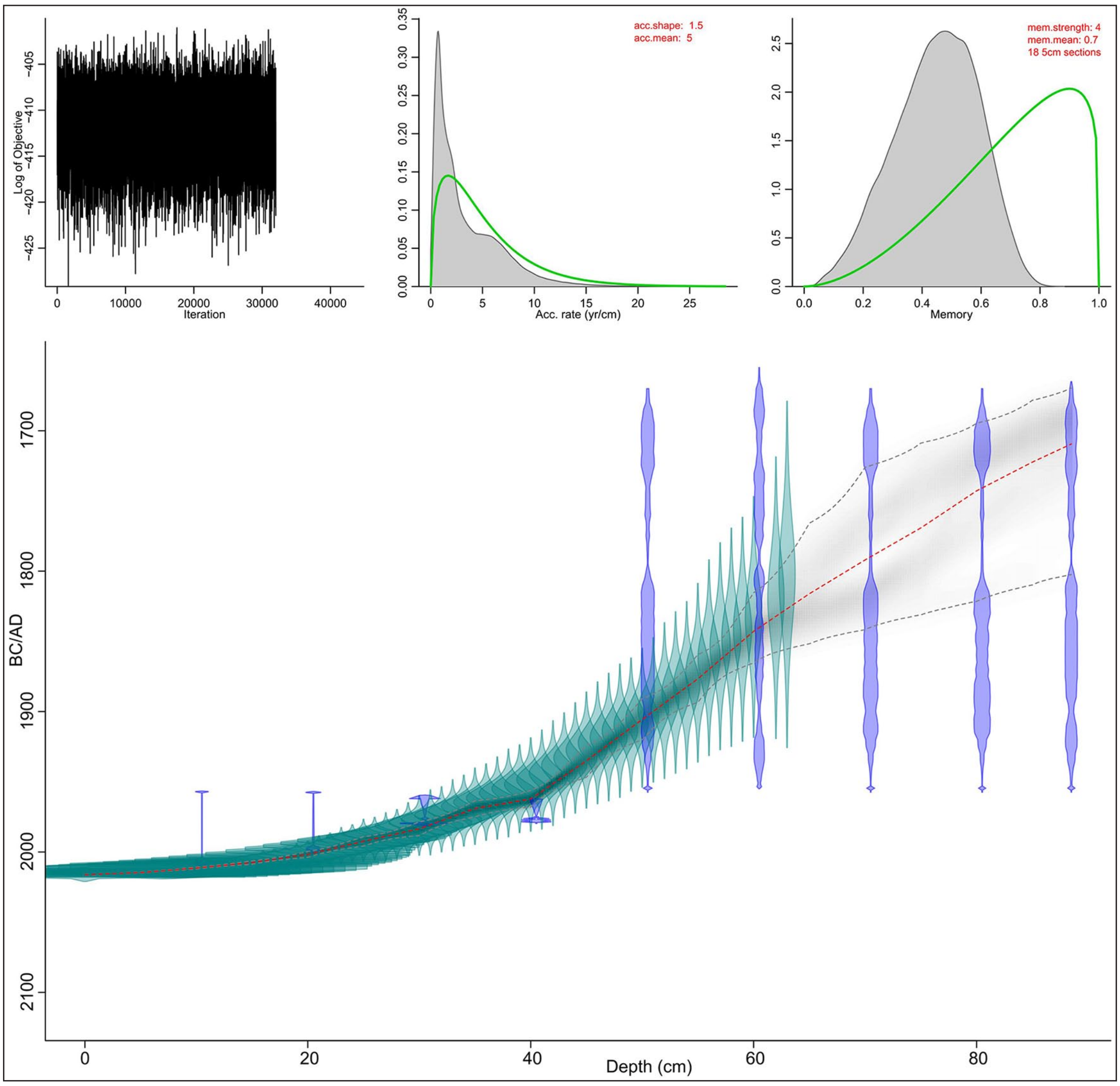

Figure 2. Age-depth model of the peat profile from Gorodetsky Moch.

the Russian Empire - Scale: 3 versts in one English inch (1:126000) (period of reflect 1850–1867, accessed on 05.2019), (6) Topographic military maps of Red Army (RKKA) (the state of the area in 1937–1941, scale 1: 50000 and 1: 100000, accessed on 05.2019). Images were classified using "Iso Cluster Unsupervised Classification" procedure. Types of land-use and forest composition were defined using the data from topographic maps, high-resolution images of Google Earth project, and expert assessment. We distinguished six different land-use categories: (1) arable land-grassland-young cuttings; (2) water bodies; (3) wetlands; (4) open soil-roads-fields after spring fire; (5) settlement; and (6) forests: coniferous (*Pinus sylvestris, Picea abies*), mixed (*Pinus sylvestris, Picea abies, Populus tremula, Betula pendula)*, and small-leaved forests (forests with *Populus tremula, Betula pendula* and sometimes *Alnus incana* domination). The proportions of changes in the land cover during the last 240 years were calculated using ArcGIS program.

Numerical analysis and visualization of the results

Palaeoecological diagrams were plotted using the software Tilia (Grimm, 1992) and C2 (Juggins, 2003). Individual zonation for pollen, charcoal, plant macrofossils, and testate amoebae was based on stratigraphically constrained cluster analysis with the CONISS method (Grimm, 1987) and was plotted using Tilia (Grimm, 1987). Common phases in the peatland development used in the description of results in the article were primarily delimited based on main changes in pollen, macrofossil, and testate amoeba analyses. The testate amoebae were used to reconstruct the hydrological variability (depth to the water table - DWT) and pH with C2 software (Juggins, 2003), using a regional Polish training set (Lamentowicz et al., 2008a). We used the tipping point if DWT=11.7 cm as the reference to define the hydrological stress in the mire (Lamentowicz et al., 2019b). Shannon diversity index (SDI) was calculated to study the community diversity of testate amoebae (Shannon, 1948) using the *vegan* package (R version 3.5.1) (Oksanen, 2013; Team, 2015). Moreover, six functional traits of the testate amoeba (metabolism – presence or absence of zoochlorella, body size – length of shell, biovolume – the volume of the shell, aperture size – the size of pseudstome, aperture position – location of the pseudostome in a shell, and body range - pseudostome size-body size ratio) were calculated (Fournier et al., 2015; Jassey et al., 2015; Koenig et al., 2018; Lamentowicz et al., 2015; Marcisz et al., 2016) using unpublished trait database using the functional diversity (FD) and *vegan* packages in R (Laliberté and Legendre, 2010; Oksanen, 2013). TA traits are expressed as the community-weighted mean (CWM) of each functional trait.

Results

Environmental changes in Gorodziecky Moch peatland

Four common phases (Gor-A-D) of the main developmental stages of the peatland were delimited based on pollen (Figure 3), plant macrofossils (Figure 4), testate amoebae (Figure 5), charcoal (Figure 4) and land cover changes (Figure 7).

Phase Gor—A (1710–1765 CE, 89–74 cm). In this phase, the tree pollen relative abundance varied from ca 78% to 90%. Here, as well as in the whole section, *Betula* and *Pinus* dominated with the participation of *Alnus. Picea* reached the maximum values in the peat core, and its share increased from ca 6% to 29%. Among herbaceous plants, *Poaceae* pollen dominated. Microscopic charcoals were remaining at low values (from 6 to 256 particles/cm^2/year), whereas macroscopic charcoals practically were absent. In this phase, *S. fuscum/rubellum* community with *Sphagnum magellanicum* dominated accompanied with *Scheuchzeria palustris*. In addition, the phase was characterized by the high share of wet species of testate amoebae and typical species for *Sphagnum* habitats such as *A. flavum*, accompanied by *H. papilio* and *Hyalosphenia elegans*. We recorded an episode of a higher water table indicated by *A. wrightianum.* Water table fluctuated in the range of 3.4–7.5 cm, and pH was in the range of 3.95–4.4. Proteinaceous testate amoebae dominated in this phase.

Phase Gor—B (1765–1960 CE, 74–40 cm). The second phase showed a distinct change in the local vegetation. The relative abundance of AP (arboreal pollen) decreased gradually from ca 83.5% to 53.5%, and the highest decrease in trees pollen occurred in the early 20th century CE. The relative abundance of *Picea* pollen decreased by few percentages at the beginning of this phase. The relative abundance of *Pinus* was between 13% and 36.1%, and that of *Betula* was between 14.4% and 51.7%. *Poaceae* and pollen human indicators reached the maximum values of 19% and 21%, respectively, in the early 20th century CE. The changes of pollen human indicators were included, among others, the increased to 8% of cultivated plants and also a minor peak of *Rumex* sum (*Rumex acetosa, Rumex acetosella*), and *Artemisia* was recorded at this time. The percentage of *Sphagnum* spores also increased and remained high during the whole phase. A few macrocharcoal peaks (to 25 particles/cm^2/year) were recorded. Microscopic charcoal were remaining at low values to 1870. Since then, we recorded an increase of microscopic charcoal (25–890 particles/cm^2/y). *S. fuscum/rubellum* dominated, with hydrophilous species forming the hummock complex, in this phase also appears *Sphagnum* sect. *Cuspidata.* Moreover, plant macrofossils indicated a decrease in *Sphagnum* and an increase in *Ericaceae*, monocots, and *Carex* sp. roots during the first half of the 19th century. The phase was characterized by moderate water table changes, oscillating between 7.4 and 13.6 cm, whereas pH between 4.1 and 4.5. Testate amoebae with proteinaceous shells such as *A. flavum, H. papilio*, and *H. elegans* were still dominant. Concurrently, the share of wet indicator species—*Heleopera petricola* — increased with a distinct peak ca.1775 CE. We also noted a high percentage of *A. discoides* at the end of the phase.

Phase Gor—C (1960–2000 CE, 40–19 cm). The proportion of AP pollen varied from around ca. 81% to 93% in this phase. We observed a decrease in *Pinus* and an increase in *Alnus* and *Betula* at the beginning of phases C. *Poaceae* dominated among the herbaceous plants' pollen percentage with a minor peak of *Vaccinium* at the beginning of this phase. The values of microscopic charcoal were still high (from 91 to 1285 particles/cm^2/year), whereas macroscopic charcoal (100–500 μm) increased and ranged from 0.5 to 79 particles/cm^2/year. The maximum values were reached between 1980 and 1990 CE. The phase was characterized by the decrease in *Sphagnum* moss and an increase in *Ericaceae*, monocots, and *Carex sp*. roots. *Sphagnum magellanicum* and *Sphagnum* sect. *Cuspidata* disappeared at the end of the 20th century. The peatland experienced abrupt water table changes that fluctuated in the range of 8.3–17.7 cm. Testate amoebae species such as: *C. oviformis, A. muscorum*, and in particular *A. militaris* and *A. discoides* reached the maximum growth, whereas *A. flavum* and *H. papilio* disappeared. We also observed a rapid increase of *D. pulex* at the end of the phase. The abundance of proteinaceous testate amoebae decreased in the favor of xenosomic taxa, that built tests from the recycled organic or mineral particles. The pH fluctuated in the range of 3.6 to 4.0.

Phase Gor—D: (2000–2016 CE, 19–0 cm). The last phase was characterized by a high percentage of AP that increased to 97%. Tree species that were abundant in the peatland vicinity are represented by *Betula, Alnus*, and *Pinus*. This phase was also characterized by the high values of microscopic charcoal (from 31 to 848 particles/cm^2/y) and macroscopic charcoal (100–500 μm: from 0 to 66 particles/cm^2/y; >500 μm: from 0 to 2 particles/cm^2/y). *Sphagnum* increased to above 95%, together with two species of testate amoebae: *A. flavum* and *H. papilio*. Concurrently, proteinaceous tests dominated. Testate amoeba biodiversity decreased at the beginning of this phase. The testate amoebae assemblage revealed a decreasing trend of the water level and pH. Water table oscillated between 10.7 and 15.4 cm, whereas the pH was between 3.9 and 4.5.

Functional traits of the testate amoebae

The analysis of functional traits of testate amoebae showed a relatively high variability during the last 300 years (Figure 6). In particular, traits such as body size, biovolume, and aperture size revealed similar changes over time. A visible decreasing trend in metabolism in the peat profile implies the decreasing abundance

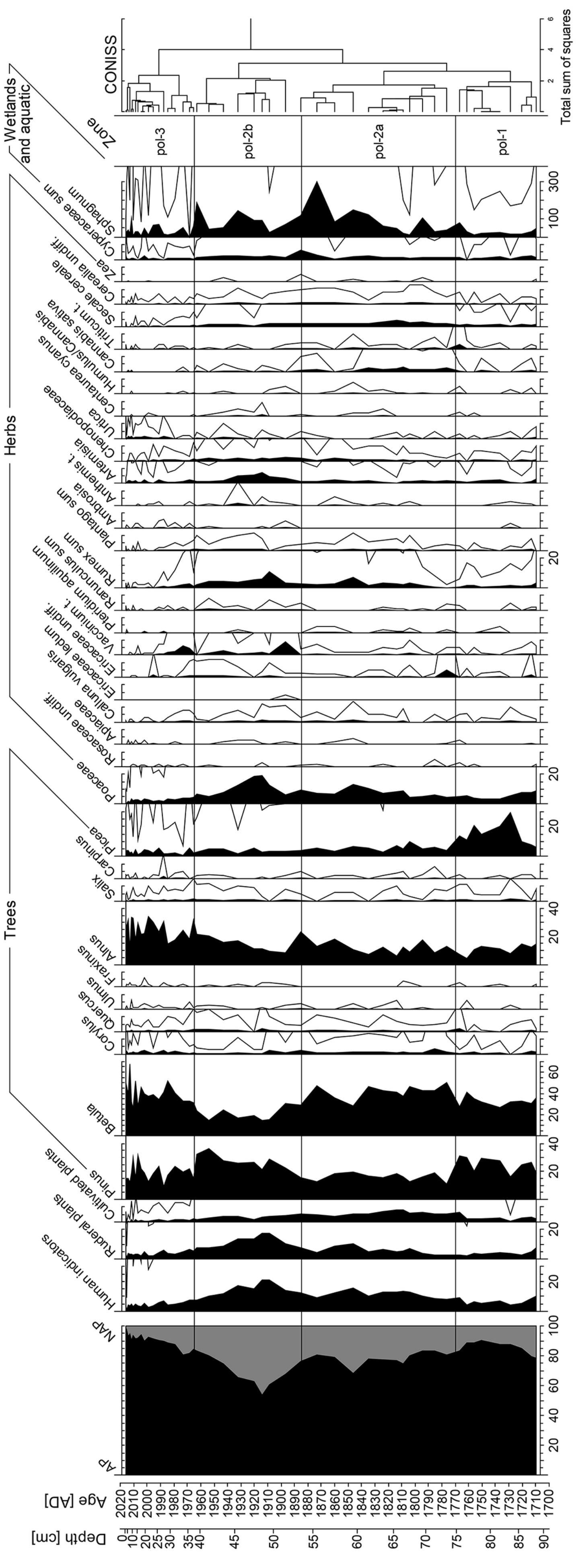

Figure 3. Pollen percentage diagram for Gorodetsky Moch peatland; 10 times exaggeration is presented as For Peer Review black lines.

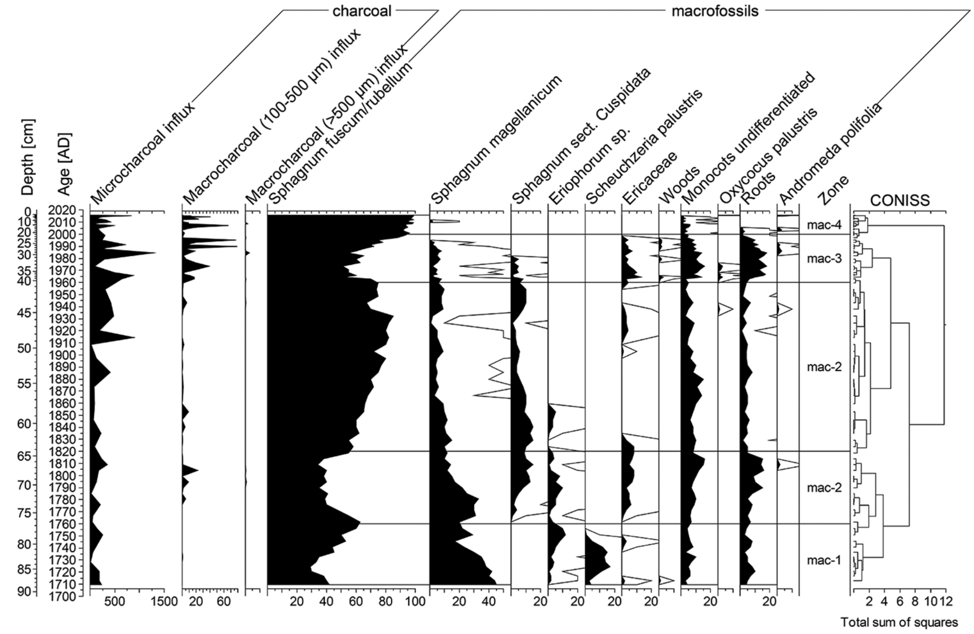

Figure 4. Charcoal diagram presenting fire history and plant macrofossils percentage diagram presenting local vegetation changes in Gorodetsky Moch; 10 times exaggeration is presented as black lines.

of mixotrophs. Metabolism CWM values reached minimum between 1965 and 1995 CE, and then started to increase abruptly suggesting higher mixotrophs abundance. Aperture position reached minimum between 1960 and 1970 CE. The maximum fluctuations in the functional diversity started together with the hydrological disturbance during the second half of the 20th century CE. Considering the low water table reconstructed in that time, the all trait CWMs are the most possibly connected with the hydrological fluctuations.

Land-use changes

During 1784–1786 CE, the land covered by forest and used for agriculture occupied 41% and 50% of study area of the Gorodziecky Moch peatland vicinity (Figure 7). The share of wetlands, rivers, lakes, and villages was low. Until CE 1867, forest cover increased up to 60%, while the percentage of agricultural lands decreased to 31%; simultaneously, other land-use types did not change significantly. During 1923–1941 CE, the area of settlements (8%) and agricultural lands (51%) increased, and deforestation was visible (forest area in 1939 CE decreased to 34%). In 1971 CE, many settlements disappeared, and fields were abandoned; therefore, their area decreased (4% and 36%, respectively) and forest cover increased to 54%. The process of depopulation and abandonment of fields continues from 1971 CE to date. Reforestation prevails and forest area increases. The percentage of wetlands and open water reservoirs changed slightly during the last 250 years, it oscillated between 5% and 6.5%.

Discussion

The Gorodetsky Moch profile represents a continuous record of peat accumulation during the last 300 years. The multiproxy data with detailed chronology records allowed to identify disturbances to the peatland and their impact on the ecosystem dynamics and palaeohydrology (Figure 8). According to the intensity of human impact on the peatland and local environment, we focused on the changes in the surrounding landscape, dry phase from the second half of the 20th century CE, and peatland recovery after the stress.

Changes in the surrounding landscape

The important factor that changes the landscape of the peatland vicinity is that at various time periods the region was a border area and an integral part of different states: Grand Duchy of Lithuania (14th–16th century CE), Grand Duchy of Moscow (16th century CE; until 1582 CE), Polish–Lithuanian Commonwealth (16th–18th century CE; 1582–1772 CE), Russian Empire (18th–20th century CE; 1772–1917 CE), Soviet Russia (20th century CE; 1917–1922 CE), Soviet Union (20th century CE; 1922–1991 CE), and Russian Federation (at present, since 1991 CE) (Eremeev, 2010; Shumskaya, 2007). A vulnerable location may have affected the occupation pattern and ancient economy of the region as well as the population density.

Increasing deforestation was observed during the last 300 years (Tarasov et al., 2019). This was also confirmed by the results of research on gully erosion in the lower Serteyka River valley (Piech et al., 2018). In 1714 CE, King Augustus II the Strong (August II Mocny in Polish) allowed for tree cutting in the area of Velizh and privileged the city for producing clapboards, sticks, and logs, among others, resulting in large deforestation and lack of wood in 1773 CE (Eremeev, 2010; Kachulina, 2010). A significant decrease of spruce abundance in the 70s of the 18th century resulted from intense forest exploitation (Figures 3 and 8). However, the forests were not cut out for a longer period until the early 20th century, which confirms Eremeev (2010), as well as the growth of forest cover documented in the pollen analysis results (Figure 3) and on the land cover change maps between 1786 and 1867 CE (Figure 7). Intense felling of forest trees began in the beginning of the early 20th century (Figure 8), as a result of wood industry was developed at that time in the region. A sawmill was built in 1913 CE in Selezni village, and a year later, a shipyard was built in Goriane village for the construction of barges for the army (Eremeev, 2010; Ivanov, 2007). Deforestation is also clearly visible on the map from 1939 (Figure 7). It is highly probable that humans were responsible for deforestation in peatland region during the last 300 years (Figures 3 and 8). However, we did not find significant relationships between the regional vegetation (deforestations) and hydrological changes of the peatland that time (Figure 8). The shift is correlated with decreasing abundance of mixotrophic species and

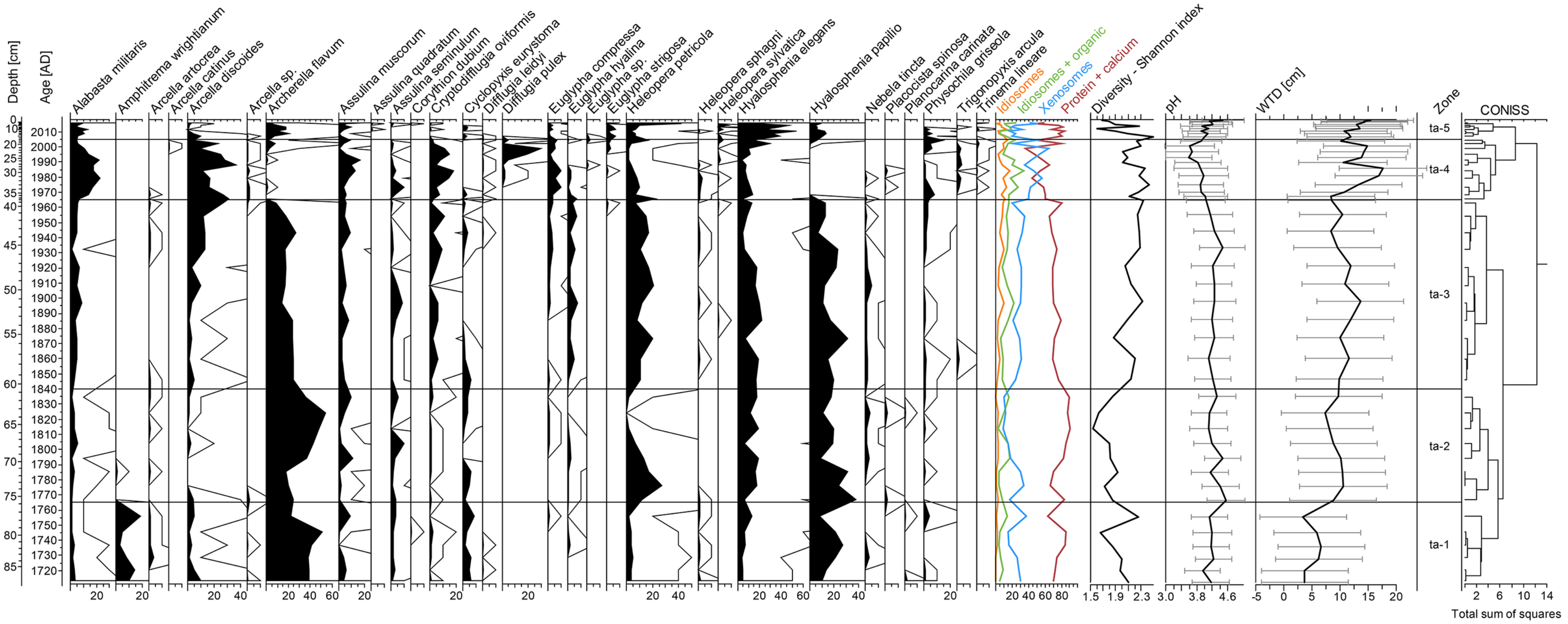

Figure 5. Testate amoeba percentage diagram presenting pH and water table changes in Gorodetsky Moch; 10 For Peer Review times exaggeration is presented as black lines.

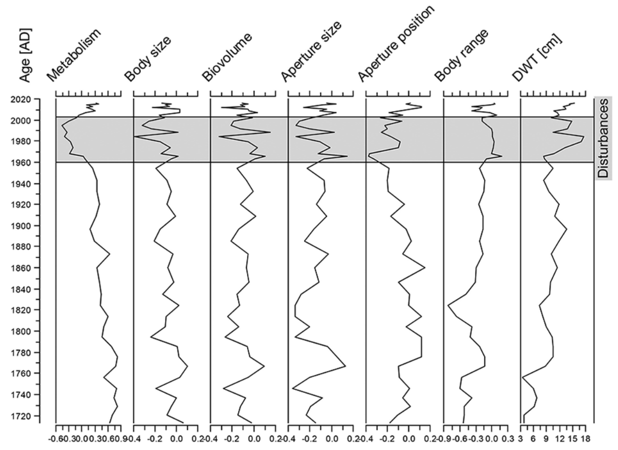

Figure 6. Functional traits of testate amoeba communities calculated from Gorodetsky Moch.

decreasing water table trend since ca 1840 CE. The *S. magellanicum to S. fuscum* shift is synchronous with the testate amoebae data and might be connected with autogenic succession (Birks and Birks, 1980; Charman, 2002; Zobel, 1988).

The changes in the surrounding landscape of the peatland in the 19th and 20th centuries CE were mostly related to the intense development of human occupation. In that time, the area of agricultural lands and settlements increased significantly (Figure 7). In 1906 CE, 58.6 thousand people lived in the region and only ca 200 people in the Gorodets village in the immediate bog neighborhood in 1912–1913 CE (Eremeev, 2010; Kachulina, 2010; velizh.admin-smolensk.ru). Local human activity was the most intensive in the early 20th century CE (Figure 8). The vicinity of the peatland was used for farming and grazing in that time. This was mostly the result of "the Emancipation Reform in Russian Empire" (from 1861 CE) and of the liberal "Stolypin agrarian reforms" in the early 20th century CE (1906) (Kosonits, 1999). Agriculture, cattle breeding, craftsmanship and fishing developed actively toward the end of the 18th century and the beginning of the 19th century CE in the estate of Selezni village adjoining Serteyka River valley from the west, which was one of the richest properties in the Velizhsky region until 1917 CE (Eremeev, 2010).

During 1929–1932 CE, the forced consolidation of individual peasant households into collective farms called "kolkhozes" was introduced and the private ownership of land (collectivization) was abolished in Soviet Union; moreover, millions of peasant families were dispossessed and deported (dekulakization) (Conquest, 1986). The abundance of cereals in pollen record during that time reached around 2.5% (Figure 3). Depopulation of rural areas of the Soviet Union was observed after 1926 CE (Becker et al., 2012). During that time, the rural population accounted for around 83% of the total population and then dropped to 66% in 1939 CE and to 48% in CE 1952 (Becker et al., 2012). After the German Army occupied the Velizh region, the population decreased, and only ca 600 to 700 people lived in Velizh city in 1943 CE. The higher fire activity during the first half of the 20th century CE (Figure 2) could be partially due to the fire of villages located in the south of the peatland in 1920s CE and because of warfare, as the Velizh region was occupied by the German Army during World War 2. The pollen values of cereals (Figure 3) decreased at the same time as that in the Staroselsky bog, which reflects the decline in agriculture in the area of the forest zone of the former Soviet Union at the end of the 20th century CE (Novenko et al., 2017). Presently, Gorodets village, like many other neighboring villages, was abandoned.

Disturbance and resilience

The results of testate amoeba and macrofossil analyses indicate a layer documenting disturbance (C zone, 1960–2000 CE) in the core starting from the second half of the 20th century CE (Figure 8). After moderate deforestation state and stable wet conditions, a dry phase appeared for about 40 years. It is highly probable that human activity was responsible for the decrease in the water level on the peatland during this time. Gorodetsky Moch was drained, and according to the map from 1989 CE, the location of the ditch is clearly visible, but the exact date of the origin of the melioration works is unknown. However, it is known that the drainage were carried out in Pskov Oblast between 1965 and 1985 CE, in both forest area (148000 ha) and open area (18000 ha) (2009–2010, 2011). This is highly probable that the drainage ditch at Gorodetsky Moch peatland was dug during the 1960s CE.

The disappearance of wet indicator, mixotrophic species of testate amoebae (*A. flavum* and *H. papilio*) (Lamentowicz and Mitchell, 2005b) and increased abundance of dry indicators such as *C. oviformis*, *A. muscorum*, *A. militaris* (Lamentowicz and Mitchell, 2005a), and *D. pulex* indicate dry conditions (Hendon, 1998; Schnitchen et al., 2003). Such composition of testate amoebae, may also suggest a human-induced hydrological disturbances causing peatland habitat instability which has become vulnerable in the periods of drought, what we now observe in results of ecological investigations (Marcisz et al., 2014; Słowińska et al., 2010; Lamentowicz et al., 2020) and in palaeoecological data (Lamentowicz et al., 2008b, 2010; Marcisz et al., 2016). Moreover, *A. discoides* might be the indicator of hydrological instability (Marcisz et al., 2015; Lamentowicz et al., 2019a) associated with temporal droughts and inundations of peatland surface. This hydrological instability of surface wetness can also be observed in the peatland vegetation cover (Figure 4), namely follows the relationship between species, we note a decrease of *Sphagnum fuscum/rubellum* and an increase in the abundance of vascular plants. The disturbance phase characterized also by a high diversity of the species composition of testate amoebae, and the SDI was high and fluctuated between 2.0 and 2.5 (Figure 5). We associate the high testate amoebae diversity with drainage, which influenced the seasonal hydrological instability in the ecosystem, and which generated new hydrological conditions with high seasonal fluctuations. This seasonal hydrological instability affects the generation of alternative ecological states, but for a relatively short period causes the possibility of occurrence of a wide range of species. Our research showed that the diversity of testate amoebae was lower immediately after the disturbance (1.5) (Figure 5). SDI ranged from 1.5 to 2.5 for the whole peat core. Moreover, analyzing the functional traits variability (body size, biovolume, and aperture size), we also observed rapid changes within the disturbances phase (during the second half of the 20th century). This phase was simultaneous with a decrease in metabolism and a slight increase in body size (Figure 6). Before disturbance, the body size, biovolume, and aperture size increased, together with a decrease in aperture position, whereas during the disturbance, these traits highly varied. A similar relationship was recorded in a previous study (Marcisz et al., 2016). Different response of proxies to disturbances of Gorodetsky Moch peatland could be related to their sensitivity (Słowiński et al., 2017, 2018), while the value of the multiproxy approach is particularly important when analyzed profile is sampled in high-resolution, that allows to assess the timing of disturbance as well as the regeneration (Colombaroli et al., 2018).

Currently (D zone, 2000–2016 CE), despite the dry phase in the second half of the 20th century CE (C zone), which is caused most probably by digging drainage ditch, the peatland is moderately wet and most likely still retains its original characteristic.

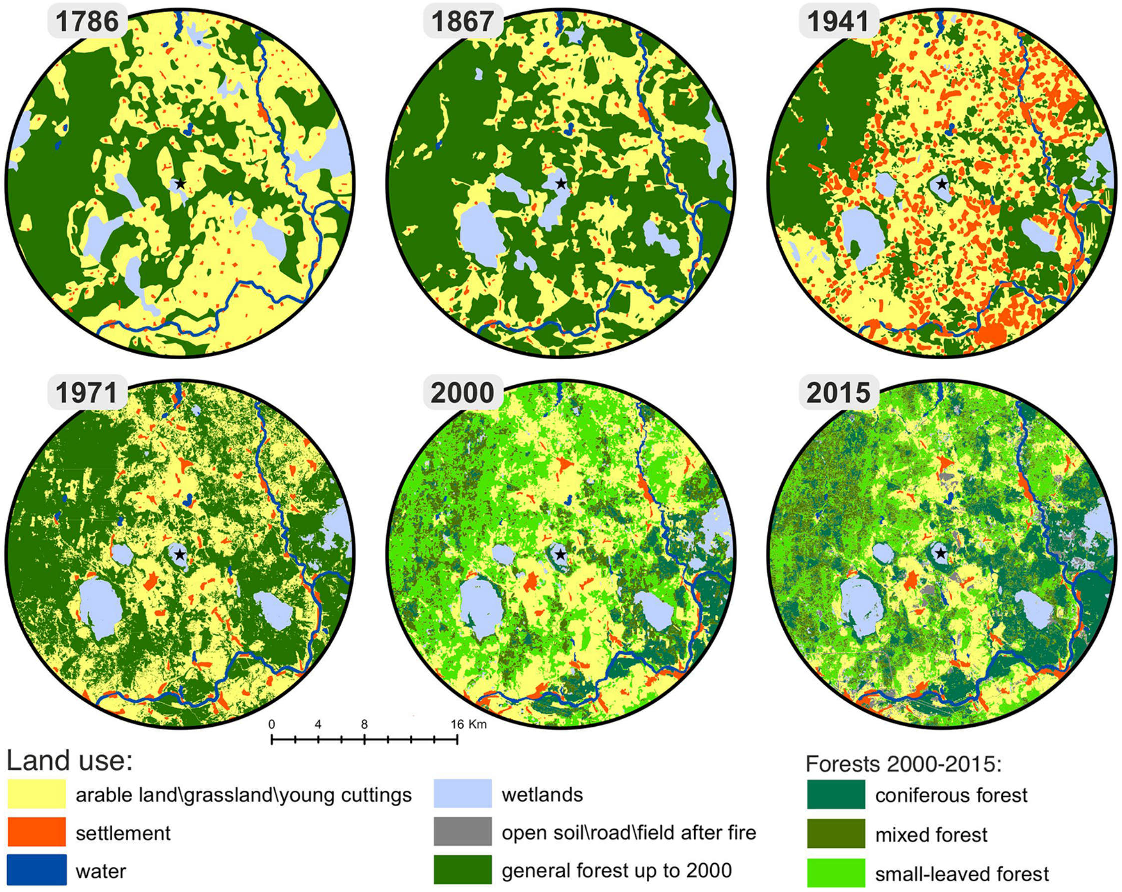

Figure 7. Land cover change map of 1780, 1850, 1939, 1971, 2000, and 2015. The maps distinguished six different land-use categories: (1) arable land-grassland-young cuttings; (2) water bodies; (3) wetlands; (4) open soil-roads-fields after spring fire; (5) settlement; and (6) forests: coniferous (*Pinus sylvestris*, *Picea abies*), mixed (*Pinus sylvestris*, *Picea abies*, *Populus tremula*, *Betula pendula*), and small-leaved forests (forests with *Populus tremula*, *Betula pendula* and sometimes *Alnus incana* domination).

The relative abundance of *Sphagnum* increased together with wet indicator species of testate amoebae (*A. flavum* and *H. papilio*) in the top part. Obtained patterns indicate regeneration and confirm that degraded raised peatlands in Europe can sometimes regenerate. Moreover, our study provides another example of high indicative value of mixotrophic testate amoebae (represented by the metabolism trait). Loss of this group should be regarded an early warning signal of *Sphagnum* peatland disturbance, and their recovery is a promising signal of ecosystem resilience (Jassey et al., 2015).

Climatic background and a forecast for the future

It is also highly probable that climatic conditions impacted the development of the Gorodetsky Moch peatland during the last 300 years. Spinoni et al. (2014) reported that Russia was one of the regions most exposed to prolonged and severe droughts between years 1951 and 1970. This period precedes the disturbed layer and drainage of the Gorodetsky Moch peatland in the second half of the 20th century. The annual precipitation between 1951 and 1970 CE was between 382 and 863 mm, whereas the average annual air temperature was lower than those in previous and later years (Weather and climate, 2016). During 1946–2016 CE, the lowest rainfall (below 500 mm) was recorded in 1946 (439 mm), 1951 (382 mm), and 1959 (458 mm) (Supplementary Figure 1). Studies show that droughts can be the main factor affecting the peatland ecosystem (Ireland et al., 2012). The extended periods with low water table can contribute to changes in the structure of vegetation, especially among mosses (Malmer et al., 1994) such as *Sphagnum*, which are very sensitive to hydrological changes (Rydin et al., 2006). It was recently revealed that vegetation changes considerably when the water table drops below 11.7 cm in the long time scale (Lamentowicz et al., 2019b). However, it is unlikely that only climate change in such a short time lead to hydrological stress, vegetation composition shift and, as a result the collapse of mixotrophic testate amoebae on the Gorodetsky Moch peatland.

Despite the peatland recovered recently fires are a real threat to this ecosystem considering recent drainage, lower water levels on the peatlands, climate changes and climatic predictions. Global warming in recent decades has significantly increased the risk of the occurrence and spread of fires (Supplementary Figure 1). The effect of prolonged drought and high air temperatures was the reason of the summer fires of forest and peatlands in many regions of the European part of Russian Federation in year 2010 (Hansen et al., 2012; Gilbert, 2010; Shvidenko et al., 2011; Witte et al., 2011). Peat fires were noted mainly in the Moscow Oblast, but also, among others, in the Tver Oblast and Pskov Oblast. Drained peatlands such as Gorodetsky Moch are more susceptible to fires. It is estimated that about 3.8 million ha of peatland in Russian Federation territory (mainly in the European part) have been drained (Päivanen and Paavilainen, 1996). A forecasted increase in the intensity of fires in the current century in Europe (Flannigan et al., 2013) will potentially affect peatlands hydrology and carbon balance. Moreover, the peatlands can often be the only source of water for animals in the face of climate change and the growing hydrological crisis. Therefore, it is important to maintain peatlands in a proper hydrological state and restoring degraded peatlands.

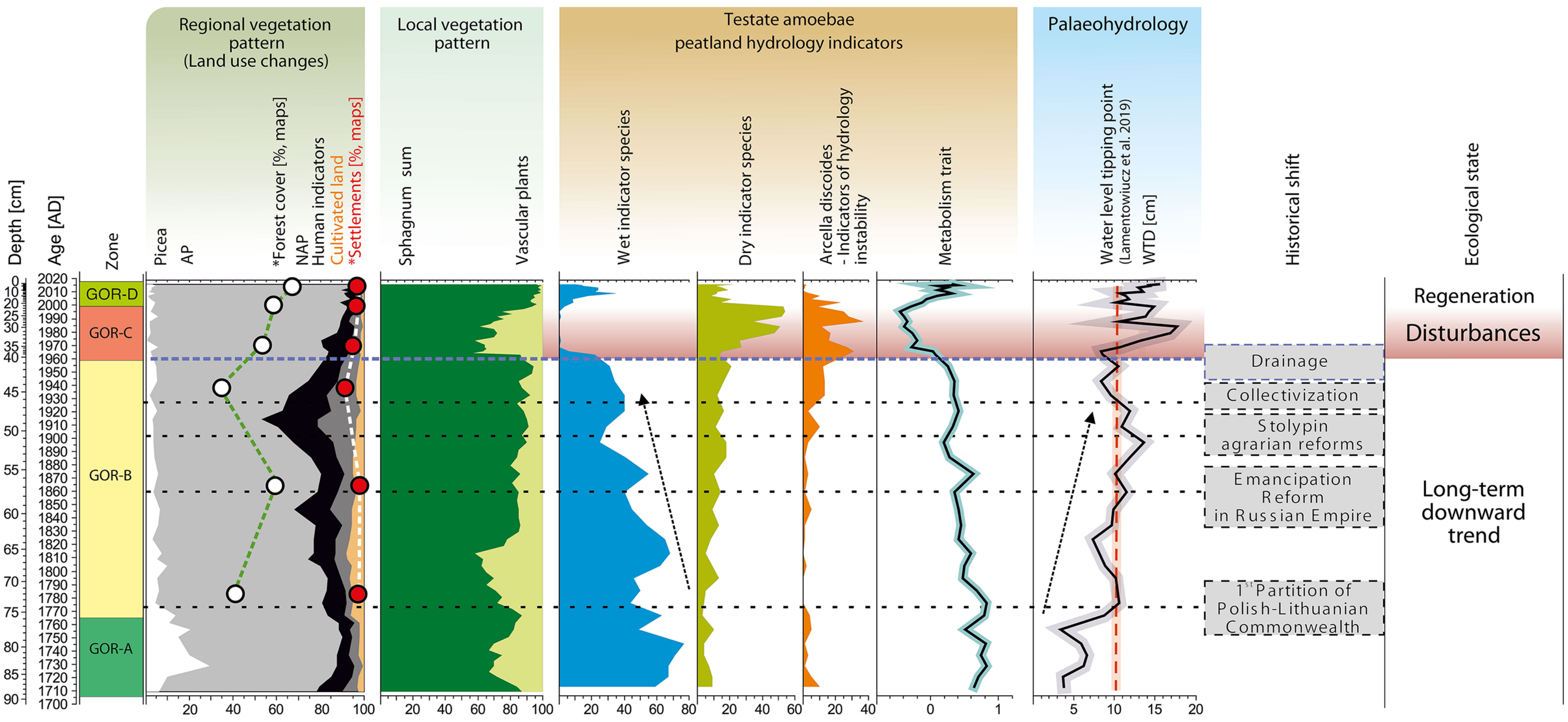

Figure 8. Summary of the most essential trends Gorodetsky Moch peatland. The figure contains: (1) regional vegetation pattern (land-use changes) based on data of pollen, and Historical maps and Corona images; (2) local vegetation pattern based on data of plant macrofossil; (3) testate amoebae peatlands hydrology indicators; (4) hydrology based on testate amoebae; (5) the significant historical shift and (6) ecological state of peatland.

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Supplemental material

Supplemental material for this article is available online.

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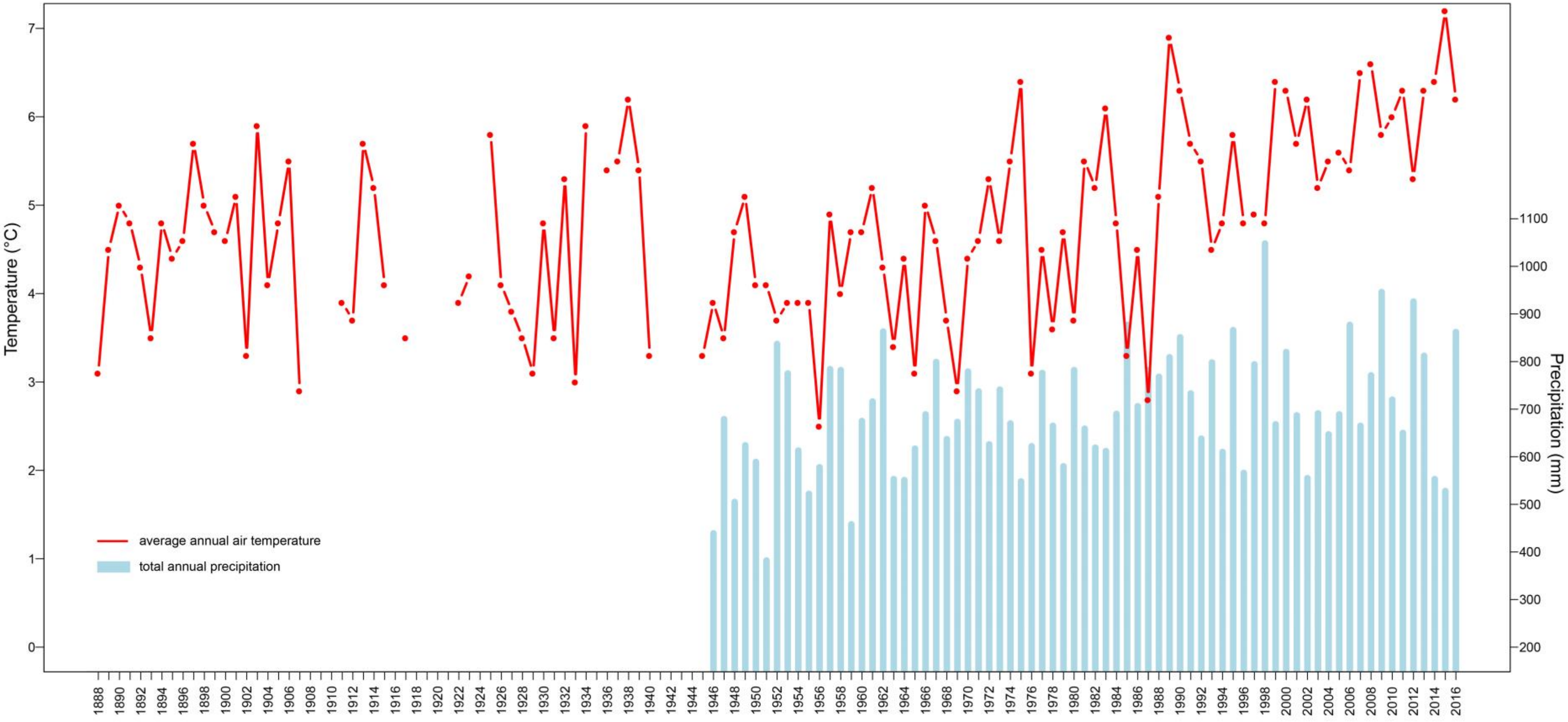
Supplementary Fig. 1. Total annual precipitation from 1946 to 2016 and average annual air temperature from the 1888 to 2016 (no data for 1908-1910, 1916,1918-1921, 1924, 1935 and 1941-1944) for Smolensk based on climate data from the Smolensk Meteorological Observatory (Weather and climate, 2016)



Supplementary Table 1. List of herbaceous pollen taxa included in the diagram curves

	Land-use category	**Indicator taxa**
Human indicators	Cultivated land	*Secale cereale, Triticum* t., Cerealia undiff., *Zea mays, Centaurea cyanus, Cannabis sativa, Fagopyrum*
	Ruderals (minor and major)	*Artemisia, Chenopodiaceae, Rumex acetosa/acetosella, Plantago lanceolata, Plantago media, Plantago major, Urtica, Polygonum aviculare, Brassicaceae,*

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Searching for an ecological baseline: Long-term ecology of a post-extraction restored bog in Northern Estonia

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ABSTRACT

The exploitation of peatlands in Estonia, which began in the 17th century, has degraded them to a great extent. Consequently, cutover and drained peatlands have become the sources of CO_2. Global warming has led to a need for policies focusing on the protection and restoration of drained and degraded peatlands. Hence, to compare the effect/progress of restoration with the past pristine ecosystem baseline before the peatland was destroyed by cutting, we examined a peat core from North Estonia using chronology based on ^{14}C by analyzing several proxies in high resolution including testate amoebae, plant macrofossils, pollen, non-pollen palynomorphs, and diatoms. The results revealed a striking ecological contrast between the pristine (ca. 2 kyrs) and restored state (currently) of the peatland. The pristine state was characterized by a domination of *Sphagnum fuscum/rubellum* and *Archerella flavum*, suggesting that extraction area of Hara peatland was a wet and stable ombrotrophic bog. As a result of peat exploitation, deposits comprising the last ca. 2 kyrs were cut. In turn an important feature of the restored section of the peat core was the domination of a green algae (Chlorophyta) and *Eriophorum vaginatum* as well as testate amoebae species *Arcella discoides*, which is considered an indicator of hydrological instability. The main difference between the predisturbed and restored parts of the peat core section was that a minor cover of peat-forming *Sphagnum* and mixotrophic testate amoebae was present in the top inundated part. We state that a healthy raised bog—the target of restoration—should consist abundant mixotrophic testate amoebae such as *Archerella flavum* and *Hyalosphenia papilio* which are good indicators of a well-functioning *Sphagnum* bog ecosystem even if the *Sphagnum* species differ from the reconstructed ecological baseline conditions. Our study highlights the extensive damage caused to the peat-forming ombrotrophic peatland by extraction and how difficult, challenging, and time-consuming is the process of ecological restoration.

1. Introduction

Peatlands store around one-third of the global soil carbon (Gorham, 1991; Rydin and Jeglum, 2013); however, peat extraction and drainage for forestry and agricultural purposes have resulted in the degradation of most of the peatlands in Europe (Joosten, 1997). Today, the disturbed peatland ecosystems act as a source of CO_2 for the atmosphere, but many of them still have the potential of increasing biodiversity and accumulating carbon. The current policies and efforts focusing on minimizing the effects of climate change (IPCC, 2014a; IPCC, 2014b) indicate the need to protect and restore drained and exploited peatlands (Charman, 2002).

Peat is one of the most important natural resources in Estonia. Its exploitation began in the 17th century which resulted in the destruction of about 9% of Estonian peatlands (Kohv and Salm, 2012). An increase in peat cutting was observed in the 20th century when peat was started to be used as a source of fuel for power stations, and later used by the garden industry, where new products such as horticultural and litter peat found application (Paal, 2005). The majority of Estonian peatlands have been drained as part of their exploitation. Thick peat layers were cut from many peatlands. It is estimated that approximately 70% of mires have been affected by drainage (Bragg and Lindsay, 2003).

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Currently, Estonian peatlands cover an area of approximately 1,009,100 ha, which accounts for 22.3% of the country's total area (Bragg and Lindsay, 2003). The area of an untouched or pristine peatland measures less than 300,000 ha (Paal, 2005).

Damaged peatlands are often in the focus of ecological restoration (Bonn et al., 2016). The range of disturbance is very wide, from simple drainage to peat exploitation to the bedrock (Chapman et al., 2003a). Therefore, restoration practices need to be adapted to above-mentioned conditions. Peatlands that were destroyed in the past might be restored through the ditch damming, plant transplantation or local deforestation (Minayeva et al., 2017). There were number of experiments that aimed at developing best practices of peatland restoration (Gorham and Rochefort, 2003; Kotowski et al., 2016) to run the peat accumulation process again. However, the success of restoration is very difficult to be predicted, as it depends on the climate and local factors, as well as it needs ecohydrological monitoring to see the final effect (Bonn et al., 2016) that might be related to improved hydrology and peat/carbon accumulation. In this context often ecological baselines might be regarded as the target for the ecological restoration, however, return to the past not disturbed pristine ecosystem is often impossible.

The measures of success taken for peatland ecological restoration, whenever possible, should consider the long-term ecology (Froyd and Willis, 2008; McCarroll et al., 2016; Tobolski, 2003), preferably based on data from high-resolution multiproxy studies (Payne et al., 2015; Roland et al., 2015; Słowiński et al., 2016). For the restoration of postextraction *Sphagnum* peatland, it is important to compare the current hydrological conditions with the past, i.e. undisturbed ecosystem baseline (Andersen et al., 2017; Valentine et al., 2013). In this case, testate amoebae might be of particular use (Mitchell et al., 2007a). Due to the hydrological sensitivity of testate amoebae and decay resistance of the tests in peat, testate amoebae are considered as the main quantitative bioindicators in palaeoecological and ecological studies on peatlands (Booth, 2001; Charman and Warner, 1992; Marcisz et al., 2014; Payne and Mitchell, 2007). They are also used to monitor the habitat changes in peatlands and their regeneration (Buttler et al., 1996; Davis and Wilkinson, 2004; Jauhiainen, 2002; Laggoun-Défarge et al., 2008; Swindles et al., 2016; Valentine et al., 2013). In recent years, there has been an increase in the number of studies on testate amoebae (Ireland and Booth, 2012; Lamentowicz et al., 2015; Mazei et al., 2017; Swindles et al., 2014; van Bellen and Larivière, 2020). However, palaeoecological and ecological studies based on the analysis of testate amoebae are rare in the case of Estonian peatlands (Niinemets et al., 2011; Portsmuth et al., 2011; Sillasoo et al., 2007; Väliranta et al., 2012). Furthermore, a multiproxy approach, combining many proxies from peatland studies, might provide a wider look at the functioning of an ecosystem and the effects of various disturbances. In this study, we used several proxies in high resolution, including testate amoebae, plant macrofossils, non-pollen palynomorphs (NPPs), pollen, and diatoms. We paid exceptional attention to mixotrophic testate amoebae that are reliable indicators of the *Sphagnum* peatland ecosystem state (Marcisz et al., 2020). While pollen and plant macrofossils are commonly used in peatland related palaeoecological studies, diatoms are very rarely analyzed in palaeoecological studies based on ombrotrophic peatlands due to their possible preservation issues related to low pH in these ecosystems/environments (Bennett et al., 1991). Nevertheless, diatoms are well represented in different types of peatlands, where they are usually most widespread among the other algal groups. The harsh and distinctive conditions in peatlands are favored by many unique diatom assemblages (Chen et al., 2016; Fránková et al., 2009; Poulíčková et al., 2013). The main environmental conditions that affect diatoms in peatlands are water availability, water chemistry, and pH. If these conditions are suitable, diatom assemblages can be found diverse and abundant (Gaiser and Rühland, 2010; Hargan et al., 2015; Küttim et al., 2017a). Thus, diatoms can act as a good indicator for tracking local or large-scale environmental changes (e.g., changes in water level and vegetation, ecological succession, human disturbances) in peatlands (Chen et al., 2016; Poulíčková et al., 2013).

Moreover, to the best of our knowledge, diatoms have been rarely used as proxies of peatland restoration, and such proxies have never been employed to track the effectiveness of the restoration of exploited peatlands (Carballeira and Pontevedra-Pombal, 2020). The resulting, palaeoecological data enabled the reconstruction of the ecosystem functioning before and after the disturbance. Additionally, to explore the available species pool of testate amoebae and diatoms in space (which can immigrate into the restored *Sphagnum* carpet) we also analyzed the modern samples for testate amoebae, diatoms, and plant communities, as well as the data on environmental monitoring as the modern reference of the conditions present in the area under restoration. Our main aim was to explore the past ecological baseline using multiproxy approach in the exploited ombrotrophic peatland ecosystem after restoration-related inundation in space and time, thus connect the record of initial peatland development with conservation action and restoration goals.

2. Data and methods

2.1. Study area

We selected the former peat extraction area of Hara peatland for this study. Hara peatland is an ombrotrophic bog which covers an area of 747 ha in northern Estonia (Fig. 1) in the Kuusalu parish in Harjumaa county (59°33′N, 25°36′E, 27.5 m a.s.l.). The study site belongs to the Lahemaa National Park and is located at the former lagoon, between the coastal formations of the Ancylus Lake stadium of the Baltic Sea (Vandel et al., 2019). Peat is underlain by sand originating from the sea. The local forest consists of *Pinus sylvestris* along with *Picea abies*. The area has a climate characterized by average annual precipitation of 648 mm (1985–2015) and an average annual temperature of 5.3 °C (Estonian Weather Service, 2018).

Peat was industrially extracted in the years 1975–1994, in the northeastern part of the Hara peatland. The extraction area of the peatland (107.66 ha) includes a peat milling area of 99.4 ha and an old peat mine of 9.26 ha in the northeastern section (Ramst et al., 2005). Water from the drainage system flows into the Pudisoo River. The bottom of the central ditch is at 25.5 m a.s.l. (Širokova, 1993). On average, 0.8 m of peat is left after extraction (Ramst et al., 2005). The maximum depth of the peat layer in the unexploited part of Hara bog is more than 4 m, of which about 2 m on top consists mainly of *Sphagnum* peat (Orru, 2020). The degraded part of the Hara peatland was rewetted in 2011–2013 by the Estonian State Forest Management Centre. The goal was to restore the near-natural peatland landscape within the Lahemaa National Park, and decrease the risk of fire and emission of greenhouse gases. During the restoration, the upper peat layer (the topmost 20–50 cm layer of degraded peat) was peeled at 46 ha, six dams were built, tree cover was removed, and the depth of the water table as well as water temperature was monitored at five measuring points. The peatland vegetation is slowly recovering due to restoration efforts - the extraction area of Hara peatland comprises mainly scattered hummocks of *Eriophorum vaginatum* and small patches of *Sphagnum.*

2.2. Fieldwork and subsampling

A peat monolith (37-cm deep; 30 × 30-cm wide) was collected in November 2017, using a shovel from the recently rewetted peat extraction area of the Hara peatland (Fig. 1) at the coring point bare peat without alive *Sphagnum* mosses or other peatland plants. Modern samples (n = 10) were collected in close vicinity to the coring point. To represent the two extremes of the microtopography of the extraction area (Fig. 1D), we collected samples from hummocks (n = 5; as *Sphagnum* moss; isolated hummock) and hollows (n = 5; as frozen surface peat; places between hummock). Vegetation was identified to a species or taxon level using macrofossils analysis, and the depth of the

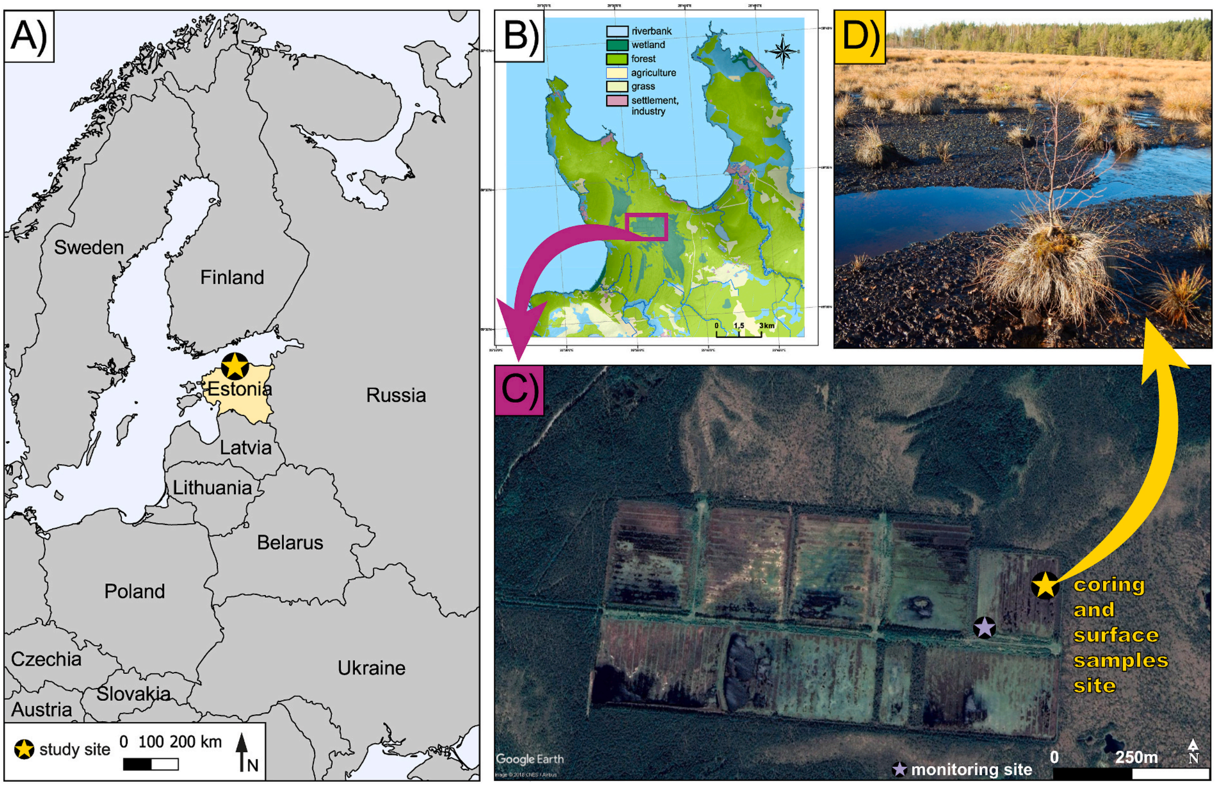

Fig. 1. A) Map of Europe showing the location of the Hara bog. B) Map of the northwestern part of Lahemaa National Park from Google Earth (from 2019), presenting the position of the peat extraction area of the Hara bog. C) Satellite map from Google Earth (from 2019) presenting the peat extraction area and the site of peat monolith sampling and surface samples in the year 2017. D) Picture of peat extraction area with hummocks of *Eriophorum vaginatum* and *Sphagnum* mosses and sampling place of peat monolith and surface samples in the autumn of 2017.

water table was measured at each sampling point using centimetre measure (Table 1). The percentages of each plant species from surface samples were determined based on an analysis of plant macrofossils obtained from the surface samples ($n = 10$) used in the analysis of testate amoebae. The peat monolith and modern samples were transported to the laboratory and refrigerated at 4 °C before they were used for further analysis. The monolith was divided into 1-cm slices and was subsequently analyzed for testate amoebae, diatoms, plant macrofossils, pollen, and NPPs, while the modern samples were divided and used for the analysis of testate amoebae, plant macrofossils, and diatoms.

2.3. Absolute chronology

The absolute chronology for peat core was obtained using four ^{14}C AMS dates determined in the Poznań Radiocarbon Laboratory (Poland) (laboratory code: Poz-; Table 2). The Bayesian age–depth model was employed using OxCal 4.3 software (Bronk Ramsey, 1995) by applying the *P_Sequence* function with parameters: $k_0 = 1$, $\log_{10}(k/k_0) = 1$, and interpolation = 1 cm (Bronk Ramsey, 2008; Ramsey and Lee, 2013). The IntCal13 atmospheric curve was used as the calibrating set (Reimer et al., 2013). The profile sections with potential changes in accumulation rate of peat ($\mathrm{AR}_{\mathrm{peat}}$) were introduced to the model as boundaries (Boundary command). These sections were as follows: (i) 37 cm—the bottom of the model, (ii) 30.5 cm—decline in *Sphagnum* percentages and total pollen concentration, (iii) 14.5 cm—decline in *Vaccinium*-group pollen and increase in *Sphagnum* percentages, and (iv) 0 cm—the top of the model. We assumed the year of coring, i.e. 2017.9 as the age of the top, because it was not possible to unequivocally reject the possibility of presence of modern deposits at the top. For better readability, a μ (mean) value rounded to 10 was selected as the modeled age, which was expressed as cal. BP (a year before AD 1950). The $\mathrm{AR}_{\mathrm{peat}}$ values were calculated using OxCal 4.3 software.

2.4. Peat properties

The degree decomposition of each peat monolith sample was assessed according to the von Post scale (Rydin and Jeglum, 2013). The dry matter, organic matter, and mineral content of the peat layers was established by loss on ignition. For the thermogravimetric analyses, we used about 3 cm^3 of peat from each sample (Precisa prepASH 340 Series). The samples were heated to a constant weight at a temperature of 105 °C and 550 °C to determine their dry matter and mineral content, respectively, while organic matter was assumed to be removed at 550 °C (Heiri et al., 2001).

2.5. Testate amoebae analysis

Testate amoeba analysis was carried out in subsamples of 2 cm^3 obtained from each modern sample from hollow and peat monolith (at 1-cm intervals). To analyze the modern testate amoebae from hummock, *Sphagnum* shoots were obtained from the upper 3 cm of the collected modern samples. Briefly, the paleo and modern samples were placed in a 500-ml beaker, shaken in distilled water, and then washed through a sieve with a mesh of 300 μm, following the procedure by Booth et al. (2010). A total of 100 tests of testate amoebae were identified at the species level (Payne and Mitchell, 2008) in each sample, based on the available identification guides (Mazei and Tsyganov, 2006; Siemensma, 2020), using a microscope at a magnification of×200 and × 400. Quantitative reconstruction of the water table and analysis of pH changes based on testate amoebae from peat monolith were carried out in C2 program (Juggins, 2003), using a regional Polish training set compiled by Lamentowicz et al. (2008). We used the *vegan* package in the R program (R version 3.5.1) (Oksanen, 2013; Team, 2015) to calculate the Shannon diversity index and functional traits (metabolism, body size, biovolume, aperture size, aperture position, and body range)

Table 1
Details of modern samples taken from the extraction area of Hara peatland.

No.	Code	Microtopography	Botanical content of modern samples	WTD [cm]
1	Hum1	hummock	*Sphagnum magellanicum* (95%), *Sphagnum fuscum/rubellum* (5%)	19
2	Hum2	hummock	*Sphagnum fuscum/rubellum*	17
3	Hum3	hummock	*Sphagnum fuscum/rubellum*	20
4	Hum4	hummock	*Sphagnum fuscum/rubellum*	15
5	Hum5	hummock	*Sphagnum fuscum/rubellum*	23
6	Hol1	hollow	Surface frozen sediment: *Microspora* sp. (Chlorophyta): (90%), *Scheuchzeria palustris* (7%), Herbaceous plants and Ericaceae roots	2
7	Hol2	hollow	Surface frozen sediment: *Microspora* sp. (Chlorophyta): (90%), Herbaceous plants (5%), *Scheuchzeria palustris*, Ericaceae roots, *Sphagnum fallax*, *Sphagnum fuscum/rubellum* and *Sphagnum magellanicum*	2
8	Hol3	hollow	Surface frozen sediment: *Microspora* sp. (Chlorophyta): (88%), Herbaceous plants (8%), *Scheuchzeria palustris*, Ericaceae roots, *Sphagnum fallax*, *Sphagnum fuscum/rubellum* and *Sphagnum magellanicum*	1
9	Hol4	hollow	Surface frozen sediment: *Microspora* sp. (Chlorophyta): (90%), Herbaceous plants (4%), *Scheuchzeria palustris*, *Eriophorum vaginatum* – spindles, Ericaceae roots, *Sphagnum fallax*, *Sphagnum fuscum/rubellum* and *Sphagnum magellanicum*	1
10	Hol5	hollow	Surface frozen sediment: *Microspora* sp. (Chlorophyta): (78%), *Scheuchzeria palustris* (6%), Ericaceae roots (6%), Herbaceous plants (5%), *Eriophorum vaginatum* – spindles, woods, *Sphagnum fallax*, *Sphagnum fuscum/rubellum* and *Sphagnum magellanicum*	1

Table 2
Radiocarbon dates from the extraction area of Hara peatland. Abbreviations: BP—before present (i.e., the year 1950 CE); Poz—Poznań Radiocarbon Laboratory.

Laboratory code-number	Depth [cm]	^{14}C date [^{14}C year BP]	Calibrated date [calibrated year BP; cal. BP] (2σ – 95.4%)	Dated material
Poz-107009	5	1965 ± 30	1990–1958 (9.7%) 1950–1824 (85.7%)	*Sphagnum* stems
Poz-106990	12	2125 ± 30	2292–2269 (7.8%) 2151–2000 (87.7%)	*Sphagnum* stems
Poz-108016	25	2240 ± 30	2339–2292 (26.1%) 2269–2151 (69.4%)	*Sphagnum* stems
Poz-107179	35	2355 ± 30	2487–2479 (1.3%) 2468–2332 (94.1%)	*Sphagnum* stems

(Fournier et al., 2015; Jassey et al., 2015; Koenig et al., 2018; Marcisz et al., 2020) based on an unpublished trait database (measured traits on the samples from the another peatland) (Jassey, Lamentowicz and Marcisz, unpublished data) and using the functional diversity and vegan packages in R program for paleo samples (Laliberté and Legendre, 2010; Oksanen, 2013). Four categories of test construction of testate amoebae (idiosomes, idiosomes + organic, protein, and xenosomes) were distinguished, as described by Mitchell et al. (2007b). High-water table indicators of testate amoebae (*Archerella flavum*, *Hyalosphenia papilio*, *Cyclopyxis arcelloides* type, and *Amphitrema wrightianum*) (Diaconu et al., 2016; Mazei and Tsyganov, 2006; Swindles et al., 2016), dry indicators (*Assulina muscorum*, *Corythion dubium*, and *Cryptodifflugia oviformis*) (Marcisz et al., 2015; Mazei and Chernyshov, 2011; Warner and Chmielewski, 1992), and an indicator of hydrological instability - *Arcella discoides* (Lamentowicz et al., 2009; Lamentowicz and Mitchell, 2005a; Łuców et al., 2020; Sullivan and Booth, 2011) were marked on the diagrams. Moreover, the average percentages of testate amoebae determined in the modern samples from hummocks and hollows are summarized in two pie charts.

2.6. Diatom analysis

To analyze the modern diatom assemblages in Hara, *Sphagnum* shoots were obtained from the upper 3 cm of the collected modern samples. For the analysis of paleo diatoms, subsamples of peat were obtained from the sediment cores. Approximately 3 cm^3 of peat was collected, and samples were taken at every 2 cm (from 1 to 2 cm until 35–36 cm), which resulted in a total of 18 subsamples. Modern *Sphagnum* samples were dried for 72 h at 45 °C. Both modern samples and samples from the peat core were treated with 33% H_2O_2 to remove organic matter, followed by which $K_2Cr_2O_7$ was added to remove all vascular plant remains and HCl to remove the carbonates. (Van der Werff, 1953). Permanent slides were mounted with Naphrax® resin (R.I. (refractive index) ≥ 1.74). Diatoms were examined at a magnification of × 1000 under an Olympus BX41 microscope (immersion oil nd = 1.518). Around 300 diatom cells were counted from each permanent slide. Identification was made to the lowest possible taxonomic level using keys and atlases (Hofmann, 2013; Krammer, 1988, 2000, 2003; Lange-Bertalot, 1999–2004, 2001, 2011).

2.7. Plant macrofossils analysis

Plant macrofossils obtained from peat monolith were analyzed in the subsamples of 2 cm^3, taken at 1-cm intervals between 0 and 5 cm, and then at 2–3 cm intervals from the depths between 8 and 37 cm. In total, 27 samples were prepared using the methods described by Birks (2007). Sediment samples were sieved through a 0.2-mm mesh under running water and were then analyzed. The macrofossils were identified based on identification guides (Grosse-Brauckmann, 1974; Mauquoy and van Geel, 2007; Tobolski, 2000) using a stereoscopic microscope at a magnification of × 200.

2.8. Pollen and non-pollen palynomorph (NPPs) analysis

A total of 11 samples (1 cm^3 in volume), were prepared using standard laboratory procedures for palynological analysis (Berglund, 1986). Samples were heated in 10% KOH to remove humic compounds and then subjected to acetolysis. One *Lycopodium* tablet (Batch 3862 containing 9666 spores per tablet; produced by the Lund University) was added to each sample for calculating the concentration of microfossils (Stockmarr, 1971). Pollen, spores, and NPPs were counted under an upright microscope until the number of total pollen sum (TPS) grains in each sample reached at least 500. The pollen grains were identified using atlases and keys (Beug, 2004; Moore et al., 1991), whereas NPPs on the basis of literature cited in Miola (2012). The percentages of pollen grains, spores, and NPPs were calculated based on the ratio of an individual taxon to the TPS (i.e., the sum of arboreal pollen and nonarboreal pollen), excluding aquatic and wetland plants including Cyperaceae, cryptogam spores, and NPPs.

2.9. Presentation of the results

All the results of the analysis of testate amoebae, diatoms, plant macrofossils, pollen, and NPPs are presented in the diagrams, which were plotted using Tilia (version 2.0.41) (Grimm, 1992), C2 (Juggins, 2003) and R programs (R version 3.5.1) (Team, 2015). Due to clear changes in the palaeoecological records of plant macrofossils and testate amoebae, and for the description of the results, we introduced individual zonation for plant macrofossils and testate amoebae based on a stratigraphically constrained cluster analysis carried out with the CONISS method (Grimm, 1987).

3. Results and interpretation

3.1. Absolute chronology, accumulation rate and peat properties

The age–depth model revealed a reliable agreement index for the model (A_{model}) equaling to 100.5% (>60% is recommended for model robustness) (Fig. 2A) (Bronk Ramsey, 2008). The results of age–depth modelling revealed that the bottom of the profile reached ca. 2420 ± 90 cal. BP. In the beginning, from ca. 2420 cal. BP (37 cm) up to ca. 2250 cal. BP (15 cm), the following quasi-stable AR_{peat} values were determined: (i) 0.05–0.1 cm yr^{-1} at ca. 2410–2310 cal. BP (37–30 cm) and (ii) 0.19–0.24 cm yr^{-1} at ca. 2310–2250 cal. BP (31–15 cm) (Table 2). A decline to 0.04–0.02 cm yr^{-1} was recorded at ca. 2250–1900 cal. BP (15–5 cm), while the lowest AR_{peat} value of 0.004–0.002 cm yr^{-1} was detected at a depth of 5–0 cm (1900–68 cal. BP). In the latter section, the highest σ error for the entire profile chronology (i.e., 250–410 calibrated years) was determined. This section probably reflects the contact of bare peat, exposed due to peat exploitation with modern deposits. The age–depth model revealed that the peat layer removed by exploitation at the coring site spanned ca. 2000 years, and also indicated that at least the topmost 5 cm should be interpreted with caution, but it most likely reflects modern times. Nonetheless, the structure of ^{14}C dates, which revealed a chronological consequence, pointed rather to the lack of vertical disturbances in the peat section of 37–4.5 cm.

The decay curve showed a little variation, with a slight decline at 32 and 24 cm (ca. 2330 and 2280 cal. BP) and a slight increase at 29, 18, and 3 cm (2330, 2260, and 1230 cal. BP; Fig. 2B). The content of water and organic matter also showed a little variation, except for the top zone (3-0 cm; 1230–68 cal. BP) where the content of organic matter was found to be decreased.

3.2. Surface samples

3.2.1. Testate amoeba analysis

A total of 14 taxa of testate amoebae were recorded in the modern samples (Fig. 3). The number of species was relatively low and similar in both the samples from hollows and hummocks—11 species were noted in hummocks and 12 in hollows. The modern samples from hummocks and hollows showed a strong dominance of one taxon, and the species composition within each of the two microforms was similar.

Hollow samples were dominated by *Arcella discoides* (57.8% of the total number of testate amoeba shells), accompanied by the species that prefer more wet conditions, including *Cyclopyxis arcelloides* type (15.6%) and *Archerella flavum* (7.2%) (Diaconu et al., 2016; Swindles et al., 2016), and others such as *Euglypha compressa* (7.9%), *Assulina muscorum* (5%), *Assulina seminulum* (0.6%), *Corythion dubium* (1.4%), *Euglypha rotunda* (1.6%), *Heleopera sphagni* (0.4%), *Nebela collaris* (2.2%), and *Heleopera sylvatica* (0.2%) (Fig. 9A). Modern samples from the hummocks tended to be dominated by *A. muscorum* (45.8%), accompanied by other species that prefer drier conditions, including *C. dubium* (13.8%) (Beyens et al., 1992) and also *A. seminulum* (8%), *E. rotunda* (10.2%), *N. collaris* (6.9%), *Euglypha compressa* (6.4%), *Trigonopyxis arcula* (4.2%), *A. discoides* (1.3%), *A. flavum* (0.8%), and *Arcella catinus* (0.6%).

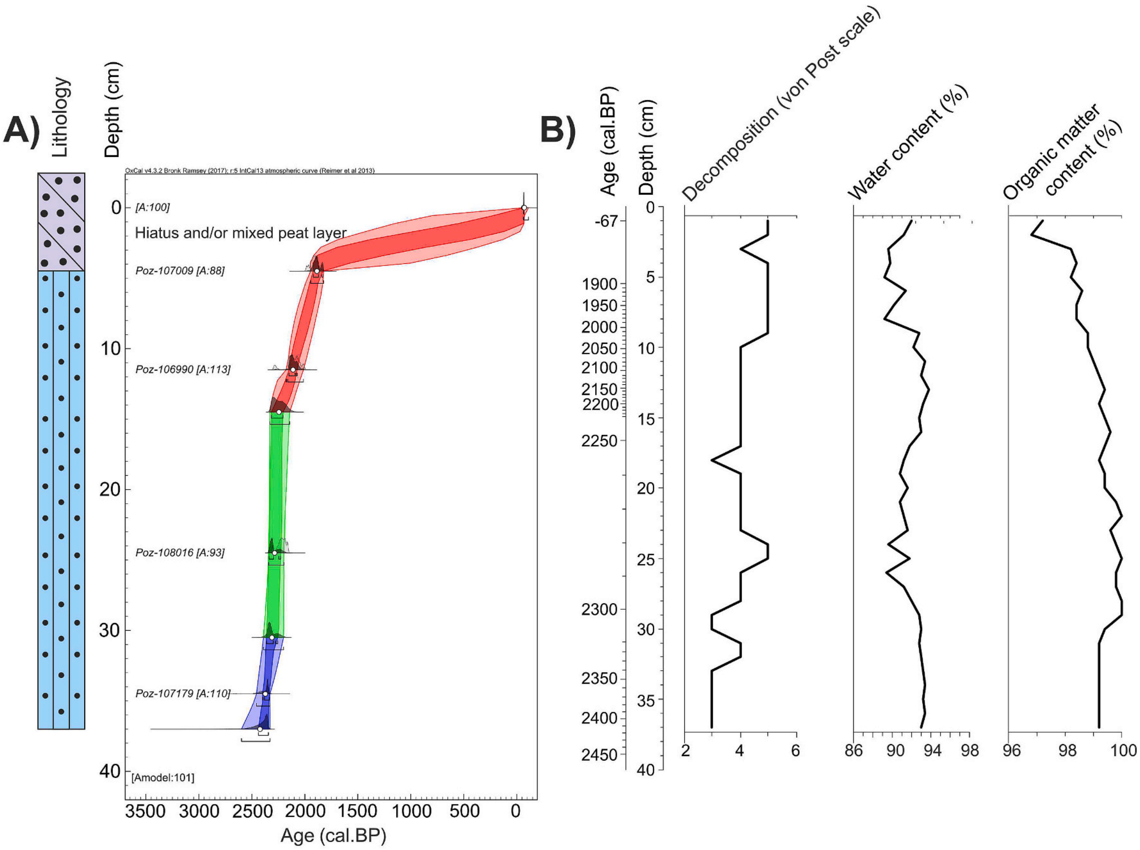

Fig. 2. A) Age–depth model of the peat monolith. B) Variations observed in the decomposition rate, water content, and organic matter content for the peat extraction area of Hara peatland.

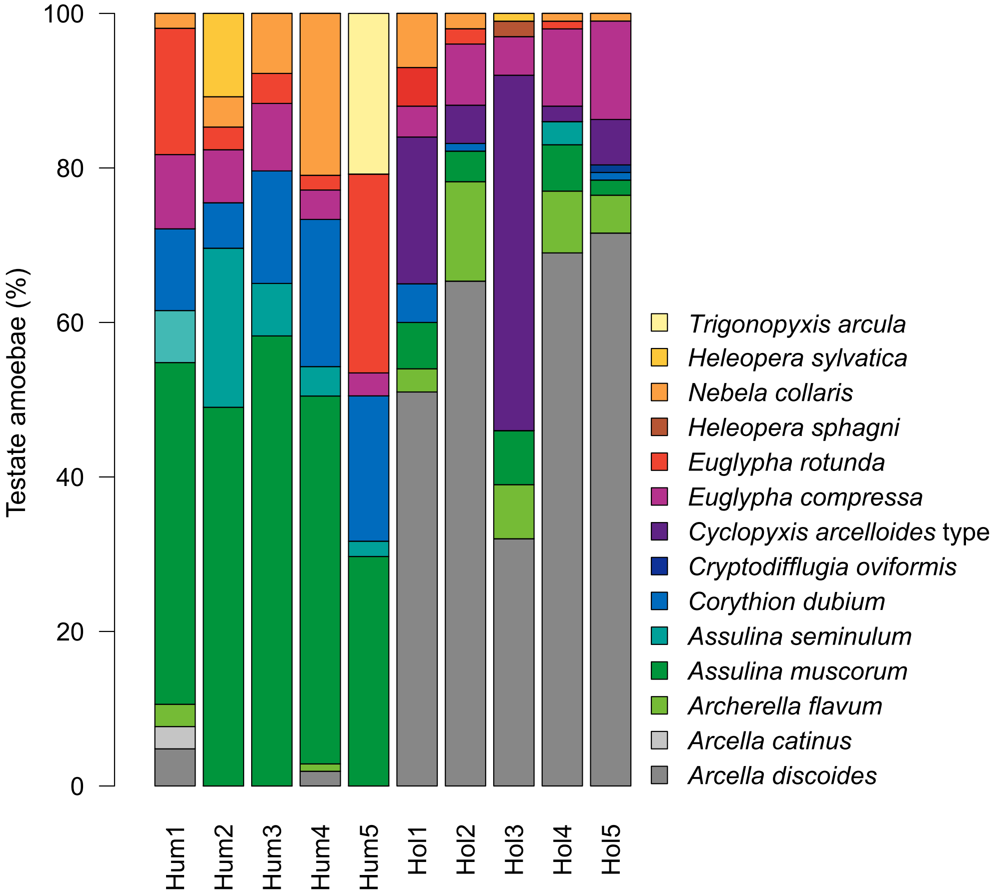

Fig. 3. Percentage of testate amoeba assemblages determined in modern samples from hummocks and hollows obtained from the excavation part of Hara peatland.

3.2.2. Diatom analysis

Comparing the results of the diatom analysis for hollows and hummocks, the distribution of diatom assemblages in modern samples was found to be more influenced by the sampling point rather than microhabitats. It is visible in Fig. 4 that the diatom composition and the abundance of *Eunotia paludosa* is more similar between sites. For example, in sampling points no. 2 and 3 both microhabitats have similar distribution of diatoms with a dominance of *E. paludosa* (98–100%). Similar disturbance pattern is also visible in sampling point no. 5, where the diatom composition differs the most from other sampling points with the lowest abundance of *E. paludosa* (86–87%). Also, in sampling point no. 5 the percentage of *Pinnularia subcapitata* is the highest of all sampling points. However, in previous studies (Chen et al., 2016; Küttim et al., 2017a) have found that the distribution of diatom assemblages in bogs is more connected to the microhabitats along the hummocks-hollow gradient.

Even though the diatom assemblages in modern samples were found to be more influenced by the sampling point rather than microhabitats, the number of different diatom species was low in the modern samples from Hara peatland. Although the investigated diatom assemblage was found to be characteristic of bogs, species richness was generally much higher in pristine bogs. The most common diatom species belonged to the genera *Eunotia*, *Pinnularia*, and *Kobayasiella*, which are commonly found in the bog environment (Cantonati and Lange-Bertalot, 2011; Küttim et al., 2017b; Poulíčková et al., 2013). The species *Hantzschia amphioxys* prefers drier habitats and therefore is more common in hummocks where the pH is higher (Chen et al., 2016). It is also considered a pioneer species in peatlands and is typically found in these

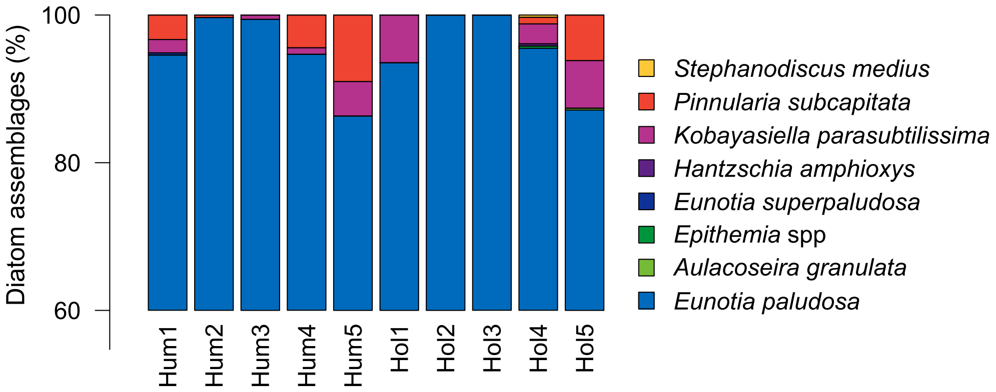

Fig. 4. Percentage of diatom assemblages determined in modern single samples from hummocks and hollows obtained from the excavation part of Hara peatland.

sites where environmental changes continuously take place and so diatom assemblages do not fully develop (Rühland et al., 2000).

3.3. *Peat monolith*

3.3.1. *Testate amoeba analysis*

A total of 25 testate amoeba taxa were recorded in the peat monolith. The monolith was characterized by dominant proteinaceous tests, low species diversity, and strong dominance of two species (*A. flavum* and *A. discoides)* (Fig. 5). Moreover, the clear changes in the peat monolith indicated three zones (A–C).

The dominant species in zone A (37–10 cm, ca. 2410–2060 cal. BP) was *A. flavum* (mixotrophic testate amoeba) which represented on average 70% (57–88%) of the total community. The high relative abundance of this species indicated wet and stable conditions at the Hara peatland between ca. 2420 and 2040 cal. BP (Sullivan and Booth, 2011; Swindles et al., 2016). The rest of the testate amoeba community was constituted mainly by *Hyalospenia papilio* (mixotrophic indicator of wet habitats) (Lamentowicz et al., 2010), *A. muscorum*, and *A. seminulum* (both are indicators of dry habitats) (Warner and Chmielewski, 1992), with percentages ranging from 0% to 9%, 1%–23.5%, and 0%–13.5%, respectively. The large abundance of species that prefer drier conditions, as well as the dominance of *A. flavum*, may indicate short-term environmental variability (Sullivan and Booth, 2011). The Shannon diversity of the testate amoeba communities was the lowest in the whole peat monolith, varying between 0.8 and 1.3. The testate amoebae – based reconstruction showed that the water table was stable and oscillated between 5 and 8.9 cm, while the pH ranged from 4 to 5.5.

An important change in the testate amoeba communities was observed in zone B (10–5 cm, ca. 2260–1900 cal. BP) (Fig. 5), where we recorded a decline in the relative abundance of *A. flavum* to 38.5%, an increase in the abundance of *A. discoides* to 11% (indicator of hydrological instability (Lamentowicz and Mitchell, 2005a; Sullivan and Booth, 2011) and a large relative abundance of *A. muscorum* (12–20%) and *C. dubium* (4.6–8.8%) (both are dry habitat indicators) (Beyens et al., 1992), accompanied by *C. arcelloides* type and *E. compressa glabra*. Moreover*, H. papilio* was not found and *A. seminulum* was found to be decreased in this zone. The contribution of proteinaceous testate amoebae was low, whereas the diversity of xenosomic and idiosomic testate amoebae was increased (1.4–2). Water table was decreased slightly (6.8–11.5 cm), while the pH oscillated between 4.2 and 4.5. All the described changes in the community of testate amoebae can indicate the change in hydrological dynamics.

In the top layer (zone C, 5–0 cm, modern times), *A. discoides* was found to be dominant (Fig. 5), accounting for an average of 73.5% of the total community at a depth from 1 to 2 cm. *A. flavum* decreased to a few per cents. The rest of the testate amoeba community was mainly constituted by *A. muscorum*, *C. dubium*, *C. arcelloides* type, and *E. compressa glabra*. The contribution of proteinaceous testate amoebae was increased, while the Shannon diversity of the communities was decreased to 1. The reconstruction of the water table depth based on testate amoebae indicated an increase in the water level from 8.7 to 2 cm in this zone; however, the peatland most likely experienced fluctuations in the water table (intermittent flooding), as was indicated by the dominance of *A. discoides* (Lamentowicz et al., 2009) (Fig. 9). The pH of this zone oscillated between 3.9 and 4.4.

3.3.2. *Diatom analysis*

Diatom assemblages in the peat monolith showed higher species richness than the assemblages from the modern samples (Fig. 6). A total of 56 different diatom species, belonging to 25 genera, were identified in the monolith. Among the identified genera, the most abundant were *Eunotia* (13 species), followed by *Pinnularia* (8), *Aulacoseira* (3), *Fragilaria* (3), *Hantzschia* (3), and *Nitzschia* (3). In all the analyzed layers, *E. paludosa* was found to be dominant (93%), followed by *Eunotia nymanniana* (3%), *Aulacoseira granulata* (1%), and *Eunotia bilunaris* (1%). The remaining 52 diatom species were present in a very low count, accounting altogether for only 1%. The diatoms were well preserved in the peat, however, only in the layer between 29 and 27 cm (ca. 2300 cal. BP), the diatom preservation was poor and the counts did not reach to the minimum of 300 specimens. The genus *Eunotia* represents a very large proportion of the diatom assemblages of Hara peatland. Throughout the peat monolith, *E. paludosa* was dominant, accounting for approximately 60–99% of the diatoms.

In the layer at 33 cm (ca. 2350 cal. BP), a major shift was noted in diatom assemblage, where the number of *E. paludosa* was decreased to 63.8% and *E. nymanniana* was increased (28.9%). An increase in *Eunotia neocompacta* (4.7%) was also recorded. The layer 31–19 cm (ca. 2320–2260 cal. BP) did not show any remarkable changes. The dominant species was *E. paludosa*, and no major shifts were observed in the diatom assemblage. At the depth from 29 to 27 cm (ca. 2300 cal. BP), the diatom preservation was poor.

In the layer 17–13 cm (ca. 2250–2180 cal. BP), the percentage of *E. paludosa* was decreased to values between 81.9% and 63.8%. The

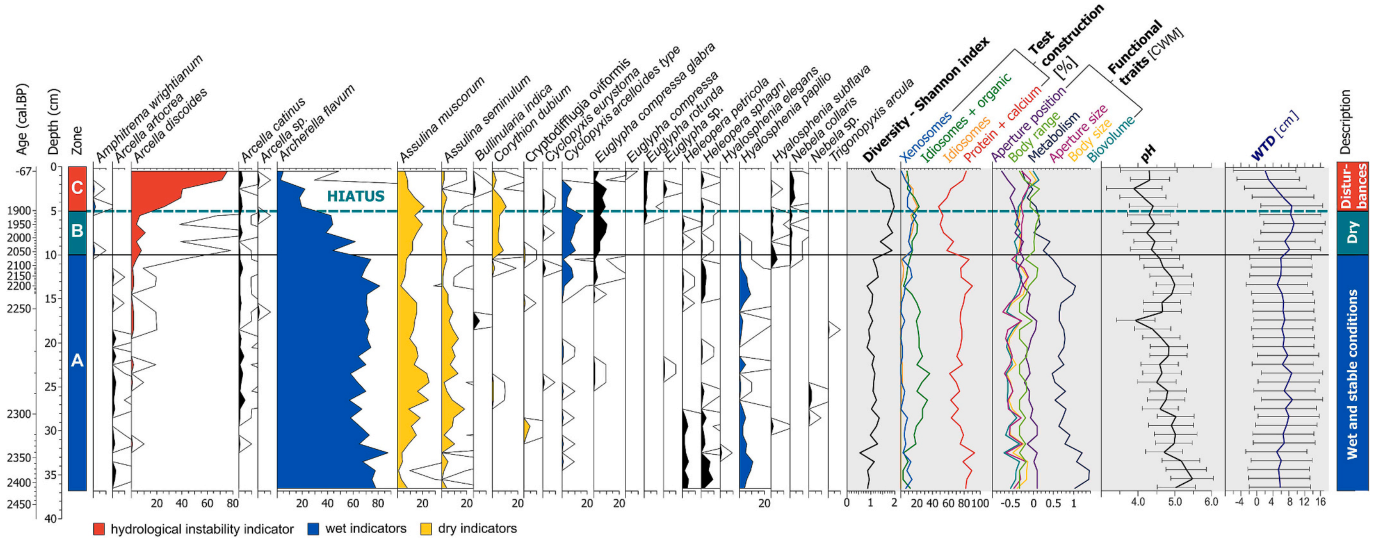

Fig. 5. Percentage testate amoeba diagram with 10 times exaggeration (presented as black lines) and values (CWM - community-weighted means of species traits) of the functional traits of the testate amoeba communities calculated from the extraction area of Hara peatland.

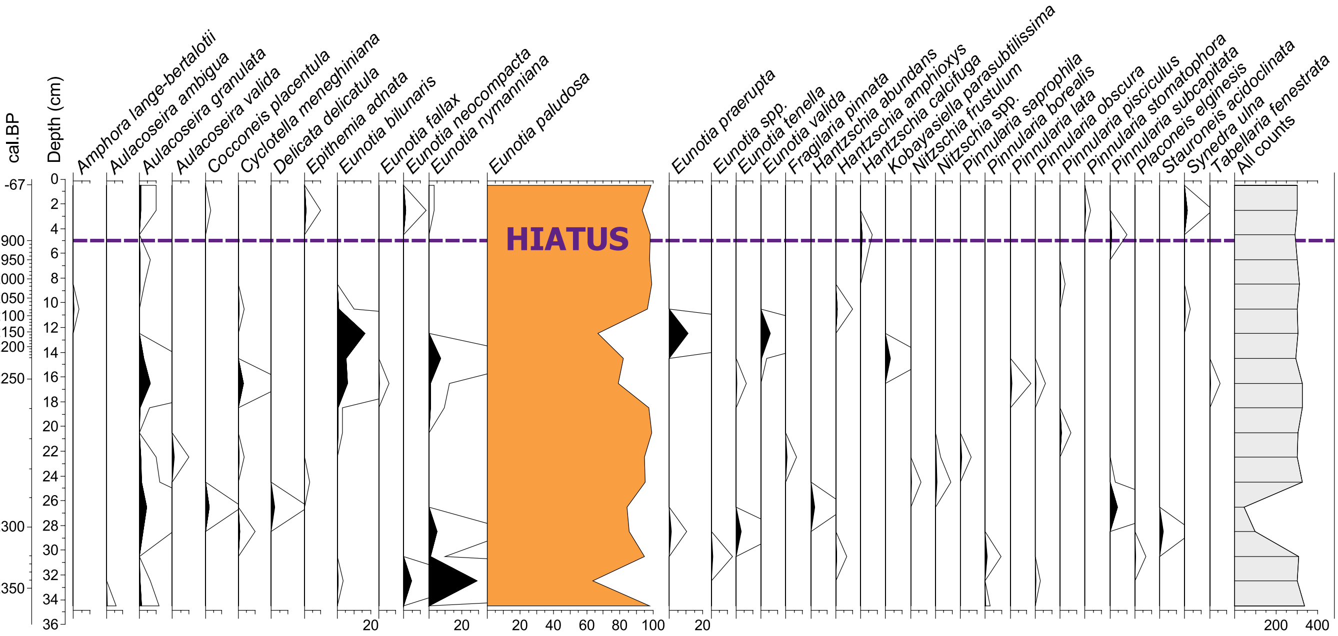

Fig. 6. Simplified percentage diatom diagram for the exploitation part of Hara peatland, with 10 times exaggeration (presented as black lines).

diatom assemblage was more species-rich, with *E. bilunaris*, *E. nymanniana*, *E. praerupta*, and other *Eunotia* species. Furthermore, at a depth of 17 cm (ca. 2250 cal. BP), *A. granulata* was slightly increased to 6.7%. These changes might indicate that the environment was wetter and pH was higher. The species *E. bilunaris* and *E. nymanniana* prefer wetter conditions with a higher pH in comparison to *E. paludosa (*Lange-Bertalot et al., 2003*)*.

Diatom assemblage was quite homogeneous with no remarkable changes noted in the upper part of the peat monolith (11–1 cm; ca. 2090–370 cal. BP), where a change in testate amoeba assemblage was recorded indicating a shift from pristine mire to peat mine state. The stable diatom assemblage, dominated by *E. paludosa* (93.3–99.4%), showed that the site was characterized by rather harsh conditions, with high acidity and relatively unfavorable conditions for diatoms. Moreover, the diatom assemblage consisted of a low number of different species.

3.3.3. *Plant macrofossils analysis*

The results of the plant macrofossils analysis, shown in Fig. 7, suggested four zones (A–D). The dominant species in zone A (37–31 cm, ca.

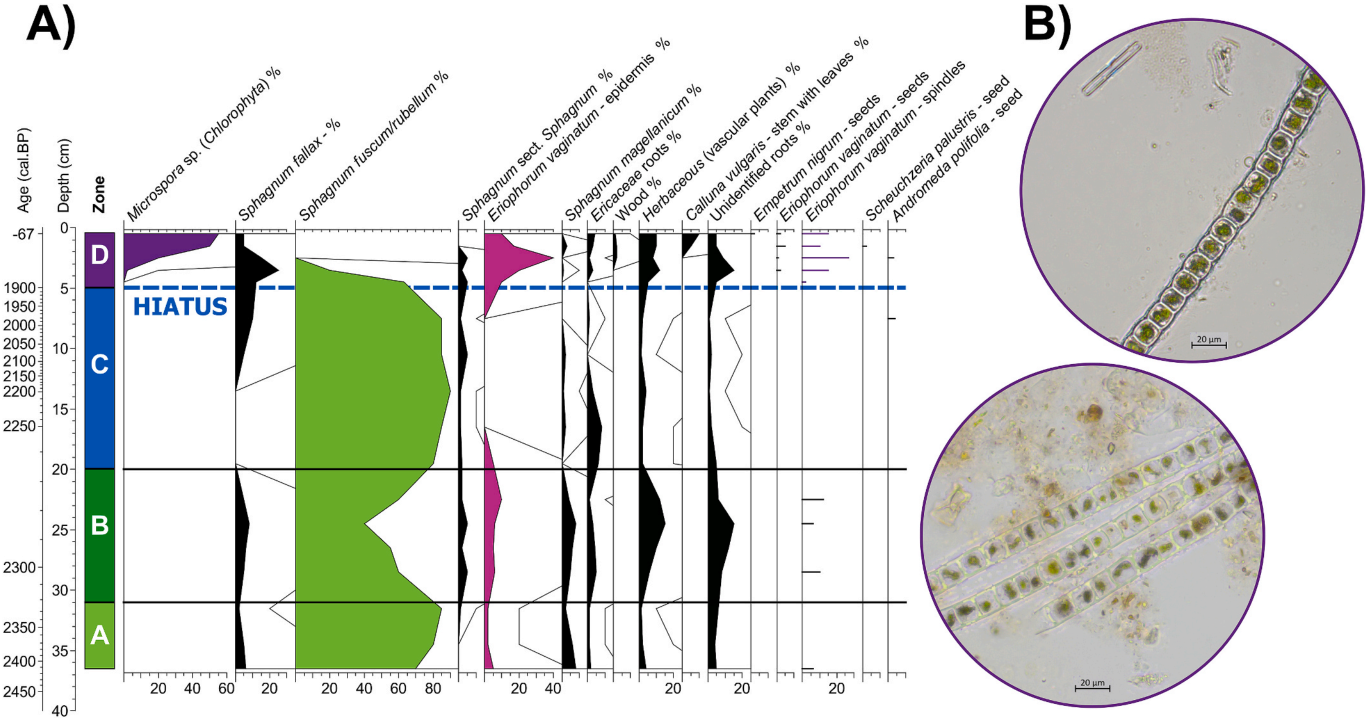

Fig. 7. A) Percentage plant macrofossil diagram for the exploitation part of Hara peatland with 10 times exaggeration (presented as black lines). B) Photographs of *Microspora* sp. (Chlorophyta) from the top of the profile.

2410–2320 cal. BP) was a hummock species, *Sphagnum fuscum/rubellum* (McCarter and Price, 2014), with a percentage ranging from 70% to 85% of the total plant macrofossils. The rest was composed mainly of *Sphagnum fallax*, *Eriophorum vaginatum* (epidermis), *Sphagnum magellanicum*, Ericaceae roots, herbaceous plants*,* and unidentified roots.

In zone B (31–20 cm, ca. 2320–2265 cal. BP), the percentage of *S. fuscum/rubellum* was decreased to 40%, whereas the abundance of *S. fallax*, *E. vaginatum* (epidermis), *S. magellanicum*, Ericaceae roots, herbaceous plants, roots, and *Sphagnum* sect. *Sphagnum* was increased to 8%, 10%, 8%, 5%, 15%, 15%, and 5%, respectively.

In zone C (20–5 cm, ca. 2265–1900 cal. BP), the percentage of *S. fuscum/rubellum* was increased to 80–90%, whereas the share of herbaceous plants and unidentified roots was decreased, compared to the previous zone. These changes in the total plant macrofossil count seemed to indicate an increase in wetness of conditions in surface peat. Between 2265 and 2100 cal. BP, an increase was observed in the share of Ericaceae roots, whereas *E. vaginatum* was absent between ca. 2050 and 1990 cal. BP and *S. fallax* between ca. 2265 and 2220 cal. BP. The species *S. magellanicum* and *Sphagnum* sect. *Sphagnum* were also present in this zone.

The D zone (5–0 cm, modern times) was characterized by a sharp decrease in the dominant *S. fuscum/rubellum* and an increase in the share of vascular plants. Herbaceous plants, roots, wood, and shrubs were increased to 12%, 15%, 2%, and 4%, respectively. The species *E. vaginatum* was increased to 40%, and the presence of its seeds and spindles in this zone indicated fluctuations in the water table (Słowiński et al., 2016), similar to the monitoring data for the exploited part of the peatland (Fig. 4B, Supplementary Figure 1). This zone was dominated by the filamentous green algae, *Microspora* sp. (Chlorophyta), which is found in acidic waters (Biggs and Kilroy, 2000; Foster, 1982; John, 2003). Its percentages varied from approximately 0%–50% of the total plant macrofossil count. A peak percentage of *S. fallax* (to 25%) was noted at a depth of 3.5 cm. Other species of *Sphagnum* moss, including *S. magellanicum* and *Sphagnum* sect. *Sphagnum,* were also present but were not abundant. At the top of this zone (2–0 cm), stems with leaves of *Calluna vulgaris* were observed. Due to the proximity of the coring site to the edge of the extraction area, the macrofossils of *C. vulgaris* might have come from the nonexploited part of the Hara peatland.

3.3.4. Pollen and non-pollen palynomorphs (NPPs) analysis

Domination of *Pinus sylvestris* (*P. sylvestris type*: 16–50%), *Betula* (23–39%), and *Picea abies* (6–24%) indicates the presence of hemiboreal forest (Fig. 8). Additional components were *Corylus avellana* (1–6%), probably *Quercus* (0.7–2.5%) and *Tilia cordata* (0–1.2%) (Fig. 8). Alder (*Alnus glutinosa* type, 11–25%) grew probably in inundated depressions and on the outskirts of the peatland. About 2080 cal. BP (10.5 cm), *P. sylvestris* expanded, probably contributing to the retreat of *P. abies*. The pollen taxa included in the TPS did not show any significant changes, which would be indicative of hiatus in the peat monolith at ca. 5 cm.

Wetland sporomorphs revealed three stages of bog development in the coring spot area: (i) at ca. 2420–2310 cal. BP (37–30.5 cm) with distinct optima of *Sphagnum* spores (2–111%) and Ericales pollen (*Vaccinium* group, 8.8–14.5%), indicating more shrubby vegetation (drier conditions); (ii) at ca. 2310–2240 cal. BP (30.5–14.5 cm) when the abundance of *Sphagnum* decreased and Ericales pollen became more frequent (more *Ledum* type); and (iii) at ca. 2240–1880 cal. BP (14.5–4.5 cm) when *Sphagnum* spores became more frequent with a probable decline in *Vaccinium* group (0.7–2%). In the case of pollen and spores characteristic of oligotrophic conditions, no substantial difference was noted between the pollen spectrum from the surface of the peatland and the depth of 4.5 cm (ca. 1880 cal. BP).

The most pronounced change in NPP was detected in the layer corresponding to ca. 2240 cal. BP (14.5 cm), with a distinct change in assemblages, marked by a decrease in the percentages of HdV-22, HdV-23, HdV-63 A *Lasiosphaeria caudata* and HdV-83. During ca. 2310–2260 cal. BP, an increased percentage of HdV-368 coprophilous fungi was noted indicating the possible presence of herbivores/omnivores in the coring area (Baker et al., 2013). This might have been a result of relatively dry conditions, as suggested by the simultaneous stable presence of fungal NPP HdV-3A (van Geel, 1978). Moreover, a high percentage of HdV-90, until ca. 2260 cal. BP, may be related to rather dry conditions (Lamentowicz and Mitchell, 2005a). From ca. 2240 cal. BP to the top of the profile, the fungal NPPs HdV-10, HdV-27 *Tilletia sphagni*, and HdV-30 *Helicoon pluriseptatum* were more frequent. HdV-10 is associated with Ericaceae roots, mainly *C. vulgaris*, which points to the *in situ* occurrence of this dwarf shrub. On the other hand, the occurrence of *T. sphagni* indicates the presence of sporulating *Sphagnum*. This set of NPPs suggests the relatively dry (hummock) conditions. The constant presence of HdV-35 and HdV-74 in the topmost section (from ca. 2080 cal. BP) indicates the possibility of at least seasonal/temporal inundations of peatland (van Geel, 1978). On the other hand, it might indicate the increase in the water table after the introduction of restoration procedures. The topmost sections of peat, which are better

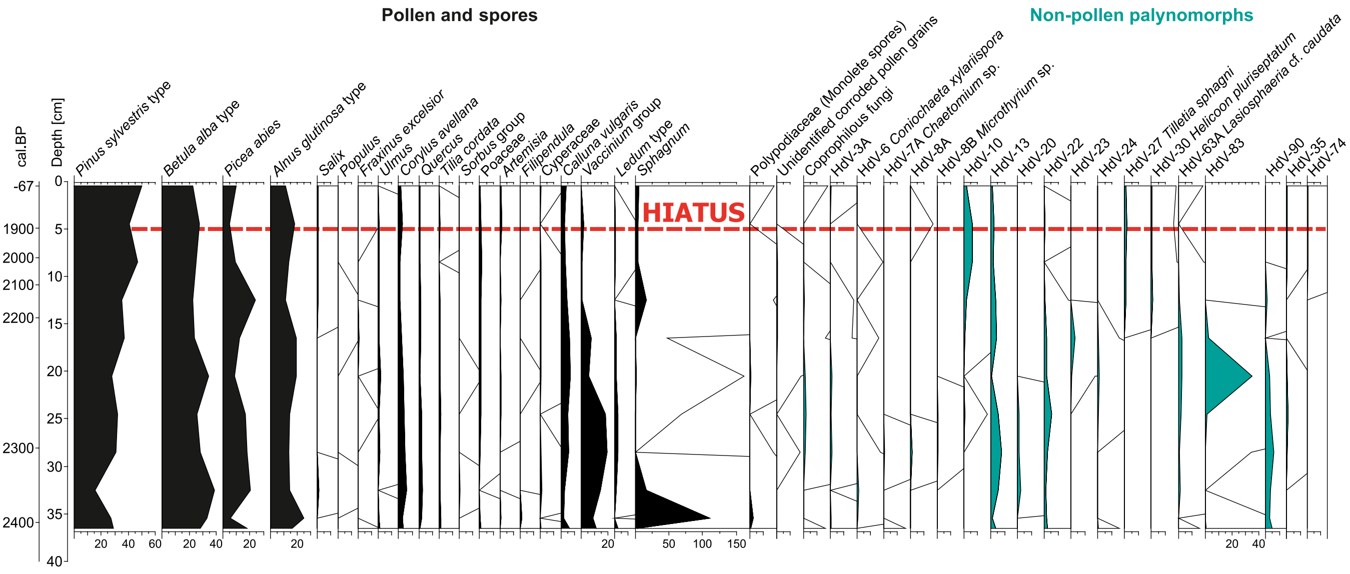

Fig. 8. Pollen and nonpollen palynomorph percentage diagram for the excavation part of Hara peatland with 10 times exaggeration (presented as black lines).

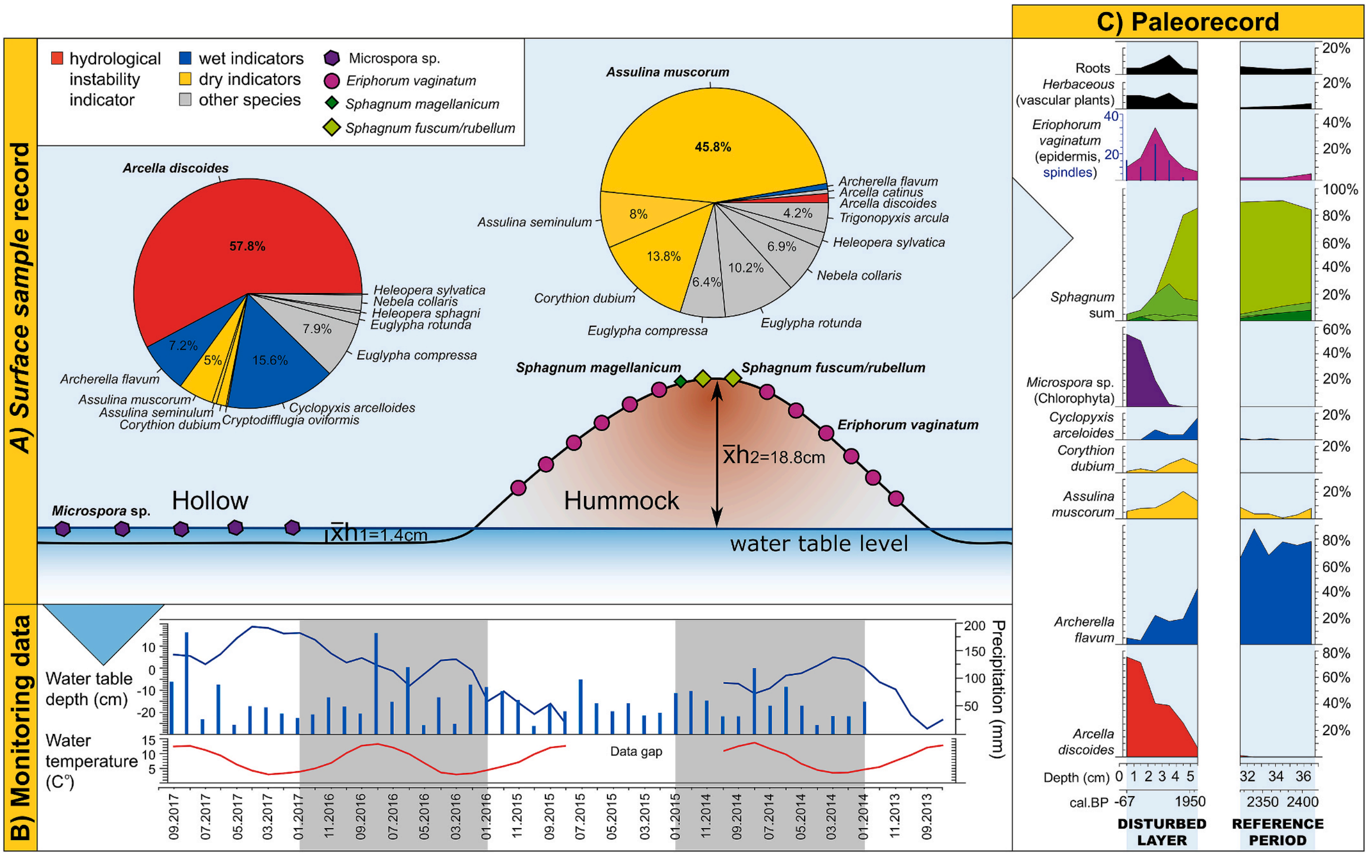

Fig. 9. A) Percentage chart of testate amoebae from modern hummock and hollow samples. B) The average monthly water temperature and water table depth of the exploited part of Hara peatland (data for the closest measuring point: hara02), with the annual sum of precipitation for Tallinn-Harku (Estonian Weather Service, 2020). C) Summary of the palaeoecological data (testate amoebae and plant macrofossils) with the reference state for peat extraction.

hydrated and softer, were more prone to be penetrated by modern aquatic organisms.

4. Discussion

4.1. Ecological baselines

The recent ecological baselines (closer in time than 2420 cal. BP) are not possible to be recognised in the analyzed core. However, this deep temporal horizon provided us with a picture of the stable ecohydrological conditions that were present in many Baltic bogs until the 200 years ago (Swindles et al., 2019). Our data show how the peatland dramatically shifted from the baseline into degraded conditions. However, it was recently recognised that even small ground water changes are affecting the peatland ecosystem in terms of vegetation structure, microbial communities and carbon fluxes (Jassey et al., 2018). Water table overrides all other ecosystem- and management-related controls on greenhouse gas fluxes (Evans et al., 2021; Jurasinski et al., 2016; Tanneberger et al., 2021). Therefore the restoration effort should be focused on the target water table that was also recognised in the palaeoecological records (Lamentowicz et al., 2019) in the context of climate change to achieve key EU sustainability objectives. Hence, we need the data from the past to better understand the potential of ecological restoration of peatlands including pristine baselines (Andersen et al., 2004).

The Hara bog record represents an industrially exploited peatland and revealed three phases in the history of peatland: 1) pristine bog, probably at a fairly early stage of its development, 2) hiatus as a result of peat of exploitation and 3) probably modern peat as a result of restoration (Figs. 3, 5 and 7). Our record begins at ca. 2420 cal. BP, when the pristine peatland ecosystem was surrounded by a hemi-boreal forest (Fig. 8). The pollen data showed the dominance of pine and birch with a high abundance of spruce and alder, which is similar to the results reported by other studies from Estonia (Niinemets and Saarse, 2006; Poska and Saarse, 1999, 2002). The analysis of plant macrofossils and testate amoebae suggested that the extraction area of Hara peatland was a wet ombrotrophic bog dominated by *S. fuscum/rubellum* (Figs. 5, 7 and 9C). The wet and stable baseline phase, with the dominance of mixotrophic testate amoebae possessing organic shell—*A. flavum* between ca. 2420 and 1900 cal. BP (Fig. 5), agrees with the record of testate amoebae from Männikjärve bog (eastern Estonia) presented by Väliranta et al. (2012). In both studies, the possible changes in moisture conditions were reconstructed using analyses of testate amoebae and plant macrofossils.

Similar to Männikjärve bog, which is located 100 km away from the southeast of Hara peatland (Väliranta et al., 2012), the results of both proxies showed different patterns of hydrological conditions. In the case of our reconstruction, the period indicated by the plant macrofossil record as drier than the average conditions (Fig. 7) and by the testate amoeba record as wetter than the average conditions (Fig. 5) was shorter and occurred between ca. 2380 and 2330 cal. BP. Väliranta et al. (2012) provided several reasons for this incoherent episode (ca. 2500 and 1750 cal. BP).

From the multiproxy studies (Figs. 5–8), we could not find another stressor that could have affected the peatland ecosystem between ca. 2420 and 1900 cal. BP. Hence, we can interpret this stage (without considering the unexplained and inconsistent episode between ca. 2380 and 2330 cal. BP) as pristine and an ecological baseline (reference period) (Fig. 9C) that might be a potential target for ecological restoration (Farrell and Doyle, 2003; Froyd and Willis, 2008; Natlandsmyr and Hjelle, 2016). However, we can also state that this target is difficult to be reached.

4.2. Degradation

Our research documented a dramatic event in the peatland ecosystem—the top part of the peatland was completely degraded due to peat cutting, and as a consequence, the peat record for the last ca. 1900 years is missing (Fig. 2). Subsequently, analyses of testate amoebae and plant macrofossils indicated changes related to rewetting (Figs. 5, 7 and 9C). Changes recorded in the testate amoeba community of the exploited part of the Hara peatland agreed well with those in plant macrofossils than the changes noted in other proxies (diatoms and pollen).

We explored the testate amoeba communities from modern hummock and hollow samples and compared them with the average monthly water temperature, water table depth, an annual sum of precipitation, and current paleorecord, as well as with the reference period for the excavation part of Hara peatland (Fig. 9). The presence of *E. vaginatum* on the surface of the old peat surface (Fig. 1D) indicated significant fluctuations in the water level (Sullivan and Booth, 2011; Tobolski, 2003), similar to the monitoring data for the exploited part of the peatland (Fig. 9B, Supplementary Fig. 1) which showed dynamic changes in the water table between 2013 and 2017 (Fig. 9B) influencing the communities of testate amoebae and plant macrofossils (Figs. 3, 5 and 7).

Restoration efforts made on the Hara peatland caused high hydrological variability. Water level fluctuations between −90 and + 30 cm, contributing to the development of *E. vaginatum* hummocks, were recently noticed in the plant macrofossils and presently on the composition of the mire surface (Mauquoy et al., 2010). Moreover, Rober et al. (2012) suggested that an increase in the abundance of filamentous green algae, including *Microspora* sp., may result from the increasing frequency of drying and rewetting events on wetlands due to climate change, or frequent fluctuations in the water table in shallow ecosystems. Therefore, the presence of *Microspora* sp. mats in the top zone of the peat monolith may also be associated with inundation and eutrophication. We assume that the development of this alga, as a potential food source, might affect the composition of testate amoebae and be linked with the increase in *A. discoides*, which is a pioneer species that immigrated to the inundated bare peat surface (Figs. 5 and 8). This monospecific testate amoeba community was the most abundantly found in the top part of the bog profile (similar to the pattern of *Microspora* sp.) (zone C, Fig. 5), and it can be related to intermittent flooding and drying of the exploited peat surface (Lamentowicz et al., 2009). We have shown in a previous study that dynamic changes occurring in the water table are the primary environmental influencing factor of the composition of testate amoebae and algae (Kołaczek et al., 2020; Lamentowicz and Mitchell, 2005a; Łuców et al., 2020; Sullivan and Booth, 2011). This study also validates our former assumption that this species is an early immigrant to not stable, novel habitats such as those recorded in *Sphagnum–E. vaginatum*-dominant (intermittently inundated) peatland laggs in Tuchola pine forest in northern Poland (Lamentowicz and Mitchell, 2005b). Attention should be also paid also to *C. arcelloides* type (Fig. 5). This species has been recorded from dry (Booth, 2007) to wet (Diaconu et al., 2016) conditions in the previous research. However, in our study, it was noted only in samples from the hollows (Fig. 3); therefore, in our study, we considered this species as an indicator of wet conditions (Fig. 8).

The diatom assemblages in Hara peatland correlates better with changes in pollen data compared to testate amoeba data. There are mostly diatoms typical of bogs, but their assemblages in modern *Sphagnum* samples from Hara were species-poor compared to the diatom assemblages found in the peat monolith (Figs. 4 and 6). All sampling points were dominated by *E. paludosa*, a characteristic species of the bog environment (Chen et al., 2012; Hargan et al., 2015; Küttim et al., 2017a). Since the typical vascular plant community is not fully recovered, it is understandable that such diatom composition (e.g., *A. granulata* and *H. amphioxys*) is characteristic of the still-developing/changing bog environment (Brugam and Swain, 2000; Chen et al., 2012).

The top recovery phase of the peat monolith (5–0 cm) was found to be a very dynamic environment (Fig. 2A). We cannot rule out the decomposition of bare peat surface under oxygenated conditions (Rydin and Jeglum, 2006) and/or mixing of the sediments in the past (due to exploitation) or at present (through restoration). However, the modern record of testate amoebae (Fig. 9A) and modern vegetation (i.e. the presence of the same species/domination of the same species in modern samples and modern sediment of peat core) probably partially support the palaeoecological record. In particular, the *in situ* presence of the spindles of *E. vaginatum* in the paleo record points to the modern record at a depth of 5–0 cm (Mauquoy et al., 2010).

4.3. Restoration

Since industrial exploitation leads to the loss of peat (and carbon store) along with local species pool (Table 1 and Figs. 7 and 9) the disturbance is so dramatic that makes the restoration of a raised bog vegetation a complex and time-consuming process (Chapman et al., 2003b). From a long-term perspective, we tried to assess the progress of the restoration process in the extraction area of Hara peatland, which is still in an initial phase (Figs. 3–7 and 9). The baseline/pristine *S. fuscum/rubellum* community that dominated during ca. 2000 cal. BP in the peat record (Fig. 9C) might be a good target for the final stage of restoration. This is mainly due to the fact *S. fuscum* is a typical species of Baltic bogs in the past (Lamentowicz et al., 2009). Moreover, *S. fuscum* is recommended for restoration in sites that have a water table depth exceeding approximately 20 cm below the surface as well as in drier sites (Karofeld et al., 2020). However, it is pointed out that an average water table depth should be higher than 20 cm in restoration sites (Karofeld et al., 2020), which contributes to the better development of *Sphagnum* mosses. Nevertheless, the baseline hydrology (former vegetation structure with a water table depth of approximately 10–12 cm) (Evans et al., 2021; Lamentowicz et al., 2019) might never be reached, and the most important aim is to trigger the peat accumulation process. At present, European peatlands are drier than they were in previous centuries (Swindles et al., 2019), and thus, their restoration is challenging. The amount and frequency of rainfall will have a large impact on the further regeneration of the ecosystem due to the sensitivity of ombrotrophic peatlands to climate change (Charman, 2002; Rydin and Jeglum, 2006). However, a promising indicator of restoration might be the fact that mixotrophs have already arrived at the community of testate amoebae (Fig. 9A). We state that the restoration target – a healthy raised bog should consist of mixotrophic testate amoeba such as *A. flavum* that are good indicators of well-functioning *Sphagnum* peatland (Jassey et al., 2015; Marcisz et al., 2020) ecosystem state even if the *Sphagnum* species is different than in the baseline. Palaeoecological assessment of the peatland restoration using the multiproxy approach is very rare.

Palaeoecological assessment of the peatland restoration using the multiproxy approach is not a common approach. Such studies have consisted significant limitations to studying post-restoration sites using proxy methods, especially using stratigraphic methods (hiatuses, mixing, differential preservation/oxidation), whereas surface sampling and monitoring are more feasible and likely to yield more informative results. Despite those limitations, we think that a combination of the palaeo approach with monitoring is a key to evaluate the restoration progress.

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Data availability

Łuców, Dominika (2021), "Łuców, D., Küttim, M., Słowiński, M., Kołaczek, P., Karpińska-Kołaczek, M., Küttim, L., Salme, M., & Lamentowicz, M. (2021). Searching for an ecological baseline: Long-term ecology of a post-extraction restored bog in Northern Estonia. QI 10.1016.", Mendeley Data, V1, doi: 10.17632/f9rw5x58zs.1.

CRediT authorship contribution statement

Dominika Łuców: Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Martin Küttim:** Conceptualization, Investigation, Data curation, Writing – original draft, Project administration. **Michał Słowiński:** Conceptualization, Investigation, Data curation, Writing – original draft, Project administration. **Piotr Kołaczek:** Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Monika Karpińska-Kołaczek:** Investigation, Data curation, Writing – original draft. **Liisa Küttim:** Investigation, Data curation, Writing – original draft. **Meryt Salme:** Investigation, Data curation. **Mariusz Lamentowicz:** Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Project administration.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2021.08.017.

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was as follows:

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Declaration of contribution to an article published in Frontiers in Ecology and Evolution

Hereby I confirm that my contribution to the article:

> Łuców, D., Lamentowicz, M., Słowiński, M., **Kołaczek, P.,** Łokas, E., Marcisz, K., Obremska, M., Theuerkauf, M., Tyszkowski, S., and Słowiński, M. (2021). Pine forest management and disturbance in Northern Poland: combining high-resolution 100-year-old paleoecological and remote sensing data, Frontiers in Ecology and Evolution, 9:747976, doi 10.3389/fevo.2021.747976

was as follows: I contributed to the **pollen analysis and interpretation of data and writing the manuscript.**

With kind regards,

Piotr Kołaczek

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> Łuców, D., Lamentowicz, M., Kołaczek, P., **Łokas, E.,** Marcisz, K., Obremska, M., Theuerkauf, M., Tyszkowski, S., and Słowiński, M. (2021). Pine forest management and disturbance in Northern Poland: combining high-resolution 100-year-old paleoecological and remote sensing data, Frontiers in Ecology and Evolution, 9:747976, doi 10.3389/fevo.2021.747976

was as follows: I contributed to **the analysis and interpretation of data and writing the manuscript.**

With kind regards,

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was as follows: I contributed to **the collecting peat core in the field, the interpretation of data and writing the manuscript.**

With kind regards,

Katarzyna Marcisz

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With kind regards,

Milena Obremska

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was as follows: I contributed to **the analysis and interpretation of data and writing the manuscript.**

With kind regards,

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was as follows: I contributed to the analysis and interpretation of data, graphic processing of the results and writing the manuscript.

With kind regards,

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was as follows: I contributed to **the conceptualization, collecting peat core in the field, laboratory preparation of samples, analysis and interpretation of data, graphic processing of the results, and writing the first draft of the manuscript. I was the PI of the TORNADO project.**

With kind regards,

Słowiński Michał

Michał Słowiński

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Łuców, D., Lamentowicz, M., Obremska, M., Arkhipova, M., Kittel, P., Łokas, E., Mazurkevich, A., Mróz, T., Tjallingii, R., and Słowiński, M. (2020). Disturbance and resilience of a *Sphagnum* peatland in western Russia (Western Dvina Lakeland) during the last 300 years: a multiproxy, high-resolution study. The Holocene, 30 (11), 1552-1566, doi.org/10.1177/0959683620941064

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was as follows:

- Laboratory preparation of samples,
- Testate amoebae and macro charcoal analysis of samples,
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With kind regards,

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With kind regards,

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was as follows: I contributed to **the interpretation of data and writing the manuscript.**

With kind regards,

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was as follows: I contributed to **the analysis and interpretation of data and writing the manuscript.**

With kind regards,

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was as follows: I contributed to **the interpretation of data and writing the manuscript.**

With kind regards,

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> Łuców, D., Lamentowicz, M., Obremska, M., Arkhipova, M., Kittel, P., Łokas, E., Mazurkevich, A., **Mróz, T.,** Tjallingii, R., and Słowiński, M. (2020). Disturbance and resilience of a Sphagnum peatland in western Russia (Western Dvina Lakeland) during the last 300 years: a multiproxy, high-resolution study. The Holocene, 30 (11), 1552-1566, doi.org/10.1177/0959683620941064

was as follows: I contributed to **the analysis.**

With kind regards,

Tomasz Mróz

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was as follows: I contributed to **the interpretation of data and writing the manuscript.**

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was as follows: I contributed to **the conceptualization, collecting peat core in the field, laboratory preparation of samples, analysis and interpretation of data** and **writing the manuscript.**

With kind regards,

Michał Słowiński

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Łuców, D., Küttim, M., Słowiński, M., Kołaczek, P., Karpińska-Kołaczek, M., Küttim, L., Salme, M., and Lamentowicz, M. (2022). Searching for an ecological baseline: Long-term ecology of a post-extraction restored bog in Northern Estonia. Quaternary International, 607, s. 65-78, doi.org/10.1016/j.quaint.2021.08.017

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was as follows:

- Collecting peat core and samples in the field
- laboratory preparation of samples,
- testate amoebae of samples,
- statistical analysis of the results,
- graphic processing of the results,
- interpretation of data,
- data synthesis,
- writing the first draft of the manuscript and editing the manuscript,
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was as follows: I contributed to **conceptualization, the collecting peat core and samples in the field, laboratory preparation of samples, analysis and interpretation of data, writing the manuscript.**

With kind regards,

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was as follows: I contributed to **conceptualization, the analysis and interpretation of data and writing the manuscript.**

With kind regards,

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With kind regards,

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was as follows: I contributed to **the non-pollen palynomorph analysis and interpretation of data and writing the manuscript.**

With kind regards,

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was as follows: I contributed to **the analysis**.

With kind regards,

Meryt Salme

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was as follows: I contributed to **the conceptualization, the analysis and interpretation of data and writing the manuscript.**

With kind regards,

Mariusz Lamentowicz

ZAŁĄCZNIK NR 1

FOTOGRAFIE STANOWISK BADAWCZYCH

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Rycina 1. Torfowisko Martwe.

Fot. **1**	Pobór rdzenia torfowego próbnikiem torfowym typu Wardenaar z torfowiska Martwe w kwietniu 2016 roku przez dr hab. Michała Słowińskiego, Prof. IGiPZ (PAN) oraz Prof. dr hab. Mariusza Lamentowicza (UAM) (Fot. K. Kajukało, 2016).
Fot. **2**	Rdzeń torfowy o długości 56 cm pobrany z południowej części torfowiska Martwe, oznaczony symbolem MAR1 (Fot. K. Kajukało, 2016).
Fot. **3**	Torfowisko Martwe w kwietniu w 2016 roku (Fot. M. Lamentowicz, 2016).
Fot. **4**	Torfowisko Martwe w sierpniu w 2019 roku z widocznym pasem brzóz wokół torfowiska od strony ścieżki tornada z 2012 roku (Fot. 2019).
Fot. **5**	Obecny stan roślinności w miejscu przejścia tornada w otoczeniu torfowiska Martwe z jego południowej strony (Fot. 2019).
Fot. **6**	Obszar zniszczeń spowodowanych przez tornado w 2012 roku. Nasadzenia drzewostanu odpowiadają rozmiarowi pasa tornada i zostały posadzone na miejscu uprzątniętych uprzednio uszkodzonych drzewostanów. Widok z wieży widokowej w Trzebcinach (Fot. 2019).

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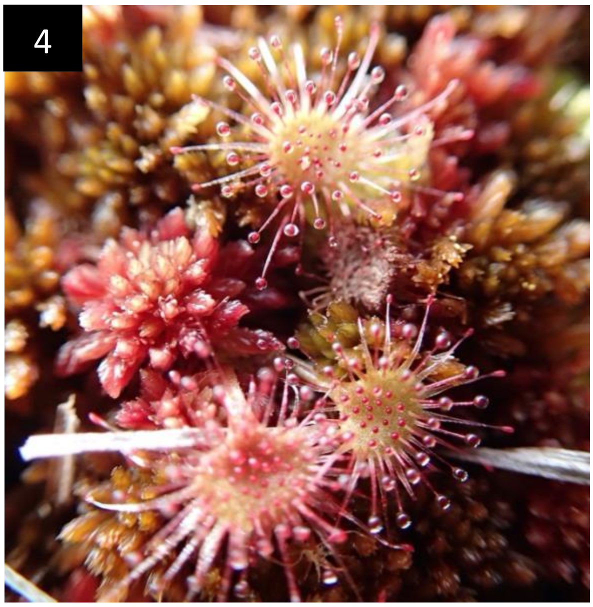


5

Rycina 2. Torfowisko Gorodziecky Moch.

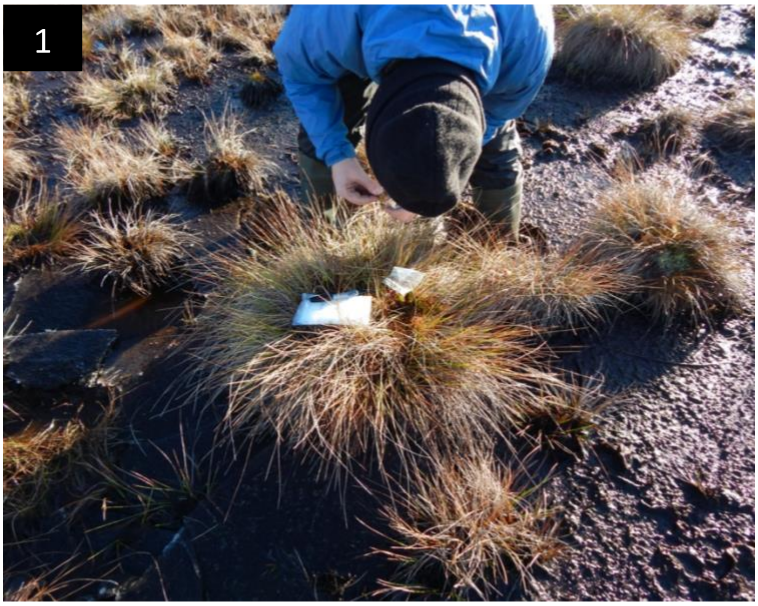
Fot. **1** Prace terenowe związane z poborem rdzenia na torfowisku Gorodziecky Moch latem w 2016 roku przez dr hab. Michała Słowińskiego, Prof. IGiPZ (PAN) oraz dr Mateusza Kramkowskiego (IGiPZ, PAN) (Fot. B. Kotrys, 2016).

Fot. **2** Pobór rdzenia torfowego z torfowiska Gorodziecky Moch przez dr hab. Michała Słowińskiego, Prof. IGiPZ (PAN) oraz dr Mateusza Kramkowskiego (IGiPZ, PAN) (Fot. B. Kotrys, 2016).

Fot. **3** Roślinność torfowiska Gorodziecky Moch. Charakterystyczna dla torfowiska wysokiego kępa z mchami torfowcami (*Sphagnum* spp.) i rosiczką okrągłolistną (*Drosera rotundifolia*) (Fot. M. Słowiński, 2016).

Fot. **4** Rosiczka okrągłolistna (*Drosera rotundifolia*) z mchami torowcami (*Sphagnum* spp.) porastająca jedną z kęp na torfowisku Gorodziecky Moch (Fot. M. Słowiński, 2016).

Fot. **5** Torfowisko Gorodziecky Moch latem w 2016 roku (Fot. M. Słowiński, 2016).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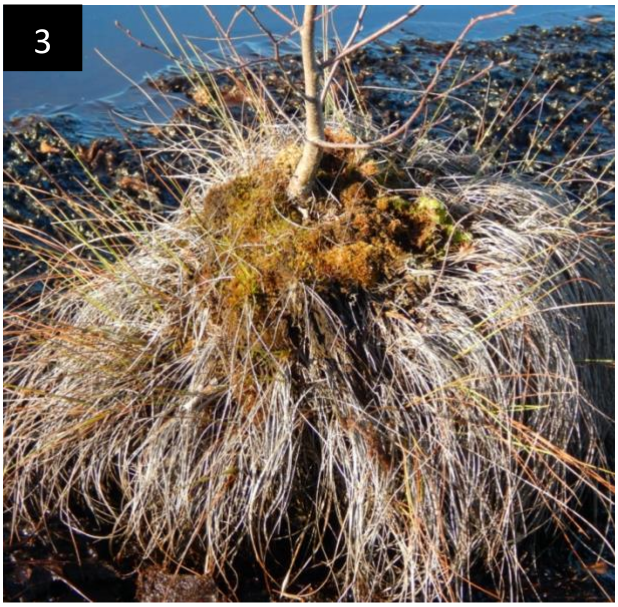
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Rycina 3. Obszaru wydobycia torfu torfowiska Hara podlegający restytucji.

Fot. **1**	Pobór prób powierzchniowych z jednej z kęp w listopadzie 2017 roku przez dr Martin Küttim (TU) z obszaru wydobycia torfu torfowiska Hara podlegającego restytucji (Fot. 2017).
Fot. **2**	Prace terenowe związane z poborem rdzenia torfowego na obszaru wydobycia torfu torfowiska Hara podlegającego restytucji w listopadzie 2017 roku (Fot. 2017).
Fot. **3**	Kępa wełnianki pochwowatej (*Eriophorum* vaginatum) z mchami torowcami (*Sphagnum* spp.) z której pobrano próby powierzchniowe do dalszych badań (Fot. 2017).
Fot. **4**	Kępy wełnianki pochwowatej (*Eriophorum* vaginatum) na obszarze wydobycia torfu podlegającego restytucji (Fot. 2016).
Fot. **5**	Obszar wydobycia torfu torfowiska Hara podlegający restytucji w listopadzie 2017 roku (Fot. 2017).
Fot. **6**	Obszar wydobycia torfu torfowiska Hara podlegający restytucji w listopadzie 2017 roku (Fot. 2017).

ZAŁĄCZNIK NR 2

FOTOGRAFIE AMEB SKORUPKOWYCH

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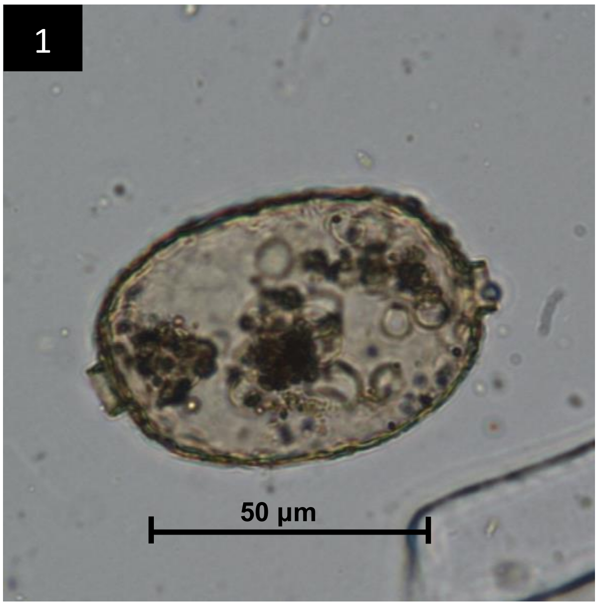

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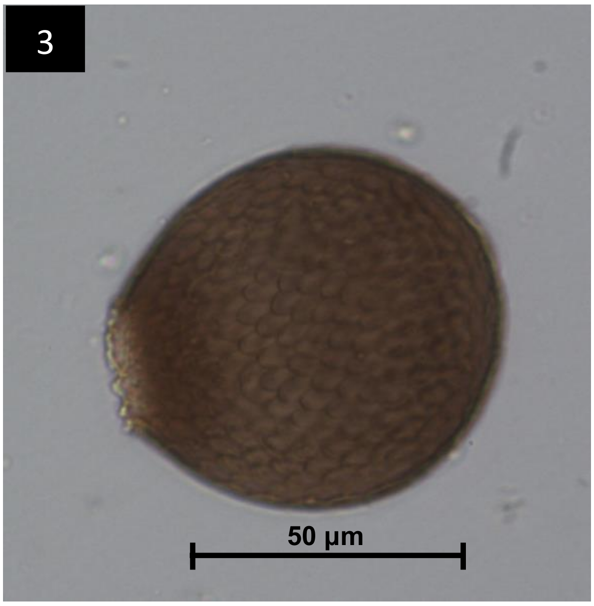

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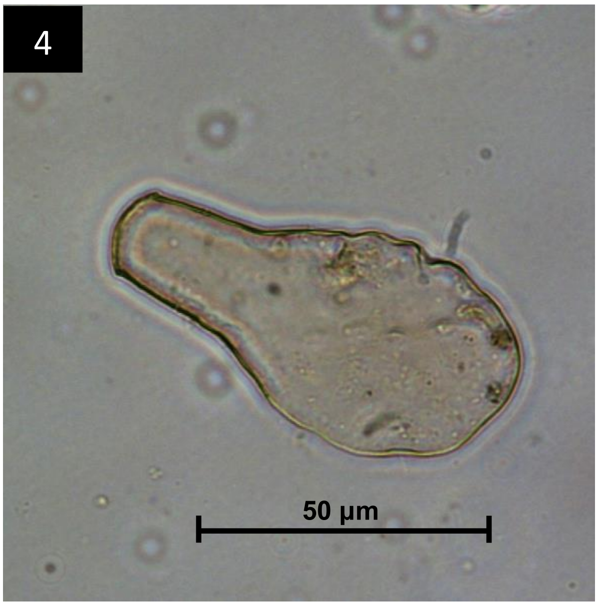

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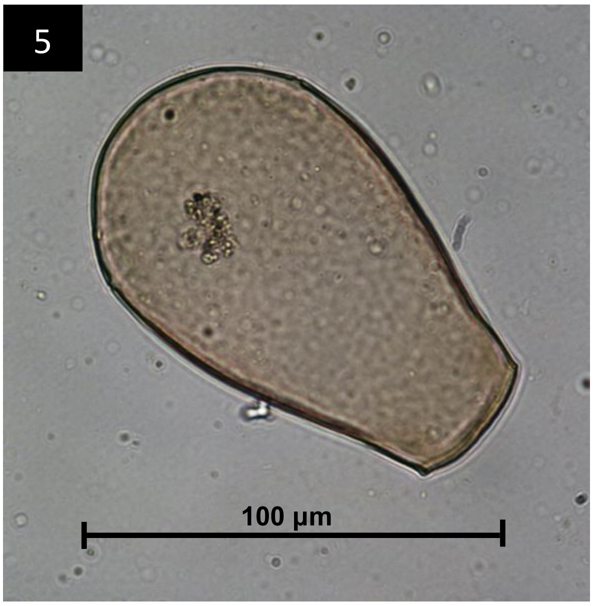


6

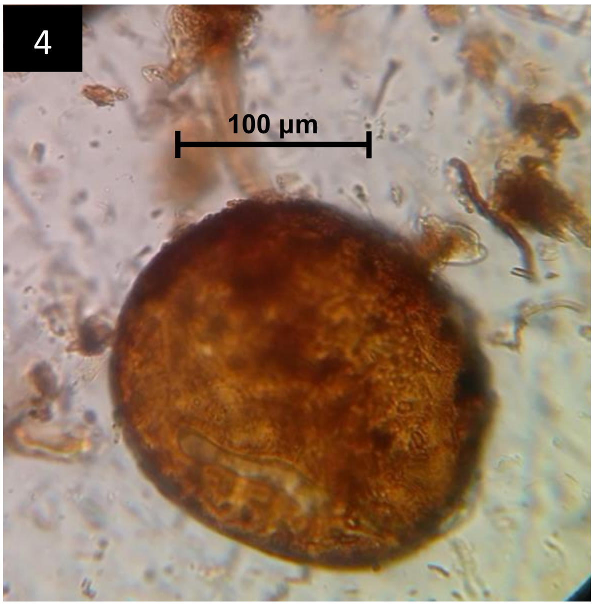
Rycina 1. Ameby skorupkowe

Fot. **1**	*Amphitrema wrightianum* (Archer, 1869) - fot. 2016
Fot. **2**	*Nebela collaris* (Ehrenberg, 1848) - fot. 2017
Fot. **3**	*Assulina seminulum* (Ehrenberg, 1848) - fot. 2016
Fot. **4**	*Hyalosphenia elegans* (Leidy, 1874) - fot. 2016
Fot. **5**	*Hyalosphenia papilio* (Leidy, 1874) - fot. 2017
Fot. **6**	*Nebela tincta* type (Kosakyan et Lara, 2012) - fot. 2016


1
100 µm


2
100 µm


3
50 µm


4
100 µm


5
50 µm


6
100 µm

Rycina 2. Ameby skorupkowe

Fot. **1**	*Galeripora discoides* (*Arcella discoides*) *(*González-Miguéns et al., 2021; Ehrenberg, 1871) - fot. 2017
Fot. **2**	*Archerella flavum* (*Amphitrema flavum*) (Archer, 1877) - fot. 2017
Fot. **3**	*Euglypha strigosa* (Ehrenberg, 1848*)* - fot. 2017
Fot. **4**	*Bullinularia indica* (Penard, 1907) - fot. 2017
Fot. **5**	*Hyalosphenia subflava* (Cash and Hopkinson, 1909)- fot. 2017
Fot. **6**	*Trigonopyxis arcula* (Penard, 1912) - fot. 2017

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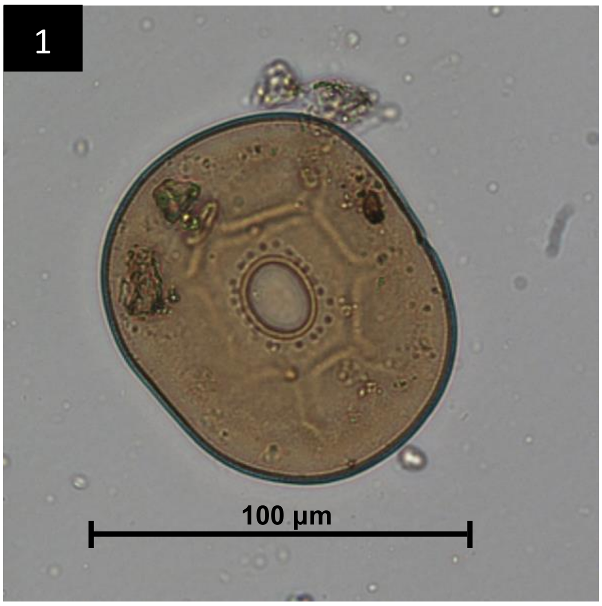

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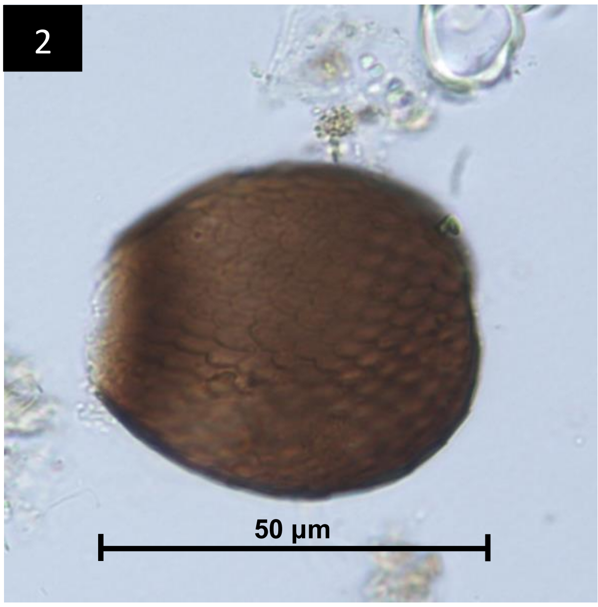

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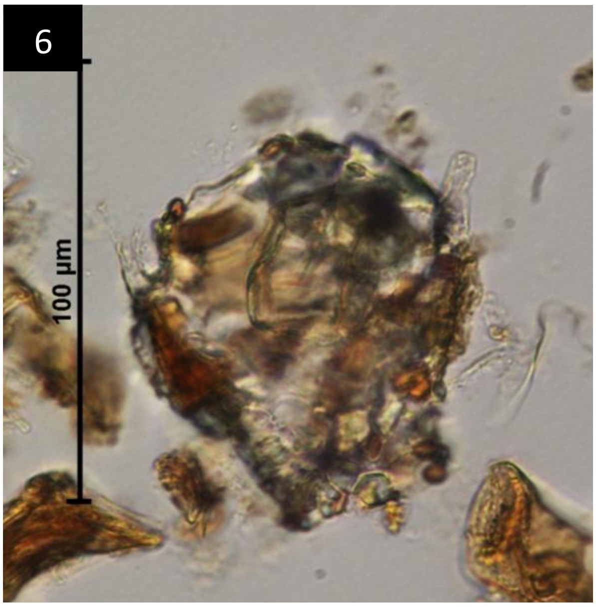


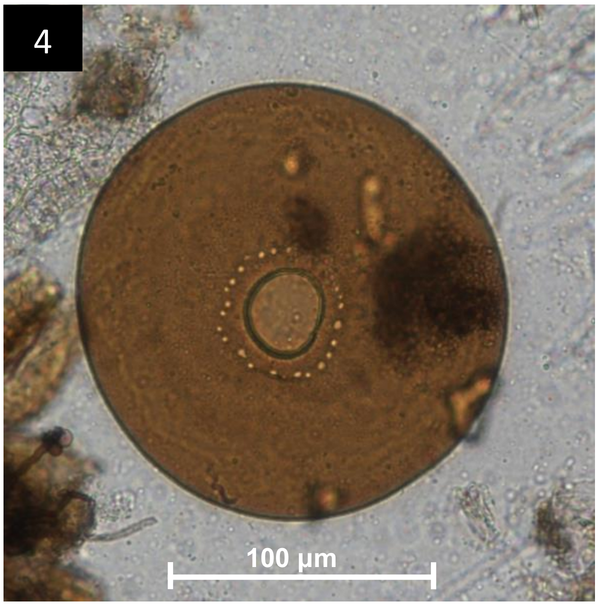
Rycina 3. Ameby skorupkowe

Fot. **1**	*Galeripora catinus* (*Arcella catinus*) (González-Miguéns et al., 2021; Penard, 1890) - fot. 2017
Fot. **2**	*Assulina muscorum* (Greeff, 1888) - fot. 2017
Fot. **3**	*Cyclopyxis eurystoma* type (Deflandre, 1929) - fot. 2017
Fot. **4**	*Alabasta militaris* (*Nebela militaris*) (Penard, 1890) - fot. 2017
Fot. **5**	*Phryganella acropodia* (Hertwig & Lesser, 1874) - fot. 2017
Fot. **6**	*Difflugia leidyi* (Wailes, 1913) - fot. 2016


1
200 µm


2
100 µm


3
50 µm


4
100 µm


5
100 µm


6
50 µm

Rycina 4. Ameby skorupkowe

Fot. **1**	*Planocarina carinata* (*Nebela carinata*) (Archer, 1867; Kosakyan et al., 2016) - fot. 2017
Fot. **2**	*Difflugia pulex* (Penard, 1890) - fot. 2017
Fot. **3**	*Trinema lineare* (Penard, 1890) - fot. 2017
Fot. **4**	*Galeripora artocrea* (*Arcella arocrea*) (Leidy, 1876; González-Miguéns et al., 2021)- fot. 2017
Fot. **5**	*Heleopera sphagni* (Leidy, 1874) - fot. 2017
Fot. **6**	*Corythion dubium* (Taranek, 1871) - fot. 2017