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Long-term vegetation dynamics and land-use history: Providing a baseline for conservation strategies in protected *Alnus glutinosa* swamp woodlands

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ABSTRACT

Alnus glutinosa (alder) swamp woodlands are in danger of disappearing in Europe and, in Norway, several habitats with alder are threatened. Knowledge about the dynamics of alder swamp woodlands is crucial for the conservation and management of this vegetation. Our studied site, Rambjøra, in western Norway encompasses the Rambjøra Landscape Protected Area. We combined information from three sources—recent alder swamp woodland ecology, vegetation history, and agricultural history—to reveal the long-term vegetation dynamics of Rambjøra in relation to land-use. Dynamic changes in the predominance of forest or semi-natural grassland over 2800 years, concurrent with varying anthropogenic disturbances are inferred. At the investigated site, alder swamp woodland developed after forest clearance and changes in the water balance. The abundance of alder swamp woodlands have varied through time, increasing with low-impact land-use and declining with intensified use or abandonment. The highest biodiversity is found in periods with grazing, hay mowing, and probably fodder and fire wood collection. This indicates that agricultural practices of moderate intensity (grazing and hay cutting) should be part of the future management in order to maintain the biodiversity and meet the objective of the protection of Rambjøra. The study demonstrates the advantages of combining vegetation surveys, pollen records, and land-use history to provide a long-term perspective on vegetation development, and in our case also as an aid when establishing conservation strategies. Our findings need to be considered in future conservation and restoration of ecosystems with alder swamp woodlands.

1. Introduction

The main European habitats of *Alnus glutinosa* ((L.) Gaertn.), alder, are alluvial forests and other habitats on wet or moist ground. Several of these habitat types are regarded as in danger of disappearing by the EU's Habitats Directive (Council Directive 92/43/EEC; Interpretation Manual of European Union Habitats – EUR28, 2013). Among them are Fennoscandian deciduous swamp woods and alluvial forests with *A. glutinosa* and *Fraxinus excelsior*, which are listed as priority habitat types. Their conservation status is considered to be "unfavourable – bad" at an EU biogeographical level (European Topic Centre on Biological Diversity, 2012). In Norway, variants of alder swamp woodlands are regarded as vulnerable (Fremstad and Moen, 2001; Lindgaard and Henriksen, 2011). *A. glutinosa* is distinguished from most European tree species by two qualities: its good supply of nitrogen due to symbiosis with nitrogen-fixing bacteria (Franche et al., 2009), and its adaptation to growth in waterlogged soils (Ellenberg et al., 1992; Glenz et al., 2006). In the humid climate of western Norway alder is also common on comparably dry soils and it is often the first tree species to invade grasslands after agricultural abandonment (Fremstad, 1983). To establish baselines for conservation and restoration of vulnerable vegetation types, knowledge of the targeted vegetation's ecology, dynamics and responses to environmental changes is crucial. A further challenge is that today's vegetation, including woodlands, is strongly influenced by former human impact (e.g. Birks, 1996; Foster et al., 1990, 2003; Willis and Birks, 2006). Despite this insight, knowledge of past vegetation and land-use is limited, even in many areas protected for their nature values (Setten and Austrheim, 2012). Palaeoecological research in specific alder swamps or woodlands with alder have shown temporal variations in the abundance of alder over a long

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time scale (Barthelmes et al., 2010; Brown, 1988; Jeffers et al., 2015; Pokorny et al., 2000; Saarse et al., 2010). However, the general picture of the long-term dynamics of alder swamp woodlands in relation to human impact is still insufficient.

To remedy this shortcoming, we explored the *A. glutinosa* swamp woodlands in Rambjøra in western Norway, which includes the Rambjøra *landskapsvernområde* (Landscape Protected Area; LPA). The objective of the Rambjøra LPA is to "preserve a rare combination of several distinctive habitat types, and to protect rare plant and animal species" (our translation). Agricultural land-use has a long history in Rambjøra (Larsen, 1980), but mainly ceased before 1960. In 1981, when Rambjøra LPA was established, shrub encroachment characterised the vegetation (Losvik, 1981). Studies by the first author (Natlandsmyr Lunde, 2000, 2003) suggest that alder swamp woodlands in abandoned cultural landscapes tend to develop towards various deciduous woodland communities, with alder losing its predominance. This led to the idea that alder is favoured by weak agricultural impact. We hypothesise that alder swamp woodlands may occur temporarily in the balance between forest and semi-natural grassland, favoured by low-impact land-use, but decline with intensified use, or with the converse: abandonment and reforestation.

The aim of this paper is to explain the long-term dynamics of *A. glutinosa* swamp woodland in relation to variations in land-use in a protected area. Three sources of information were used: (1) surveys of recent alder swamp vegetation, (2) analysis of fossil pollen assemblages revealing the vegetation dynamics on a longer time scale, and (3) long-term variations in settlement and land-use as recorded in historical data. The focus is on temporal vegetation variability: particularly the alternations between alder swamp woodland and open grassland, and between alder swamp woodland and other deciduous woodland communities. This is made visible through analysis of gradients and temporal changes in the recent vegetation (1975–1995) and of fossil pollen revealing the vegetation dynamics on a longer time scale (ca. 2800 years). By reconstructing the land-use history of the area, changes in the intensity of disturbance associated with farming/grazing management is proposed as a possible driver of change. Based on the results, a conservation baseline and management strategy to meet the conservation aim of Rambjøra LPA is suggested. The findings will also contribute to the conservation of alder swamp woodlands in general.

2. Study area

2.1. Natural conditions

Rambjøra (60.34°N, 5.36°E) is situated in the lowlands of western Norway, about 6 km south of the city centre of Bergen (Fig. 1). The peat core for pollen analyses was taken within Rambjøra LPA, whereas vegetation surveys also include a larger area to the east. The settlement and land-use history encompasses a 4 × 4 km area centred on Rambjøra.

Western Norway belongs to the Atlantic biogeographical region of Europe (EEA, 2005). The climate is oceanic, with relatively cool summers and mild winters. Annual rainfall in Rambjøra is about 2000 mm (Førland, 1993). The growing season is long considering the latitude: with day temperatures exceeding 6 °C for more than 210 days a year (Moen, 1999). The topography of Rambjøra, at both a small and larger scale, is rather rough and uneven, and includes some steep cliffs. The bedrock in most of the protected area and northward is dominated by rather soft rocks: amphibole–garnet mica schist, and locally amphibolite, greenstone or the harder rocks trondhjemite and meta-chert, while harder gneisses, and in the valley bottom in Sandal some moraine material, are sources to the soil farther to the south and east (Fossen and Thon, 1988; Geological Survey of Norway, 2015). The soft rocks weather easily, and the smaller areas of harder bedrock which alternate with the softer create a landscape with ridges and rocks between depressions where erosion and redeposition generates a rather nutrient-rich soil.

The vegetation in Rambjøra LPA today is a mosaic of woodland vegetation and partly overgrown meadows and pastures. The surroundings are of similar vegetation, albeit with increased settlement since 1945. *A. glutinosa* is the most abundant tree species, both on waterlogged soil and, together with *Betula pubescens*, on well-drained soil. Numerous stands of alder swamp woodland were recorded in the area surveyed in 1975 and 1995 (Fig. 1), ranging in size from a few up to a thousand square metres. Only negligible areas of alder swamp woodlands were found within 1 km north- and westwards of the LPA. Rich deciduous woodland with, for example, *Ulmus glabra*, *Tilia cordata*, and *F. excelsior* grows on the steep north- and west-facing slopes of Rambjøra. Several foreign tree species, including *Fagus sylvatica* were planted in the southernmost part of the LPA in 1898–1916. *Picea abies* has been planted in the area since the 1920s.

2.2. Land-use and settlement history

Agricultural activity with cereal cultivation and animal husbandry is likely in the region since the Late Neolithic (2300–1800 BC), as indicated by pollen analysis from the lake Tveitevatnet, 2 km north of Rambjøra (Hagebø, 1967) and lake Kalandsvatn, 6 km to the south (Mehl and Hjelle, 2015). This is in accordance with the general pattern of agricultural expansion in western Norway (Hjelle et al., 2006). The nineteenth century infield–outfield system in the region involved the use of resources in relatively large outfield areas (Byrkjeland, 1958), where the most common practices were livestock grazing, hay mowing, harvesting of leaves and twigs from trees for fodder, and selected tree felling for building material and firewood. Manure was only used on the cultivated fields and hay meadows in the infields. Rambjøra LPA mainly belongs to the farms of Nattland (Nedre and Øvre), Sandal and Tveiterås (Fig. 1), and has probably been used as outfields for these farms. Traditionally the hay meadows were grazed in spring and autumn, and the grass was cut in July or later. No ploughing, reseeding or fertilisation took place in the outfields, and no farm machinery was used (Losvik, 1978; Natlandsmyr Lunde, 2000). Even when artificial fertiliser became common in the region from about 1880, the outfields were hardly ever fertilised (Nedkvitne et al., 1995). Overall, this suggests that agricultural land-use has intermediate disturbance impacts on outfield vegetation.

Rambjøra is located in the former Fana municipality. A settlement history of Fana has been given by the historian Larsen (1980, 1984), based on historical sources, names, and archaeological data. We prepared maps based on his assumptions for the farms in the surroundings of Rambjøra (Fig. 2). The history of these farms may have been as follows (Larsen 1980, 1984): The most ancient farms were taken up along the sea by Nordåsvatnet in the Pre-Roman or early Roman Iron Age (500 BC–AD 200). The first farm in Rambjøra, Nattland, was cleared during the Migration Period (AD 400–570). Nattland covered most of Rambjøra until the beginning of the Viking Period (AD 800–1030). Later Sandal was taken up, Nattland was divided into Øvre and Nedre Nattland, and Tveiterås came into use. Agricultural expansion is reflected on a regional scale from AD 200, with maximum openness of the landscape between AD 600 and 1990 (Mehl and Hjelle, 2015). The existence of a king's farm in Bergen in the Viking Period reflects the importance of the region at that time, which also represents the starting point for development towards the medieval town of Bergen (Helle, 1982; Krzywinski and Kaland, 1984; Hjelle, 2001).

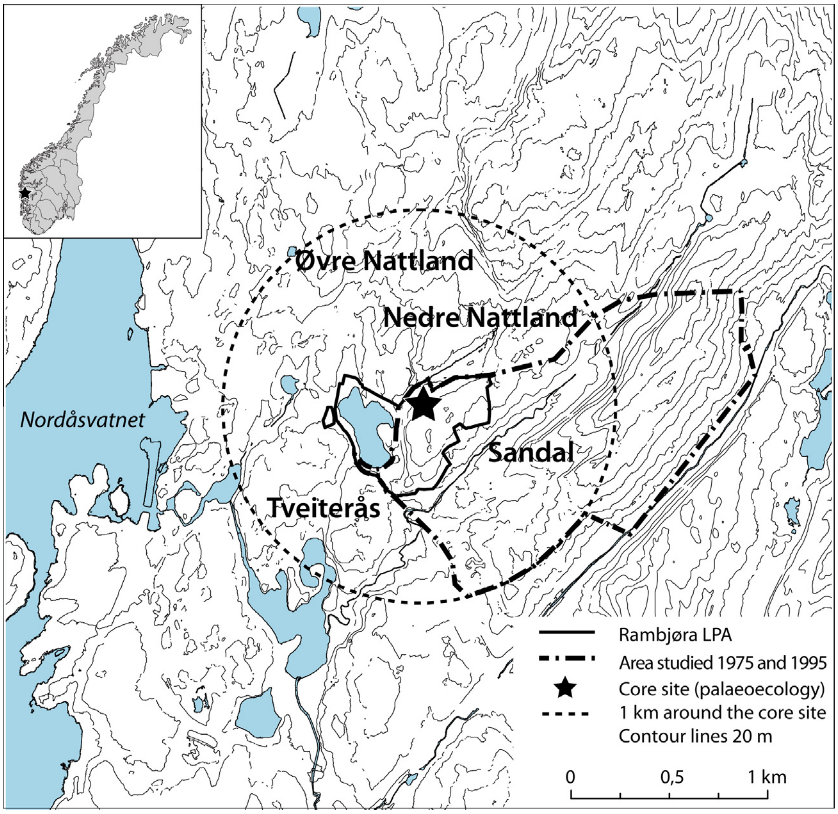


Fig. 1. Topographic map of the Rambjøra area in Bergen, western Norway. The Rambjøra Landscape Protected Area (LPA), the 1975 and 1995 vegetation surveys, and the coring site with a circle of 1 km radius centred on the core site, are marked.

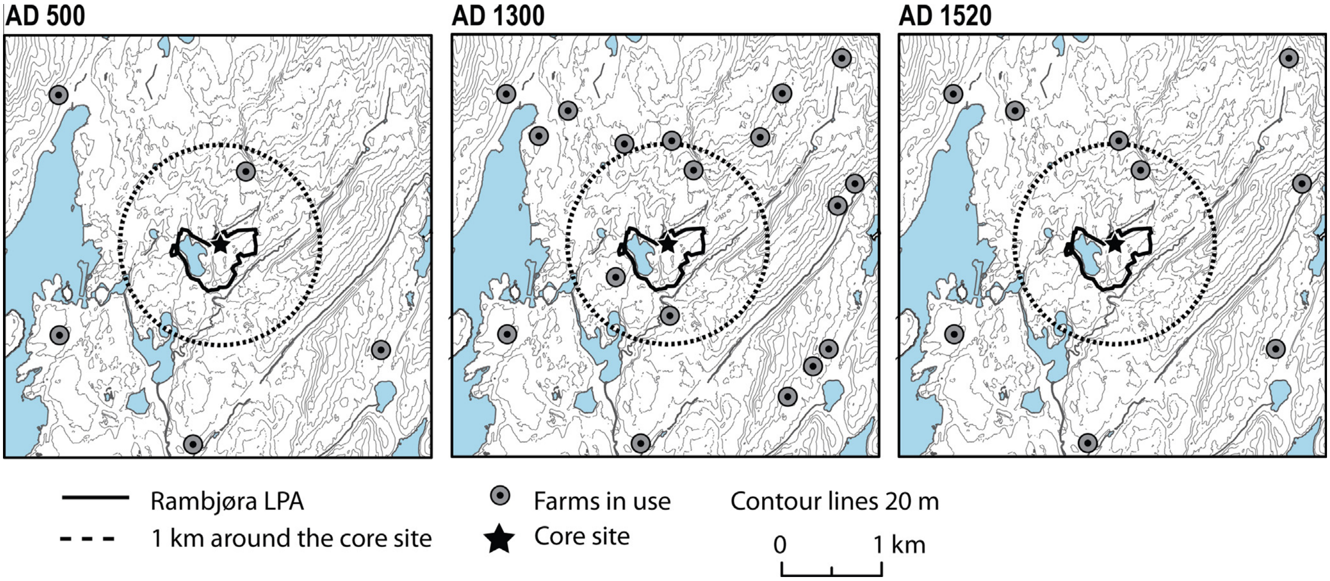


Fig. 2. Temporal development of land-use in the vicinity of Rambjøra, compiled from Larsen's (1980) estimates for each farm. The left map shows farms likely to have been in use by the end of the Early Iron Age (AD 500). The most ancient farms, settled in the Early Roman Iron Age (AD 1–200), are the two farms located near the sea by Nordåsvatnet. The central map shows farms likely to have been in use at the end of the high medieval period (AD 1300) and the map to the right, at the end of the late medieval period (AD 1520).

In the high medieval period (AD 1130–1350), a total of 18 farms existed in the surroundings of Rambjøra. Following the Black Death in AD 1349 half of the 18 farms were abandoned and three farms never came into use again (Larsen, 1980). Both Sandal and Tveiterås probably lay waste during the late medieval period (AD 1350–1537). Not until the seventeenth century the number of farms in the surroundings of Rambjøra came close to high medieval levels.

By the time of Norway's first property registration in AD 1665 each farm was generally run by one family. Later most farms were parcelled out, and each larger farm (*gård*) may comprise several smaller farm holdings (*bruk*) with different owners. The smaller farms are still registered according to the larger farm unit to which they belong. Two farms (*bruk*) taken up on Nedre Nattland around 1800 (Larsen, 1984), lie in the vicinity of the core site in Rambjøra LPA, indicating agriculture intensification at this time. One farm was in use from 1750 until 1960, and farmed by two families between 1898 and 1930. The other farm was farmed between 1813 and 1970 and used by a riding school until 2002. Between the Second World War and about 1960, farming in Rambjøra mainly came to an end.

Within Rambjøra LPA, the easternmost part was grazed by cattle until 2006, and later by sheep. This pasture has been fertilised yearly since the conservation area was established. Some of the south- and west-facing slopes were grazed by sheep until about 1980. Parts are now maintained by yearly cutting and removal of the grass, but with no ploughing, reseeding or application of fertiliser. A restoration project started in Rambjøra LPA in 2005, to open up some of the stands of alder swamp woodlands.

3. Methods

3.1. Recent vegetation

Knowledge of the recent vegetation in the alder swamp woodlands in Rambjøra was gained from vegetation surveys and analyses of soil samples in 1975 and 1995 (Losvik, 1978; Natlandsmyr Lunde, 2000, 2003). Soil samples were collected from five points within all quadrats in 1995 and from 12 of the quadrats in 1975, mixed, and analysed for loss-on-ignition. The vegetation sampling was based on analyses of all homogenous stands (Nordhagen, 1943) of alder swamp woodland, defined as areas with *A. glutinosa* as the most abundant tree species and high ground-water level, often above the ground. The cover of each vascular plant species was recorded within one to five quadrats in each stand, comprising 17 quadrats (4–25 m^2) in 1975 and 35 quadrats (each 25 m^2) in 1995. The exponential Hult-Sernander scale was used (1 =< 1/16 of the quadrat, 2 => 1/16–1/8, 3 => 1/8–1/4, 4 => 1/4–1/2, 5 => 1/2–3/4, 6 => 3/4–1). To compare vegetation data and pollen percentage data, the recorded Hult-Sernander values were converted into percentages prior to the numerical analysis. This was done by using the middle value of the cover in the Hult-Sernander scale (e.g. 1 = 1/32, 2 = 3/32, ..., 6 = 7/8). 100% equals the sum of cover values of all species in the plot. By sampling all stands of alder swamp woodland in both sampling years, the floristic variation within this vegetation is reflected even though the plots were not permanent. The nomenclature used in this paper follows Lid and Lid (2005).

3.2. Palaeoecology

Palaeoecology is based on a pollen core from Øvrebøen (100 m a.s.l.), a rather flat area on a north-facing slope in Rambjøra LPA (Fig. 1). Until about 1950 this was an unfertilised hay meadow, thereafter pasture until 1960 (Natlandsmyr Lunde, 2000, 2003). The core was taken in April 2007, using a 1 m long Russian-type peat corer of 11 cm diameter.

The size of the pollen source area reflected in the pollen core depends on the surrounding vegetation and will change through time. The investigated pollen site is today a "forest hollow", located within an open alder swamp woodland (tree canopy cover < 40%), which is estimated to have a relevant pollen source area of 50–150 m (Bunting et al., 2005; Calcote, 1995; Sugita, 1994). The relevant source area for pollen as defined by Sugita (1994) is the area beyond which the relationship between vegetation and pollen does not improve. The size of the area is found to depend on the patchiness of the surrounding vegetation (e.g. Bunting et al., 2004) and only 30–45% of the pollen deposited may come from within this area (Sugita, 1994). Most herbs, however, are thought to reflect the vegetation at or close to the site (Bunting, 2003; Hjelle, 1997, 1999; Waller et al., 2005). Based on estimates of a relevant source area of 400 m for moss polsters in southern Sweden and estimates of ca. 1000 m for lakes <20 ha in western Norway (Hjelle and Sugita, 2012), an area of radius 1000 m centred on the pollen site is thought to contain the main pollen contributors to the Rambjøra site through time.

In the laboratory, samples for pollen analysis (0.5 cm thickness, volume 1 cm^3) and loss-on-ignition (0.5 cm thickness) were taken from the pollen core. *Lycopodium* spores (Stockmarr, 1971) were added to the samples to enable the calculation of pollen concentrations. The pollen samples were processed using KOH, acetolysis, and HF treatment following Fægri and Iversen (1989). Identification of pollen and spores follows the keys in Fægri and Iversen (1989) with additional use of Beug (2004), Punt and Hoen (1995), and the modern pollen reference collection at the University of Bergen. Two *Alnus* species are found in Norway: *A. glutinosa* and *A. incana*, of which only *A. glutinosa* is growing in Rambjøra today. *A. incana* is rare along the coast of Norway (Lid and Lid, 2005) and we suppose that it is pollen of *A. glutinosa* that we find in the pollen core. *Glyceria fluitans* is included in *Hordeum* type pollen (Beug, 2004), but has in the present study been separated based on a more narrow annulus (Beug, 2004) and more scattered columella than *Hordeum*, according to the reference collection. None of the other wild grass species included in *Hordeum* type following Beug (2004) are thought to have grown in Rambjøra. A minimum of 1000 terrestrial pollen grains (1001–1157) were counted from each sample. In the pollen diagram, percentages for terrestrial pollen and pteridophyte spores are calculated based on the sum of these. Percentages of aquatics (AQP), non-pollen palynomorphs (NPP), and charcoal are based on the same sum + x, where x is the number of the microfossil in question.

The diagram is separated into four pollen zones where each zone reflects a period of stability and zone boundaries represent periods of change. The limits are based on SPLITLSQ and SPLITINF (Birks and Gordon, 1985), using the programme Zone 1.2 (Juggins, 1991).

Three bulk peat samples, two samples of hazel-nut shells and three wood samples were radiocarbon dated (AMS) at Beta Analytic Inc., Miami, USA. The dates were calibrated and plotted using the program Clam, R-code for classical age-depth modelling version 2.2 (Blaauw, 2010), with the Intcal 13 calibration curve (Reimer et al., 2013). All ages are given in calibrated years BC/AD.

3.3. Loss-on-ignition

Samples for loss-on-ignition analysis were dried for 24 h at 105 °C and burned for 6 h at 550 °C. Loss-on-ignition (*Loi*) is calculated as percentage of dry weight.

3.4. Data analysis

Ordinations were performed both with the vegetation data and the pollen data, to illustrate patterns of floristic variation in the recent alder swamp woodlands, and to help reveal the main gradients of the long-term vegetation dynamics. As we wanted to understand the relationship between the long-term vegetation development and the recent alder swamp vegetation, the recent data were treated as supplementary (passive) data in the ordinations of the fossil pollen data. This was made possible by expressing the species in the vegetation data as their palynological equivalents (here called taxa) (see Appendix). To evaluate this method, we compared an ordination of the recorded species with an ordination of species expressed as palynological equivalents. All ordinations were performed by principal components analysis (PCA) as recommended for short gradients (Lepš and Šmilauer, 2003; ter Braak and Prentice, 1988). Detrended correspondence analysis (DCA; Hill and Gauch, 1980) produced gradient lengths of 3.14 (species) and 2.39 (species as palynological equivalents) standard deviations (sd) for the vegetation data, and 1.06 sd for the pollen data. The ordinations were done with square-root transformation of the percentage data to down-weight the effect of species or pollen/spore types with high abundances. The program CANOCO version 4.5 for windows (Lepš and Šmilauer, 2003; ter Braak, 2002), was used for the ordinations, and the diagrams were drawn using Canodraw for Windows 4.0 (Šmilauer 1999–2009).

For the vegetation data, the number of species (*species*) and species expressed as palynological equivalents (*taxa*) per plot were calculated as an aid for evaluating the effects of expressing samples in terms of species composition and the species' palynological equivalents. This relationship was tested by Pearson's product-moment correlation. For the pollen and pteridophyte data, palynological richness was measured using rarefaction analysis in the programs RARECEP and RAREPOLL (Birks and Line, 1992). Rarefaction analysis gives an estimate of the expected number of taxa assuming that the same number of terrestrial pollen and pteridophyte spores had been counted in all samples. The lowest counting sum of identified terrestrial pollen grains and pteridophyte spores, 1125, made the basis for the analysis. The difference in palynological richness between the four pollen zones was tested by a Welch two sample t-test. The statistical analyses were done in R version 2.15.3 (R Core Team, 2013).

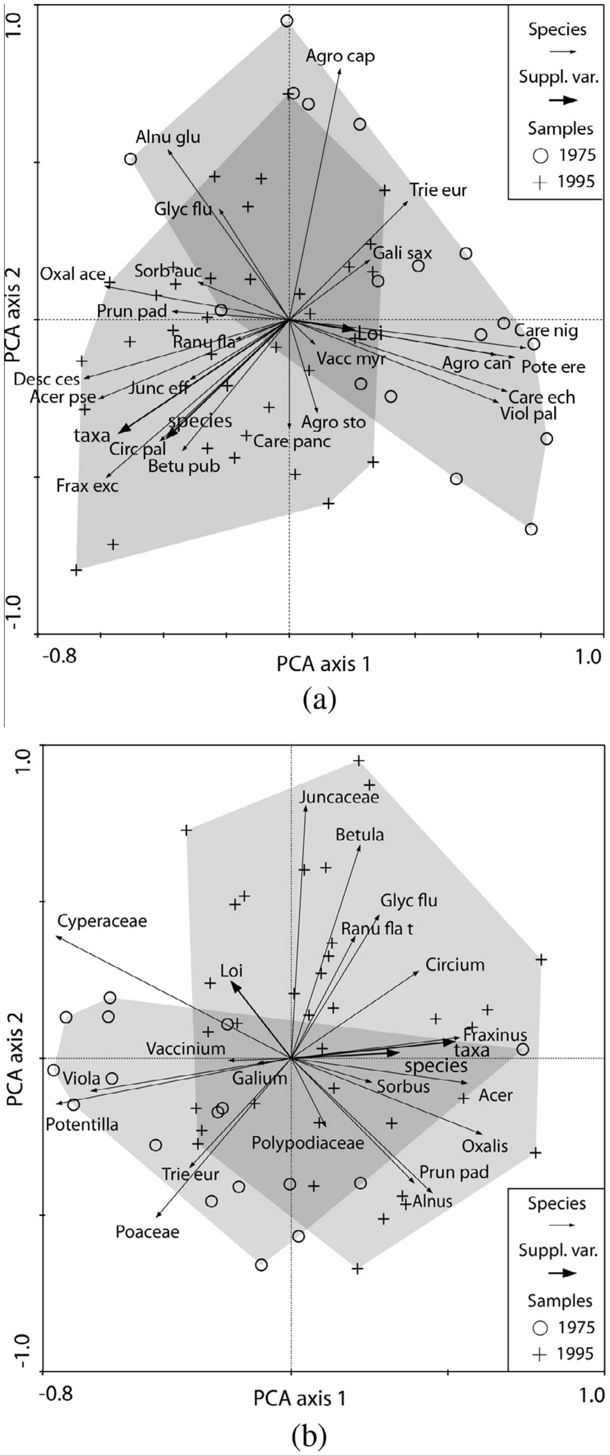
3.5. Historical maps

Maps showing animal husbandry and grazing pressure in selected years from 1665 to 1959 within a 4 × 4 km square around Rambjøra, were prepared to get a picture of the overall variation in land-use in historical time periods. While the maps of the earliest settlements (Fig. 2) are based on historic assumptions (Larsen, 1980), the maps of land-use from 1665 and later are based on public records from the first property registers of Norway and the Norwegian censuses of agriculture (obtained from Larsen, 1984). Grazing pressure was calculated as number of domestic animals per km^2 for each farm, where 1 domestic animal = 1 cow or 1 horse, 3 calves/heifers/bullocks, or 5 sheep/goats, according to their relative fodder uptake (Lein, 1977). Missing data for two farms on the outskirts of the area were replaced by averages from the other farms for the actual years.

All maps were prepared using the software package ArcMap version 9.3.1 (© 1999–2009 ESRI Inc.). The map data were obtained from The Norwegian Mapping Authority.

4. Results

4.1. The vegetation of the recent A. glutinosa swamp woodlands



(a)

(b)

Fig. 3. Principal components analysis biplot of the samples from the alder swamp woodland surveys in 1975 and 1995: (a) using plant species (axis 1: explained variance 18%; axis 2: 9%) and (b) using the species' palynological equivalents (axis 1: explained variance 20%; axis 2: 13%). Species or taxa occurring in at least 1/3 of the plots are shown. Loss-on-ignition (*Loi*) and number of species (*species*) or palynological equivalents per plot (*taxa*) are shown as supplementary variables. See supplementary material for abbreviations, and the relationships between species and their palynological equivalents.

A. glutinosa was prominent in the vegetation plots in the alder swamp woodlands, as stated in the selection criteria. In total, 113 vascular plant species were recorded in the surveys (Fig. 3; see supplementary data for details). The species are grouped into 65 palynologial equivalents (taxa). The major herbs are *Potentilla erecta* and *Trientalis europaea*. Semi-natural grassland species are common, among others *Galium saxatile*, Poaceae, and Cyperaceae (grasses and sedges: e.g. *Deschampsia cespitosa*, *Agrostis capillaris*, *A. canina*, *A. stolonifera*, *Carex panicea*, *C. echinacea*, *C. nigra*). Polypodiaceae (ferns) occur in most plots. Wet-site indicators such as *Viola palustris*, *Glyceria fluitans*, and *Ranunculus flammula* are common. The state of the alder swamp woodlands in 1975 and 1995 reflects vegetation change 15 and 35 years, respectively, after the cessation of farming in 1960. *A. glutinosa* dominated the tree layer almost completely in 1975, but had lower than average cover in

Table 1
Radiocarbon dates from Rambjøra. Calibrations using Clam (Blaauw, 2010) with IntCal13 calibration curve (Reimer et al., 2013).

Laboratory ID	Depth, cm	Material dated	^{14}C age, BP	Calibrated age, 2σ	Outliers
Beta-242312	18–18.5	Peat bulk	510 ± 40	AD 1319–1449	
Beta-242313	38–38.5	Wood	200 ± 40	AD 1642–1954	[a]
Beta-253836	58–58.5	*Corylus* nutshell	520 ± 40	AD 1316–1447	[a]
Beta-237589	68–68.5	*Corylus* nutshell	1200 ± 50	AD 688–962	
Beta-242314	120–120.5	Wood	2710 ± 40	927–803 BC	[a]
Beta-253837	120.5–121	Peat bulk	2370 ± 40	732–381 BC	
Beta-253838	149–149.5	Peat bulk	2640 ± 40	895–778 BC	
Beta-252315	149.5–150	Wood	2220 ± 40	385–198 BC	[a]

[a] Samples treated as outliers in Clam (see Fig. 4).

1995. Other deciduous trees, on the other hand, constituted a substantial part of the tree layer by the latter date, particularly *Acer pseudoplatanus*, *Betula pubescens,* and *Fraxinus excelsior*. The lower abundance of grasses and sedges, and higher abundance of ferns in 1995 compared to 1975 is probably related to the discontinuation of grazing. An accumulation of biomass is expected when hay mowing and grazing come to an end. Loss-on-ignition, which is, on average, 60% in the alder swamp vegetation, showed a slight increase, but is not significantly different from 1975 (56%) to 1995 (62%).

The ordination of the species (Fig. 3a) also indicates ongoing vegetation change, with the first axis reflecting a major gradient from relatively well-lit, nutrient-poor conditions on the right (e.g. *Carex nigra*, *Agrostis canina*, *G. saxatile*, *P. erecta*) to higher abundance of trees and more shady conditions on the left (*Oxalis acetocella*, *A. glutinosa*, *B. pubescens*, *F. excelsior, A. pseudoplatanus*, *Prunus padus*).

The ordination of the species expressed as their palynological equivalents (Fig. 3b) captures the same major gradient along the first axis, with tree taxa to one side and light-demanding field-layer taxa (e.g. Poaceae, Cyperaceae, *Galium*, *Potentilla* type) on the other side (the reversal of the two axes is merely a technical artefact). The samples are distributed similarly along the main gradient in both diagrams, the 1975 samples towards the well-lit conditions and the 1995 samples towards the more shady conditions with trees, implying changes in the alder swamp woodlands from 1975 to 1995. The supplementary variables *species*, *taxa* and *Loi* have their maxima in the same area of the biplot in both analyses.

The similarity between the two diagrams with regard to both the underlying gradients and the location of samples and variables indicates that the species expressed as their palynological equivalents give a good representation of the vegetation in the recent alder swamp woodlands. The two variables (*species* and *taxa*) are strongly and significantly correlated ($r = 0.8984$; $p < 0.001$).

4.2. Long-term vegetation and land-use development

Based on radiocarbon dates (Table 1, Fig. 4), the pollen diagram encompasses a time period from ca. 800 BC until today. The dating results are open to alternative age-depth models and the chronology is based on the following criteria: (1) in the two lowest levels dated, the wood remains gave reversed ages in relation to depth and the dates based on peat samples are used, (2) loss-on-ignition indicates increased organic production from around 75 cm and the date of the lowermost nut shell is accepted as the most reasonable scenario, (3) the loss-on-ignition values decrease in the upper 20 cm and pollen concentration increases. Increased pollen concentration is supposed to reflect lower, not higher, accumulation rate and the date based on peat is used. (4) The upper four cm, with increased *Loi*, are thought to represent the last ca. fifty years with practically no agricultural use of the land, (5) three dates treated as outliers in the model are supposed to represent younger plant material. This could be due to penetration of peat by younger roots included in the dated wood remains, whereas the nutshell may have fallen into a potential open channel in the peat. One date gave an older than expected age which could be due to resedimentation of old wood remains.

The pollen diagram (Fig. 5) is divided into four local pollen zones, RA1–RA4. In zone RA1 (from the Late Bronze Age to the Late Iron Age, ca. 800 BC–AD 650) forest dominated the area, with broadleaved deciduous trees (*Alnus*, *Corylus*, *Tilia*, *Ulmus*) on moist, nutrient-rich ground and mixed *Pinus* – *Quercus* on drier ground, poorer in nutrients. Relatively high values of *Betula*, *Corylus*, and *Sorbus*, as well as the continuous curve of *Juniperus* indicate open woodland. This is further supported by the continuous curve of Poaceae and sporadic occurrence of light-demanding and grazing-tolerant herbs such as *Plantago lanceolata*, *Ranunculus acris* type, *Rumex* sect. *acetosa*, and *Galium* type. Fern spores (Polypodiaceae) are abundant, indicating low grazing pressure compared to later time periods. Fluctuations in the percentages of trees, e.g. *Alnus*, *Pinus*, *Quercus*, *Tilia*, and a general decrease in *Ulmus* may also reflect some utilisation of the woodland. The estimated palynological richness is at its lowest in this zone (mean 26.3), significantly lower than in the three top zones, both together (mean 39.8, $p < 0.001$) and separately (each $p < 0.001$). The low values (<30%) of loss-on-ignition indicate minerogenic soil (Fig. 4). Nattland farm may have been cleared by the end of this zone, while fluctuations in the abundance of trees and the sparse grazing indicators before this may be associated with land-use from farms further away, e.g. those closer to the sea (Nordåsvatnet, Fig. 2, AD 500). Another explanation is that the Nattland area was in use earlier than estimated from the historical evidence of farm establishment. This is supported by recent archaeological excavations indicating agricultural settlement in the Late Bronze Age and Early Iron Age ca. 900 m north of the pollen core site (Halvorsen, 2010; Joki and Ramstad, 2010).

At the start of pollen zone RA2 (Late Iron Age and early medieval period, about AD 650–AD 1150) a decrease in tree pollen (*Pinus*, *Quercus*, *Tilia*, *Ulmus*) is apparent, reflecting forest clearance. The light-demanding taxon *Fraxinus* is continuously present, indicating expansion of ash in an open forest. Increased light is also indicated by an increase in *Juniperus*, *Calluna*, Cyperaceae, and taxa reflecting semi-natural grasslands, such as Poaceae, *P. lanceolata*, *Rumex* sect. *acetosa*, and *Potentilla* type. Human impact is further supported by a decrease in fern spores (Polypodiaceae), the presence of dung-indicating fungal spores (Sordariaceae), and by increased palynological richness (mean 39.6) compared to zone RA1 ($p < 0.001$). The higher amount of microscopic charcoal compared to the previous zone, indicates increased use of fire. Contrary to the other major tree species, the pollen concentration of *Alnus* is relatively constant at the transition from zone RA1 to RA2 (Fig. 4) and a considerable increase in percentages is evident, reaching a maximum level at ca. AD 750, followed by a sharp decrease (Fig. 5). An

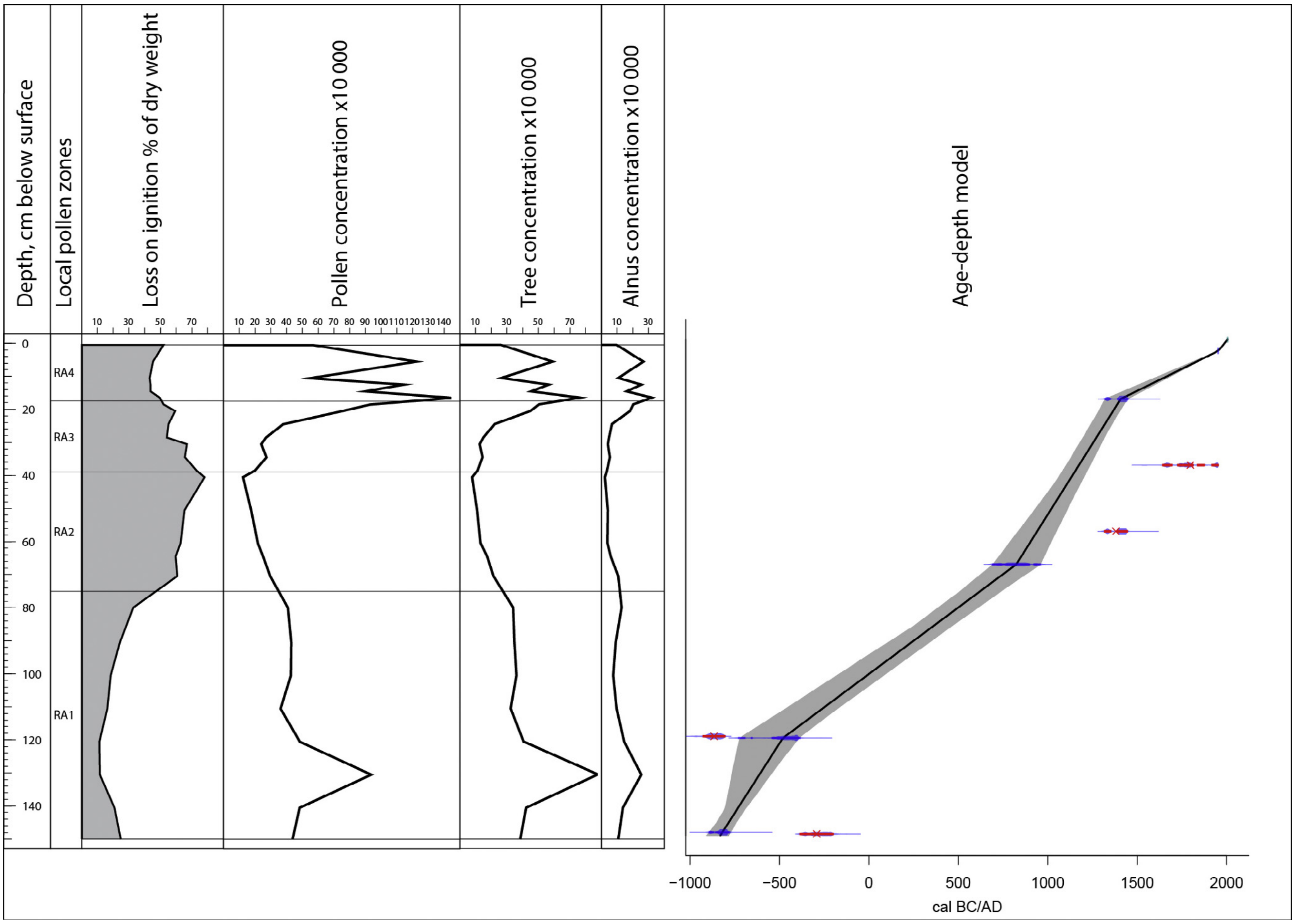


Fig. 4. Loss on ignition, pollen concentration for three groups – total pollen, trees without *Alnus*, and *Alnus*, and age-depth model for Rambjøra using linear interpolation in the program Clam (Blaauw, 2010) with Intcal 13 calibration curve (Reimer et al., 2013). Dates treated as outliers are shown in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increase in loss-on-ignition reflects local peat development, and zone RA2 contains the first pollen of the characteristic wet-site indicators: *Caltha*, *G. fluitans*, and *R. flammula*. The continuous presence of *Clasterosporium caricinum* spores, which grow on *Carex* (van Geel and Aptroot, 2006) is supported by high values for Cyperaceae pollen, and reflects the local development of sedge peat. Altogether, this indicates that alder swamp woodland with sedge was growing locally on the site, and that semi-natural grasslands existed in the area. The increase in semi-natural grasslands coincides with increased settlement in the surroundings of Rambjøra as well as within 1000 m of the coring site where the number of farms increased from one to four between AD 500 and 1300 (Fig. 2).

At the transition to pollen zone RA3 (high and late medieval period, ca. AD 1150–1450), a further drop in tree pollen percentages and increase in *Juniperus* takes place. *Alnus* maintains the values from the end of the previous zone, whereas *Betula* and *Pinus* decrease, indicating further utilisation of *Pinus* and the clearance, and possible browsing, of *Betula*. *Tilia* and *Ulmus* have low values probably reflecting their absence in the vicinity of the site and/or pollarding of *Ulmus*. Taxa indicating semi-natural grassland increase in RA3, a further reduction in fern spores takes place, and dung spores (Sordariaceae) are present. Estimated palynological richness is high (mean 38.5). In the lower part of zone RA3 and during the transition to RA4, burning is indicated by a rather abrupt increase in the amount of microscopic charcoal. Both incidents coincide with a small decline in the amount of tree pollen, indicating clearance by fire. The increased values of anthropogenic indicators indicate increased impact on the local environment compared to the previous zone. Both pollen and loss-on-ignition indicate a high water table which allowed the continued accumulation of waterlogged organic sediment and provided a suitable habitat for alder swamp communities. This vegetation development matches the history of increased farming settlement between AD 500 and 1300 (Fig. 2). After the Black Death in AD 1349, many of the farms in the area were abandoned (Fig. 2, AD 1520). Higher *Alnus* and tree pollen concentration at the end of zone RA3 may reflect some forest regrowth, but the presence of grazing indicators suggests that Rambjøra was most likely still used for grazing throughout this period of recession.

Pollen zone RA4 (end of the late medieval period, ca. AD 1450, until present day) reflects a small decrease in woodland and *Juniperus*, and an increase in semi-natural grassland. Brassicaceae, *Cirsium* type, Poaceae, and *Rumex* sect. *acetosa* increase at the start of the zone, whereas Cyperaceae decreases. A further increase in Poaceae and Brassicaceae as well as in *R. acris* type and Apiaceae takes place in the middle of the zone. Scattered finds of cereal pollen are present. Estimated palynological richness is at its highest, on average 42.0, significantly higher than zone RA3 ($p = 0.03$), and total pollen concentration increases. Increased pollen concentrations may reflect a decrease in the sediment accumulation rate as indicated in the age-depth model (Fig. 4), an increase in the pollen accumulation rate or a combination of these components. In contrast to the previous zones where tree pollen dominates

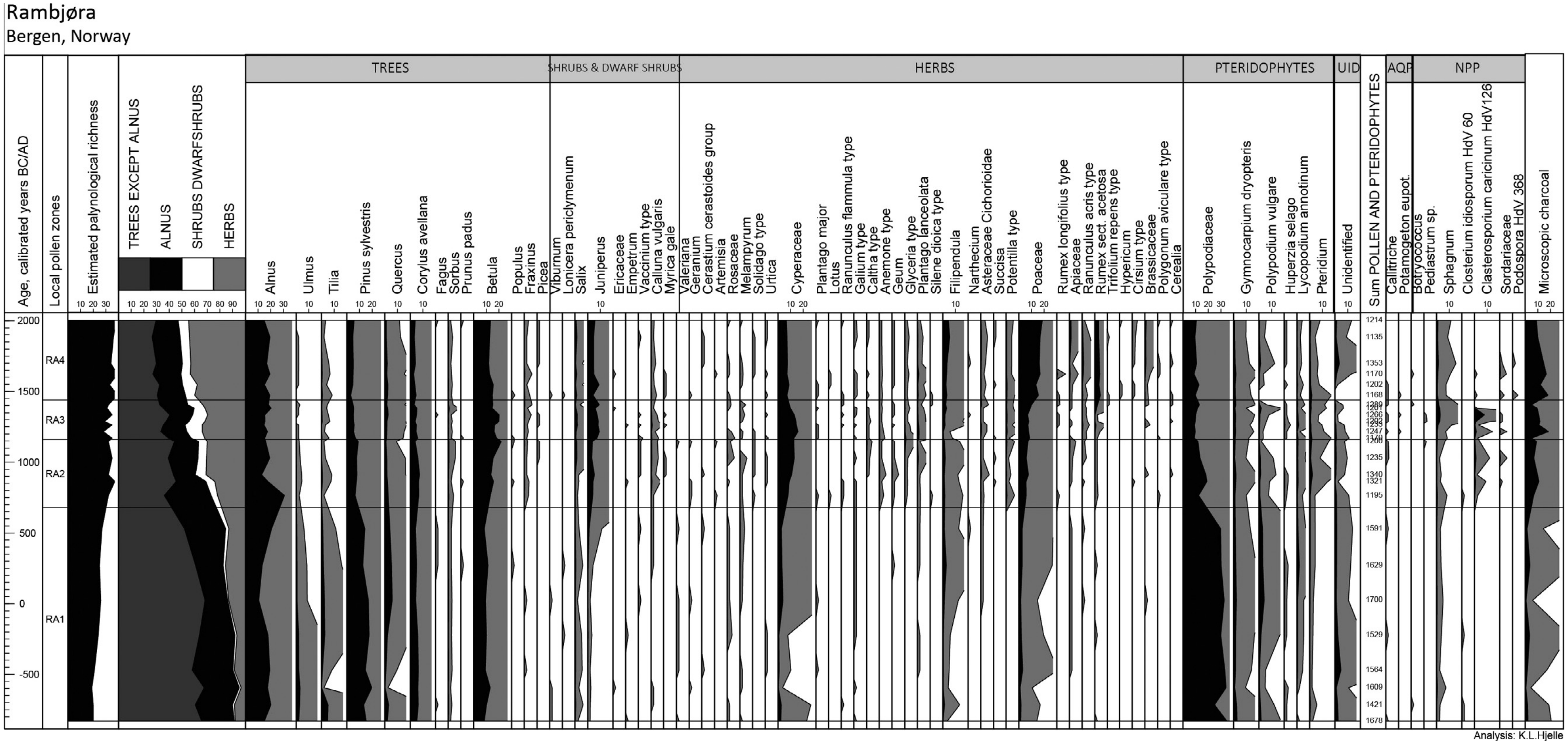


Fig. 5. Pollen percentage diagram and estimated palynological richness from Rambjøra, showing the time period from 800 BC (to the left) until today (to the right). Black curves show percentages, grey 10× exaggerations. Pollen/spore types present in one (*Astragalus* type, *Centaurea nigra* type, *Dianthus* type, Orchidaceae, *Prunella* type, *Rhinanthus* type, *Sagina*, *Spergula arvensis*, *Trifolium pratense* type) or two samples (*Rubus*, *Sedum*, *Cerastium fontanum* type, *Veronica*, *Achillea* type, *Humulus* type, *Pedicularis*, *Alchemilla*, *Allium ursinum* type, *Nymphaea*, *Selaginella*) are omitted from the pollen diagram.

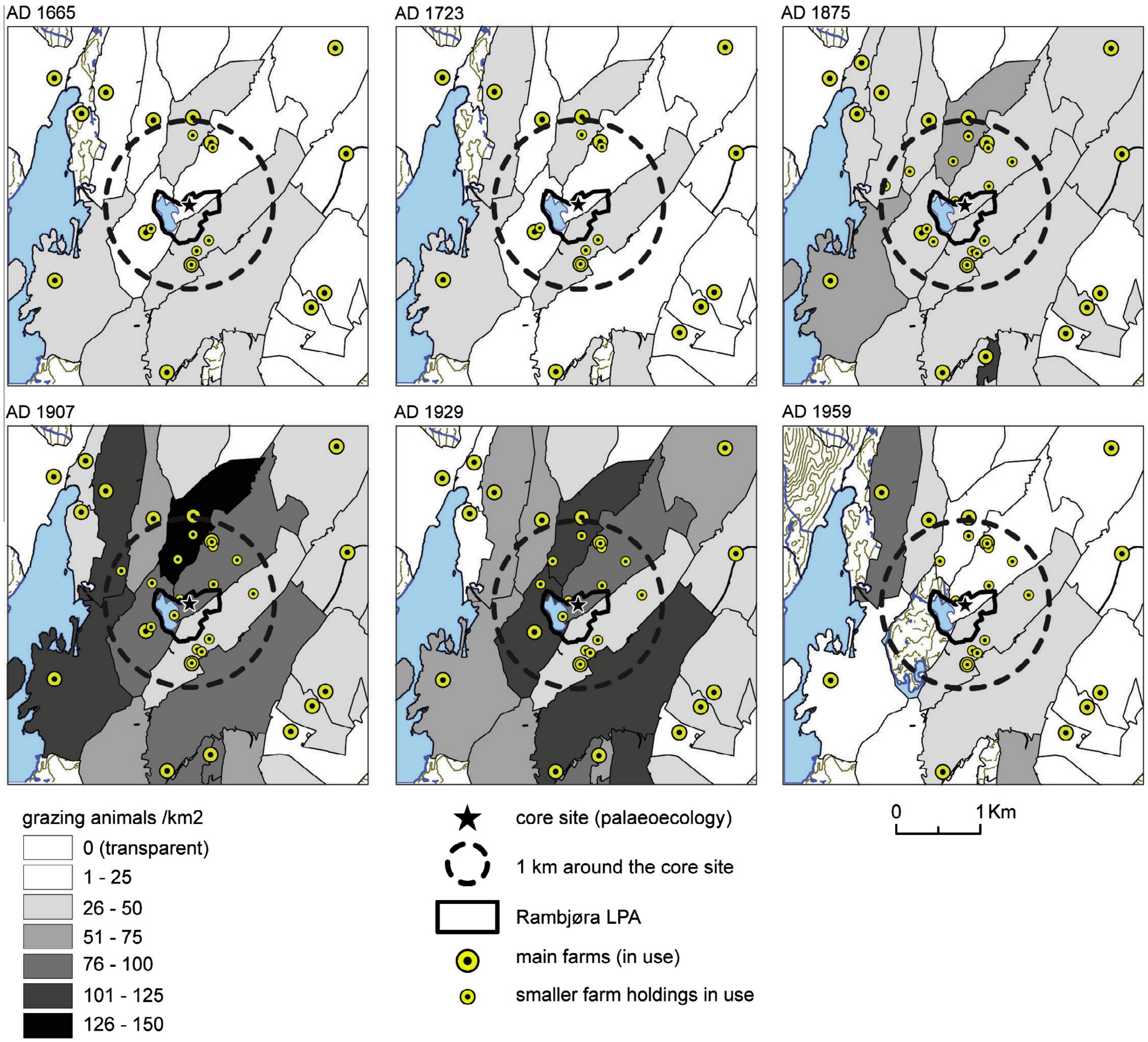
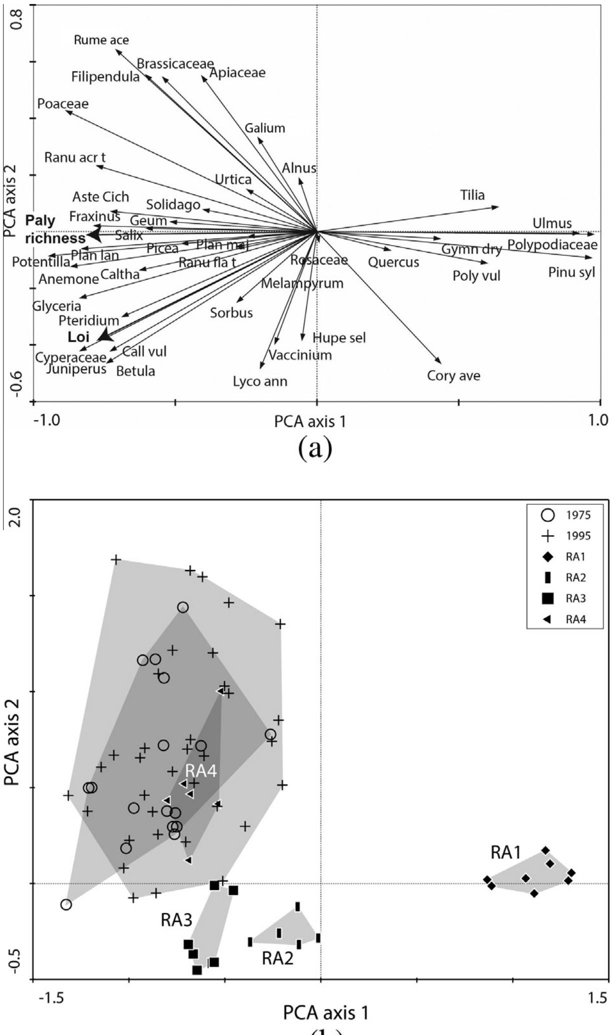


Fig. 6. Farmyards and farms in use in and around Rambjøra between AD 1665 and 1959. Within Rambjøra, smaller farms (*bruk*) under the umbrella of a principal farm are shown as smaller symbols. Grazing pressure is shown for the major farms, calculated as total farm animals per km^2 where 1 farm animal corresponds to 1 cattle/horse, 3 young heifers/calves or 5 sheep/goats.

pollen concentrations, herb pollen contributes up to ca. 50% of the concentration in zone RA4. This marked change together with decrease in *Loi* may reflect a change towards drier conditions and a possible hiatus at the site. There is, however, no increase in taxa resistant to decay, such as Polypodiaceae, *Tilia*, Asteraceae Cichorioideae or corroded (unidentified) pollen grains (Havinga, 1984; Bunting et al., 2001), which could indicate taphonomic processes caused by drying. Neither the gradual decrease in *Loi* starting at the RA2/RA3 transition nor the continuity in several pollen curves supports the existence of a hiatus. The observed changes are more likely to reflect change in the type and intensity of land-use practices at the site and in the surroundings. A decrease in loss-on-ignition may indicate the removal of plant material by hay mowing or grazing, which causes decreased accumulation of organic matter. *Loi* around 50% is lower than in the investigated alder swamp woodlands (mean 60%) and some mineral input due to more intensive use of the surroundings of the core site is likely. Both processes may have contributed to the high pollen concentration in zone RA4. Pollen of *Rumex* sect. *acetosa*, *R. acris* type, *P. lanceolata*, Asteraceae Cichorioideae, and Poaceae are common both in grazed and mowed vegetation communities, but their high percentages together with high values of Apiaceae may indicate mowing (Hjelle, 1999). Hay mowing locally at the pollen core site is known in the first part of the last century. The high degree of similarity in the pollen assemblages through zone RA4 may support that mowing took place already at the end of the medieval period, or at least from the 17th century, when a reduction in *Juniperus* and *Betula* and an increase in Poaceae and Apiaceae appear. Several farms may have utilized the area in the 17th century and the intensity of land-use in Rambjøra LPA increased considerably after the 18th century (Fig. 6). During the last century the use of the area was probably at its maximum, resulting in a reduction in *Alnus* as indicated in the youngest analysed samples. The mixture of light-demanding grassland taxa and alder swamp



(a)

(b)

Fig. 7. Principal components analysis (PCA) biplot of the pollen data set (axis 1: explained variance 59%; axis 2: 12%) as taxa (a) and sites (b). Loss on ignition (*Loi*) and palynological richness (*Paly richness*) are shown as supplementary variables. The samples from the alder swamp woodland vegetation surveys have been added passively. Only taxa occurring in at least 1/3 of the samples are shown. See supplementary material for abbreviations.

woodland taxa indicates a mosaic of vegetation communities where the type and intensity of land-use has changed through time and space.

4.3. A. glutinosa swamp woodlands in the past

Alder swamp woodlands at or near the pollen core site can be recognised in the pollen diagram when *Alnus* is found together with several common species of the recent alder swamp woodlands. *G. fluitans* and *R. flammula* (Fig. 5) are particularly good indicators, as both grow only on very wet or waterlogged soil. Other typical plants of the alder swamp woodlands are less suitable indicators; some are just as common in other habitats, such as grasses and sedges in semi-natural grasslands or ferns in well drained forests. Some have pollen which is recognisable only to a lower taxonomic level, e.g. *Galium*. Others, such as *T. europaea* and *V. palustris*, are entomophilous (insect pollinated) species which are underrepresented in pollen diagrams (Hjelle, 1997) and not found in the pollen core from Rambjøra.

The ordination of the pollen samples reflects vegetation dynamics through time (Fig. 7). The distribution of taxa along the first axis, which explains most of the variability in the data set, indicates an underlying gradient from forest (*Corylus*, *Quercus*, *Pinus sylvestris*, *Tilia*, *Ulmus*, Polypodiaceae) to semi-natural grasslands and open woodlands (Poaceae, herbs such as *P. lanceolata*, *Rumex* sect. *acetosa*, *R. acris* type, and the light-demanding shrub and tree taxa *Juniperus*, *Betula,* and *Fraxinus* (Fig. 7a)). *Alnus* is located in the middle of this gradient, implying that alder takes an intermediate position in the vegetation dynamics between semi-natural grassland and forest. Characteristic taxa of the alder swamp vegetation such as Cyperaceae, *Glyceria* type, *R. flammula* type, *Potentilla* type, are correlated with another in the ordination, but uncorrelated to *Alnus.* This supports the intermediate status of *A. glutinosa* in the vegetation dynamics of alder swamp woodlands, as well as the presence of *Alnus* in other woodland communities through time.

The samples from each pollen zone are clustered along the main gradient (Fig. 7b). Their positions indicate the dominance of semi-natural grassland and open woodland in the three top pollen zones and of forest habitat in RA1. The samples from RA1 are clearly separated from all other samples. This demonstrates that the vegetation in the oldest period was noticeably different from both the vegetation in later periods and the recent alder swamp vegetation. The difference is probably a result of the lower anthropogenic influence in RA1, supported by the evidence of the land-use history (Fig. 2). Areas with alder swamp woodlands may have been rather limited prior to the Late Iron Age, at least locally, as zone RA1 contains practically no pollen of the typical alder swamp woodland species *G. fluitans* and *R. flammula*. However, these may have been overshadowed by high tree pollen producers, and alder swamp woodland may have existed elsewhere. Alternatively, *Alnus* may also have been common in the well-drained forests, as it makes up between 15% and 20% of the pollen assemblage, the same as in later periods (Fig. 5).

The vegetation plots from the alder swamp woodlands are located close to the pollen samples from the top three zones, indicating similarities in the vegetation from the seventh, and especially from the 15th, century to present day. Their position along the main gradient suggests the dominance of semi-natural grassland, in line with the anthropogenic influence in these periods (Figs. 2, 5 and 6). The location of the samples from zones RA2, RA3, and RA4 in the ordination suggests that the vegetation varied concurrently with the anthropogenic influence when semi-natural grassland dominated the landscape. The samples from RA2 are located closest to RA1, suggesting a stronger element of woodland in the Late Iron Age and early medieval time (RA2) than later, as also indicated by the number of farms (Fig. 2). The samples from zones RA3 and RA4 have a similar position along the first ordination axis, but are separated along the second. This axis, which is of minor importance compared to the first (eigenvalues 0.12 and 0.59, respectively), seems to reflect an underlying gradient from pasture (Cyperaceae, *Pteridium*, *Juniperus*) to hay meadow (*R. acris* type, Poaceae, *Rumex* sect. *acetosa*). The samples from RA4 are placed among the vegetation samples along the second axis. Pollen percentages of grasses show a marked increase in the more recent centuries (RA4), probably caused by mowing at the core site and the surroundings. The abundance of sedges decreases in the same period, which may indicate that grasses are favoured by mowing at the expense of sedges.

5. Discussion

5.1. Evaluation of the approaches

In this study we have combined vegetation data and pollen data by transforming species to their palynological equivalents (taxa), and further compared these taxa with pollen data through ordinations. Some inconsistencies might have been caused by the case that the species is known in the vegetation, while most grasses, sedges, ferns and many herbs are determined jointly to family level in the pollen data. However, the vegetation data expressed as both species and their palynological equivalents reveal the same main gradients using ordination methods, indicating that the transformation retains the same information. Previous studies have shown an overall good relationship between vegetation data expressed as pollen equivalents and pollen in modern surface samples (Hjelle, 1997, 1999), supporting our approach of comparing vegetation data and fossil pollen data. The observed underrepresentation of entomophilous taxa in the pollen record compared to the vegetation, and corresponding overrepresentation of wind pollinated taxa is also in accordance with previous studies. In contrast to the study of Hjelle (1999) based only on herbs and dwarf-shrubs, we have included shrubs and trees in the present investigation. These are mainly wind pollinated and may reflect a larger source area than the investigated *Alnus* swamp woodlands. In forested periods, most of the pollen probably arrives from the nearest 50–150 m of the coring site (Binney et al., 2005; Bunting et al., 2005; Sugita, 1994). This is the case for zone RA1 in particular. In periods with open vegetation at and around the pollen core site, a larger area is reflected. Most of the pollen, however, will come from the nearest surroundings, and the amount from further away will decrease with distance.

Whereas the pollen assemblages reflect a mixture of the vegetation communities in Rambjøra and its surroundings, the vegetation data come from several stands of *Alnus* swamp woodlands within the Rambjøra area, both in the vicinity of the pollen core and quite far from the core site. They capture the variation and development in a 20-year period within these woodlands. Although the vegetation data only includes one vegetation community, because of their spatial and temporal distribution, they are likely to take in variation in alder swamp woodlands which could improve the comparability of our two data sets. The ordination results show that our approach of comparing recent vegetation and fossil pollen data helps to identify periods with alder swamp woodland at the local site as well as identifying changes in the management of the woodland through time.

The approach of making use of the vegetation history and land-use history in context provided increased insight into the development of Rambjøra, but also created several challenges as the two sources are different in scale, temporally and spatially (Davies and Watson, 2007; Swetnam et al., 1999). The pollen data covers the last 2800 years, whereas the spatial representation will vary through time depending on the forest cover and patchiness of the vegetation (cf. Binney et al., 2005; Bunting et al., 2004, 2005; Hellman et al., 2009). The historical data comes from systematic, farm-specific written sources over the last 350 years, whereas the land-use history before 1665 is based on incomplete sources (Larsen, 1980, 1984). We do not know how changes in the number of domestic animals in Rambjøra and on nearby farms affected the grazing pressure locally around the pollen core site. The same applies to the local effects of historical events at a broader scale (e.g. the Black Death), and how they appear as floristic changes in the pollen data. On the other hand, local events that are not captured by the land-use history at a larger scale may be the drivers of local land-use and vegetation changes (cf. Davies and Watson, 2007). This demonstrates some aspects of the complex interaction of land-use and vegetation. However, the interpretations of the palynological data independently provide a good match for the historical sources which supports the reliability and suitability of our approach.

5.2. Long-term dynamics of *A. glutinosa* swamp woodlands

In the pollen core, *Alnus* pollen has high values through all four zones, indicating that alder has been growing at or close to the site for around 2800 years. The local pollen production by *Alnus* will result in low representation of other tree taxa, especially in time periods with *Alnus* swamp woodland at the coring site (Binney et al., 2005; Bunting et al., 2005). However, the small-scale topographical pattern in the study area with short distances (<20 m) from dry hill sides to wet depressions will probably reduce some of this effect in Rambjøra. With few exceptions, periods of high pollen concentration of *Alnus* coincide with high concentrations of total tree pollen (Fig. 4) and changes in loss-on-ignition together with variation in pollen composition indicate the time periods when alder swamp vegetation existed locally. The variations in abundance of alder are closely related to land-use, as demonstrated both by the pollen record and the alder swamp vegetation data. The increased relative abundance of alder pollen in periods when other tree species decline, most prominently at the transition between pollen zones RA1 and RA2, is a natural result of human land-use causing a more light-open forest, with improved sprouting opportunities for alder (McVean, 1956; Tapper, 1993). The reduced abundance of trees leads to increased soil water and anoxic conditions which further favour *A. glutinosa* (Claessens et al., 2010; Ellenberg et al., 1992). A decline in alder was observed in our study area ca. AD 800 subsequent to the increase at the RA1/RA2 boundary. Comparable decline or disappearance of alder observed elsewhere have been connected to either natural or anthropogenic causes (Barthelmes et al., 2010; Brown, 1988; Douda et al., 2009; Muller et al., 2012; Pokorny et al., 2000; Saarse et al., 2010). In Rambjøra the decline in the Late Iron Age coincides with increased settlement in the area (Fig. 2), hence it is likely that the decline is caused by a further intensification of agricultural land-use, probably including clearance for livestock grazing, hay mowing, and increased utilisation of alder, for example, for firewood.

The increase in alder swamp woodlands that is indicated in the pollen composition after the Black Death may be related to a phase of forest recovery and succession due to agricultural abandonment. With time, abandonment would probably result in the reduction of *Alnus*, similar to that observed in the vegetation between 1975 and 1995. Vegetation surveys of the alder swamp woodlands in Rambjøra demonstrated a decline in abundance of alder 15–35 years after cessation of the land-use in 1960, concurrent with a succession that involves replacement of alder by other tree species. The shift in the tree layer was probably caused by more shady conditions as the trees grew and the canopy became denser. *A. glutinosa* is unable to regenerate under a dense canopy due to toxic substances in non-decomposed litter from standing alder trees, and because the seedlings require good light intensity and suitable hydrological conditions to establish and grow (Claessens et al., 2010; McVean, 1955, 1956). Furthermore, a denser tree canopy will use more water and result in relatively drier soil, which favours tree species other than *A. glutinosa* (Cramer, 1985; Latham and Blackstock, 1998; Natlandsmyr Lunde, 2000, 2003; Schrautzer et al., 1991; Tapper, 1993). The changes in the field layer, with a decrease in grazing-tolerant grassland species and an increase of species intolerant of grazing, point towards the cessation of land-use as the cause of the vegetation development in Rambjøra since 1975.

The abundance of alder in 1975 probably resulted from the invasion of alder into the semi-natural grasslands shortly after agricultural abandonment (Douda et al., 2009; Fremstad, 1983; Vinther, 1983). It is likely that *A. glutinosa* was favoured during this period due to its good supply of nitrogen (Franche et al., 2009), which may be deficient in unfertilised semi-natural grasslands and thereby a limiting factor for other tree species.

5.3. Possible drivers of change

Our results provide strong support for human impact as the main driver of vegetation changes in Rambjøra during the last 2800 years, while past climate changes have had less importance to the vegetation processes. The first development of local *Alnus* swamp woodland ca. 650 AD is probably related to a change in the balance between precipitation and evaporation/transpiration due to forest clearance. Whereas a relatively warm and dry climate characterises the period from AD 1 to medieval times, the "Little Ice Age" from c. AD 1500 to 1850, was the coldest episode in northern Europe during the study period and is associated with increased humidity (Nesje et al., 2008; Seppä et al., 2009). *A. glutinosa* is favoured by humid conditions (Ellenberg et al., 1992), but there is no increase in loss-on-ignition in this time period that could indicate increased ground water level with anoxic conditions and limited decomposition of organic content. Low humidity is further supported by decreases in Cyperaceae, *Sphagnum*, and aquatics in zone RA4. The observed increase in microscopic charcoal indicates burning from human activities, and the presence of cereals and several other anthropogenic indicators document agricultural activity. However, climate may have had an indirect impact on the vegetation via its interaction with human activities, with more favourable climate contributing to agricultural improvements, and thus also to vegetation changes. During the last 150 years we have experienced a markedly warmer climate (Nesje et al., 2008; Seppä et al., 2009). In a warmer climate, biological processes are faster, which will lead to a rapid regrowth of semi-natural grasslands after abandonment (Lindner et al., 2010). Any future climate change towards higher precipitation is likely to favour *A. glutinosa* and swamp woodlands. The literature differs substantially regarding biodiversity and ecological trends under climate change (Bellard et al., 2012; Lenoir et al., 2013; Moritz and Agudo, 2013; Willis and Bhagwat, 2009). Hence it is uncertain how climate changes will affect biodiversity in the alder swamp woodlands.

Variations in the abundance of alder pollen over time have been explained as cyclical developments due to regeneration characteristics of the alder itself (Pokorny et al., 2000), or environmental factors that influenced the vegetation development (Brown, 1988). The life span of alder is about 120 years, and *A. glutinosa* has difficulties regenerating under a dense canopy (Claessens et al., 2010; McVean, 1955, 1956). In the case of Rambjøra, however, the alternations in alder are so closely linked to changes in land-use that the impact from agricultural practices is likely to overshadow any cyclical variation over time. Agricultural influence has helped maintain the stands of alder woodlands for a longer time than what would have been the case in a natural cycle. The forest has been kept open and the conditions have been favourable, providing opportunities for alder to regenerate by seed or at least for rejuvenation by new shoots from trunks. The disturbance caused by agricultural land-use thus stands out as the main factor responsible for the longevity of the alder swamp communities.

5.4. A baseline for management in Rambjøra LPA

Our study has demonstrated that the dynamic processes between the alder swamp woodlands and drier deciduous woodland or semi-natural grasslands are closely related to land-use practices and contribute to the richness of habitats in Rambjøra. Although alder has been present in the area for many centuries, the composition and hydrology of these habitat types have varied. Alder presence alone is therefore not sufficient to conserve all of the currently valued (e.g. understorey) species, as species which are associated with alder swamp woodlands may be lost, at least locally, due to the likelihood of a successional shift away from swamp conditions following reduced disturbance.

In order to follow up on the protection of Rambjøra LPA, the managers should aim to maintain the 'rare combination of several distinctive habitat types'. Presumably the protection objective refers to the habitats found in Rambjøra when the area was protected in 1981. At that time, the vegetation was undergoing a recovery after the cessation of agricultural disturbances, demonstrated in our surveys of 1975 and 1995. Accordingly, such a management strategy will be based on a recent snapshot of a dynamic landscape where our results show that the community composition has varied over the last three millennia.

The species richness gives an impression of the richness of habitat types in the area. The estimated palynological richness, a proxy for species richness, increased in Rambjøra concurrent with increased settlement and was high from the Late Iron Age onwards. The highest values are found between the 16th and 20th centuries, when a large population needed to exploit all available resources in the landscape (Larsen, 1984; cf. Fig. 2). However, the traditional farming in the outfields in Rambjøra involved only intermediate levels of disturbance (extensive livestock grazing, hay mowing, collection of fodder from trees, felling of single trees, and no use of fertiliser or machinery). This trend in species richness is similar to what has been shown elsewhere (e.g. Bengtsson et al., 2000; Berglund et al., 2008; Lindbladh, 1999; Hjelle et al., 2012; Mehl and Hjelle, 2015). Increased palynological richness may, however, also reflect the opening-up of the landscape and a change in dominance from trees with high pollen productivity and wind dispersal to herbs with lower pollen production (cf. Odgaard, 1999). The combination of pollen types from different vegetation communities that characterises the fossil pollen assemblages from the 16th century onwards, indicate that high palynological richness is related to high habitat heterogeneity. Accordingly, the human-influenced periods which include the situation at the time of the protection, seem to be the most obvious baseline.

Habitats and species existing in Rambjøra in the Bronze Age and Early Iron Age might get overlooked if more recent periods are used as a baseline for the management strategy. Forest plants (e.g. *Tilia*, *Ulmus*, *Valeriana*, ferns) were more abundant in the most ancient period. However, these plants also grow in the woodlands of Rambjøra today (Losvik, 1978; Natlandsmyr Lunde, 2000, 2003). Therefore, this is no argument against developing a management strategy based on the vegetation of later, more human influenced time periods. On the other hand, continued abandonment of the former land-use may lead to conditions similar to those prior to the Early Iron Age, when woodlands prevailed. This may, in turn, cause a loss of species diversity and a decline in many of the communities which currently characterise Rambjøra.

The considerations above lead us to recommend the human-influenced periods of the Late Iron Age and later as the baseline for the conservation management of Rambjøra LPA.

To achieve the habitat types of Rambjøra aligned with this baseline, it is necessary to re-establish some traditional agricultural measures, and thereby the ecological processes caused by such land-use (cf. Franklin et al., 2002). The habitat types and the particular land-uses are interdependent, and may be transient and unstable components of a dynamic landscape. Management interventions to reinstate agricultural practices will secure the dynamic alternations between woodland and open semi-natural grasslands, which will thus favour the stands of alder swamp woodlands. This implies, in particular, the need for extensive livestock grazing and optimally also hay mowing. No fertiliser must be applied, and no drainage carried out. The management measures need to be spatially dynamic as alder may shift its location to overcome limited regeneration beneath its own canopy. Tree felling in some stands of alder swamp woodlands is recommended at the start of the maintenance measures, targeting the desired dynamic processes. The management strategy should aim for a moderate impact of the agricultural measures. The effects must be monitored (Noss, 1999) and evaluated on an ongoing basis to be able to decide the optimal intensity of the management to achieve the desired effect. It must be taken into account that, because the extent of each stand of alder swamp woodland is rather small, they are vulnerable to changing hydrological regime and liable to dry up. The Intermediate Disturbance Hypothesis (Connell, 1978), suggests that species richness should be highest with a moderate intensity of disturbance and overly intensive grazing is likely to reduce habitat and species richness. The situation today does not indicate an immediate risk of too intensive agricultural land-use. On the contrary, abandonment is evident in many European landscapes and is predicted to increase (e.g. Macdonald et al., 2000; Navarro and Pereira, 2012). The protection objective of Rambjøra implies conservation of the habitats and protection of the species in these ecosystems. The management practices which are already carried out, are paid for by the local authorities. Recently these are supplemented by a project involving restoration by tree felling and later maintenance by cutting and removal of grass. If these measures are continued, and targeted more closely to specific alder swamp communities, the dynamic ecological processes may still support the upholding of these vulnerable habitat types.

Taking a longer time perspective, if an intermediate disturbance regime is not adopted, then the present abandonment may cause a continued replacement of alder by other deciduous trees in the alder swamp woodlands in Rambjøra, and the system may change from alder swamp woodlands towards mixed deciduous forest comparable to the vegetation in the Bronze Age and Early Iron Age, with associated shifts in biodiversity.

5.5. Conclusions

Dynamic changes in predominance between forest and semi-natural grassland have taken place over 2800 years, concurrent with varying anthropogenic disturbances. The abundance of alder swamp woodlands has varied temporally within this dynamic situation, increasing with low-impact land-use and declining with intensified use or abandonment.

The approach of combining three parameters – recent vegetation data, long term pollen records and historical data – clearly helped to demonstrate the relationship between the present and the past and strengthened the interpretation of the data. The study illustrates the usefulness of combining the pollen record and land-use history to provide an important long-term perspective on the vegetation development. It also demonstrates the contribution that palaeoecology can make to the establishment of conservation strategies.

Our findings should be taken into account by conservation managers and restorers of alder swamp woodlands, as well as when aiming to maintain the biodiversity of forests with elements of alder swamp woodlands. A restoration effort has already been initiated in Rambjøra LPA, that promotes the dynamics between semi-natural grasslands, alder swamp woodlands, and forest. The objective is to maintain a variety of habitats in the protected area, as stated in the protective purpose, and provide sites for a diversity of species. Further ecological and palaeoecological research is needed to confirm to what extent alder swamp woodlands in general are dependent on anthropogenic influences, as has been demonstrated in Rambjøra.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.03.049.

References

Barthelmes, A., Gerloff, D., de Klerk, P., Joosten, H., 2010. Short-term vegetation dynamics of Alnus dominated peatlands: a high resolution palaeoecological case study from western Pomerania (NE Germany). Folia Geobotanica 45 (3), 279–302. http://dx.doi.org/10.1007/s12224-010-9063-8.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377. http://dx.doi.org/10.1111/j.1461-0248.2011.01736.x.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. For. Ecol. Manage. 132 (1), 39–50. http://dx.doi.org/10.1016/S0378-1127(00)00378-9.

Berglund, B.E., Gaillard, M.-J., Bjørkman, L., Persson, T., 2008. Long-term changes in floristic diversity in southern Sweden: palynological richness, vegetation dynamics and land-use. Vegetation History Archaeobotany 17, 573–583. http://dx.doi.org/10.1007/s00334-007-0094-x.

Beug, H.-J., 2004. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Verlag Dr. Friedrich Pfeil, Munich.

Binney, H.A., Waller, M.P., Bunting, M.J., Armitage, R.A., 2005. The interpretation of fen carr pollen diagrams: the representation of the dry land vegetation. Rev. Palaeobot. Palynol. 134, 197–218. http://dx.doi.org/10.1016/j.revpalbo.2004.12.006.

Birks, H.J.B., 1996. Contributions of quaternary palaeoecology to nature conservation. J. Veg. Sci. 7, 89–98. http://dx.doi.org/10.2307/3236420.

Birks, H.J.B., Gordon, A.D., 1985. Numerical Methods in Quaternary Pollen Analysis. Academic Press, London.

Birks, H.J.B., Line, J.M., 1992. The use of rarefaction analysis for estimating palynological richness from quaternary pollen-analytical data. The Holocene 2, 1–10. http://dx.doi.org/10.1177/095968369200200101.

Blaauw, M., 2010. Methods and code for 'classical' age-modelling of radiocarbon sequences. Quaternary Geochronol. 5, 512–518. http://dx.doi.org/10.1016/j.quageo.2010.01.002.

Brown, A.G., 1988. The palaeoecology of *Alnus* (alder) and the postglacial history of floodplain vegetation. Pollen percentages and influx data from the West Midlands, United Kingdom. New Phytol. 110 (3), 425–436. http://dx.doi.org/10.1111/j.1469-8137.1988.tb00280.x.

Bunting, M.J., 2003. Pollen–vegetation relationships in non-arboreal moorland taxa. Rev. Palaeobot. Palynol. 125, 285–298. http://dx.doi.org/10.1016/S0034-6667(03)00005-8.

Bunting, M.J., Armitage, R., Binney, H.A., Waller, M., 2005. Estimates of 'relative pollen productivity' and 'relevant source area of pollen' for major tree taxa in two Norfolk (UK) woodlands. The Holocene 15 (3), 459–465. http://dx.doi.org/10.1191/0959683605hl821rr.

Bunting, M.J., Gaillard, M.-J., Sugita, S., Middleton, R., Broström, A., 2004. Vegetation structure and pollen source area. The Holocene 14 (5), 651–660. http://dx.doi.org/10.1191/0959683604hl744rp.

Bunting, M.J., Tipping, R., Downes, J., 2001. "Anthropogenic" pollen assemblages from a Bronze Age cemetery at Linga Fiold, West Mainland, Orkney. J. Archaeol. Sci. 28, 487–500. http://dx.doi.org/10.1006/jasc.2000.0607.

Byrkjeland, J., 1958. Husdyrbruket i Hordaland gjennom 100 år. Hordaland landbruksselsk, Bergen, 118 s.

Calcote, R., 1995. Pollen source area and pollen productivity-evidence from forest hollows. J. Ecol. 83, 591–602. http://dx.doi.org/10.2307/2261627.

Claessens, H., Oosterbaan, A., Savill, P., Rondeux, J., 2010. A review of the characteristics of black alder (Alnus glutinosa (L.) Gaertn.) and their implications for silvicultural practices. Forestry 83 (2), 163–175. http://dx.doi.org/10.1093/forestry/cpp038.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs-high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199 (4335), 1302–1310. http://dx.doi.org/10.1126/science.199.4335.1302.

Cramer, W., 1985. The effect of sea shore displacement on population age structure of coastal *Alnus glutinosa* (L.) Gaertn. Holarctic Ecol. 8 (4), 265–272.

Davies, A.L., Watson, F., 2007. Understanding the changing value of natural resources: an integrated palaeoecological-historical investigation into grazing-woodland interactions by Loch Awe, Western Highlands of Scotland. J. Biogeogr. 34 (10), 1777–1791. http://dx.doi.org/10.1111/j.1365-2699.2007.01725.x.

Douda, J., Cejkova, A., Douda, K., Kochankova, J., 2009. Development of alder carr after the abandonment of wet grasslands during the last 70. Ann. Forest Sci. 66 (7). http://dx.doi.org/10.1051/forest/2009065.

EEA, 2005. Biogeographical regions, Europe 2005. The European Environment Agency of the European Union http://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-2005, Website accessed 22/05/2012.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulissen, D., 1992. Indicator values of plants in central Europe. Scr. Geobotanica 18.

European Topic Centre on Biological Diversity, 2012. Online database of conservation assessments under Article 17 of the Habitats Directive for the reporting period 2007–2012 (EIONET) http://bd.eionet.europa.eu/article_17/reports2012/habitat/summary, Website accessed 27.10.2015.

Fossen, H., Thon, A., 1988. Bergen 1511 I, berggrunnskart-1:50 000, foreløpig utgave. Norges geologiske undersøkelse.

Foster, D.R., Schoonkaker, P.K., Pickett, S.T.A., 1990. Insights from paleoecology to community ecology. Trends Ecol. Evol. 5 (4), 119–122. http://dx.doi.org/10.1016/0169-5347(90)90166-B.

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The importance of land-use legacies to ecology and conservation. Bioscience 53 (1), 77–88. http://dx.doi.org/10.1641/0006-3568(2003) 053[0077:TIOLUL]2.0.CO;2.

Franche, C., Lindstrom, K., Elmerich, C., 2009. Nitrogen-fixing bacteria associated with leguminous and non-leguminous plants. Plant Soil 321 (1–2), 35–59. http://dx.doi.org/10.1007/s11104-008-9833-8.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J.Q., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155, 399–423. http://dx.doi.org/10.1016/s0378-1127(01)00575-8.

Fremstad, E., 1983. Role of black alder (Alnus glutinosa) in vegetation dynamics in West Norway. Nord. J. Bot. 3 (3), 393–410. http://dx.doi.org/10.1111/j.1756-1051.1983.tb01954.x.

Fremstad, E., Moen, A. (Eds.), 2001. Truete vegetasjonstyper i Norge. NTNU Vitenskapsmuseet Rapp. Bot. Ser. 4, pp. 1–231.

Fægri, K., Iversen, J., 1989. In: Fægri, K., Kaland, P.E., Krzywinski, K. (Eds.), Textbook of Pollen Analysis, forth ed. The Blackburn Press, New Jersey.

Førland, E.J., 1993. Nedbørnormaler, normalperioden 1961–1990. Det Norske Meteorol. Inst. Rapp. 39/93. Oslo, Norway.

Geological Survey of Norway, 2015. Maps on bedrock geology, sediments and others https://www.ngu.no/en/topic/applications, Website accessed 26.02.2016.

Glenz, C., Schaepfer, R., Iorgulescu, I., Kienast, F., 2006. Flooding tolerance of central European tree and shrub species. For. Ecol. Manage. 235, 1–13. http://dx.doi.org/10.1016/j.foreco.2006.05.065.

Hagebø, S., 1967. Pollenanalytiske undersøkelser av den postglaciale utvikling i Bergensdalen. Cand. Real. Thesis, University of Bergen. (Unpublished).

Halvorsen, L.H., 2010. Vegetasjonshistoriske undersøkelser på Nattland, gbnr. 11/728, Bergen, Hordaland. Palaeobotanisk rapport fra Bergen museum, De naturhistoriske samlinger, Universitetet i Bergen 2/2010.

Havinga, J., 1984. A 20-year experimental investigation into the differential corrosion susceptibility of pollen and spores in various soil types. Pollen Spores 26, 541–558.

Helle, K., 1982. Kongssete og kjøpstad: fra opphavet til 1536. Bergen bys historie. Bind I. Universitetsforlaget, Bergen, Norway.

Hellman, S., Bunting, M.J., Gaillard, M.-J., 2009. Relevant source area of pollen in patchy cultural landscapes and signals of anthropogenic landscape disturbance in the pollen record: a simulation approach. Rev. Palaeobot. Palynol. 153, 245–258. http://dx.doi.org/10.1016/j.revpalbo.2008.08.006.

Hill, M.O., Gauch, H.G., 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42, 41–58. http://dx.doi.org/10.1007/BF00048870.

Hjelle, K.L., 1997. Relationships between pollen and plants in human-influenced vegetation types using presence – absence data in western Norway. Rev. Palaeobot. Palynol. 99, 1–16. http://dx.doi.org/10.1016/S0034-6667(97)00041-9.

Hjelle, K.L., 1999. Modern pollen assemblages from mown and grazed vegetation types in western Norway. Rev. Palaeobot. Palynol. 107, 55–81. http://dx.doi.org/10.1016/S0034-6667(99)00015-9.

Hjelle, K.L., 2001. Eksisterte det et tettsted i Bergen i vikingtiden? Bosetningsutvikling basert på botanisk materiale. Årbok Bergen Museum 2000, 58–63.

Hjelle, K.L., Hufthammer, A.K., Bergsvik, K.A., 2006. Hesitant hunters: a review of the introduction of agriculture in western Norway. Environ. Archaeol. 11, 147–170. http://dx.doi.org/10.1179/174963106x123188.

Hjelle, K.L., Kaland, S., Kvamme, M., Lødøen, T.K., Natlandsmyr, B., 2012. Ecology and long-term land-use, palaeoecology and archaeology - the usefulness of interdisciplinary studies for knowledge-based conservation and management of cultural landscapes. Int. J. Biodiversity Sci. Ecosyst. Services Manage. 8, 321–337. http://dx.doi.org/10.1080/21513732.2012.739576.

Hjelle, K.L., Sugita, S., 2012. Estimating pollen productivity and relevant source area of pollen using lake sediments in Norway: how does lake size variation affect the estimates? The Holocene 22, 313–324. http://dx.doi.org/10.1177/0959683611423690.

Interpretation Manual of European Union Habitats-EUR28, 2013. <http://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/Int_Manual_EU28.pdf>.

Jeffers, E.S., Bonsall, M.B., Froyd, C.A., Brooks, S.J., Willis, K.J., 2015. The relative importance of biotic and abiotic processes for structuring plant communities through time. J. Ecol. 103, 459–472. http://dx.doi.org/10.1111/1365-2745.12365.

Joki, H., Ramstad, M., 2010. Arkeologiske undersøkelser av kokegropfelt og forhistorisk dyrkning på Nattland, gnr. 11, bnr. 728, Bergen kommune, Hordaland. Seksjon for ytre kulturminnevern, Bergen Museum, Universitetet i Bergen. (Unpublished).

Juggins, S., 1991. ZONE version 1.2. Unpublished computer program. University of Newcastle, Newcastle upon Tyne, UK http://campus.ncl.ac.uk/staff/Stephen.Juggins/software/ZoneHome.htm.

Krzywinski, K., Kaland, P.E., 1984. Bergen - from farm to town. The Bryggen Papers. Supplementary Series 1, 1–39.

Larsen, J.T., 1980. Fana bygdebok 1. Fra de eldste tider til 1665. Fana Bygdeboknemnd, Bergen, Norway.

Larsen, J.T., 1984. Fana bygdebok 4. Gards- og ættesoge. Fana bygdeboknemnd, Bergen, Norway.

Latham, J., Blackstock, T.H., 1998. Effects of livestock exclusion on the ground flora and regeneration of an upland Alnus glutinosa woodland. Forestry 71 (3), 191–197. http://dx.doi.org/10.1093/forestry/71.3.191.

Lein, H., 1977. Utmarksressurser i fôr og matproduksjon. Delrapport III. Norges landbruksvitenskaplige forskningsråd. Cited from: Nedkvitne, J.J., Garmo, T.H., Staaland, H., 1995. Beitedyr i kulturlandskap. Landbruksforlaget, Oslo, Norway.

Lenoir, J., Graae, B.J., Aarrestad, P.A., Alsos, I.G., Armbruster, W.S., Austrheim, G., Bergendorff, C., Birks, H.J.B., Bråthen, K.A., Brunet, J., Bruun, H.H., Dahlberg, C.J., Decocq, G., Diekmann, M., Dynesius, M., Ejrnæs, R., Grytnes, J.-A., Hylander, K., Klanderud, K., Luoto, M., Milbau, A., Moora, M., Nygaard, B., Odland, A., Ravolainen, V.T., Reinhardt, S., Sandvik, S.M., Schei, F.H., Speed, J., David, M., Tveraabak, L.U., Vandvik, V., Velle, L.G., Virtanen, R., Zobel, M., Svenning, J.-C., 2013. Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. Glob. Change Biol. 19 (5). http://dx.doi.org/10.1111/gcb.12129.

Lepš, J., Šmilauer, P., 2003. Multivariate Analysis of Multivariate Data Using CANOCO. Cambridge University Press, Cambridge, UK.

Lid, J., Lid, D.T., 2005. Norsk Flora. Det Norske Samlaget, Oslo, Norway.

Lindbladh, M., 1999. The influence of former land-use on vegetation and biodiversity in the boreo-nemoral zone of Sweden. Ecography 22, 485–498. http://dx.doi.org/10.1111/j.1600-0587.1999.tb01277.x.

Lindgaard, A., Henriksen, S. (Eds.), 2011. Norsk rødliste for naturtyper 2011. Artsdatabanken, Trondheim.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolstrom, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698–709. http://dx.doi.org/10.1016/j.foreco.2009.09.023.

Losvik, M.H., 1978. Vegetasjonsklassifikasjon og kartlegging med sikte på anvendelse i landskapsplanlegging i Bergensregionen. Cand. real Thesis. University of Bergen. (Unpublished).

Losvik, M.H., 1981. Successional pathways in former pastures and heaths at Bergen, Western Norway. Norsk Geografisk Tidsskrift - Norwegian Journal of Geography 35 (2), 79–101. http://dx.doi.org/10.1080/00291958108552064.

MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Lazpita, J. G., Gibon, A., 2000. Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. J. Environ. Manage. 59 (1), 47–69. http://dx.doi.org/10.1006/jema.1999.0335.

McVean, D.N., 1955. Ecology of Alnus glutinosa (L.) Gaertn. II. Seed distribution and germination. J. Ecol. 43 (1), 61–71. http://dx.doi.org/10.2307/2257119.

McVean, D.N., 1956. Ecology of Alnus glutinosa (L.) Gaertn. III. Seedling establishment. J. Ecol. 44 (1), 195–218. http://dx.doi.org/10.2307/2257162.

Mehl, I.K., Hjelle, K.L., 2015. From pollen percentage to regional vegetation cover-new insight into cultural landscape development in western Norway. Rev. Palaeobot. Palynol. 217, 45–60. http://dx.doi.org/10.1016/j.revpalbo.2015.02.005.

Moen, A., 1999. National Atlas of Norway: Vegetation. Norwegian Mapping Authority, Hønefoss, Norway.

Moritz, C., Agudo, R., 2013. The future of species under climate change: resilience or decline? Science 341, 504–508. http://dx.doi.org/10.1126/science.1237190.

Muller, S.D., Miramont, C., Bruneton, H., Carre, M., Sottocornola, M., Court-Picon, M., de Beaulieu, J.L., Nakagawa, T., Schevin, P., 2012. A palaeoecological perspective for the conservation and restoration of wetland plant communities in the central French Alps, with particular emphasis on alder carr vegetation. Rev. Palaeobot. Palynol. 171, 124–139. http://dx.doi.org/10.1016/j.revpalbo.2011.12.005.

Natlandsmyr Lunde, B., 2000. Vestnorske svartorsumpskoger. Klassifikasjon, økologi og dynamikk, særlig med henblikk på utviklingstendenser etter opphørt bruk. Cand. scient. Thesis. University of Bergen. (Unpublished).

Natlandsmyr Lunde, B., 2003. Vegetasjons- og landskapsutvikling i et vernet kulturlandskap i Bergen fra 1975 til 2000. In: Austad, I., Hamre, L.N., Ådland, E. (Eds.), Gjengroing av kulturmark, 15. Bergen Museums Skrifter, pp. 21–28.

Navarro, L.M., Pereira, H.M., 2012. Rewilding abandoned landscapes in Europe. Ecosystems 15 (6), 900–912. http://dx.doi.org/10.1007/s10021-012-9558-7.

Nedkvitne, J.J., Garmo, T.H., Staaland, H., 1995. Beitedyr i kulturlandskap. Landbruksforlaget, Oslo, Norway.

Nesje, A., Dahl, S.O., Thun, T., Nordli, Ø., 2008. The ‘Little Ice Age’ glacial expansion in western Scandinavia: summer temperature or winter precipitation? Climate Dyn. 30, 789–801. http://dx.doi.org/10.1007/s00382-007-0324-z.

Nordhagen, R., 1943. Sikilsdalen og Norges fjellbeiter. Bergens Museums Skrifter 22, 1–607.

Noss, R.F., 1999. Assessing and monitoring forest biodiversity: a suggested framework and indicators. For. Ecol. Manage. 115, 135–146. http://dx.doi.org/10.1016/s0378-1127(98)00394-6.

Odgaard, B.V., 1999. Fossil pollen as a record of past biodiversity. J. Biogeogr. 26, 7–17. http://dx.doi.org/10.1046/j.1365-2699.1999.00280.x.

Pokorny, P., Klimesova, J., Klimes, L., 2000. Late holocene history and vegetation dynamics of a floodplain alder carr: a case study from eastern Bohemia, Czech Republic. Folia Geobotanica 35 (1), 43–58. http://dx.doi.org/10.1007/BF02803086.

Punt, W., Hoen, P.P., 1995. The Northwest European pollen flora 7. Caryophyllaceae. Rev. Paleobot. Palynol. 88, 83–272. http://dx.doi.org/10.1016/0034-6667(95)00020-X.

R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves, 0–50,000 years cal. yr BP. Radiocarbon 55, 1869–1887.

Saarse, L., Niinemets, E., Poska, A., Veski, S., 2010. Is there a relationship between crop farming and the Alnus decline in the eastern Baltic region? Vegetation History Archaebotany 19 (1), 17–28. http://dx.doi.org/10.1007/s00334-009-0216-8.

Schrautzer, J., Haerdtle, W., Hemprich, G., Wiebe, C., 1991. The synecology and synsystematics of disturbed alder forests in the Bornhoevede lake district (Schleswig-Holstein). Tuexenia 11, 293–308.

Seppä, H., Bjune, A.E., Telford, R.J., Birks, H.J.B., Veski, S., 2009. Last nine-thousand years of temperature variability in Northern Europe. Climate Past 5 (3), 523–535.

Setten, G., Austrheim, G., 2012. Changes in land use and landscape dynamics in mountains of northern Europe: challenges for science, management and conservation. Int. J. Biodiversity Sci., Ecosyst. Services Manage. 8 (4), 287–291. http://dx.doi.org/10.1080/21513732.2012.738094.

Šmilauer, P., 1999–2009. CanoDraw for Windows 4.14.

Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen Spores 13, 615–621.

Sugita, S., 1994. Pollen representation of vegetation in quaternary sediments: theory and method in patchy vegetation. J. Ecol. 82, 881–897. http://dx.doi.org/10.2307/2261452.

Swetnam, T.W., Allen, C.D., Betancourt, J.L., 1999. Applied historical ecology: using the past to manage for the future. Ecol. Appl. 9 (4), 1189–1206. http://dx.doi.org/10.1890/1051-0761(1999) 009[1189:AHEUTP]2.0.CO;2.

Tapper, P.G., 1993. The replacement of *Alnus glutinosa* by *Fraxinus excelsior* during succession related to regenerative differences. Ecography 16 (3), 212–218. http://dx.doi.org/10.1111/j.1600-0587.1993.tb00211.x.

ter Braak, C.J.F., 2002. Program CANOCO Version 4.5 – 1988–2002 Biometris – Quantitative Methods in the Life and Earth Sciences. Plant Research International, Wageningen University and Research Centre, Wageningen, the Netherlands.

ter Braak, C.J.F., Prentice, I.C., 1988. A theory of gradient analysis. Adv. Ecol. Res. 18, 93–138. http://dx.doi.org/10.1016/S0065-2504(08)60183-X.

Vinther, E., 1983. Invasion of *Alnus glutinosa* (L.) Gaertn in a former grazed meadow in relation to different grazing intensities. Biol. Conserv. 25 (1), 75–89. http://dx.doi.org/10.1016/0006-3207(83)90032-0.

Waller, M.P., Binney, H.A., Bunting, M.J., Armitage, R.A., 2005. The interpretation of fen carr pollen diagrams: pollen-vegetation relationships within the fen carr. Rev. Palaeobot. Palynol. 133 (3–4), 179–202. http://dx.doi.org/10.1016/j.revpalbo.2004.10.001.

Van Geel, B., Aptroot, A., 2006. Fossil ascomycetes in quaternary deposits. Nova Hedwigia 82 (3–4), 313–329. http://dx.doi.org/10.1127/0029-5035/2006/0082-0313.

Willis, K.J., Bhagwat, S.A., 2009. Biodiversity and climate change. Science 326, 806–807. http://dx.doi.org/10.1126/science.1178838.

Willis, K.J., Birks, H.J.B., 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science 314 (5803), 1261–1265. http://dx.doi.org/10.1126/science.1122667.