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Abrupt Alnus population decline at the end of the first millennium CE in Europe – the event ecology, possible causes, and implications

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	outbreak. Following current observations of the decline of alder stands in Europe due to a Phytophthora outbreak, we suggest that a similar process may have occurred in the past. This study provides insight into long-term alder (mainly A. glutinosa) dynamics in a condition of climate change and illustrates its great resilience, enabling the natural, successful regeneration of alder stands after critical diebacks if environmental conditions improve. Our finding that the Alnus pollen decline reflects a roughly synchronous event indicates that the decline could be used as an over-regional chronostratigraphic marker for 800–1000 CE in pollen diagrams from a large part of the European Lowland.

Abrupt *Alnus* population decline at the end of the first millennium CE in Europe – the event ecology, possible causes, and implications

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Abstract

The study, based on the examination of 70 published and unpublished pollen profiles from Poland and supplementary data from the surrounding regions, shows that an abrupt, episodic *Alnus* population decline at the end of the first millennium CE was a much more widespread event than has been previously reported, spanning large areas of the temperate and boreal zones in Europe. The data from Poland suggest that the decline was roughly synchronous and most likely occurred between the 9th and 10th centuries, with strong indications for the 10th century. The pollen data indicate that human impacts were not a major factor in the event. Instead, we hypothesize that one or a series of abrupt climatic shifts that caused floods and droughts at the end of the first millennium CE could have initiated this ecological disturbance, leading to a higher vulnerability of the alder trees to a pathogen outbreak. Following current observations of the decline of alder stands in Europe due to a *Phytophthora* outbreak, we suggest that a similar process may have occurred in the past. This study provides insight into long-term alder (mainly *A. glutinosa*) dynamics in a condition of climate change and illustrates its great resilience, enabling the natural, successful regeneration of alder stands after critical diebacks if environmental conditions improve. Our finding that the *Alnus* pollen decline reflects a roughly synchronous event indicates that the decline could be used as an over-regional chronostratigraphic marker for 800–1000 CE in pollen diagrams from a large part of the European Lowland.

Key words: *Alnus* long-term population dynamics, climate change, ecological disturbance, palaeoecology, pathogen outbreak, *Phytophthora*

Introduction

Disturbances are widely recognized as one of the main factors influencing the direction and rate of forest succession in temperate and boreal biomes, where the forest composition is not only shaped by regional climate, soil, or topography but also frequently punctuated by more abrupt and less predictable factors, such as wildfires, storms, or pathogen outbreaks (Bradshaw and Sykes, 2014). Recently, the unprecedented rate of climate change predicted ~~in~~ for the 21st century is considered a likely cause of a higher frequency of different catastrophic natural events (Mann et al., 2017), leading to the potential damage of forest stands (Kramer et al., 2008; Seidl and Rammer, 2017; Veraverbeke et al., 2017) and a higher risk of insect and pathogen outbreaks among several tree species (La Porta et al., 2008; Sturrock et al., 2011; Santini et al., 2013; Flynn and Mitchell, 2018).

To understand the role of disturbances in forest ecosystems, knowledge about their past occurrence and effects is important (Jeger and Pautasso, 2008; Cole et al., 2014). Among the most convincing evidence of past disturbances are abrupt declines in pollen values of specific tree taxa in pollen diagrams. However, a problem arises when trying to determine the disturbance agent that caused the decline based on sedimentary records. Only in the case of human impacts (Kitagawa et al., 2016; Wacnik et al., 2016), forest fires (Tinner et al., 2000; Yin et al., 2016), and sharp climatic shifts (Ammann et al., 2013; Ghilardi and O'Connell, 2013) is the causal attribution less complicated. Detecting past disturbances caused by beetle outbreaks, plant diseases, and storms is more difficult. Ascertaining the occurrence of past storms is practically impossible (but see, for example, de Jong et al., 2009; Kaniewski et al., 2016), while past beetle outbreaks have been traced in some cases using fossil beetle remains preserved in sediments (Girling and Greig, 1985; Clark and Edwards, 2004; Morris et al., 2015). Recently, progress has been achieved in analysing non-pollen palynomorphs from pollen samples, which in some cases have disclosed outbreaks of fungal pathogens (van Geel and Andersen, 1988; van Geel et al., 2013; Latałowa et al., 2013).

The complexity of this issue is well illustrated by the debates on a European-wide elm decline c. 6300 –5800 cal BP (Iversen, 1941; Troels-Smith, 1960; Peglar, 1993; Parker et al., 2002; Batchelor et al., 2014) and a hemlock decline c. 5500–5100 cal BP in eastern North America (Davis, 1981; Allison et al., 1986; Bennett and Fuller, 2002; Foster et al., 2006). In both cases, the conspicuous and abrupt decline of a single species was the subject of different hypotheses concerning a potential disturbance agent. Sudden climate change, a beetle or pathogen outbreak, and human impacts (in the case of *Ulmus* decline) were discussed as potential factors interacting separately or in combination (summarized by Waller, 2013).

Here, we develop our earlier finding that the episodic decline of *Alnus* at the close of the first millennium CE was a widespread phenomenon and not an effect of human impacts or the sole effect of climate change (Stivrins et al., 2017). We present pollen data from a larger region of Europe that show that the *Alnus* decline not only occurred in the Baltic countries, Finland, and western Russia but was also equally prominent and obvious in many locations in north-central Europe and that the geographic range of the event probably extended further to western Europe. Important pollen data from the event are provided by a new pollen diagram from an annually laminated lake sediment core from Lake Czechowskie in Poland. The sediments, which were analysed with high resolution for pollen and accurately dated based on the varve chronology, are used to identify the beginning, end, and duration of the event. In turn, the high-resolution analysis of pollen and non-pollen palynomorphs from peat-bog profiles serves to identify environmental changes around the decline. Finally, we discuss the potential causes of this event. Our study links a well-defined, large-scale ecological disturbance from the past with a very similar recent large-scale alder forest dieback in Europe, which is a great problem for nature protection and the management of riverine ecosystems (Jung et al., 2016).

Study area and present-day *Alnus* occurrence

The present study covers northern and central Poland between 52-55°N and 14-24°E (the northern part of the Central European Plain) (Fig. 1). The area belongs to the temperate climate zone of Europe and lies at the transition where the Atlantic and continental air masses clash. The continentality gradient increases from west to east. The climate is relatively warm and wet, with annual precipitation of 550-700 mm on average, annual mean air temperatures between 6.5 and 8.5°C, average January temperatures between 0 and -4°C, and average July temperatures between 18 and 17°C (Lorenc, 2005).

Most of this area was covered by an ice sheet during the last glacial period. In the northern regions, the ice sheet and its meltwaters left, among other forms, ranges of terminal moraines dissected by a dense network of interconnected lake channels and river valleys. The hills of the moraines are higher than 300 m a.s.l. at their highest points. Flat or gently undulating ground moraine, which usually does not exceed 200 m a.s.l., is the main landscape element in central Poland. Patches of outwash plains and kame terraces are distributed throughout the region (Gilewska, 1991). Common features of such deglaciated environments are large lakelands and numerous mires of various origins that fill lake channels, river valleys, and kettle holes, providing perfect conditions for palaeoecological studies; therefore, a number of sites have been investigated here by means of pollen analysis.

Large proportions of wetlands in the study area are habitats for riparian alder-elm forests (Alno-Ulmion) and alder-carr (*Alnetea glutinosae*), where *Alnus glutinosa* is the main species. Two alder species – black alder (*A. glutinosa* (L.) Gaertn.) and grey alder (*A. incana* (L.) Moench) – occur in this region (Zając and Zając, 2001).

A. glutinosa has a wide geographical distribution covering most of Europe west of 30°E longitude, while to the east of this line, its range extends as far as western Siberia. With increasing aridity and a decline in summer temperatures, it appears in restricted areas and dispersed locations. It is absent from northern and central Scandinavia and the southern and eastern Iberian Peninsula and is scarce in some areas of southern and eastern Europe (Kajba and Gracan, 2003). Black alder is a temperate species that is demanding with respect to minimum summer temperatures (12°C) but sustains strong winter frosts of -39 to -43°C for northern populations and -30 to -34°C for southern populations (Dewald and Steiner, 1986). Its occurrence is closely linked to the availability of water, so water deficits during dry and warm periods in summer have a negative impact on alder tree fitness. Because of several adaptations to very wet and anaerobic soil, it forms forest communities in marshy sites that are waterlogged throughout the year and in riverside sites where seasonal flooding occurs, but it also appears in admixture with other species in plateau sites under conditions of high soil moisture. The species is of considerable interest for its place in riparian ecosystems, where it plays a beneficial role in flood control and stabilizing riverbanks as well as water filtration and purification in waterlogged soils. It also supplies the ecosystem with nitrogen by way of symbiosis with nitrogen-fixing bacteria (Claessens et al., 2010).

A. incana is considered a boreal and mountain species, and its geographic range is divided into two parts. The northern area includes the eastern Baltic region, all of Scandinavia, and northeastern Europe up to western Siberia. In the southern area, it occurs in most mountain ranges except for the Pyrenees (Jalas and Suominen, 1976). Its present-day occurrence is strongly affected by plantation, which impedes the delimitation of the natural range. Compared with *A. glutinosa*, *A. incana* is less demanding concerning growing season temperatures and tolerates long harsh winters better. It grows mostly on young alluvial soils, does not tolerate long-lasting flooding and is more tolerant to drought than black alder (Boratyński, 1980; Pancer-Kotejowa and Zarzycki, 1980).

Black alder is one of the most common species, and grey alder is distinctly less frequent in the study region (Zając and Zając, 2001). Thus, it is probable that the potential proportion of *A. incana* pollen in the profiles examined in the present study is insignificant and that the alder pollen present in this material represents mostly *A. glutinosa*.

Materials and Methods

The pollen data selected for this study derive from original publications, data stored in the European Pollen Database (EPD, *www.europeanpollendatabase.net*), and in a few cases, from unpublished materials provided by the study authors (ESM Table S1, available online). The suitability of a pollen profile for examination of the presence/absence of the *Alnu*s decline was determined according to the stratigraphic resolution of pollen sampling in the section under concern. In addition to the pollen percentage values, we used the pollen influx data (pollen accumulation rate) from three sites to explore the decline of the *Alnus* population in more quantitative terms.

Seventy one pollen profiles (69~~8~~ sites) were included in this paper. The basic information concerning their geographical position, category, dating methods and results, *Alnus* decline characteristics, and references are included in ESM Table S1 (available online). The metadata for each site, such as the basin type (lake or peat-bog), its surface, the presence of an inlet or outlet, the distance to a river valley, and potential habitats for *Alnus*, are consolidated in ESM Table S2 (available on-line). Selected palaeoenvironmental data on local hydrological changes at the event, human impacts, and pollen data from the main tree taxa are provided in ESM Table S3 (available online).

The sites were grouped into two categories. The "primary sites" (A) category includes 31 profiles with high pollen sampling resolution and age/depth models based on a series of radiocarbon dates in the section of interest or with ^{14}C dates related directly to the *Alnus* decline event. New age/depth models were developed based on the radiocarbon dates listed in original publications and using the current calibration curve (Reimer et al., 2013) and OxCal software (version 4.2; Bronk Ramsey and Lee, 2013). The most precise dating has been provided for the record from annually laminated sediments in Lake Czechowskie, Lake Żabińskie and Lake Szurpiły~~,~~ where the chronological information is based on ~~a~~ multiple dating approaches~~ (Wulf et al., 2016).~~. The Lake Czechowskie chronology is based on varve counting, tephrochronology, AMS ^{14}C dating on terrestrial plant remains, in-situ ^{10}Be and ^{137}Cs activity meauserments; the chronological uncertainty for the period around 1000 CE does not exceed ± 10 varve years (Czymzik et al., 2018; Ott et al., 2016; Wulf et al., 2016). In Lake Żabińskie different methods of varve counting, AMS ^{14}C dates, ^{137}Cs activity and cryptotephra were used to establish the sediment chronology; in this case the averaged chronological uncertainty in the section under concern was calculated to $^{+12}/_{-24}$ varve years (Żarczyński et al., 2018, 2019). The Lake Szurpiły chronology was established by using different methods of varve countig and independent radiometric dating (AMS ^{14}C, ^{210}Pb and ^{137}Cs); the dating uncertainty in the section around the *Alnus* decline is ±42 varve years (Kinder et al., 2013; Kinder, oral inf.).

The "secondary sites" (B) are those of weaker quality concerning their independent chronologies. In 40% of the sites, the *Alnus* decline was dated to approximately the 9th-10th centuries according to the indirect premises (ESM Table S1, available online); the main comparison was with the nearest well-dated pollen profiles and a cross-check of the palynological indications of the human occupation phases with knowledge of the chronology of a nearby early medieval settlement development. These kinds of data did not add to the establishment of the exact timing and duration of the decline but did enable the identification of *Alnus* events recorded in particular profiles as roughly concurrent with those at other sites.

The statistical significance of the decline was analysed using 11 *Alnus* pollen curves selected on the basis of their relatively high temporal resolution. We used SiZer analysis (Significant Zero crossings of derivatives) (Chaudhuri and Marron 2000) to detect significant declines and rises in the *Alnus* population. SiZer analysis has been shown to be a powerful tool in ecology to detect the significant change points in time series data inferred as ecological thresholds (Sonderegger et al., 2009; Clements and Rohr, 2009; Clements et al., 2010). When applied to time series, SiZer analysis applies a nonparametric smoothing to a signal and detects the time intervals where the smooth is significantly increasing or decreasing. A wide range of smoothing levels are considered to reveal the salient features in the signal at all time scales. When compared to many other change point detection methods, the strength of the SiZer analysis is in its flexibility. It allows for a trend in the data, the detection of multiple change points and changes in the temporal sampling distribution, and adapts to temporal changes in the error variance of the signal. The results of SiZer analysis are visualized using a colour map where the time is on the horizontal axis and the smoothing level is on the vertical axis, and for each pixel, its colour represents the significance of the derivative of the smooth for the corresponding time point and scale. A SiZer map is an efficient tool that helps discover all the significant declines and rises in the data at a glance (ESM Figure 1, available online). The SiZer analyses were performed with the SiZer package (Sonderegger, 2012) in R 3.1.2 (R Development Core Team, 2014).

To illustrate the *Alnus* decline in a broader context of environmental changes reflected by palynological data and to show that the decline is distinct irrespective of the site type, local conditions and pollen representation of human activity, we present two sample sets of pollen diagrams from lakes (Fig. 2) and peat bogs (Fig. 3); the sites strongly differ with respect to their surface size, which indicates different source areas of pollen (cf. Prentice, 1985; Sugita, 1993), and are located along the 600 km-long W-E transect running through different geographic and historical regions of northern and central Poland.

Results

Characteristics, statistical significance and chronology of the *Alnus* pollen decline

The *Alnus* pollen curve decline is one of the striking features in the early medieval sections of many profiles in Poland (Fig. 1; ESM Table S1, available online). In 85% of the 71~~0~~ pollen diagrams considered in the present study, the decline was abrupt, with the magnitude ranging from 40 to 90% reductions from pre-decline levels. Sharp declines were also displayed in the *Alnus* pollen influx values (pollen accumulation rates – PAR) calculated in three profiles: Lake Czechowskie (from c. 12000 to 2000 grains cm^{-2} a^{-1}), Lake Suminko (from c. 6000 to 1800 grains cm^{-2} a^{-1}) (Fig. 2), and Bagno Kusowo (from c. 1800 to 400 grains cm^{-2} a^{-1}) (Fig. 3). The decline was distinct in both the lake sediment and peat-bog profiles (Figs. 2, 3 and 4). The review of the pollen diagrams in terms of the presence/absence of the event *versus* environmental factors such as basin morphometry and some features of the catchment showed no correlation (ESM Table S2, available online). The detailed characteristics of the *Alnus* pollen decline differed among the sites mostly because of the different sediment thicknesses and the different sampling resolutions in the relevant parts of the profiles. It seems that the weak expression or absence of the decline was (in most cases) caused by lower sampling resolution with respect to the sedimentation rate or sediment loss in the section of the pollen profiles of concern. In fact, in many profiles, a clear lithological limit occurred around the decline (ESM Table S3, available online).

The results of the SiZer analyses (Fig. 5, ESM Figure S1, available online) from 11 sites highlight all the significant decline-rise events in the *Alnus* curves during the last 2000 years. They show that a statistically significant decline was followed by a statistically significant rise at the end of the first millennium in eight of the 11 analysed time series. The sampling density in Białowieża 314D and 131C, and in Bukrzyno was too low, which hampered the detection of the *Alnus* decline so that even the lowest values were observed at the end of the first millennium; the result was not statistically significant. Furthermore, two other statistically significant decline-rise events were detected in the Czechowskie and Racze records around the 4th-5th century and then around the 15th century. The earlier, minor shift, although not statistically significant, was also detectable in some other sites.

~~Due to the annually laminated sediments and the high sampling resolution, the record from Lake Czechowskie (Fig. 2) offered~~ T~~t~~he ~~most precise~~best chronology for the early medieval event is available for the lakes with annually laminated sediments (Table 1). In Lake Czechowskie (Fig. 2)~~At this site~~, the *Alnus* values were 14% until the decline began at 970 CE. The decline was extremely abrupt, so that by 1020 CE, the *Alnus* percentages were down to a minimum of 1.7%, where they stayed until a rise began at 1090 CE, reaching over 10% by 1120 CE. ~~, which is practically the same level as before the decline.~~ Thus, in the Lake Czechowskie record, the event lasted approximately 150 years. In Lake Żabińskie the *Alnus* curve declined by 870 CE to 1.7% between 920 and 1000 CE, a rise began by 1060 CE and by 1090 CE the *Alnus* curve reached 11% (Żarczyński et al., 2019). Considering relatively large dating uncertainty (± 42 varve years), similar results were obtained in Lake Szurpiły (Kupryjanowicz and Fiłoc, 2016; Kupryjanowicz, unpubl. data). In this site the decline started at 830 CE, the minimum of 2.4% was reached at 930 CE, and already by 980 CE the *Alnus* pollen curve started to rise reaching 10.5% at by1010 CE.

Similar data have been obtained from other lake and bog profiles in which this event was dated using age/depth models based on radiocarbon dates ("primary sites") or according to the AMS ^{14}C dates for plant remains selected directly from the *Alnus* decline level (Table 1, ESM Table S1, available online). Keeping in mind the differences in the pollen sampling resolution in particular profiles and the large range of dating uncertainty, the ages (median) calculated in the individual profiles based on the age/depth models were surprisingly consistent, ranging from 800 to 970 CE for the start of the decline, from 900 to 1020 CE for the minimum values, and from 1040 to 1210 CE for the full recovery of the *Alnus* pollen curve. According to these data, the whole period from the decline to the recovery lasted for 150 to 330 years in the individual sites, giving an average of 250 years. The collection of 30 radiocarbon dates from 20 sites performed specifically for the *Alnus* decline (Table 1) offered important support for an even more detailed determination of the age of the event. In most sites, the dates (median) for the *Alnus* pollen curve depression point to the 10th century, which is in agreement with the age calculated from the annually laminated sediments. ~~of Lake Czechowskie.~~

In only a few sites, the dates for the major *Alnus* decline in the first millennium CE estimated according to the published original data were older (ESM Table S1, available online). The earliest decline (c. 5th-6th centuries) was recorded in the Wojnowo site (Wacnik et al., 2012); this decline roughly coincides with the first statistically significant *Alnus* declines in Lake Czechowskie and Lake Racze and with the additional negative shifts preceding the main *Alnus* decline in some other sites (Fig. 5).

The *Alnus* pollen decline *vs*. indicators of human impact

The relationship of the *Alnus* pollen decline to the palynological indicators of settlement activity varied among the sites (Figs. 2 and 3, ESM Table S3, available online). In the majority of the sites, it was slightly preceded by the decline of some other tree pollen and the initial rise of pollen typical of the human land occupation phase. Such a situation is illustrated by the diagrams from Lake Suminko (Fig. 2) and Słowińskie Błota/85 (Fig. 3), for example, where already in the section preceding the *Alnus* fall, *Carpinus* and *Quercus* started to decline, the frequency of Poaceae, meadow plants and fallow indicators (*P. lanceolata*) and some weed pollen (*Artemisia*, *Rumex acetosa/acetosella* t.) slightly increased and the scattered pollen of cereals was present. In Lake Mełno (Fig. 2), an abrupt *Alnus* decline was preceded by a strong *Carpinu*s decrease and distinctly increasing pollen curves of anthropogenic indicators, including cereals. In some sites, such as Lake Zarańskie (Fig. 2), the decline of *Alnus* pollen occurred in the already advanced human impact phase confirmed by cereal and *P. lanceolata* pollen, both exceeding 1%.

There are also a few profiles in which the clear signature of the *Alnus* decline does not coincide with the indicators of settlement development. In the peat profiles from Białowieża Forest (Fig. 3), only weak negative shifts of the pollen curves of other deciduous trees (mainly *Carpinus* and *Ulmus*) occurred, and a few scattered pollen grains of anthropogenic indicators appeared at this level. In Lake Czechowskie, pollen evidence for human activity was very weak throughout the whole section of the profile (Fig. 2); moreover, at the *Alnus* decline level, cereal pollen entirely disappeared, while pollen of other taxa typical of human-made habitats was scarce. In contrast to other trees, in most sites, *Alnus* pollen curves regained their earlier levels, rising with increasing proportions of indicators of human impacts.

The relation of the *Alnus* decline to the frequency of microscopic charcoal particles found in some of the profiles did not show any consistent results either (Figs. 2 and 3). In Białowieża Forest, the charcoal particles declined in two profiles and rose in one. In Lake Czechowskie, their proportions decreased immediately at the *Alnus* decline and then rose again. In Bagno Kusowo, we observed the opposite pattern, while in Lake Suminko, the charcoal frequency did not change.

The *Alnus* pollen decline vs. indicators of hydrological shifts

The palaeoecological data point to hydrological shifts around the *Alnus* decline in all the peat profiles and in some lakes (Fig. 3, ESM Table S3, available online); however, the record of the hydrological changes in the peat bogs is much clearer than in the lake sediments. Only in a few shallow lakes (sites 3, 15, 22, 26 and 63 in ESM Table S3, available online), the lithological limits indicated distinct water level lowering. In deeper and larger lakes, the composition of the sediments did not show any clear change or display increases in mineral matter and changes in algae remains, which may have been the result of different factors, including water table lowering but also increased denudation and/or higher productivity caused by anthropogenic eutrophication or a warmer climate. The same explanation may underlie the discrete change in lithology in Lake Suminko (Fig. 2), where delicate, unclear lamination was present below the *Alnus* decline but disappeared entirely above it.

Changes in the hydrological conditions in the peat bogs are shown by examples presented in Fig. 3. In the profiles from Białowieża Forest (CE Poland), the decline in *Botryococcus* and Cyperaceae was followed by small peaks of *Ledum* and *Entophlyctis lobata* (BIA/314D) and *Calluna* (BIA/318C) and then a strong increase in *Sphagnum.* In Czerlon, a distinct shift from minerotrophic to ombrotrophic conditions was punctuated by a decline of Cyperaceae and *Botryococcus,* which were substituted by raised bog taxa: *Sphagnum* spores strongly increased while testate amoeba, such as *Amphiterma wrightianum*, *Archerella flavum*, *Assulina* spp., *Heleopera* sp., and *Hyalosphenia papillo* appeared concurrently with a depression in the *Calluna* pollen curve and then declined. Similar results have been obtained in the profile from Słowińskie Błota/85 (NW Poland), where a thin layer of *Eriophorum vaginatum* concurrent with a peak of *Calluna* and a deep depression in *Sphagnum* occurred immediately before the alder decline, indicating a dry spell. At the decline, the proportions of *Sphagnum* spores rose abruptly; at this level, *A. flavum*, *Assulina* spp., and *Arcella discoides* appeared at higher frequencies and then declined. All the above data and similar records from many other sites (ESM Table S3, available online) seem to illustrate a dry phase immediately prior to the *Alnus* decline, a short wet shift at the decline and then drier conditions again. Furthermore, a striking difference between the pollen data from lakes (Fig. 2) and peat bogs (Fig. 3) concerning the trajectory of the *Pinus* pollen curves might be an argument for the involvement of a dry period in the low *Alnus* pollen phase. In all of the peat bog sites, the *Alnus* decline was accompanied by prominent peaks of *Pinus* pollen, which were absent in the profiles from the lakes. This pattern suggests that the increase in *Pinus* reflects on-site disturbances, most likely the encroachment of pines onto the bogs in the dry period.

At most sites, the *Alnus* pollen decline was concurrent with an increase in pollen proportions of Poaceae and of pioneer trees growing in riverine forests and wetlands (*Salix* spp., *Betula* sp.), and fluctuations in *Ulmus* and *Fraxinus* pollen values (also in *Picea* in eastern Poland); this decline most likely reflects changes in the local vegetation after the reduction of the alder stands.

Discussion

Geographic range and timing of the event

The report by Stivrins et al. (2017) indicates that the *Alnus* decline was a widespread event in northeastern Europe, while the present data extend the range into north-central Europe (northern and central Poland). Furthermore, the event is well marked in some sites in Germany, Denmark, and southern Sweden (Fig. 1). A further, systematic examination of the pollen diagrams from Europe is needed to determine the area affected by the *Alnus* decline in more detail.

The review of the pollen profiles from Poland (ESM Table S3, available online) suggests that hydrological disturbances around this event with a clear dry period were involved. The temporary water deficit could have resulted in the formation of short-lived hiatuses or in a slowing down of the sediment accumulation rate in the peat bogs, which might be one of the potential reasons for the weak expression of the decline in some diagrams, while dating uncertainty makes it difficult to observe the event in some other records. The main challenge in reconstructing the exact timing and duration of palaeoecological events is the limited accuracy of the chronologies of the sediment sequences, which should be borne in mind, particularly when discussing the dating of short-lived events (cf. Bennett and Fuller, 2002), their synchronicity among sites (Parnell et al., 2008) and their correlation with other data (Blaaw, 2012). However, the chronological data provided in this paper, based not only on age/depth models but also on 30 radiocarbon dates performed on samples taken in 20 sites directly at the decline level or immediately next to it and a varve chronology in three lakes (Lake Czechowskie, Lake Szurpiły and Lake Żabińskie), allow us to suggest that the decline was roughly synchronous, starting approximately in the 9th-10th centuries, with a strong indication of the 10th century. These new data from Poland permit a narrowing of the chronology of the major *Alnus* decline event in relation to the

600-1000 CE timespan suggested in our earlier paper, which was based mainly on data from northeastern Europe (Stivrins et al., 2017). It is worth noting that in that area, the majority of the dates for the decline are between 900 and 1000 CE (Saarse et al., 2010; Stivrins et al., 2017). Similar results are shown in the pollen diagrams from Germany (Litt et al., 2009; Dörfler et al., 2012), Denmark (Aaby, 1988) and southern Sweden (Lagerås, 1996; de Jong and Lagerås, 2011; Fredh et al., 2013). After a detailed revision of the original pollen diagrams analysed in this study and considering the basis for their chronostratigraphy, it seems that the earlier dates might be, in most cases, an artefact caused by poor dating accuracy resulting from the inadequate number of radiocarbon dates used for the age/depth models or the sediment disturbances following dry shifts in the local hydrology. However, we should also accept that at least some of these earlier *Alnus* declines could have been separate events resulting from human impacts (e.g., Wojnowo site; Wacnik et al., 2012) or natural factors devastating local alder populations. This explanation seems to be reinforced by the results of the SiZer analysis provided in this study, indicating distinct shifts in alder pollen curves at approximately half of the first millennium CE preceding the major decline.

The results of this study, especially the data from the annually laminated sediments of three lakes~~Lake Czechowskie~~, demonstrated the very fast recovery rate of the early medieval alder population. According to the varve chronology, the alder population minimum was reached after approximately 50-100 -years from the start of the decline, it stayed at this low level for approximately 50-70-140 years, and during the next approximately 30 years, the population reached the pre-disturbance level. This demonstrates the great resilience of alder forest ecosystems, even if they are exposed to severe natural disturbances. The early age when *A. glutinosa* starts its reproduction (12-20 years according to Tallantire, 1974) is certainly among the important factors here. Another point worth mentioning is that our calculation of the alder recovery rate is close to the average recovery time for forest ecosystems (42 years) given by Jones and Schmitz (2009).

Potential causes of the *Alnus* decline

The *Alnus* pollen decline shows individual features that are distinctly different from the pollen curve trajectories of other tree taxa, suggesting that the alder population dieback was triggered by a specific factor. Knowing the cause of the *Alnus* decline is critical for understanding the significance and implications of this event in long-term forest dynamics. As with *Tsuga* (Foster et al., 2006) and *Ulmus* (Parker et al., 2002) declines, abrupt climate changes, human influences, or disturbances such as pathogen outbreaks or fires should all be considered in the discussion of potential factors involved in this event.

In earlier papers, Sarmaja-Korjonen (2003) and Saarse et al. (2010) suggested human influence as the likeliest candidate for the *Alnus* declines in southern Finland and Estonia, respectively. In fact, most of the pollen sites studied by these authors lie in areas where the event was concurrent with settlement development. However, according to a more recent study, the decline also occurred at many boreal sites where evidence of contemporary human activity is absent, indicating that changes in agricultural practices cannot explain the sudden decrease of the *Alnus* population in this region (Stivrins et al., 2017).

Similar results were obtained in the present study. Although in a great portion of the sites, the *Alnus* decline overlapped with the beginning of settlement development (e.g., Noryśkiewicz, 2013; Pędziszewska et al., 2015; Pędziszewska and Latałowa, 2016), making it difficult to separate the results of human-induced deforestation and natural disturbances in alder stands, other pollen data from Poland and those from other regions indicate that the widespread alder population decline took place regardless of the state of local settlement development. A strong decline has been recorded in the profiles from Białowieża Forest (this paper) and Mechacz Wielki (Gałka et al., 2017), for example, in which anthropogenic indicators are almost absent, in those that reflect weak early medieval occupation (e.g., Lake Suminko – this paper), and in many sites where settlement was already developed, as in north–central Poland (Noryśkiewicz, 2013), northwestern Poland (Latałowa, 1992; Noryśkiewicz, 2014; Bloom, 2015; Lamentowicz et al., 2015) and northeastern Germany (Dörfler et al., 2012). There are also sites where the *Alnus* decline was concurrent with the evidence of decreasing agricultural activity or even a short-lived disruption in settlement development (e.g., Kupryjanowicz and Fiłoc, 2016; Lake Czechowskie – this paper). Fires as a triggering factor may also be rejected. The available microcharcoal data do not show any consistent results in this respect. In some sites, high charcoal peaks occurred with the *Alnus* decline (Marcisz et al., 2015); in others, the charcoal frequency was low at the event level (Lake Suminko and Lake Czechowskie – this paper). Similar results have been provided by Stivrins et al. (2017).

An additional argument against the human impacts explanation is the fast recovery of the *Alnus* population even when the pollen values for the anthropogenic indicators were rising, which was clearly expressed in most of the pollen diagrams. Thus, arguing for human influence would require answering why humans not only suddenly began to use/destroy *Alnus* stands but also why they suddenly stopped doing so. Moreover, an explanation invoking human impacts does not provide a sound rationale for the event, especially for its alder-specific character, abruptness, and synchronous occurrence over the large geographic range.

Abrupt climate shifts would be another potential factor for the *Alnus* decline. The wet episode recorded in some peat bogs concurrently with the early phase of the decline and the subsequent dry period reflected in most sites analysed in this study might be of interest here.

The wet shift indicated in some sites presented in this study seems to conform with the dendrochronological and historical data from Europe, which show that the generally warm and dry period of the 9th century and the first half of the 10th century was punctuated by several short, cold shifts (Yavuz et al., 2007; Büntgen et al., 2016) and flooding events (Stothers, 1998). Historical sources indicate that Europe experienced several harsh winters every few years in the 9th and the first half of the 10th century when the Danube, Elbe, and Rhine rivers and even the Adriatic Sea were frozen (Yavuz et al., 2007). Some of the harsh winters directly followed the major volcanic eruptions of Katla in 822-823 CE (Büntgen et al., 2017), Eldgjá in 934 CE (Stothers, 1998) and Changbaishan (Tianchi Paektu) in 946 CE (Sun et al., 2014). Harsh, long winters usually result in floods and the transport of ice blocks, which may damage alder trees, making them more vulnerable to infection by pathogenic fungi (Ballesteros et al., 2010). Volcanic eruptions may also be followed by high precipitation events, which are another cause of flooding (Gao and Gao, 2017) affecting riparian forests. Historical sources reviewed by Stothers (1998) reported excessive flooding in France and Germany in the period following the Eldgjá eruption. In fact, our data from Gdańsk confirm the presence of floods prior to the *Alnus* decline (Święta-Musznicka et al., 2011; Święta-Musznicka and Latałowa, 2016), which is in agreement with other studies showing that in Poland, floods were particularly frequent around the 10th century (Maclin et al., 2006; Gębica and Wojtal, 2011). Thus, one or a series of floods could have initiated the *Alnus* decline.

Certainly, the subsequent dry period was unfavourable for alder fitness as well. *A. glutinosa* is adapted to a wide range of temperatures, but its occurrence depends on the availability and abundance of water. Its leaves have no mechanism for controlling transpiration, and its roots, when exposed to air, are extremely vulnerable to cavitation (Hacke and Sauter, 1996; Claessens et al., 2010); thus, water deficits during dry and warm summers may affect the tree. Drought as the possible agent for the *Alnus* decline has already been suggested by Noryśkiewicz (2013) and Święta-Musznicka and Latałowa (2016). In fact, the occurrence of a dry period reflected in several sites analysed in this study agrees with the data from many regions of northern and central Europe. The prevalence of dry conditions in the 9th–10th centuries has been documented in such distant locations as Kontolanrahka Bog in southern Finland (Väliranta et al., 2007), Männikjärve Bog in Estonia (Sillasoo et al., 2007), and Misten Bog in eastern Belgium (De Vleeschouwer et al., 2012; Streel et al., 2014). A drop in the effective humidity in the raised bogs in southwest Sweden (predominantly dry summers) in the 9th (8th)-10th centuries has been reported by de Jong et al. (2007, 2009). These data seem to be concordant with the results of the dendroclimatological study by Helama et al. (2009), indicating distinct and persistent summer droughts from the early 9th to the early 13th centuries that were caused by a prolonged rainfall deficit in Finland. High-resolution hydroclimatic data from lowland Central Europe also indicate a dry spell for at least part of the 10th century (Büntgen et al., 2011) and strong negative extremes (droughts) in this period (Dobrovolný et al., 2015). Low water levels in the mid-European lakes have been reconstructed by Magny (2004). Persistent droughts at the end of the first millennium CE and the beginning of the second millennium occurred in various regions of Europe and globally (Cook et al., 2015).

The coincidence between the *Alnus* decline and the period in which flash floods and summer droughts occurred seems to be a good argument for the event. However, it still does not explain the alder-specific character and suggests a possible impact of additional factors. Therefore, we hypothesize that a cumulative effect of climate change and the outbreak of pathogens provides an explanation that is most consistent with the characteristics of the *Alnus* decline.

The role of pathogens as a cause of the *Alnus* decline was also speculated by Sarmaja-Korjonen (2003), who considered it, however, a less likely reason for the event because of doubts about whether a pathogen would destroy *Alnus* on such a scale that it would appear in pollen diagrams and whether the damage caused by a pathogen would persist for hundreds of years. We now know that pathogen outbreaks can occur on continental spatial scales, covering hundreds of thousands of square kilometres and impacting trees and forests to an extent that can be clearly reflected in the pollen values of the host species (Bradshaw and Sykes, 2014) and the abundant presence of parasite spores (van Geel and Andersen, 1988). In addition, the decline would not be an event where one generation of trees is killed, but rather the pathogen would exert influence over tens or hundreds of years (Latałowa et al., 2013; Waller, 2013).

One possible cause of such a pathogen outbreak could be ~~is~~ *Phytophthora* sp. *Phytophthora* is a genus comprising about 150 known taxa of fungi that are responsible for over 66% of fine root diseases and over 90% of collar rots of woody plants in different parts of the world. Currently, in Europe, about

20 indigenous and alien *Phytophthora* taxa have been detected, most of them heavily devastating tree nurseries and forests. Since the early 1990s, a root and collar rot epidemic caused by interspecific hybrids of *Phytophthora* has led to high levels of mortality of alder in riparian forests in most parts of Europe (Jung et al., 2016). Although the present-day ~~fungus is~~ most virulent to ~~the~~ alder *Phytophthora alni* subsp. *alni*~~,~~ is a recent hybrid (Brasier et al., 2004), we may suspect a similar process in the past, especially because several *Phytophthora* species are probably indigenous in European forests (Santini et al., 2013), and experimental studies have shown that a range of non-host-specific taxa of this genus may be a serious threat to *A. glutinosa* (Haque and Diez, 2012). Floods and droughts are generally recognized as the main risk factors for *Phytophthora* epidemics (Strnadová et al., 2010; Sturrock et al., 2011; Aguayo et al., 2014). As a relatively soft-xylem species, *A. glutinosa* has been found to be vulnerable if exposed to flash floods because high discharge and debris transport often result in wounded trees, increasing their exposure to pathogens (Ballesteros et al., 2010). Moreover, summer flooding and persistent stagnant water after the event may damage alder roots because of anoxia, as has been recorded along several European rivers in recent times (Bjelke et al., 2016). *Phytophthora* zoospores are transported by water, and floods are thus an important vector for their effective and rapid spread. The recently observed alder dieback spread over large areas of Europe roughly over a decade (Jung and Blaschke, 2004).

We thus propose that the *Alnus* decline at the end of the first millennium CE was an effect of factors similar to those involved in the present-day mass damage to alder forests. The decline may have been initiated by large-scale flood events that damaged the alder stands and disseminated *Phytophthora* spores over large areas. The subsequent dry period would reinforce the effect of a pathogen outbreak. According to Desprez-Loustau et al. (2006), field observations confirm the stimulating effect of alternating wet and dry periods on the disease.

As already discussed in our earlier paper (Stivrins et al., 2017), the difficulty of detecting whether the pathogen outbreak was the cause of the *Alnus* decline is the lack of direct fossil data that would reflect the occurrence of any pathogen in our records. The remains of some fungi are preserved in a fossil state and sustain the chemical treatment used for preparing pollen samples (van Geel and Aptroot, 2006), but in the case of *Phytophthora*, only molecular biology methods would be effective (Stivrins et al., 2017). Considering some indirect arguments, it is interesting to note the mass occurrence of the remains of *Coniochaeta lignaria* concurrent with the on-site *Alnus* decline in Gdańsk (Święta-Musznicka and Latałowa, 2016). Although this endophytic fungus has a wide spectrum of occurrence, it is also known from its concomitance with *Phytophthora* and from its antagonistic effects against this plant pathogen (Kokaew et al., 2011).

Conclusions

An abrupt, episodic *Alnus* population decline at the end of the first millennium CE was a widespread event that has been so far well documented for southern Finland, western Russia, the Baltic countries, and northern and central Poland. It has also been identified in some sites in Germany, Denmark, and southern Sweden. The data collected in the present paper suggest that the decline was roughly synchronous and most likely took place at around the 9th –10th century, with a strong indication for the 10th century. However, further examination is needed for a more precise determination of both the geographic range of the *Alnus* decline and its dating. This information would help to address whether the earlier *Alnus* decline records reflect earlier, separate events or if the *Alnus* decline was a time-transgressive process. In this case, a reconstruction of the spatio-temporal pattern of the geographical range of the *Alnus* decline would be important.

Our current hypothesis on the causes of the *Alnus* decline involves distinct climatic shifts as a factor initiating the widespread collapse of the alder forests. Our data intrinsically preclude the precision of dating the *Alnus* decline that would enable us to correlate it with any concrete climatic event dated by a dendrochronological method or shown by historical sources (see Blaauw, 2012). We may only hypothesize that one or a series of sharp climatic extremes that occurred in the 9th-10th centuries would initiate this ecological disturbance. Our core idea here is that the climatic events were followed by the spread of a pathogen and its subsequent outbreak. According to current observations on the decline of alder stands in many European regions due to *Phytophthora* outbreaks, we hypothesize that a similar process could have occurred in the past. For a more definitive identification of the potential disease agents, specific studies involving molecular biology methods are needed.

Two important aspects of the present study require emphasis. First, our finding that the *Alnus* pollen decline reflects a roughly synchronous event indicates that it can be used as an over-regional chronostratigraphic marker for c. 800-1000 CE in pollen diagrams from a large portion of the European Lowland. Second, our study provides insight into the role of abrupt, short-term climatic shifts as a primary stress factor leading to the higher vulnerability of alder (mainly *A. glutinosa*) populations in Europe against a potential pathogen outbreak. This critically important species in river valley ecosystems has been seriously threatened in many European regions in recent years, so knowledge about a similar, catastrophic decline occurring one thousand years ago is of special importance for the management of riverine forests following both nature conservation and economic issues. Considering the synchronicity of the *Alnus* decline over a large geographic region and that the location of the most important habitats for alder are in connection with rivers, which is similar to the present-day observation, the critical role of floods is strongly suggested as both a stress factor for alder trees and an agent for rapidly disseminating pathogen propagules. Our study also illustrates in a long-term perspective the great resilience of alder that enables natural, successful regeneration of its stands if environmental conditions improve.

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Figure legends

Fig. 1 (A~~a~~) Location of the study area and the *Alnus* decline sites outside Poland; (B~~b~~) the area of Poland covered by the present paper; and (C~~c~~) the area covered by earlier papers on the *Alnus* decline

(Sarmaja-Korjonen, 2003; Saarse et al., 2010; Stivrins et al., 2017). ~~On map ‘b’, green dots were used for~~a- pollen sites where the *Alnus* decline was well expressed, b- ~~and yellow dots were used if~~pollen sites where the event was lacking or weakly expressed; site numbers follow the list of sites (Table S1): Bråtamossen (Lagerås, 1996), Fiolen Lake (Fredh et al., 2013), Store Mosse Bog (de Jong and Lagerås, 2011), Holmegaard Bog (Aaby, 1988), Belau Lake (Dörfler et al., 2012), Felchowsee and Grosser Krebssee (Jahns, 2000), Holzmaar Lake and Meerfelder Maar Lake (Litt et al., 2009)

Fig. 2 Simplified pollen diagrams from selected lakes illustrating the *Alnus* decline against changes in other tree taxa, indicators of settlement activity and selected indicators of lake environment: Lake Czechowskie (Obremska and Ott, unpubl.), Lake Suminko (Pędziszewska et al., 2015), Lake Mełno (Noryśkiewicz, 2013), and Lake Zarańskie (Noryśkiewicz, 2014); dating of Lake Mełno and Lake Zarańskie sediments acc. to indirect premises (see Methods); site numbers as in Fig. 1 and ESM Table S1 (available online)

Fig. 3 Simplified pollen diagrams from the selected peat bogs illustrating the *Alnus* decline against changes in the other tree taxa, indicators of settlement activity and selected indicators of local hydrology: BIA/314D and BIA/318C (Zimny, 2014), Czerlon (Latałowa et al., 2016), Bagno Kusowo (Lamentowicz et al., 2015), and Słowińskie Błota/85 (Latałowa, unpubl.); site numbers as in Fig. 1 and ESM Table S1 (available online)

Fig. 4 *Alnus* pollen percentage values for the period AD 300-1400 in selected sites in Poland: BIA/340G, BIA/131C, BIA/314D and BIA/318C (Zimny, 2014), Czerlon (Latałowa et al., 2016), Lake Czechowskie (Obremska and Ott, unpubl.), Bukrzyno (Pędziszewska, 2008), (Lake Suminko (Pędziszewska et al., 2015), Bagno Kusowo (Lamentowicz et al., 2015), and Słowińskie Błota/85 (Latałowa, unpubl.); Lake Racze/Miedwie (Bloom, 2015); site numbers as in Fig. 1 and ESM Table S1 (available online)

Fig. 5 Analysis of the statistical significance of the decline-rise events in the *Alnus* populations in 11 selected sites in Poland (see the caption of Fig. 4 for site information) using the SiZer analysis (see ESM Figure S1, available online). a- ~~A~~ statistically significant declines, b- ~~is shown with red and a~~ statistically significant rises~~ is shown with a blue line~~; the strongest decline at the end of the first millennium is shown with a dashed line. Because the data for three records was too sparse (BIA/131C, BIA/314D and Bukrzyno/BI), no statistically significant decline-rise events were detected

Supporting information

ESM Table S1 *Alnus* decline – pollen sites; Site category: A – primary sites, B – secondary sites; Decline: a– present, b– no recovery, c– weak or not recorded; Age of the event: start of the decline, minimum value, recovery to the earlier level; EPD – European Pollen Database

ESM Table S2 Environmental metadata for the sites; site type concerns a period of the *Alnus* decline event; o- outflow, i- inflow; site numbers as in ESM Table S1 (available online) and Fig. 1

ESM Table S3 Palaeoecological characteristics around the *Alnus* decline; HI – human impact: h – high, m – moderate, l – low, a – absent; NPPs – *non-pollen palynomorphs*; site numbers as in ESM Table S1(available online) and Fig. 1; for references, see Table S1

ESM Figure S1 The results of the SiZer analyses of *Alnus* pollen curves in selected sites in Poland (for site information, see the caption of Fig. 4 in the main text). In the maps, the horizontal axis represents the time, the vertical axis represents the scale and the colour of each pixel represents the significance of the derivative of the smooth of the curve at the corresponding time and scale. Red, blue and purple indicate that the derivative is significantly negative, positive or neither, respectively. Grey means that the data are too sparse for inference. The most suitable scales for the detection of the significant decline-rise events in the data are shown with vertical lines. The scale that reveals the decline-rise event at the end of the first millennium is shown with a yellow line, and the scales for the other events are shown with green lines

Table 1 Radiocarbon dates and results of their calibration for the *Alnus* decline in Polish sites, with site numbers as in Fig. 1 and Table S1; for references see Table S1

Site No.	**Site name**	**Lab. No.**	**Age ^{14}C BP**	**Median AD**	**Calibration (2σ) AD**	**Position of the date in relation to the event**
1	Lake Racze/Wolin	Poz-74501	1135±30	919	777–986	Decline
		Poz-74500	805±30	1235	1170–1273	Full recovery
3	Wolin II/00	Poz-29758	1015±30	1014	971–1149	Decline
		Poz-29760	900±30	1123	1039–1210	Recovery
4	Lake Racze Miedwie	Poz-49125	955±30	1096	1022–1155	Minimum/early
		Poz-49124	935±30	1105	1030–1175	Full recovery
7	Bagno Kusowo	Poz-55359	1055±35	988	895–1028	Decline/minimum
9	Słowińskie Błota	Gd-1879	1000±40	1032	975–1155	Start of the recovery
10	Kluki	Gd-565	865±60	1166	1038–1261	Recovery
11	Darżlubie Forest	Gd-1032	1125±55	911	774–1014	Decline
12	Gołębiewo (G/I)	Poz-3624	1030±30	1005	901–1116	Decline
		Poz-49034	895±35	1130	1039–1215	Full recovery
13	Gdańsk-Pszenna	Poz-45048	1155±30	881	775–969	Decline
		Poz-31661	840±35	1202	1152–1267	Full recovery
14	Gdańsk-Żytnia	Poz-31658	1215±30	812	694–889	Before the decline
		Poz-31657	1110±30	937	879–1013	Minimum
16a	Stążki/2008	Poz-15781	1100±30	946	887–1013	Minimum
		Poz-15782	1090±30	954	892–1014	Minimum
		Poz-15780	1025±30	1005	945–1110	Recovery
17	Bukrzyno (B/I)	Poz-19361	1030±30	1005	901–1116	Minimum
18	Lake Suminko	GdA-2517	930±30	1099	1025–1165	Recovery
19	Lake Czechowskie	Varves		970	±10 varve years	Decline
				1020		Minimum
				1090		Early recovery
				1120		Full recovery
31a	Linje	Poz-56402	1145±35	896	776–978	Decline/minimum
		Poz-54918	995±35	1035	995–1145	Full recovery
42	Lake Żabińskie	Varves		870	+12/-24 varve years	Decline
				920		Minimum
				1060		Early recovery
				1090		Full recovery
43	Mechacz Wielki	Poz-46146	1095±30	950	890–1013	Early recovery
44	Lake Szurpiły	Varves		830	±42 years	Decline
				930		Minimum
				980		Early recovery
				1010		Full recovery
48	BIA/318C	Poz-39678	1080±30	966	894–1018	Decline/minimum
49	BIA/314D	Poz-52241	1115±30	933	779–1013	Decline/minimum
		Poz-58946	850±25	1195	1154–1258	Recovery
52	BIA/131C	Poz-39672	1220±40	803	684–892	Below the decline
		Poz-35662	685±30	1296	1267–1389	Full recovery
54	Czerlon	Poz-78644	1080±30	966	894–1018	Decline/minimum

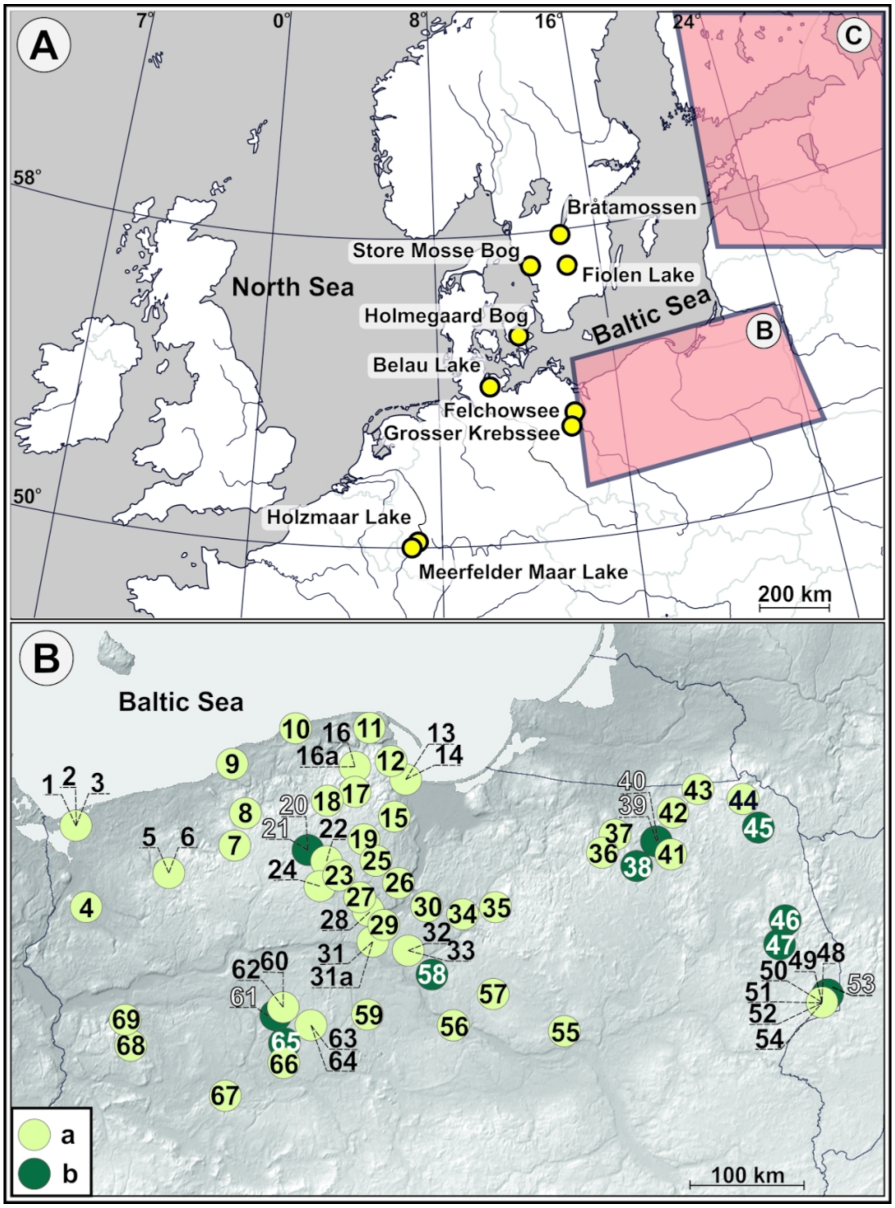

Fig. 1 (A) Location of the study area and the Alnus decline sites outside Poland; (B) the area of Poland covered by the present paper; and (C) the area covered by earlier papers on the Alnus decline (Sarmaja-Korjonen, 2003; Saarse et al., 2010; Stivrins et al., 2017). a- pollen sites where the Alnus decline was well expressed, b- pollen sites where the event was lacking or weakly expressed; site numbers follow the list of sites (Table S1): Bråtamossen (Lagerås, 1996), Fiolen Lake (Fredh et al., 2013), Store Mosse Bog (de Jong and Lagerås, 2011), Holmegaard Bog (Aaby, 1988), Belau Lake (Dörfler et al., 2012), Felchowsee and Grosser Krebssee (Jahns, 2000), Holzmaar Lake and Meerfelder Maar Lake (Litt et al., 2009)

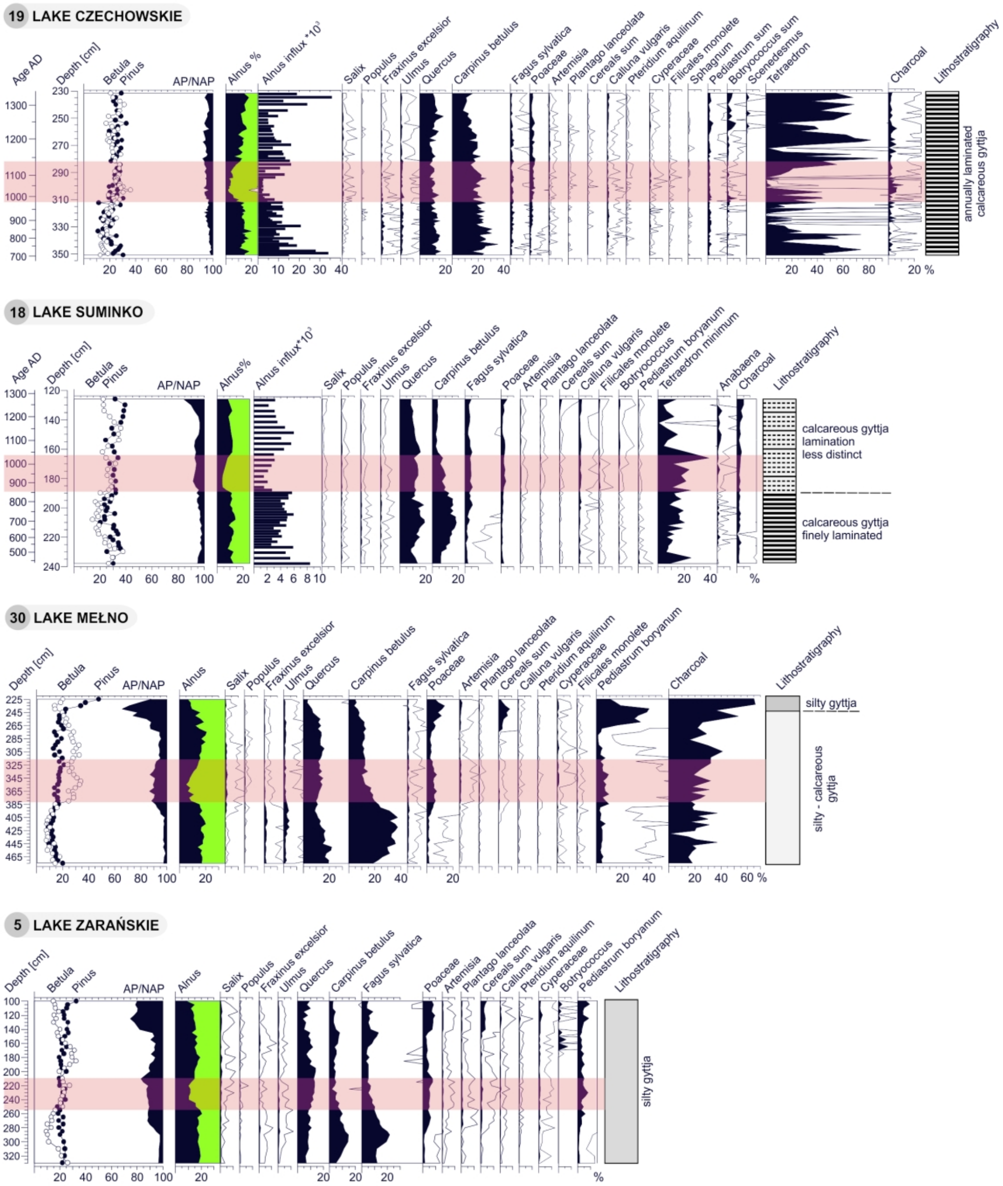

Fig. 2 Simplified pollen diagrams from selected lakes illustrating the Alnus decline against changes in other tree taxa, indicators of settlement activity and selected indicators of lake environment: Lake Czechowskie (Obremska and Ott, unpubl.), Lake Suminko (Pędziszewska et al., 2015), Lake Mełno (Noryśkiewicz, 2013), and Lake Zarańskie (Noryśkiewicz, 2014); dating of Lake Mełno and Lake Zarańskie sediments acc. to indirect premises (see Methods); site numbers as in Fig. 1 and ESM Table S1 (available online)

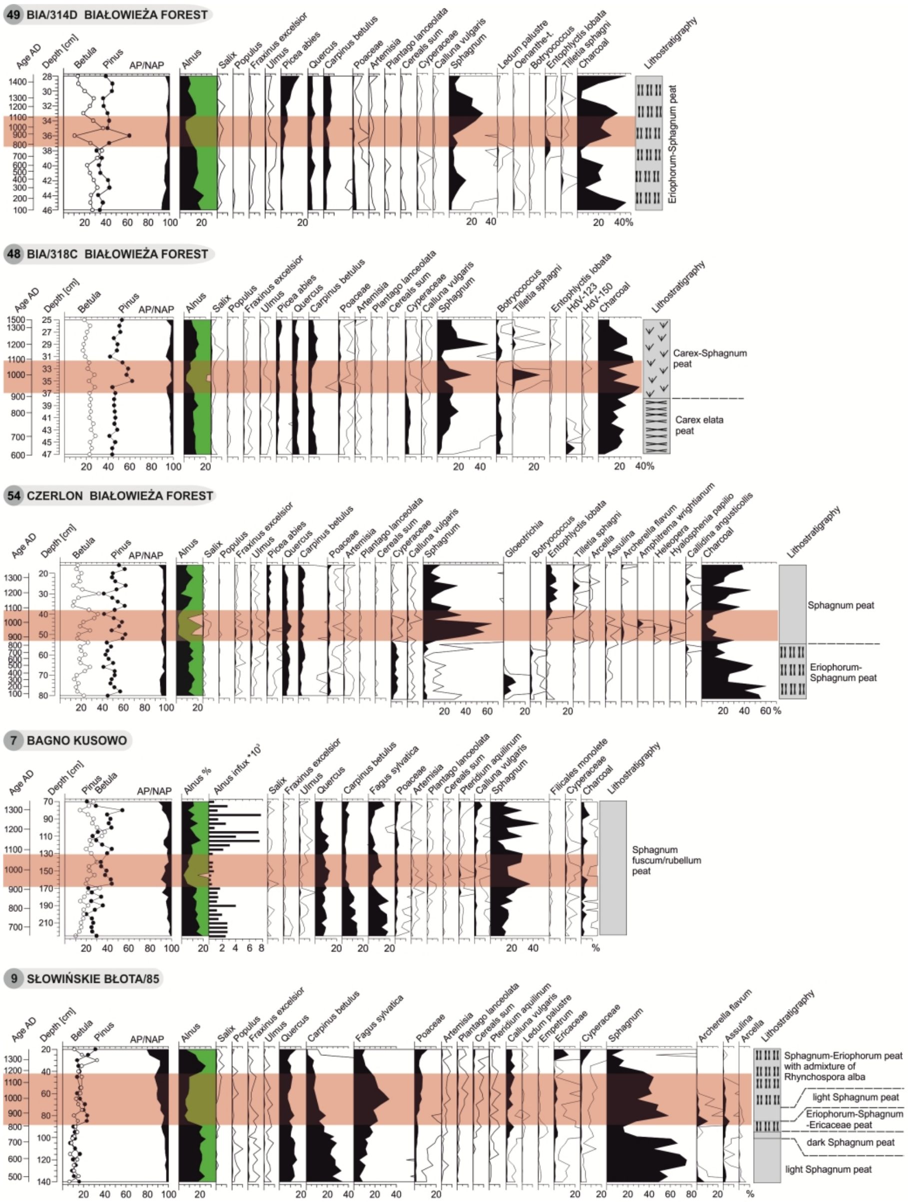

Fig. 3 Simplified pollen diagrams from the selected peat bogs illustrating the Alnus decline against changes in the other tree taxa, indicators of settlement activity and selected indicators of local hydrology: BIA/314D and BIA/318C (Zimny, 2014), Czerlon (Latałowa et al., 2016), Bagno Kusowo (Lamentowicz et al., 2015), and Słowińskie Błota/85 (Latałowa, unpubl.); site numbers as in Fig. 1 and ESM Table S1 (available online)

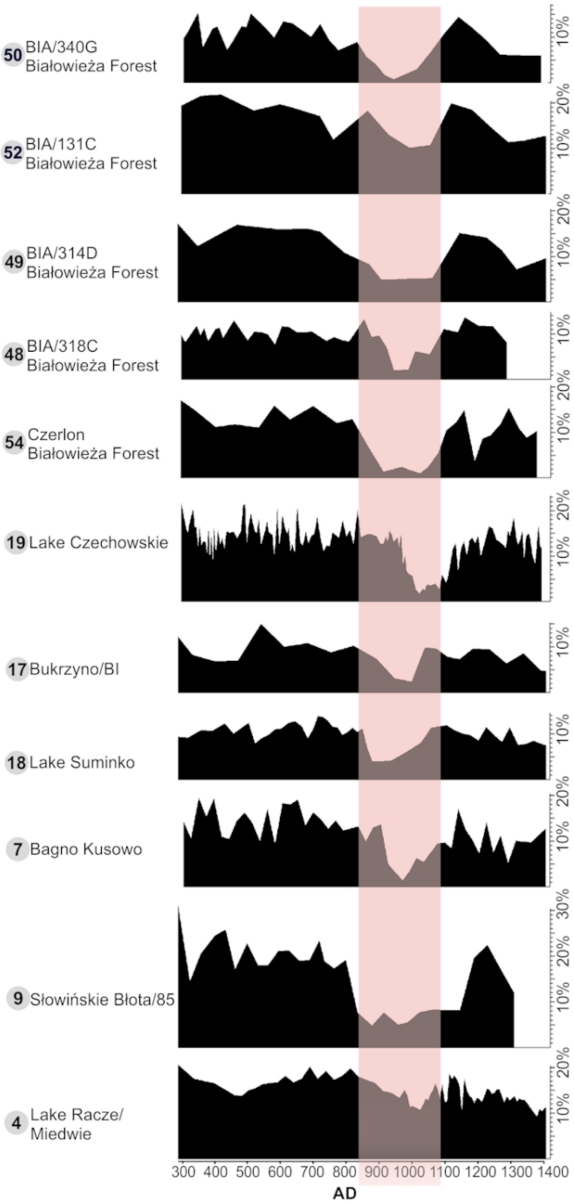

Fig. 4 Alnus pollen percentage values for the period AD 300-1400 in selected sites in Poland: BIA/340G, BIA/131C, BIA/314D and BIA/318C (Zimny, 2014), Czerlon (Latałowa et al., 2016), Lake Czechowskie (Obremska and Ott, unpubl.), Bukrzyno (Pędziszewska, 2008), (Lake Suminko (Pędziszewska et al., 2015), Bagno Kusowo (Lamentowicz et al., 2015), and Słowińskie Błota/85 (Latałowa, unpubl.); Lake Racze/Miedwie (Bloom, 2015); site numbers as in Fig. 1 and ESM Table S1 (available online)

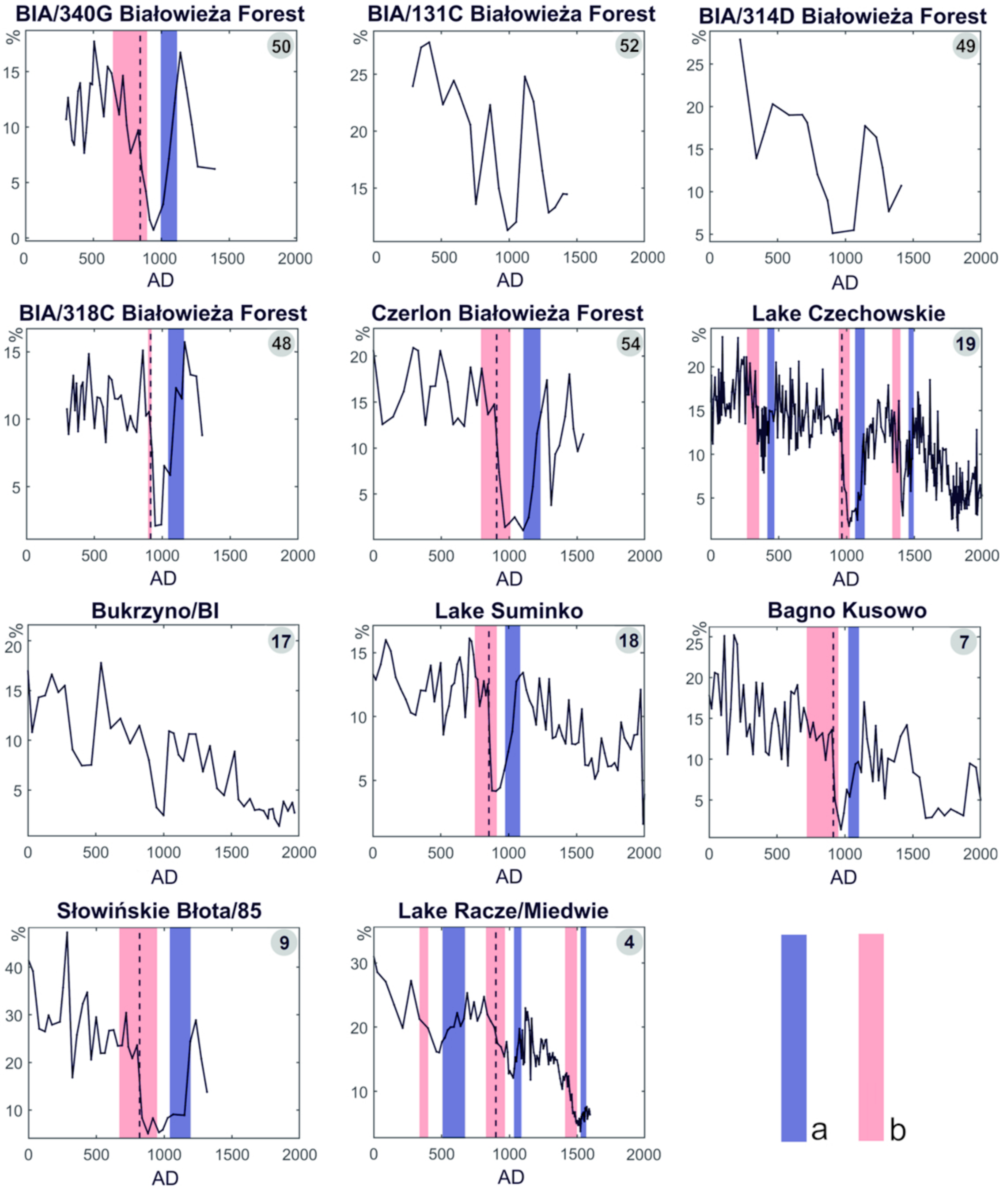

Fig. 5 Analysis of the statistical significance of the decline-rise events in the Alnus populations in 11 selected sites in Poland (see the caption of Fig. 4 for site information) using the SiZer analysis (see ESM Figure S1, available online). a- statistically significant declines, b- statistically significant rises; the strongest decline at the end of the first millennium is shown with a dashed line. Because the data for three records was too sparse (BIA/131C, BIA/314D and Bukrzyno/BI), no statistically significant decline-rise events were detected

ESM Table S1 *Alnus* decline – pollen sites; Site category: A – primary sites, B – secondary sites; Decline: a– present, b– no recovery, c– weak or not recorded; Age of the event (median): start of the decline, minimum value, recovery to the earlier level; EPD – European Pollen Database.

Site No.	Site Name	Geogr. coordinates	Site cat.	Decline			Decline from-to (%)	Dating method	Age of the event (AD)	Comment	Source of data
				a	b	c					
1	Lake Racze/ Wolin Island	53°55’N 14°40’E	A	x			18.5-8.4 (54.6%)	^{14}C dates	800 900 1100		Latałowa M (1992)
2	Kołczewo	53°55’N 14°40’E	A	x	x		26.7-9.7 (63.7%)	^{14}C dates	9th c.	Lack of the top of the profile	Latałowa M (1992)
3	Wolin II/00	53 °50’N 14 °37’E	A	x			10.7-2.1 (80%)	^{14}C dates	10th c.		Pędziszewska A (unpubl.)
4	Lake Racze/Miedwie	53°18’N 14°51’E	A	x			20.2-10.8 (46.5%)	^{14}C dates	800 975 1070		Bloom K (2015)
5	Lake Zarańskie	53°34’N 15°49’E	B	x			20.4-10.6 (48%)	Pollen stratigraphy	ca. 9-10th c.		Noryśkiewicz AM (2014)
6	Lake Gągnowo	53°37’N 15°48’E	A	x			21-9.3 (56%)	^{14}C dates	10th c.		Noryśkiewicz AM (unpubl.)
7	Bagno Kusowo	53°48’N 16°35’E	A	x			ca. 13-<5 (61.5%)	^{14}C dates	900 950 1100		Lamentowicz M et al. (2015)
8	Lake Kwiecko	54°01’N 16°42’E	B	x			ca. 30-5 (83.3%)	Pollen stratigraphy	9-10th c.		Madeja J (2012)
9	Słowińskie Błota/85	54°25’N 16°30’E	A	x			24.2-4.9 (79.8%)	^{14}C dates	860 960 1170		Latałowa M (unpubl.)
10	Kluki	54°42’N 17°17’E	A	x			20.6-3.7 (82%)	^{14}C dates	9-10th c.		Tobolski K (1987); EPD
11	Darżlubie Forest	54°42’N 18°10’E	A	x	x		10.8-4.2 (61.1%)	^{14}C dates	10th c.	Lack of the top of the profile	Latałowa M (1982)
12	Gołębiewo/GI	54°27’N 18°30’E	A	x			11.2-3.2 (71.43%)	^{14}C dates	1040		Pędziszewska A and Latałowa M (2016)

Site No.	Site Name	Geogr. coordinates	Site cat.	Decline		Decline from-to (%)	Dating method	Age of the event (AD)	Comment	Source of data
13	Gdańsk-Pszenna Granary Island	54°20’N 18° 39’E	A	x		44.1-2.2 (95%)	^{14}C dates	880 940 1200	A hiatus around the decline	Święta-Musznicka J and Latałowa M (2016)
14	Gdańsk-Żytnia Granary Island	54°20’N 18° 39’E	A	x		49.5-3.7 (92.5%)	^{14}C dates	9-10th c.		Święta-Musznicka J and Latałowa M (2016)
15	Lake Godziszewskie	54°5’N 18°33’E	B	x		30.1-3.8 (87.4%)	Pollen stratigraphy	ca. 9-10th c.		Miotk G (1986); EPD
16	Stążki/2013	54°25’N 18°05’E	B	x		ca. 15-2 (87%)	Age/depth model	ca. 10th c.		Gałka M et al. (2013)
16a	Stążki/2008	54°25’N 18°05’E	A	x		ca. 10-3 (ca. 70%)	^{14}C dates	10th c.		Lamentowicz M et al. (2008a)
17	Bukrzyno/BI	54°14’N 18°01’E	A	x		10.3-2.4 (76,7%)	^{14}C dates	890 1000 1040		Pędziszewska A (2008)
18	Lake Suminko	54°11’N 17°47’E	A	x		11.1-4 (64%)	^{14}C dates	860 940 1060		Pędziszewska A et al. (2015)
19	Lake Czechowskie	53°52’N 18°14’E	A	x		14.5-1.8 (88%)	^{14}C dates varves	969 1024 1135		this paper
20	Lake Wielkie Gacno	53°47’N 17°30’E	B		x	-	Age/depth model	-	The event unclear	Hjelmroos-Ericksson M (1981)
21	Lake Ostrowite	53°47’N 17°35’E	B		x	-	Age/depth model	-	The event unclear	Milecka K (2005)
22	Lake Suszek	53°43’N 17°46’E	B	x		ca. 22-12 (45.5%)	Pollen stratigraphy	ca. 9-10th c.		Miotk-Szpiganowicz G (1992)
23	Tuchola	53°34’N 17°54’E	B	x		ca.8-2 (75%)	Pollen stratigraphy	9-10th c.	“One sample event”	Lamentowicz M et al. (2008b)
24	Lake Kęsowo	53°33’N 17°43’E	B	x		ca. 20-11 (45%)	Pollen stratigraphy	9-10th c.		Miotk-Szpiganowicz G (1992)
25	Lake Jelonek	53°45’N 18°23’E	B	x		ca. 10-3 (70%)	Pollen stratigraphy	ca. 9th c.		Filbrandt-Czaja A (2009)

Site No.	Site Name	Geogr. coordinates	Site cat.	Decline			Decline from-to (%)	Dating method	Age of the event (AD)	Comment	Source of data
26	Zawada	53°37’N 18°35’E	B	x			17.8-11,4 (36%)	Pollen stratigraphy	ca. 9-10th c.	A hiatus around the decline	Noryśkiewicz B (2004)
27	Lake Mukrz I	53°31’N 18°07’E	B	x			19.6-10.2 (48%)	Pollen stratigraphy	ca. 9-10th c.		Noryśkiewicz AM (2006)
28	Gruczno	53°22’N 18°19’E	B	x			19-3.7 (80.5%)	Pollen stratigraphy	ca. 9th c.		Noryśkiewicz AM (2016)
29	Lake Czyste	53°17’N 18°29’E	A	x			12.9-4,8 (62.8%)	^{14}C dates	770 820 850		Noryśkiewicz AM (2013)
30	Lake Mełno	53°26’N 19°00’E	B	x			20.5-5,2 (74.1%)	Pollen stratigraphy	9-10th c.		Noryśkiewicz AM (2013)
31	Linje	53°11’N 18°18’E	B	x	x		17.9-4 (77.7%)	Pollen stratigraphy	10th c.		Noryśkiewicz AM (2013)
31a	Linje	53°11’N 18°18’E	A	x			ca. 16-8 (50%)	^{14}C dates	9-10th c.		Marcisz K et al. (2015)
32	Lake Kamionkowskie	53°08’N 18°46’E	B	x			14.7-5,5 (62.6%)	Pollen stratigraphy	ca. 10th c.		Noryśkiewicz AM (2013)
33	Gronowo	53°06’N 18°48’E	A	x			15.5-3,6 (76.8%)	^{14}C dates	880 990 1210		Noryśkiewicz AM (2013)
34	Lake Strażym	53°20’N 19°27’E	B	x			19.2-4,5 (76.6%)	Pollen stratigraphy	ca. 9-10th c.		Noryśkiewicz B (1987); EPD
35	Lake Zwiniarz	53 °26’N 19° 50’E	B	x			19.3-5,6 (71%)	Pollen stratigraphy	ca. 9-10th c.	“One sample event”	Noryśkiewicz A (unpubl.)
36	Gązwa	53°52’N 21°13’E	A	x			ca. 15-3 (80%)	^{14}C dates	ca. 8th c.	„One sample event”	Gałka M et al. (2015)
37	Lake Salęt	53°56’N 21°19’E	B	x			-	^{14}C dates	-	-	Szal M et al. (2014)
38	Lake Mikołajki	53°46’N 21°35’E	B			x	-	Pollen stratigraphy	-	Slight decline difficult to date	Ralska-Jasiewiczowa M (1966); EPD

Site No.	Site Name	Geogr. coordinates	Site cat.	Decline			Decline from-to (%)	Dating method	Age of the event (AD)	Comment	Source of data
39	Lake Wojnowo	53°57’N 21°49’E	B	x			-	Age/depth model	ca. 5th c.	Problem with dating?	Wacnik A et al. (2014)
40	Lake Miłkowskie	53°51’N 21°50’E	B			x	-	Age/depth model	-	The event unclear	Wacnik A et al. (2014)
41	Lake Łazduny	53°51’N 21°57’E	B	x			ca. 15-3 (80%)	^{14}C dates	ca. 890	Short, distinct decline	Wacnik A et al. (2012)
42	Lake Żabińskie	54°07’N 21°58’E	A	x	x		ca. 11-2 (82%)	^{14}C dates varves	870 920 1090		Żarczyński M et al. (2019)
43	Mechacz Wielki (MW/I)	54°18’N 22°18’E	A	x			ca. 12-3 (75%)	^{14}C dates	10th c.		Gałka M et al. (2017)
44	Lake Szurpiły	54°13’N 22°53’E	A	x			ca. 12-5 (58%)	Age/depth model, varves	830 930 1010		Kinder M et al. (2013); Kupryjanowicz M and Fiłoc M (2016)
45	Lake Wigry	54°01’N 23°04’E	B			x	-	Age/depth model	-	decline difficult to date	Kupryjanowicz M (2007)
46	Kładkowe Bagno	53°18’N 23°22’E	B			x	-	Pollen stratigraphy	-	Several small episodes difficult to date	Kupryjanowicz M (2004)
47	Maliniak	53°11’N 23°19’E	B	x			6.2-3.7 (40.3%)	Age/depth model	-	The decline weakly expressed	Kupryjanowicz M and Szal M (2015)
48	BIA/318C, Białowieża Forest	52°44’40.8’’N 23°53’40.4’’E	A	x			13.1-2.1 (84%)	^{14}C dates	10th c.		Zimny M (2014)
49	BIA/314D, Białowieża Forest	52°44’45.7’’N 23°50’09.5’’E	A	x			16-4.9 (69.4%)	^{14}C dates	10th c.		Zimny M (2014)
50	BIA/340G, Białowieża Forest	52°44’11.2’’N 23°50’13.0’’E	A	x			8.9-0.7 (92.1%)	^{14}C dates	10th c.		Zimny M (2014); Latałowa M et al. (2015)
51	BIA/317C, Białowieża Forest	52°44’33.2’’N 23°52’37.1’’E	A	x			11.8-4.3 (63.6%)	^{14}C dates	10th c.		Zimny M (2014)

Site No.	Site Name	Geogr. coordinates	Site cat.	Decline		Decline from-to (%)	Dating method	Age of the event (AD)	Comment	Source of data
52	BIA/131C, Białowieża Forest	52°47’59.5’’N 23°50’51.3’’E	A	x		18.2-10.1 (44.5%)	^{14}C dates	10th c.		Zimny M (2014); Latałowa M et al. (2015, 2016)
53	BIA/161 A, Białowieża Forest	52°47’55.0’’N 23°50’48.7’’E	A	x		-	^{14}C dates	10th c.	The decline unclear; sediment disturbances	Pędziszewska A (unpubl.)
54	Czerlon	52°41’17.8’’N 23°44’09.2’’E	A	x		12.8-1.4 (89.1%)	^{14}C dates	10th c.		Latałowa M et al. (2016)
55	Lake Błędowo	52°32’N 20°40’E	B	x		14.1-7.5 (46.8%)	Pollen stratigraphy	ca. 9-10th c.		Bińka K et al. (1991); EPD
56	Lake Gościąż	52°35’N 19°21’E	B	x		18.8-11.8 (37.2%)	^{14}C dates	ca. 9-10th c.	Weak data in the section of the *Alnus* decline	Ralska-Jasiewiczowa M et al. (1998); EPD
57	Lake Białe	52°29’N 19°31’E	B	x		-	Age/depth model	ca. 10th c.	Weak data in the section of the *Alnus* decline	Wacnik A et al. (2011)
58	Lake Steklin	52°57’N 19°01’E	B		x	-	Pollen stratigraphy	-	The event unclear	Noryśkiewicz B (1982); EPD
59	Lake Gopło	52°38’N 18°21’E	B	x		12.5-4.7 (62.4%)	Pollen stratigraphy	ca. 9-10th c.		Jankowska B (1980)
60	Lake Kamionek	52°35’N 17°23’E	B	x		ca. 22-10 (50.5%)	Pollen stratigraphy	ca. 9-10th		Filbrandt-Czaja A (1998)
61	Lake Skrzetuszewskie	52°33’N 17°21’E	B		x	-	^{14}C dates	-	The event unclear	Tobolski K (1991); EPD
62	Lake Lednica I/86	52°33’N 17°23’E	B	x		17.02-7.6 (58.3%)	Pollen stratigraphy	ca. 9-10th c.		Makohonienko M (1991); EPD
63	Lake Głęboczek	52° 39’N 17°38’E	B	x		ca. 19-7 (63%)	Pollen stratigraphy	ca. 9-10th c.		Makohonienko M (2000)
64	Lake Świętokrzyskie	52°32’N 17°35’E	B	x		21.5-6.1 (71.6%)	Pollen stratigraphy	ca. 9-10th c.		Makohonienko M (2000); EPD

Site No.	Site Name	Geogr. coordinates	Site cat.	Decline	Decline from-to (%)	Dating method	Age of the event (AD)	Comment	Source of data
65	Lake Baba	52°25’N 17°22’E	B	x	-	Pollen stratigraphy	-	The event unclear	Milecka K (1998)
66	Giecz 4/90	52°19’N 17°21’E	B	x x	ca. 28-12 (57.1%)	Pollen stratigraphy	ca. 9-10th c.		Milecka K (1998)
67	Lake Wonieść	51°59’N 16°42’E	A	x	ca. 16-5 (68.8%)	Age/depth model	ca. 9th c.		Dörfler W (2011)
68	Lake Paklicko Wielkie	52 °19’N 15°30’E	B	x	13.8-4.3 (69%)	^{14}C dates	10th c.		Noryśkiewicz AM (unpubl.)
69	Lake Długie	52 °28’N 15 °26’E	B	x	18.8-4.1 (78%)	Pollen stratigraphy	10th c.		Noryśkiewicz AM (unpubl.)

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ESM Table S2 Environmental metadata for the sites; site type concerns a period of the *Alnus* decline event; o- outflow, i- inflow; site numbers as in ESM Table S1 (available online) and Fig. 1.

Site no.	Site Name	Site type	Surface (ha)	Outflow inflow	Distance to a river valley (km)	Comment on the local environment and potential habitats for *Alnus*
1	Lake Racze/ Wolin Island	Kettle-hole lake	4.95	-	0.4	Small stream close to the site; patches of *Alnus* forests present nearby to the site
2	Kołczewo	Raised bog	4	-	0.5	Small stream close to the site; local habitats for *Alnus* limited
3	Wolin II/00	Mire/Fen	undefined	-	See comment	Location in large wetland in a river valley; abundant habitats for *Alnus*
4	Lake Racze/ Miedwie	Kettle-hole lake	10	o	2.5	Small temporal outflow to Lake Miedwie; large share of hydromorphic soils and the *Alnus* forest habitats in the surroundings
5	Lake Zarańskie	Channel lake	158.6	o	3	The lake situated in a watershed; *Alnus* forest habitats are fairly common
6	Lake Gągnowo	Channel lake	86	i, o	See comment	Patches of *Alnus* forest present in the vicinity of the lake and along the lake channel
7	Bagno Kusowo	Raised bog	318.8	-	0.2	Numerous lakes, water courses and large wetlands provide suitable habitats for *Alnus*
8	Lake Kwiecko	Channel lake	127	i, o	See comment	A river flows through the lake; large patches of wetlands in the surroundings of the lake
9	Słowińskie Błota/85	Raised bog	120	-	1.5 -2	Peat-bog developed in a watershed; two rivers in the vicinity; large patches of hydromorphic soils
10	Kluki	Raised bog	700	-	1.5	Large peatland at the Baltic coast; abundant habitats for different types of *Alnus* forests
11	Darżlubie Forest	Mire	4	-	2-3.5	Habitats for alder present at the site
12	Gołębiewo	Raised bog	0.6	-	0.8	Several small streams flow through the area; alder forest ca. 2.5 km from the site
13	Gdańsk-Pszenna Granary Island	Fen	undefined	i, o	0.14	Former alluvia in the mouth of the Vistula River covered by alder forest (on the site)
14	Gdańsk-Żytnia Granary Island	Fen	undefined	i, o	0.14	Former alluvia in the mouth of the Vistula River covered by alder forest (on the site)
15	Lake Godziszewskie	Channel lake	169.4	o, i	See comment	Numerous small water courses, wetlands and lakes; alder habitats common
16	Stążki/ 2013	Raised bog	28	-	0.2	The site located in the vicinity of a river valley
16a	Stążki/ 2008	Raised bog	28	-	0.2	The site located in the vicinity of a river valley
17	Bukrzyno/BI	Peat-bog	1	-	4.5	Peat-bog adjacent to a lake; the site located in the area between the large postglacial channels; abundant habitats for *Alnus*
18	Lake Suminko	Channel lake	15	i, o	See comment	Small river flows through the lake; large channel lakes with strips of alder stands in the vicinity of the lake
19	Lake Czechowskie	Channel lake	76.6	o	1.5	Large patches of wetlands in the surroundings of the lake

Site no.	Site Name	Site type	Surface (ha)	Outflow inflow	Distance to a river valley (km)	Comment on the local environment and potential habitats for *Alnus*
20	Lake Wielkie Gacno	Channel lake	13.1	-	7; 4	The lake lies in a long channel lake complex, where patches of hydrogenic soils are limited; also outside the channel habitats for *Alnus* are not common
21	Lake Ostrowite	Channel lake	259	i, o (?)	5	The lake lies in a large channel lake complex
22	Lake Suszek	Channel lake	10	i, o	See comment	Dense river net in the surrounding area; hydrogenic soils are common
23	Tuchola	Peat-bog	2	-	0.4	A kettle-hole mire located within an outwash plain; patches of wetlands fairly common
24	Lake Kęsowo	Channel lake	23.7	??	2	Numerous lakes and patches of wetlands suitable for *Alnus*
25	Lake Jelonek	Cave-in lake	21	-	0.3	Numerous lakes and patches of wetlands; 0.3 km from a meandering river; abundant habitats for *Alnus*
26	Zawada	Peat-bog	20	-	8	Peat-bog situated close to a large channel lake (35 ha); hydromorphic soils common
27	Lake Mukrz/I	Channel lake	43.3	i, o	See comment	Small river flows through the lake; large patches of wetlands in the surroundings of the lake; common habitats for *Alnus*
28	Gruczno	Peat-bog	2.87	-	2.5	Large alluvial plain of the Vistula River; *Alnus* forest on the site
29	Lake Czyste	Channel lake	28.5	i, o	See comment	Small river flows through the lake; the area dissected by small lake channels and patches of wetlands; common habitats for *Alnus*
30	Lake Mełno	Channel lake	162.5	i	2; 2.8	Numerous lakes and patches of wetlands
31	Linje/2013	Raised bog	5.97	-	8	Large patches of alluvia being habitats for alder forests
31a	Linje/2016	Raised bog	5.97	-	8	Large patches of alluvia being habitats for alder forests
32	Lake Kamionkowskie	Channel lake	63.5	-	1.7	Dense hydrological net, numerous lakes connected by watercourses and patches of wetlands; alder carr in the vicinity of the lake
33	Gronowo	Peat-bog	2.3	-	2.7; 7.5	Peat-bog in a channel; alder carr developed on the site
34	Lake Strażym	Channel lake	73.4	i, o	See comment	Dense hydrological net, numerous lakes connected by watercourses and patches of wetlands suitable for alder forests
35	Lake Zwiniarz	Channel lake	53.7	o	See comment	Dense hydrological net including small rivers; common alder forest habitats in the lake catchment
36	Gązwa	Raised bog	204	-	6.5	Raised bog with several mineral islands, situated ca. 2.5 km from a large lake
37	Lake Salęt	Channel lake	327.7	i, o	See comment	The lake lies in the basin of a river; dense hydrological net; common alder forest habitats in the lake catchment
38	Lake Mikołajki	Channel lake	424	i	6	The lake lies in a large channel lake complex; alder carr at the edge of the lake and in the surrounding area

Site no.	Site Name	Site type	Surface (ha)	Outflow inflow	Distance to a river valley (km)	Comment on the local environment and potential habitats for *Alnus*
39	Lake Wojnowo	Channel lake	176.3	o, i	See comment	Several small rivers and watercourses, and a large lake in the vicinity; abundance of hydrogenic soils
40	Lake Miłkowskie	Channel lake	23.7	o, i	1.5	Alder forest habitats are common in the lake catchment
41	Lake Łazduny	Channel lake	10.6	o	4.5	Alder forest habitats are common in the lake catchment
42	Lake Żabińskie	Kettle-hole lake	41	o, i	0.4	The lake is connected with large Lake Gołdopiwo; it is located in the Węgorapa River catchment; local habitats for *Alnus* restricted to the eastern part of the lake catchment
43	Mechacz Wielki	Raised bog	146.7	-	-	The alder carr developed at the edge of the site
44	Lake Szurpiły	Cave-in lake	80.9	i, o	4.5	Dense hydrological net in the area; hydromorphic soils close to the lake and in the river valleys
45	Lake Wigry	Channel lake	2115	i, o	See comment	The lake lies in the basin of the Czarna Hańcza River; the river flows through the lake; abundant habitats for alder forests in the vicinity of the lake
46	Kładkowe Bagno	Raised bog	40	-	2	Patches of alder forest present close to the site
47	Maliniak	Raised bog	0.5	-	2; 3	Dense river net in the area; abundant habitats for alder forests
48	BIA/318C, Białowieża Forest	Peat-bog	0.84	-	1; 2	Rich hydrological net of rivers and small streams; hydrogenic soils are common; patches of riparian and alder carr habitats are frequent
49	BIA/314D, Białowieża Forest	Peat-bog	1.4	-	0.3	As above
50	BIA/340G, Białowieża Forest	Peat-bog	0.26	-	0.65	As above
51	BIA/317C, Białowieża Forest	Peat-bog	2.04	-	1	As above
52	BIA/131C, Białowieża Forest	Peat-bog	5.5	-	1; 0.4	As above
53	BIA/161A, Białowieża Forest	Peat-bog	2.3	-	1.4; 0.4	As above
54	Czerlon	Peat-bog	34	-	1.3	As above
55	Lake Błędowo	Lake	8	o	0.25	The lake lies close to a large river valley; hydromorphic soils in a flood plain
56	Lake Gościąż	Lake	45.5	i, o	See comment	The lake lies in the large Vistula River valley and is included to a smaller river system; wetlands in the river valleys and in the surrounding region are common and provide abundant habitats for *Alnus* forests
57	Lake Białe	Channel lake	150.2	-	0.3	Dense net of lake channels, rivers and patches of wetlands
58	Lake Steklin	Channel lake	100	i, o	1	Dense hydrological net in the area

Site no.	Site Name	Site type	Surface (ha)	Outflow inflow	Distance to a river valley (km)	Comment on the local environment and potential habitats for *Alnus*
59	Lake Gopło	Channel lake	2154.5	i, o	See comment	The lake is connected with a large river; hydromorphic soils common in the surroundings of the lake
60	Lake Kamionek	Channel lake	3	i, o	2	Dense net of lake channels and patches of wetlands provide habitats for *Alnus* forest
61	Lake Skrzetuszewskie	Lake	ca. 2.5	i, o	See comment	The lake lies immediately to the large Lake Lednica; small river flows through the lake; local habitats for *Alnus* restricted to the surroundings of lakes
62	Lake Lednica I/86	Channel lake	348	i, o	See comment	Small rivers flow through the lake; large patches of hydrogenic soils suitable for *Alnus* along the lake
63	Lake Głęboczek	Channel lake	12.5	o	0.24	Dense net of lake channels and small rivers provides habitats for *Alnus*
64	Lake Świętokrzyskie	Channel lake	14	i, o	See comment	Dense net of lake channels and small rivers provides habitats for *Alnus*
65	Lake Baba	Channel lake	2.7	i, o	2.3	*Alnus* forest habitats restricted to lake channels
66	Giecz 4/90	Peat-bog	3	-	0.5	The core taken from an archaeological trench located at the former bridge/causeway crossing wetland; a river in the vicinity of the site
67	Lake Wonieść	Channel lake	121	i, o	2.5 4.3	The lake connected with other 5 other lakes, situated between two rivers; habitats for *Alnus* are common
68	Lake Paklicko Wielkie	Channel lake	196	i, o	See comment	The lake is included to a river system; dense hydrological net and patches of wetlands; potential habitats for *Alnus* forest are common
69	Lake Długie	Channel lake	95.5	i, o	2	Dense hydrological net and patches of wetlands along a meandering river; potential habitats for *Alnus* forest are common

ESM Table S3 Palaeoecological characteristics around the *Alnus* decline; HI – human impact: h – high, m – moderate, l – low, a – absent; NPPs – *non-pollen palynomorphs*; site numbers as in ESM Table S1(available online) and Fig. 1; for references, see Table S1.

Site No.	Site Name	Concurrent decline in tree taxa	Concurrent rise in tree taxa	HI	Changes in sediments and occurrence of local ecosystem taxa (aquatic and mire organisms)	Comment on environmental changes concurrent with the *Alnus* decline
1	Lake Racze/ Wolin Island	*Fagus*	*Pinus, Betula, Salix, Quercus*	h	Sediment change: increase of mineral matter; *Pediastrum* rises	The decline was concurrent with an intensive human impact phase; increase of denudation processes and trophy of the lake
2	Kołczewo	*Fagus, Carpinus*	*Pinus, Salix*	l	*Calluna* expansion and abundant *Sphagnum* spores	Start of the decline at the beginning of a human impact phase; drier condition during the event
3	Wolin II/00	*Ulmus, Corylus, Quercus*	*Salix, Sambucus nigra*	h	Lake sediments replaced by a peat layer; aquatic taxa decline; large peak of HdV-200; rise of *Phragmites*-t. pollen and macrofossils of *Ranunculus sceleratus*, *Juncus* spp. and *Eleocharis* spp.	The decline happened during strong human impact phase accompanied by fire indicators; distinct decline in the water table
4	Lake Racze/ Miedwie	-	*Pinus, Betula, Salix, Populus, Quercus*	h	Lithological limit: an increase of organic matter and fraction of sand in mineral matter total; important trophic changes reflected by NPPs	*Alnus* declined after the *Carpinus* and *Fagus* declines, during an intensive human impact phase; increase of denudation processes and trophy of the lake
5	Lake Zarańskie	*Fraxinus*	*Salix, Betula, Pinus Quercus*	h	*Pediastrum* rises	*Alnus* declined after the *Carpinus* and *Fagus* declines, during an intensive human impact phase; trophy of the lake increased
6	Lake Gągnowo		*Quercus, Betula*	h	*Pediastrum* strongly rises	*Alnus* declined after the *Carpinus* and *Fagus* declines, during an intensive human impact phase; trophy of the lake increased
7	Bagno Kusowo	-	*Pinus, Quercus*	m	Ca. AD 850 short wet shift, recorded on the basis of macrofossils and testate amoeba; gap in *Eriophorum vaginatum*, peak of *Arcella discoides*	*Alnus* declined after the *Carpinus* and *Fagus* declines, during a human impact phase; hydrological instability at the event
8	Lake Kwiecko	-	*Pinus, Betula*	l	Increase of corroded pollen and charcoal in the sediments	*Alnus* declined slightly before the *Carpinus* and *Fagus* declines, and slightly before the beginning of a moderate human impact phase
9	Słowińskie Błota/85	-	*Pinus, Fagus*	l	Lithological limit (*E.vaginatum* layer); rise of *Sphagnum*, peak and then decline of *Assulina, Archerella* and *Arcella*	*Alnus* declined after the *Carpinus* decline at a minute human impact phase; hydrological disturbances: dry-wet-dry shifts

Site No.	Site Name	Concurrent decline in tree taxa	Concurrent rise in tree taxa	HI	Changes in sediments and occurrence of local ecosystem taxa (aquatic and mire organisms)	Comment on environmental changes concurrent with the *Alnus* decline
10	Kluki	*Carpinus*	*Betula*, *Fagus*	1	Peak of *Cladium mariscus* and appearances of *Utricularia*, *Ceratophyllum* and *Pediastrum* immediately below the *Alnus* decline; distinct decline of Cyperaceae, rise of *Calluna* and Ericaceae, and gradual rise of *Sphagnum* at the event level	Low intensity human impact phase; wet-dry hydrological shifts at the beginning of the *Alnus* decline
11	Darżlubie Forest	*Quercus, Carpinus*	*Betula, Pinus, Salix, Fagus*	1	No distinct changes in the sediment; macrocharcoal present	The *Alnus* decline was concurrent with the beginning of a human impact phase
12	Gołębiewo/GI	*Quercus*	*Populus, Quercus*, *Fagus*	1	Filicales rise (small), ombrotrophic taxa still present (*Sphagnum*, *E. vaginatum*); *Assulina* and *Archerella flavum* decrease and then reappear	*Alnus* declined before the *Carpinus* decline, at the beginning of a human impact phase; wet event ca. AD 950-1080 interrupted a dry phase (ca. AD 670-1320)
13	Gdańsk-Pszenna Granary Island	*Fraxinus, Quercus, Carpinus*	*Pinus*	1	Distinct sediment change; local alder groves and oxbows with aquatics replaced by open-fen vegetation with Cyperaceae and Filicales; high frequency of fungi developing on decaying wood	Human activity evidence negligible; distinct drop in the ground water table
14	Gdańsk-Żytnia Granary Island	*Carpinus, Fagus*	*Pinus*	1	Distinct sediment change; local alder groves and oxbows with aquatics replaced by open-fen vegetation with Cyperaceae, Filicales; high frequency of fungi developing on decaying wood	Human activity evidence negligible; distinct drop in the ground water table
15	Lake Godziszewskie	*Betula, Carpinus*	*Pinus*	1	Distinct lithological limit between algae gyttia and coarse detritus gyttia; rise of corroded pollen in the sediments; Filicales monolete spores decline, pollen of Cyperaceae strongly rises	The *Alnus* decline concurrent with the beginning of a new human impact phase; hydrological disturbances immediately before the *Alnus* fall
16	Stążki/2013	-	*Betula, Fagus*	1	*Sphagnum* sect. Acutifolia and *A. flavum* dominate; small peak of *Sph. Cuspidatum* at around AD 1000	*Alnus* declined after the *Carpinus* decline; weak human impact evidence; short dry shift at around the 9th c., wet event at around AD 1000, and then dry shift around AD 1140
16a	Stążki/2008	-	*Pinus, Betula*	1	Decline of *A. flavum*, increase of *Assulina muscorum* and *A. seminulum*	*Alnus* declined after the *Carpinus* decline; weak human impact; wet before the event, decrease of the water table at the alder decline and then wet and dry shifts before AD 1000; strong wet shift c. AD 1100

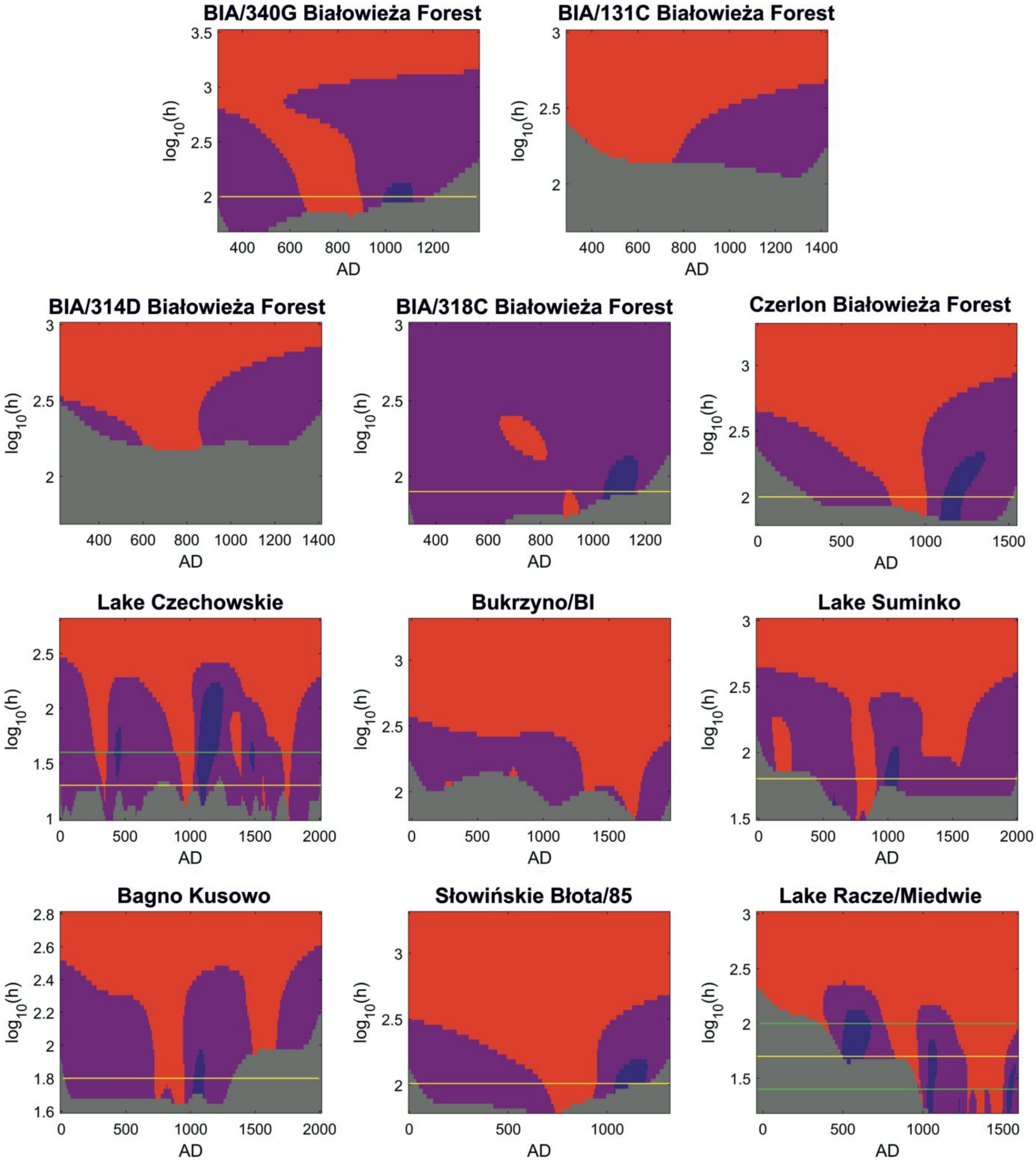
Site No.	Site Name	Concurrent decline in tree taxa	Concurrent rise in tree taxa	HI	Changes in sediments and occurrence of local ecosystem taxa (aquatic and mire organisms)	Comment on environmental changes concurrent with the *Alnus* decline
17	Bukrzyno	*Carpinus, Tilia*	*Betula, Salix, Fagus*	m	Peak of *Sphagnum* and *E. vaginatum* is present; *Daphnia* decreases; *Assulina* spp. and *A. flavum* rise at the recovery of *Alnus*	*Alnus* declined during moderate human impact phase accompanied by fire indicators; wet before the event, drier condition during the event
18	Lake Suminko	*Carpinus*	*Ulmus, Fagus, Betula, Salix*	l	Minute changes in lithology (lamination, color); small increase of Filicales spores and rise of *Anabaena* and *Tetraedron minimum*	*Alnus* declined after the *Carpinus* decline at a minute human impact phase; changing trophy of the lake
19	Lake Czechowskie	No distinct changes in tree taxa	*Betula, Salix*	l	No macroscopic changes in lithology; rapid decrease of *Tetraedron,* small rise of Cyperaceae and Filicales	*Alnus* declined in the condition of a very weak (negligible) human activity
20	Lake Wielkie Gacno	-	-	-	-	The event weakly expressed; unclear
21	Lake Ostrowite	-	-	-	-	The event weakly expressed; unclear
22	Lake Suszek	*Carpinus, Fraxinus*	*Pinus, Betula, Populus, Salix*	l	Lithological limit: algal gyttja changes onto coarse detritus gyttja; *Pediastrum* declines, Filicales, *Phragmites*-t. and Cyperaceae rise	*Alnus* decline was concurrent with the beginning of a human impact phase; lowering of the lake water table
23	Tuchola	-	*Betula*	l	Significant decline of Cyperaceae, peak of *Sphagnum*	*Alnus* declined after the *Carpinus* decline; low intensity human impact phase; dry period
24	Lake Kęsowo	*Carpinus*	*Salix, Populus, Pinus*	l	Unclear	The *Alnus* decline was concurrent with the beginning of a human impact phase
25	Lake Jelonek	*Carpinus* fluctuates	*Pinus, Betula*	l	Decrease of *Pediastrum* and pelagial diatoms, rise of epiphytic and benthic diatoms	*Alnus* declined after the *Carpinus* decline; low human impact phase; lowering of the lake water table
26	Zawada	No data	*Pinus*	l	Hiatus below the event – low water level	Lowering of the lake water table
27	Lake Mukrz I	Small decline of *Carpinus*	*Betula*	l	Change not recorded	*Alnus* declined before the main decline of *Carpinus* at a minute, initial human impact phase
28	Gruczno	-	*Betula, Pinus*	m	Decline of Ericaceae and Cyperaceae, rise of *Sphagnum* and *Amphitrema*	*Alnus* declined after the *Carpinus* and *Quercus* decline, during a human impact phase; drop of the ground water level on the bog
29	Lake Czyste	-	*Pinus, Betula, Corylus*	l	Change in the lithology: the proportions of mineral matter increase; small increase of *Pediastrum*	*Alnus* declined after the *Carpinus* decline at the beginning of a human impact phase; higher lake trophy

Site No.	Site Name	Concurrent decline in tree taxa	Concurrent rise in tree taxa	HI	Changes in sediments and occurrence of local ecosystem taxa (aquatic and mire organisms)	Comment on environmental changes concurrent with the *Alnus* decline
30	Lake Mełno	*Fraxinus, Ulmus*	*Betula, Salix, Quercus*	m	Lithology change not recorded; increase of *Pediastrum*, small peak of Cyperaceae	The *Alnus* decline was preceded by the decline of *Carpinus* and development of a settlement phase; higher lake trophy
31	Linje/2013	*Quercus, Carpinus*	*Pinus, Betula*	m	Decrease of *Assulina, Amphitrema* and *Callidina angusticollis*; increase of *Calluna*, Ericaceae, *Ledum, Sphagnum* and *Entophlictis lobata*;	The *Alnus* decline was concurrent with the beginning of a human impact phase; decrease of the water table
31a	Linje/2016	*Ulmus, Fraxinus, Carpinus*	*Betula, Salix*	m	*A. flavum* declines, *Amphitrema wrightianum* increases together with *Centropyxis aculeata* and *Difflugia globulosa*; *Sphagnum* declines (spores and macrofos dominated by *Sph. magellanicum*), while proportions of *Carex* radicelle strongly increase; *Scheuchzeria palustris* up to 20% of macrofossils at the limit between the phases	The *Alnus* decline was concurrent with the beginning of a human impact phase accompanied with fire indicators; change in the bog wetness just at the alder decline from moderately wet to wet; a short hiatus in-between?
32	Lake Kamionkowskie	*Pinus, Fraxinus*	*Betula, Salix*	l	*Pediastrum* rises	*Alnus* declined after the *Carpinus* decline at the beginning of a low human impact phase; higher lake trophy
33	Gronowo	*Ulmus*	*Pinus, Salix, Betula*	m	Increase of *Calluna* and *Sphagnum*; *Assulina, C. angusticollis Amphitrema* and *Entophlictis lobata* fluctuate	*Alnus* declined after the *Carpinus* decline and after the start of a human impact phase; wet and dry shifts
34	Lake Strażym	-	*Pinus, Betula*	l	*Pediastrum* peaks and then declines	*Alnus* declined after the *Carpinus* decline at a minute human impact phase; lowering of the lake water table (?)
35	Lake Zwiniarz	*Carpinus*	*Betula*	l	Not recorded	The *Alnus* decline was concurrent with the beginning of a human impact phase
36	Gązwa	*Picea*	*Betula*	l	Ca. AD 600 – AD 950 *Sph. fuscum/rubellum* replaced by *Sph. cuspidatum*; *A. wrightianum* rises, *A.flavum* declines; peak of *E. vaginatum*	*Alnus* decline took place at a minute human impact phase; low resolution data for the event (a hiatus?); high water level before the event, then rapid drop at the *Alnus* decline and again higher water level at the alder recovery
37	Lake Salęt	*Betula, Salix*	*Picea*	a/l	No data	The *Alnus* decline contemporary with the decline of settlement indicators
38	Lake Mikołajki	-	-	-	-	The event weakly expressed; unclear

Site No.	Site Name	Concurrent decline in tree taxa	Concurrent rise in tree taxa	HI	Changes in sediments and occurrence of local ecosystem taxa (aquatic and mire organisms)	Comment on environmental changes concurrent with the *Alnus* decline
39	Lake Wojnowo	*Populus, Salix*	*Betula, Corylus, Fraxinus*	m	Increase of Cyperaceae	The *Alnus* decline dated to the 5th century, concurrent with a distinct human impact phase
40	Lake Miłkowskie	-	-	-	-	The event unclear due to the low resolution pollen data?
41	Lake Łazduny	*Carpinus, Quercus*	*Betula, Pinus*	l	Decline of *Tetraedron* and *Botryococcus*; peaks of Cyperaceae, Filicales and *Phragmites*-t.	Low resolution data; decline of the lake water table
42	Lake Żabińskie	*Carpinus*	*Pinus, Quercus*	l	No data	The event concurrent with a low human impact phase
43	Mechacz Wielki (MW/I)	*Picea* rises and then falls	*Betula, Pinus*	l	Short peak of *Sph. cuspidatum* within a *Sph. rubellum/fuscum* phase	Indicators of human activity absent; ca. AD 800 decrease of water level and up to AD 1050 stable hydrological conditions; short wet event at the *Alnus* decline (MWII); wet phase at the alder regeneration ca. AD 1050 (Oort Minimum)
44	Lake Szurpiły	*Carpinus, Fraxinus*	*Betula, Populus, Salix*	l	No data	Scattered pollen of anthropogenic indicators
45	Lake Wigry	-	-	-	-	The decline difficult to date
46	Kładkowe Bagno	-	-	-	No data	Several *Alnus* pollen curve fluctuations
47	Maliniak	Fluctuation of most of the tree taxa	*Pinus, Betula*	l	No data	The decline weakly expressed; low human impact phase
48	BIA/318C, Białowieża Forest	Fluctuation of most of the tree taxa	*Pinus*	a	Decrease of *Calluna* and Cyperaceae; gap in *Botryococcus* and *Carex elata* (macros); peaks of *Sphagnum* and *Tilletia sphagni*	Indicators of settlement absent and strong decline of fire proxies; water table lowering on the peat-bog
49	BIA/314D, Białowieża Forest	Fluctuation of most of the tree taxa	*Pinus, Picea, Salix, Tilia*	a	Decrease of *E. vaginatum, Andromeda polifolia, Ledum,* Cyperaceae, *Entophlictis lobata* and *Botryococcus*; significant increase of *Sphagnum* and *T. sphagni*; abundant microcharcoal	Indicators of settlement almost absent, but those of fires present; water table lowering on the bog
50	BIA/340G, Białowieża Forest	Fluctuation of most of the tree taxa	*Pinus*	l	Decrease of *Sphagnum*, *T. sphagni* and *E. vaginatum*; increase of *Calluna,* Cyperaceae and Filicales	Beginning of a weak settlement; hydrological disturbances on the bog

Site No.	Site Name	Concurrent decline in tree taxa	Concurrent rise in tree taxa	HI	Changes in sediments and occurrence of local ecosystem taxa (aquatic and mire organisms)	Comment on environmental changes concurrent with the *Alnus* decline
51	BIA/317C, Białowieża Forest	*Salix, Fraxinus, Corylus*	*Pinus, Betula, Picea*	a	Disappearance of green algae (*Botryococcus, Spirogyra, Zygnema, Mougeotia*); peak of *Sphagnum* and *T. sphagni*	Indicators of settlement absent; decrease of the water level on the bog
52	BIA/131C, Białowieża Forest	*Ulmus, Fraxinus, Salix*	*Picea*	a	Increase of *Calluna,* peak of *Sphagnum,* important rise of *E. lobata*	Indicators of settlement almost absent; hydrological disturbances on the bog
53	BIA/161A, Białowieża Forest	-	-	a	-	The *Alnus* difficult to identify; hydrological disturbances on the bog; human activity negligible
54	Czerlon	*Betula*	*Pinus*, *Salix*, *Picea, Quercus*, *Carpinus*	a	Decline of the mire indicators (Cyperaceae), expansion of the raised-bog taxa: important rise of *Sphagnum*, small peaks of *A. wrightianum*, *A. flavum*, *Assulina*, *Heleopera, Hyalosphenia papillo*; rise of *E. lobata* at the end of the phase	Indicators of settlement almost absent, indicators of fires decline; wet conditions before the alder decline, then dry and wet shifts; ombrotrophication of the bog
55	Lake Błędowo	*Carpinus, Quercus, Fraxinus*	*Betula, Populus, Salix*	l	Increase of diversity and considerable fluctuation of the planktonic diatoms	The event concurrent with an early human impact phase; before and during the *Alnus* decline higher water level
56	Lake Gościąż	*Carpinus*	*Pinus, Salix, Ulmus, Fraxinus*	l	Small increase of Cyperaceae and then expansion of the pelagial Cladocera; decline of the pollen influx	The low resolution sampling in the section under concern restricts the interpretation; the *Alnus* decline seems to be concurrent with the beginning of an anthropogenic phase; lower water table before the event; after AD 1000 distinct rise of the water table
57	Lake Białe	*Carpinus*	*Pinus, Betula*	l	Poor data	The *Alnus* decline was concurrent with the beginning of a human impact phase
58	Lake Steklin	-	-	-	-	The event unclear
59	Lake Gopło		*Betula, Pinus, Quercus*	m	Not recorded	*Alnus* declined after the *Carpinus* decline, during a moderate human impact phase
60	Lake Kamionek	*Fraxinus, Ulmus*	*Betula, Pinus, Quercus*	l	Decrease of *Pediastrum*, small rise of Cyperaceae	*Al.* declined after the *Carpinus* decline at the beginning of a human impact phase; lowering of the water table

Site No.	Site Name	Concurrent decline in tree taxa	Concurrent rise in tree taxa	HI	Changes in sediments and occurrence of local ecosystem taxa (aquatic and mire organisms)	Comment on environmental changes concurrent with the *Alnus* decline
61	Lake Skrzetuszewskie	-	-	-	-	The event weakly expressed, unclear
62	Lake Lednica I/86	*Ulmus*	*Salix*	m	Significant rise of *Pediastrum* and small of Cyperaceae	*Alnus* declined after the *Carpinus* decline, concurrently with a moderate human impact phase
63	Lake Głęboczek	*Carpinus*	*Salix, Betula, Pinus*	l	Poor data	The *Alnus* decline was concurrent with the very beginning of a weak human impact phase
64	Lake Świętokrzyskie	*Carpinus*	*Betula, Populus, Salix*	m	Lithological limit: decrease of detritus gyttja, increase of calcium carbonate; increase of *Thelypteris palustris*, Filicales and Nympheaceae; peak of *Typha latifolia*	The *Alnus* decline was concurrent with the beginning of a human impact phase; lowering of the lake water table
65	Lake Baba	-	-	-	-	The event weakly expressed, unclear
66	Giecz 4/90	*Fraxinus*	*Betula, Salix, Populus*	l	Strong lithology change: layer of sand; decrease of *Pediastrum* and a rise of Cyperaceae	*Alnus* declined after the *Carpinus* decline at an early human impact phase; hydrological disturbances at the event
67	Lake Wonieść	*Quercus, Ulmus*	*Betula, Pinus*	l	No data	*Alnus* declined after the *Carpinus* decline, during an advanced, moderate human impact phase; slight decline of anthropogenic indicators at the *Alnus* minimum
68	Lake Paklicko Wielkie	*Quercus*	*Pinus, Betula*	m	Local hydrology change not recoded	*Alnus* declined after the *Carpinus* and *Fagus* declines; the decline of a human impact phase
69	Lake Długie	*Quercus*	*Betula, Pinus*	m	Local hydrology change not recoded	*Alnus* declined after the *Carpinus* and *Fagus* declines during a moderate human impact phase; slight decline of anthropogenic indicators at the *Alnus* minimum



ESM Figure S1 The results of the SiZer analyses of *Alnus* pollen curves in selected sites in Poland (for site information, see the caption of Fig. 4 in the main text). In the maps, the horizontal axis represents the time, the vertical axis represents the scale and the colour of each pixel represents the significance of the derivative of the smooth of the curve at the corresponding time and scale. Red, blue and purple indicate that the derivative is significantly negative, positive or neither, respectively. Grey means that the data are too sparse for inference. The most suitable scales for the detection of the significant decline-rise events in the data are shown with vertical lines. The scale that reveals the decline-rise event at the end of the first millennium is shown with a yellow line, and the scales for the other events are shown with green lines