The environment they lived in: anthropogenic changes in local and regional vegetation composition in eastern Fennoscandia during the Neolithic

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Abstract
Understanding about regional versus local changes in vegetation is critical in answering archaeological questions, in particular at a time when humans are assumed to have caused higher disturbances at local scales rather than regional scales; this is the case during the Neolithic. The aim of this paper is to assess the impact of Neolithic land use on regional and local vegetation dynamics, plant composition and disturbance processes (e.g. fire) in eastern Fennoscandia. We apply the Landscape Reconstruction Algorithm (LRA) to high-resolution pollen records from three lacustrine sediment cores that cover the Neolithic period. We calculate changes in vegetation composition and the rate of plant compositional change. Fire dynamics are estimated as an indicator of land use, although fire can result from both natural and anthropogenic disturbances. Our results show that during the Early Neolithic, changes were mainly driven by natural and climate-induced factors and vegetation composition and fire activity were similar at both regional and local scales. From ca. 4000 bc onwards, trends in vegetation and fire dynamics start to differ between regional and local scales. This is due to local land uses that are overshadowed at the regional scale by climate-induced factors. The use of the LOVE model in pollen analyses is therefore very useful to highlight local land uses that are not visible by using REVEALS.

Keywords Land cover · Plant compositional change · Pollen · Landscape reconstruction algorithm (LRA) · Fire · Environmental history · Human–environment interactions

Introduction
Holocene sediment archives from lakes, ponds and peat bogs in Europe provide evidence of human activities during the last ca. 12,000 years. Deforestation practices aimed at expanding areas for agriculture are commonly identified in pollen records from these archives via a decrease in tree pollen percentages and an increase in herbs and crop pollen types (e.g. Ojala and Alenius 2005; Gaillard et al.)

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Anthropogenic impact on vegetation is related to the spread of human activities in a catchment area. It is related to local activities that can expand through time to a regional scale. Based on pollen-based modelling and anthropogenic land cover change scenarios, we have increased our understanding about regional and subcontinental-scale vegetation and land use patterning in Europe, although this information mostly refers to deforestation (e.g. Trondman et al. 2015; Kaplan et al. 2017; Marquer et al. 2017; Roberts et al. 2018; Zanon et al. 2018).

The development of pollen databases (e.g. Fyfe et al. 2009; Giesecke et al. 2014) allows the assessment of changes in Holocene vegetation composition and dynamics at regional and subcontinental scales (e.g. Marquer et al. 2014, 2017; Giesecke et al. 2017). These variations are basically due to climate, environmental (e.g. soil characteristics, characteristic traits of plant species, extreme disturbance events) and/or land use factors. Recent studies have shown that climate and land use are important drivers of vegetation change during the Holocene in northern Europe and Fennoscandia (Reitalu et al. 2013; Kuosmanen et al. 2016, 2018; Marquer et al. 2017). While climate is the dominant factor during the first half of the Holocene, land use becomes one of the primary drivers during the last 2,500 years.

Pollen-based reconstruction of past vegetation at regional and subcontinental scales represents a summary of the outcomes from all the interactions between vegetation dynamics, climate influences and impacts of land use within $10^4$ km$^2$ or larger (Prentice 1985). Land use impacts on vegetation composition and dynamics based on pollen are certainly recorded differently at local scales than at regional scales. The understanding of land use consequences at a local scale is particularly important to explore changes in the landscape-scale vegetation cover during the Neolithic; Neolithic populations, with subsistence based on hunting and gathering, are assumed to have had lower impact on vegetation at a regional scale than at a local scale in some areas. Furthermore, recent studies show that forest landscapes may have been shaped by human manipulation over millennia, although to a small extent. These human activities have caused local changes in biodiversity, species distributions and biomass (Dambrine et al. 2007; Innes et al. 2013; Pini et al. 2017). A better understanding of early anthropogenic impact at a local scale can provide insights into human-nature relationships at a time when populations were highly dependent on climate and environmental variabilities (Boivin et al. 2016). However, this information can only be gained by studying known spatial resolutions and using adequate indicators of vegetation change, such as land cover, plant diversity and composition indices.

Traditional pollen data expressed as proportions provide information about a mix of the regional and local pollen assemblages, thus making it difficult to assess the local changes in vegetation. The Landscape Reconstruction Algorithm (LRA, Sugita 2007a, b) was proposed to overcome this issue and provides pollen-based reconstructions of regional and local vegetation in quantitative terms, i.e. plant cover at a defined spatial scale (a few metres to kilometres from the center of the lake/peat bog). In particular, the LRA corrects for biases caused by basin size, intertaxonomic differences in pollen productivity and dispersal deposition. The LRA has already been applied in various environmental contexts (e.g. Sugita et al. 2010; Cui et al. 2014; Poska et al. 2014; Hjelle et al. 2015; Mazier et al. 2015; Abraham et al. 2017; Marquer et al. 2020). A better understanding about regional versus local changes in vegetation is critical in answering archaeological questions, in particular at a time when humans are assumed to have caused higher disturbances at local scales than regional scales, this being the case during the Neolithic.

Recent studies suggest that the Neolithization of Eurasia was a more complex process and the Neolithic a more diverse phenomenon than traditionally assumed (Barker 2006; Fuller et al. 2011; Herva et al. 2017; Nordqvist 2018). As pointed out by Bogucki (1995) and Smith (2001), an extensive and systematic manipulation of resources and some degree of control of wild species was already taking place during the Mesolithic. This was to such a degree that the static categories of “Mesolithic” and “Neolithic” are not correct characterizations defining the Stone Age (see also Nordqvist 2018). There are examples of societies where combined foraging and low-level use of cultivars were long-term and stable strategies that maintained foraging options rather than replacing wild foods. Smith (2001) has proposed the term “low-level food production” for the “in-between territories” that are neither hunting, fishing and gathering economies based exclusively on wild plant and animals, nor farming relying heavily on agricultural products. In western Norway, Hjelle et al. (2006) have argued that cereals and domesticated animals were introduced by some hunter-fisher groups during the early and middle Neolithic without any significant changes in the traditional economy and settlement pattern. Additionally, according to Barker (2006) there was not a steady “wave of advance” of a Neolithic package of new technologies and new forms of subsistence, but rather a piecemeal process of adoption of such package components by the indigenous foraging populations in different environmental and cultural contexts. New insights around the above archaeological issues might be obtained by a deeper understanding of the consequences of land use at local scales, i.e. by studying the environment the human populations lived in.
Within this context, the aim of the present paper is to assess the impact of Neolithic land use on the regional and local vegetation dynamics, plant composition and disturbance processes (fire). The study focuses on eastern Finland, where the Neolithic period begins with the appearance of pottery, ca. 5300–5200 BC (Pesonen and Leskinen 2009; Pesonen et al. 2012; Halinen 2015). The impact of Neolithic land use has already been studied in this region by using qualitative information, i.e. conventional pollen percentages and concentrations (grains/cm³) from sediment archives. These previous studies indicate that during the Early and Middle Neolithic hunter-gatherers increasingly started to impact the flora and vegetation structure and to incorporate cultivars into their economy (Tolonen 1978; Reynaud and Hjelmroos 1980; Königsson and Possnert 1997; Vuorela et al. 2001; Poska et al. 2004; Poska and Saarse 2006; Alelänius et al. 2013, 2017; Augustsson et al. 2013; Alelänius et al. in press). Here, we apply the LRA to high-resolution pollen records from three lacustrine sediment cores that cover the Neolithic period. We estimate changes in vegetation composition, the rate of plant compositional change and fire activity. Fire occurrence is here considered as an indicator of land use (e.g. Scherjon et al. 2015), although fire can result from both natural and anthropogenic disturbances (see “Discussion”).

Materials and methods

Environmental setting and archaeological context

The study area (Fig. 1) is located in the southern boreal vegetation zone of southern Finland. It belongs to the Finnish Lake District, where lakes occupy about 25% of the region. The Lake District expands into most of central and eastern Finland and extends further east to the Karelian Isthmus and the Republic of Karelia in Russia. Forests in this area are dominated by *Picea abies, Pinus sylvestris, Betula pendula, Betula pubescens, Populus tremula, Alnus incana* and *Alnus glutinosa* (Alalammi 1988). The region is classified as lowland with a terrain relief between of 30 and 75 m a.s.l.

Both lakes Katajajärvi and Huhdasjärvi belong to the drainage basin of the River Kymijoki, and were isolated from the Baltic Sea basin at around 9650 BC (Saarnisto 1970; Björck 1995; Lunkka et al. 2004). The bedrock includes primarily metavolcanic and metasedimentary rocks and several
generations of granitoids (Lehtinen et al. 2005). The quaternary geology of the study area is dominated by till, sand, clay and organic deposits that mostly fill the depressions of crystalline bedrock. Valleys, eskers and drumlins are typical landforms in the area (Simonen 1980; Tyrväinen 1986; Alalammi 1988; Lunkka et al. 2004). Today, the length of the growing season is 160–175 days/year and the mean annual precipitation is 550 mm, of which about 200 mm is received as snow. The mean annual temperature varies between +3.5 and +4 °C, the warmest month is July (+17 °C), and the coldest are January and February (between −9 and −8 °C) (Alalammi 1988). The archaeological finds indicating Stone Age habitations around the lakes Huhdasjärvi and Katajajärvi are modest; most of the sites have not been dated more accurately than to the Stone Age or to the subsequent Early Metal Period, i.e. this corresponds to 1800 BC–AD 300 in the inland areas of Finland. More generally, eastern Finland is rich in rock paintings dated back to the Stone Age (Fig. 1), often located by the waterways and representing land is rich in rock paintings dated back to the Stone Age and the Late Glacial in the inland areas of Finland. More generally, eastern Finland is rich in rock paintings dated back to the Stone Age and the Late Glacial (Lahelma 2008; Gjerde 2010).

**Pollen and charcoal data**

Three sediment cores (Fig. 1) were sampled for pollen analyses. One of the cores was obtained from lake Katajajärvi (Alenius et al. 2009), and two (Huhdasjärvi A and C) from Pitkälahti bay about 13.4 km from lake Katajajärvi (Alenius et al. 2017). Pitkälahti bay is a small oblong area belonging to lake Huhdasjärvi. Coordinates, size of the lakes and references are given in Table 1. The two sediment cores obtained from Pitkälahti bay were situated 450 m apart. Empirical and theoretical studies in Scandinavia (e.g. Nielsen and Sugita 2005; Hellman et al. 2009; Hjelle and Sugita 2012; Cui et al. 2014; Hjelle et al. 2015; Mazier et al. 2015; Fredh et al. 2019) have demonstrated that the RSAPs (Relevant Source Areas of Pollen; sensu Sugita 1994) for small lakes correspond to a large range of values (ca. 900 to 3000 m) most likely resulting from different vegetation patch sizes, spatial structure of the local landscapes and the basin size. This means that the RSAPs of the two cores collected in Pitkälahti bay most likely overlap. An earlier analysis based on pollen proportions (ESM 1) has shown differences in the pollen data between these two cores (Alenius et al. 2017), which suggests that the two coring sites can be considered as distinct palaeoecological records. Furthermore, the squared chord distance analysis performed between the three sites shows that the differences in term of vegetation composition are higher between Huhdasjärvi A and C than between one or the other of the Huhdasjärvi sites and Katajajärvi (see Fig. 2 and “Discussion” below). This underlines that the pollen mixing during the deposition of sediment cannot be considered as homogeneous for the entire lake, but rather specific to locations defined by lake morphology. Such weak mixing of pollen within the entire lake would result in an overrepresentation of local pollen in the bays. This means that bays from a large lake might be assumed to be different small sites for LRA reconstructions. Note that a major assumption of the LRA is that lakes are of circular shape and the pollen grains, once deposited on the lake surface, are well mixed in the water column during the sedimentation processes. For the application of the LRA to our study, we therefore made the assumption that each site (Huhdasjärvi A and C) is an individual small lake of circular shape. However, this assumption has not been tested, i.e. comparison between LOVE reconstructions using modern surface pollen assemblages and actual plant cover around these sites; this might be a source of uncertainties in our LOVE estimates that should be taken into account in the interpretation of the results.

Charcoal data were collected from Huhdasjärvi A and C in order to reconstruct local fire dynamics at the two selected sites during the Holocene. The charcoal particles > 10 µm (measured along the longest axis) were counted on pollen slides and expressed as microcharcoal concentrations, i.e. number of fragments/cm³. Each charcoal record is standardized and normalized according to a protocol frequently used by the palaeofire community (Power et al. 2010). Charcoal

| Table 1 | Pollen records used for REVEALS and LOVE reconstructions. The REVEALS estimates are those published by Kuosmanen et al. (2018) |
|---------|---------------------------------------------------------------------------------------------------------------------------------|
| Lakes used for the REVEALS model | Latitude (°N) | Longitude (°E) | Size (ha) | References |
| Laihalampi | 61.49° | 26.08°E | 25.5 | Heikkilä and Seppä (2003) |
| Kirkkolampi | 61.79° | 29.99°E | 72 | Alenius and Laakso (2006) |
| Orjärvi | 61.66° | 27.21°E | 28.8 | Alenius et al. (2008) |
| Huhdasjärvi | 61.17° | 26.59°E | 29.5 | Alenius et al. (2013) |
| Kaakotinlampi | 61.41° | 25.86°E | 0.2 | Vuorela (1981) |
| Lakes used for the LOVE model | | | | |
| Huhdasjärvi A | 61.163° | 26.59°E | 22 | Alenius et al. (2017) |
| Huhdasjärvi C | 61.166° | 26.593°E | 22 | Alenius et al. (2017) |
| Katajajärvi | 61.17° | 26.84°E | 14 | Alenius et al. (2009) |
influxes are then converted to Z-scores for an interpretation of individual values with respect to variation around the long-term mean (here the interval 1,000–6,000 BP, i.e. the period most representative of the entire database). Mean Z-scores are then computed at 200-year intervals. For the study of fire dynamics at the regional scale, we used the composite charcoal curve already published in Kuosmanen et al. (2018), constructed by grouping together all available records in southeast Finland. Differently from Kuosmanen et al. (2018), where the authors focused on the period 10,000–1,000 (i.e. the time where data on human population were available), in the present paper we extend the palaeofire reconstruction over the entire Holocene. Also in this case, charcoal data are expressed as transformed charcoal influx (hereafter referred as tCHAR) Z-scores.

Chronologies of Huhdasjärvi A and C are based on palaeomagnetic dating supported by three bulk AMS radiocarbon dates (Alenius et al. 2017). An age-depth model for Lake Katajajärvi uses four calibrated AMS radiocarbon ages and linear interpolation; the age-depth model agrees well with the known regional dates for the increase of Picea, Tilia and Alnus pollen percentages obtained from the literature (Alenius et al. 2009). Age-depth models, bathymetry and coring locations for Lake Katajajärvi, Huhdasjärvi A and C are presented in ESM 2.

**The landscape reconstruction algorithm (LRA)**

The LRA approach (Sugita 2007a, b) consists of two sub-models. The first sub-model is REVEALS for plant cover reconstruction at a regional scale of ca. 50–100 km radius around a large lake (radius > 50 ha) or a mix of several lakes and/or bogs of small sizes (radius < 50 ha; Marquer et al. 2014, 2017; Trondman et al. 2015, 2016). The second sub-model is LOVE for plant cover reconstruction at a local scale of about a few metres to kilometres from each of
the small size sites from which pollen records are obtained. LOVE estimates correspond to vegetation composition within the RSAP at each site and are obtained by subtracting the regional background of pollen (calculated from the REVEALS estimates) from the overall pollen assemblages (Sugita 2007b).

For the LRA runs we use twenty-three pollen types and the relative pollen productivity estimates (RPPs) obtained from various regions in Europe (the LANDCLIM standard 2 dataset of Mazier et al. 2012) that have been previously applied for all sub-continental and regional pollen-based vegetation reconstructions (Marquer et al. 2014, 2017; Trondman et al. 2015; Kuosmanen et al. 2018). RPPs and their standard errors, fall speeds of pollen, and the different land cover categories used in this study are given in Table 2. Plant taxa are here grouped into four land cover categories: forest/woodland, meadow/grassland, cropland and wetland. The LRA results are expressed as percentage cover of plant types or land-cover categories with their standard errors.

Table 2 RPPs (relative pollen productivity estimates) and their standard errors, fall speeds of pollen and land cover categories

| Taxa               | RPP and their standard errors | Fall speeds of pollen (m/s) |
|--------------------|-------------------------------|-----------------------------|
| Woodland/forest    |                               |                             |
| *Picea*            | 2.62 ± 0.12                   | 0.056                       |
| *Pinus*            | 6.38 ± 0.45                   | 0.031                       |
| *Betula*           | 3.09 ± 0.27                   | 0.024                       |
| *Alnus*            | 9.07 ± 0.1                    | 0.021                       |
| *Quercus*          | 5.83 ± 0.15                   | 0.035                       |
| *Tilia*            | 0.8 ± 0.03                    | 0.032                       |
| *Ulmus*            | 1.27 ± 0.05                   | 0.032                       |
| *Fraxinus*         | 1.03 ± 0.11                   | 0.022                       |
| *Corylus*          | 1.99 ± 0.19                   | 0.025                       |
| *Fagus*            | 2.35 ± 0.11                   | 0.057                       |
| *Carpinus*         | 3.55 ± 0.43                   | 0.042                       |
| Meadow/grassland   |                               |                             |
| Poaceae            | 1                             | 0.035                       |
| *Juniperus*        | 2.07 ± 0.04                   | 0.016                       |
| *Calluna*          | 0.82 ± 0.02                   | 0.038                       |
| *Rumex*            | 2.14 ± 0.28                   | 0.018                       |
| *Plantago media*   | 1.27 ± 0.18                   | 0.024                       |
| *Plantago lanceolata* | 1.04 ± 0.09 | 1.04                         |
| *Filipendula*      | 2.81 ± 0.43                   | 0.006                       |
| *Artemisia*        | 3.48 ± 0.20                   | 0.025                       |
| Cropland           |                               |                             |
| *Secale*           | 3.02 ± 0.05                   | 0.06                        |
| *Cerealia-t*       | 1.85 ± 0.38                   | 0.06                        |
| Wetland            |                               |                             |
| *Cyperacea*        | 0.87 ± 0.06                   | 0.035                       |
| *Salix*            | 1.22 ± 0.11                   | 0.022                       |

Standard errors of the REVEALS and LOVE estimates are obtained by a delta method (Stuart and Ord 1994).

Regional vegetation, REVEALS estimates

The REVEALS estimates used to reconstruct southeast Finland regional land-cover over the last 10,000 years are those already published in Kuosmanen et al. (2018). Note that in Kuosmanen et al. the data are presented only for the time period 1,000 to 12,000 years ago, but we here show the whole last 12,000 years. REVEALS estimates for the last 1,000 years were not shown in Kuosmanen et al. because of the focus of the study on a comparison between REVEALS and human population estimates that did not cover the last millennium. Time intervals of 200 years were used, except in the three uppermost time windows (AD 2000–1950, 1950–1900 and 1900–1850) where time intervals of 50 years were used. These estimates were based on five pollen records (lakes Orijärvi, Kirkkolampi, Laihalampi, Kaakotinlampi and Huhdasjärvi 1; Fig. 1, Table 1, ESM 3); for all details see Kuosmanen et al. 2018. The core Huhdasjärvi 1 (Alenius et al. 2013) was collected from the same lake as Huhdasjärvi A and C (used for the LOVE reconstructions). However, the Huhdasjärvi 1 sediment core was collected from a large open area and the pollen records are assumed to represent the regional vegetation. The Huhdasjärvi A and C cores were obtained from Pitkälahti bay and the pollen records from these cores are assumed to represent the local vegetation signals (see ‘Pollen and charcoal data’).

Local vegetation, LOVE estimates

The REVEALS estimates (see previous section) are used as inputs in LOVE for the regional vegetation abundance. The RSAP can be calculated by using an inverse modelling approach including in the LOVE model, however because of the low numbers of similarly-sized sites available for our analysis it would be difficult to obtain reliable RSAPs by using this approach. RSAPs have been estimated in southern Sweden by using a forward-modelling approach (Sugita 1994; Sugita et al. 1999) and hypothetical landscapes based on modern vegetation maps (Mazier et al. 2015). The results reveal predicted RSAPs of radii of 1,740 and 1,440 m from the centres of the lakes studied by Mazier et al. Because of similarly-sized sites and the use of pollen records from bays would overrepresent local pollen (see “Pollen and charcoal data” above), the lowest RSAPs of Mazier et al. would be relevant for our study. We have therefore considered a RSAP of radius 1,400 m as the spatial unit of the LOVE reconstructions around the sites. We further assume a constant RSAP through time. For the sizes of each lake the nearest distances from the shores have been measured to calculate the lake radii (Table 1). The time interval used for the LOVE runs is...
200 years. Pollen counts falling within each time interval are pooled together. The longest time span (lasting from 7950 BC to AD 1580 with a total of 49 time windows) is obtained from Lake Katajajärvi, while the shortest span (lasting from 6550 BC to AD 450 with a total of 36 time windows) from Lake Huhdasjärvi A. We use the LOVE version 5.0 program (Sugita unpublished). Note that wind speed is set to 3 m s\(^{-1}\) and the maximum spatial extent of the regional vegetation from the centre of the study sites to 50 km. Neutral atmospheric conditions are considered for these runs. A Gaussian Plume Model (Sutton 1953; Tauber 1965; Prentice 1985; Sugita 1994) is used to describe pollen dispersal and deposition characteristics.

### Indices of change in vegetation composition and CONISS

Rate of change in vegetation composition, vegetation turnover and evenness are calculated using the REVEALS- and LOVE-based results. Rate of change aims at identifying periods of stability and change in vegetation over time. Turnover represents the magnitude of change in vegetation over time. Evenness refers to how numerically equal the plant taxa are in their abundances (i.e. if all taxa are equal in their abundances the evenness is 1, maximum evenness). For methodological details see Marquer et al. (2014, 2017). In order to identify periods of similar vegetation composition, a stratigraphically constrained cluster analysis (CONISS; Grimm 1987) is used for both REVEALS and LOVE estimates. We further performed a squared chord distance analysis to assess the differences between the three “local sites” as well as between each of the local site and the REVEALS estimates. The squared chord distances have also been calculated between the five sites that have been used for REVEALS to test the assumption that in theory the sites used for REVEALS runs should be more similar to each other than to the LOVE sites.

### Results

#### Changes in plant abundance and vegetation composition

**Regional vegetation, REVEALS**

Four major regional CONISS zones (CONISS R1 to R4) are observed based on the REVEALS estimates (Fig. 3). The main features of each CONISS zone are described in Table 3.

The results for the rate of change, turnover and evenness are presented in Fig. 4. The rate of change remains low from 6650 to 5050 BC, slightly increases between 5050 and 3250 BC, then rises (higher variation than previously) from 3250 BC onwards with the highest value reached at the present time. A high turnover between 6850 and 4850 BC is followed
Table 3 Summary of the vegetation composition changes for the main regional and local CONISS zones. Percentages presented in the brackets are the average percentages over the time interval

| Regional: CONISS R1-R4 | Huhdasjärvi A: CONISS HA1-HA4 | Huhdasjärvi C: CONISS HC1-HC4 | Katajajärvi: CONISS K1-K4 |
|------------------------|-------------------------------|-----------------------------|--------------------------|
| R4: AD 550–2000        | HA4: 1750 BC–AD 650          | HC4: 1150 BC–AD 1050        | K4: 1750 BC–AD 1650      |
| Increase in meadow/grassland (Poaceae 11.5%, Juniperus 0.8%), cropland (Secale) and wetland (Cyperaceae) taxa. Decrease in forest/woodland vegetation cover | The dominating tree taxa are Pinus (44.5%), Betula (27.5%), Picea (16.3%) and Alnus (6.7%). Corylus is the highest estimate for thermophilous trees taxa. Juniperus, Poaceae and Salix are the abundant meadow/grassland and wetland taxa | Pinus (39.7%) and Betula (23%) dominate, while Picea (8.2%) and Alnus (5.5%) decrease. Corylus is the most abundant thermophilous tree taxa, while Poaceae dominates among meadow/grassland taxa | Pinus (49%), Betula (27.9%), Picea (9.5%) and Alnus (6.5%) are the abundant tree taxa. Juniperus, Poaceae and Calluna are the main meadow/grassland taxa. Salix and Cyperaceae dominate among wetland taxa |
| R3: 4450 BC–AD 550     | HA3: 4150–1750 BC            | HC3: 4350–1150 BC           | K3: 3350–1750 BC         |
| Increase in abundance of Picea (40%), and decrease in abundances of Betula (29.8%), Pinus (15%) and thermophilous trees taxa (5.6%) | Betula (38.2%), Pinus (37.6%), Alnus (9.3%) and Picea (7.4%) dominate Corylus, Ulmus and Tilia are the most abundant thermophilous trees taxa. Juniperus and Poaceae are the most abundant meadow/grassland taxa, while Salix and Cyperaceae characterize the wetland vegetation | Picea (39%), Betula (37%) and Alnus (9.7%) dominate. Picea is present (5.4%). Corylus, Ulmus, Tilia and Fraxinus are recorded in small abundances. Juniperus and Poaceae dominate among meadow/grassland taxa | Pinus (40.5%), Betula (36.9%) and Alnus (9.5%) dominate. Estimates of Picea, Corylus, Ulmus and Fraxinus are low. Among meadow/grassland vegetation, Juniperus, and Poaceae are the most abundant taxa |
| R2: 7650–4450 BC       | HA2: 5150–4150 BC            | HC2: 6550–4350 BC           | K2: 7550–3350 BC         |
| Betula (53%) and Pinus (16.4%) dominate. Estimates of Ulmus, Alnus and Corylus are low. Meadow/grassland and wetland taxa are dominated by Poaceae and Cyperaceae, respectively | Betula (60%), Pinus (39%) and Alnus (10.3%) dominate. Estimates of thermophilous tree taxa are dominated by Ulmus (12.5%), abundances of Corylus and Tilia are low. Poaceae, Cyperaceae and Salix are the most abundant meadow/grassland and wetland taxa | Betula (42%) and Pinus (34.9%) dominate. Estimates of thermophilous trees taxa, i.e. Ulmus and Corylus, are low. Tilia increases, Poaceae, Salix and Cyperaceae have few abundances | Betula (41.8%), Pinus (34.2%) and Alnus (11.3%) dominate. Estimates of Corylus, Ulmus are few. Poaceae and Salix are the most abundant meadow/grassland and wetland taxa |
| R1: 9750–7650 BC       | HA1: 6550–5150 BC            | HC1: 6950–6550 BC           | K1: 7950–550 BC          |
| Betula (36%), Pinus (15.5%), Poaceae (28%) and Cyperaceae (9.3%) dominate. Estimates of Ulmus and Corylus are low | Betula (43.7%), Pinus (36%) and Alnus (12.5%) dominate. Estimates of Ulmus and Corylus are small. From 5550 BC onwards, Tilia increases. Of meadow/grassland taxa, Poaceae is the most abundant | Pinus (46%), Betula (32.6%) and Alnus (14.4%) dominate. Estimates of Ulmus, Corylus, Poaceae and Salix are few | Pinus (44%) and Betula (43.6%) are dominant tree taxa. Estimates of Alnus, Ulmus and Corylus are small. Salix and Cyperaceae are the most abundant meadow/grassland and wetland taxa, respectively |
by a decreasing trend until AD 1750. Then, an increase is recorded until the present time. Evenness is high between 6850 and 3450 BC, then a decreasing trend characterizes the period 3450 BC–AD 550. A new increase is visible from AD 550 until 1875.

Local vegetation, LOVE

The four major CONISS zones identified in Huudasjärvi C (HC1 to HC4), Huudasjärvi A (HA1 to HA4) and Katajajärvi (K1 to K4) are shown in Fig. 5 and described in Table 3.

Considering the indices of change in vegetation composition, a low rate of change from 6650 BC until 2650 BC is followed by increasing and highly variable values between 2650 BC and AD 950. Turnover is high from 6850 to 3850 BC, and a decreasing trend characterizes the period between 3850 BC and AD 1350. Evenness is stable/slightly increasing from 6850 BC until 3850 BC, then it decreases during the period between 3850 BC and AD 1350.

Regional versus local vegetation dynamics

In general, similar trends in Holocene forest development (Fig. 6) are visible at both the regional and local scales. However, open land (meadow/grassland, cropland and wetland) and forest/woodland categories are respectively less and more abundant at the local scales than the regional scale. Some individual tree taxa (e.g. Picea) are, nevertheless, more common at the regional scale. In detail, one important difference is the spread of Picea. Between 5550 and 4750 BC in REVEALS Picea constitutes 1.8%, while LOVE estimates for this taxon are still very low (0.1–0.2%). Differences can also be seen in the relative abundances of tree taxa. Regionally, between 4750 and 1800 BC, Picea constitutes 26.8% (percentages are averaged REVEALS and LOVE values over the time interval) and Pinus 15% of forest/woodland vegetation, while at the local scales Picea abundance is lower than 6% and Pinus is more abundant (37.8–39%). With respect to broadleaved trees, during the same time period the regional abundance of Betula and Alnus together reaches 39%, while locally their vegetation cover is ca. 48%. Therophilous trees (i.e. Corylus, Fraxinus, Tilia, Ulmus) are also more abundant regionally (9.7%) than locally (ca. 7%). Of meadow/grassland taxa, Juniperus shows an increase in Huhdasjärvi A around 4150 BC, Huhdasjärvi C around 4350 BC and in Katajajärvi around 3350 BC (more noticeably around 1750 BC), while such an increase is only visible at the regional scale at AD 550. Of wetland taxa, Salix is present in 0.3–0.8% in the local and regional reconstructions.

Trends in evenness and turnover are similar between the local and regional scales. Differences are observed in terms of timing and amplitude of changes. The decrease in evenness between 3250 BC and AD 550 is more pronounced at the regional than at the local scales. While the local rate of change is in general higher than the regional one for the same time periods, values remain low at both the regional and local scales until 3250 and 2650 BC, respectively. Note that the rate of change at Lake Katajajärvi does not show an increasing trend.

The squared chord distance analysis (Fig. 2) shows few differences between the three local sites; the main differences are observed between Huudasjärvi A and C. The dissimilarity between Huudasjärvi A and C is essentially caused by differences in abundances of Betula, Picea, Pinus and Salix, in particular a high dissimilarity is observed at ca.
1400 bc due to Picea. Differences between the regional and local signals are increasing from ca. 4250 bc; they are higher than between the LOVE sites. The squared chord distances between the five sites that have been used for REVEALS (Fig. 2) support the assumption that in theory the sites used for REVEALS are similar to each other with a mean of squared chord distances lower than 0.2 and little variability between sites. There are more differences and variabilities between the REVEALS and LOVE estimates than between the sites that have been used for the REVEALS runs.

**Fire dynamics at regional and local scales**

Main trends of the regional and local fire-dynamics are presented in Fig. 6. At the regional scale, fire activity is above the long-term mean (i.e. positive tCHAR Z-scores) between 9750 and 3000 bc. A period with negative values occurs from 3000 bc until ad 600. Finally, fire activity is higher than the long-term mean during the last 1,400 years (between 600 ad and the present day).

At the local scale, trends in fire activity slightly differ between the two sites analyzed. Huhdasjärvi A is characterized by higher tCHAR Z-scores compared to the long-term mean between 6450 and 3800 bc, with a short period of lower fire activity between 5300 and 5000 bc. Then the values start to decrease, with negative tCHAR Z-scores during the period 3700–1200 bc. From 1200 bc to ad 400 the site is characterized by higher fire activity. Negative tCHAR Z-scores are finally recorded between ad 400 and 750. At Huhdasjärvi C, tCHAR Z-scores are characterized by higher values compared to the long-term mean between 6650 and 3400 bc. Despite some oscillations, fire activity between 3400 bc and ad 600 is similar to the long-term mean (tCHAR Z-scores around 0). Since ad 600, fire activity increases, with a peak at ad 950.

**Discussion**

**Roles of climate and environmental factors in vegetation composition**

Our results show similar trends in Holocene forest development at both the regional and local scales. Between 6850 and 4850 bc both the regional and local turnovers reach maximum values and the regional rate of change is the lowest. These changes likely relate to the spread of new tree taxa in the region, such as Tilia and Picea around 6000 bc. The highest abundances in thermophilous taxa (21–23%) are reached during the Early Neolithic, between 4750 and 4350 bc. This coincides with the Holocene Thermal Maximum (HTM), ca. 6000–3000 bc in southern Fennoscandia, when temperatures were ca. 1.5–2.5 °C higher than the present time (Heikkilä and Seppä 2003; Ojala et al. 2008; Seppä et al. 2009b).

The HTM was followed by an overall cooling and the southward retreat of noble deciduous tree taxa. A gradual decrease in thermophilous tree taxa is clear in both the regional and local vegetation reconstructions since around 4400 bc. This significant change in the Fennoscandian ecosystem is related to the spread of Picea after ca. 4000 bc (Giesecke and Bennett 2004; Seppä et al. 2009a). Oxygen isotope records in sediments show an increase in relative humidity after 3000 bc in the region (Hammarlund et al. 2003; Heikkilä and Seppä 2010; Kostrova et al. 2018), with an effect on the natural fire frequency. This is in agreement with our regional charcoal results, showing a long period of low fire activity from 3000 bc until ad 600. This period 4450 bc–ad 550 is further characterized by a gradual decline of turnover and evenness in vegetation. It can be argued that the reason for such changes is the progressive replacement of “former” species-rich mixed forests with more homogeneous “modern” boreal forests dominated by Picea, Pinus and Betula.

Compared to the regional abundances, local abundances are lower for Picea and thermophilous taxa (only 7.6% between 4850 and 4250 bc in Huhdasjärvi A), and higher for Pinus; this explains part of the increasing differences between the local and regional vegetation composition in Fig. 2. This difference is probably caused by the distribution of surface deposits. Till deposits dominate the area, while sorted glaciofluvial deposits, such as eskers, are less represented but favour Pinus that predominantly grows on these drier and nutrient-poor patches. Shade-tolerant Picea prefers moist and nutrient-rich soils (Sutinen et al. 2002) and forms the typical boreal forest zone on till-dominated soils of Finland. Thus it is not a surprise that Picea dominates the late Holocene regional vegetation based on REVEALS estimates from five basins across the area, while Pinus can be locally more common, in particular around Huhdasjärvi, located by a large area of glaciofluvial deposits. There are also differences between the two sites from Pitkälahti bay, as Picea has been (according to LOVE-based estimates of the local vegetation composition) slightly more common at the end of the bay than the middle part. We assume that the results reflect real differences in vegetation around the bay rather than major differences in pollen dispersal and/or deposition patterns, since the cores were collected from two individual small accumulation basins within the bay. This is supported by the uniform sediment accumulation rates between the cores through time.
The trend in the rate of vegetation change is increasing from 3250 BC at regional scale, and later (from 2650 BC) at local scales. Our results agree with turnover, evenness and rate of change observations studied at regional and subcontinental scales (Marquer et al. 2017) and are likely to be caused by Holocene climate changes.

Role of late Mesolithic and Neolithic land use in vegetation composition and fire activity

From late Mesolithic to Middle Neolithic (6450–3200 BC)

Fire activity  Between 6450 and 3800 BC both the regional and local fire activity are generally characterized by values above the long-term mean. Despite some oscillations, the local and regional fire activities are higher than the long-term mean until 3800 and 3000 BC respectively, suggesting the widespread use of fire. As there is plenty of evidence of human activity around the lake Huhdasjärvi during this period (detected from pollen and loss on ignition), human induced fires could be a reason for high values in fire activity. In the earlier study from Huhdasjärvi (analysed from Huhdasjärvi 1; Alenius et al. 2017) an abrupt erosion phase was dated to between 6340–5810 BC, and was found to coincide with phases of increased fire intensity. This was then followed by the increase in species richness from ca. 5260 BC, simultaneous with a decrease in Pinus and Betula, indicating an increase in the openness of the landscape. Also in the cores obtained from Pitkälahti bay, the earliest human impact was earlier dated to between ca. 4400 and 3900 BC. It includes some use of fire and cultivation of hemp and barley. In addition, a sudden erosion phase was dated between 4165 and 4090 BC. In addition to the cultivated plants Hordeum and Cannabis, apophytes such as Plantago major/media, Rumex, Fabaceae, Campanula and Caryophyllaceae are recorded.

During the Neolithic burning practices are known to have played an important role in opening up landscapes to
favour the growth of edible plants such as raspberry, juniper
(Juniperus), hazel (Corylus) and wild strawberry (Fragaria vesca) (Vanhanen and Pesonen 2015). All these species have a competitive advantage in early successional communities but decline in abundance during later successional stages (Smith 2001). During this period fire could also have been used to clear forests for increasing grazing lands for large ruminants, such as moose that prefer young forests. Osteological material obtained from eastern Finland shows that people used moose and forest reindeer as mammal resources, in addition to aquatic resources, such as beaver and Saimaa ringed seal (Ukkonen 1996; Oinonen et al. 2014).

**Early decrease of Tilia abundance at a regional scale** In the local reconstructions, Tilia abundances are decreasing in lakes Katajajärvi and Huhdasjärvi from ca. 4000–3200 bc. This decrease is also observed at the regional scale but a bit earlier than at the local scales, ca. 4600 bc. This decrease in Tilia abundance can be interpreted as a consequence of the natural gradual decrease in Tilia abundance due to the overall cooling and the southward retreat of noble deciduous tree taxa (Huntley and Birks 1983; Seppä et al. 2009a, b). These results suggest that the decreases in Tilia abundances have not been simultaneous in the studied region, which can be seen at the local scales. The difference in timing of local Tilia declines might be caused by land use, e.g. differences in the intensity and extent of land use between various locations. Tilia fluctuations at lake Huhdasjärvi, occurring synchronously with other settlement indicators (increase in Juniperus, Cannabis, Rumex), might suggest management of Tilia woodlands by small-scale human groups that can only be detected at the local scale. In the northern German Neolithic, the synchronous decline of Tilia values together with the simultaneous occurrence of settlement indicators has been interpreted as an anthropogenic influence on the woodland composition (Kirleis et al. 2012).

Manufacture of lime bast cordage has been an unbroken tradition from the Mesolithic to the present day in northern Europe (Myking et al. 2005). In eastern Baltic Sea regions, lime fibres are known in prehistory to be utilized for binding material for stationary wooden fishing structures (Bérzinš 2008) and lime bast is also widely used as a raw material for different textiles (Bender Jørgensen 1990; Schweinigruber 1990; Rimkutė 2010; Mannering et al. 2012). Lime bast is usually obtained from young trees. COPPERING i.e. the periodic cutting-off at ground level is a traditional way to encourage the growth of multiple young shoots. Note that it has been demonstrated that the amount of pollen produced by Tilia cordata is heavily reduced as a result of periodic coppicing and is therefore likely to be ‘palynologically invisible’ (Waller et al. 2012). In addition to being used for bast, coppiced lime has also been used for leaf fodder for livestock in many parts of Europe (e.g. Rasmussen 1989). Pollen spectra from eastern and northern Denmark have revealed felling and burning of lime woodlands for livestock grazing and cereal cultivation (Andersen 2012). In Finland, osteological evidence of domesticated animals (excluding dogs) for this time period is missing. The earliest sheep/goat bone dates to end of the third millennium bc (Bläufer and Kan tanen 2013). However, it should be noted that unburnt bone does not generally preserve in the acidic soil conditions of Finland and all the available osteological material is burnt.

**Towards local semi-open landscapes from ca. 4000 bc** From ca. 4000 bc, differences in vegetation composition between the local and regional scales are increasing; see Fig. 2. The most notable difference is visible in Juniperus percentages, as the LOVE estimates for Huhdasjärvi and Katajajärvi show an increase in its abundance; from 4350 bc at Huhdas järvi C, 4150 bc at Huhdasjärvi A and 3350 bc at Katajajärvi (with a more noticeable increase from 1750 bc onwards). Increase in Juniperus percentage cover indicates a change in vegetation structure towards semi-open landscapes, where light-demanding Juniperus grows better. This might be due to the local land use that is not visible at the regional scale. Changes in Juniperus abundance might be more influenced by climate and environmental factors at the regional scale than at the local scale. Juniperus increases at the local scale were probably caused by land use. This hypothesis of change in land use towards semi-open landscapes is supported by the simultaneous, yet sporadic evidence of cultivation of Cannabis and Hordeum, earlier dated in lake Huhdasjärvi pollen sequences to between ca. 4400 and 3200 bc, also indicating longer occupation at the site (Alenius et al. 2017). Earlier, increase in Juniperus percentage cover was likewise dated to between 4480 and 3250 bc in Lake Bol’shojye Zavetnoye (about 180 km to the east in the Karelian Isthmus, Russia) and was interpreted as indicating intensified human activity and prolonged human occupation at the site (Alenius et al. 2020).

In timing, this change in vegetation pattern towards semi-open landscapes agrees with the arrival of a new pottery tradition called Typical Comb Ware (TCW in Finland: 4000–3400 bc). During the early TCW period, there was an increasing tendency to locate housepit sites in unsheltered and aquatically-oriented locations, coincident with the appearance of village-like clusters of housepits. These changes have been interpreted as reflecting a growing degree of sedentism (Mökkönen 2011). The appearance of TCW is marked by new contact networks that are in some regions explained through small-scale migration and in other areas through cultural diffusion, the movement of new ideas and material goods (Nordqvist and Herva 2013; Herva et al. 2014; Nordqvist and Kriska 2015).

If we accept the identification of the earliest Cerealia- and Cannabis-types of pollen as a proof of the growing of
domesticated plant taxa, interesting questions regarding the nature and scale of these activities arise. The term *cultivation* usually refers to the growing of domesticated crops for food and other purposes, but it can also refer to non-agricultural contexts of wild-plant exploitation. The meaning has expanded to include a range of activities that promote plant growth such as tillage, land clearance, plant sowing, weeding, harvesting and deliberate burning of vegetation (Harris 2007; Harris and Fuller 2014; Fuller and Lucas 2017). If the sites were settled for a longer period than before, it is likely that shifting cultivation was not taking place but, instead, cultivation took place in longer-term, permanent plots. Sometimes the terms *horticulture* and *garden cultivation* are used in the literature for traditional agricultural systems. According to Harris (2007), *gardens* are smaller and are floristically more diverse than fields. In that sense, the growing of domesticated species around lakes Huhdasjärvi and Katajajärvi might relate to garden cultivation in permanent plots and possibly included other wild-plant management and activities. Nevertheless, it is clear that between ca. 4400 and 3200 bc cultivation did not form the basis of subsistence in southeastern Finland (a region situated in the boreal forest zone beyond 60° N latitude) and was not in the form of intensive field cultivation as in Central Europe (see also Núñez 1999; Mökkönen 2010; Nordqvist and Kriiska 2015). Hunting, fishing and gathering remained as subsistence sources even when the knowledge of cultivation had reached the area.

The highest HTM summer temperatures and the lowest relative humidity took place in Fennoscandia at ca. 4000 bc (Seppä et al. 2009b; Heikkilä et al. 2010; Salonen et al. 2014). The climatic conditions appear to correlate with: (1) the increase in *Juniperus* (from 4350–4150 bc onwards) and (2) the earliest sporadic signals of cultivation of domesticated species (in lake Huhdasjärvi between ca. 4400 and 3200 bc), both suggesting in situ human occupation, together with (3) the spread of TCW. In this respect, at that time there should not have been climatic limitations for the onset of small-scale, sporadic growing of cultivars, especially with the onset of a new, more sedentary, style of life. Coincident with the HTM and related high productivity of terrestrial, lacustrine and marine ecosystems, human population proxies indicate a substantial growth in hunter–gatherer populations supported by an increase in resource availability (Ömønen et al. 2010; Tallavaara et al. 2010; but see also Crombé and Robinson 2014).

**From local to regional land use: from Late Neolithic (3200–1800 bc) to Preindustrial period**

A significant increase in the rate of change takes place from 2450 bc onwards in Huhdasjärvi A and 2050 bc onwards at Huhdasjärvi C. This increase corresponds to a first decrease in *Betula* and increases in the abundances of *Picea* and *Pinus*, based on LOVE reconstructions. A climate-induced change in vegetation composition might be suggested as a main explanation for this increase in the rate of change; an increase in boreal forest components, particularly *Picea*, at that time is commonly assumed to be climate-induced.

However, an increase in organic matter input into the bay, potentially caused by erosion due to human activities near to the shores of Huhdasjärvi, was recorded by earlier studies at both coring sites between ca. 2600 and 1840 bc, with the highest peak in organic content dated to ca. 2300 bc (Alenius et al. 2013, 2017). Furthermore, a *Hordeum*-type pollen grain was identified at ca. 2160 bc (Alenius et al. 2017), also indicating human occupation around the lake. The rates of change at the regional scale and at lake Katajajärvi are not as notable as in Huhdasjärvi A and C. All of this might indicate a local-scale land-use activity located near Huhdasjärvi.

Both the regional and local trends in fire activity decrease during this period. At the regional scale, the charcoal composite curve shows values lower than the long-term mean between 3000 bc and AD 600. Locally, Huhdasjärvi A is characterized by negative tCHAR Z-scores between 3800 and 1200 bc, while negative values are recorded at Huhdasjärvi C between 3700 bc and AD 600. This might suggest few human-induced fires at those times.

From 1750 bc onwards the local vegetation near lakes Huhdasjärvi A and Katajajärvi are both characterized by a decline in *Betula, Ulmus* and *Corylus* and an increase in *Picea* and *Juniperus*. The plausible reason might be the grazing of domesticated animals and those feeding in broadleaved forests (Behre 1981; Pykälä 2001). In timing, the LOVE results agree with the earliest osteological evidence. In Finland, the earliest secure appearance of livestock dates to the end of the Late Neolithic, ca. 2500–950 bc (Bläuer and Kantanen 2013; Cramp et al. 2014; Ukkonen and Mannermäa 2017; Ahola et al. 2018). The REVEALS results however do not show similar patterns, change in forest plant composition, suggesting that the land use has remained small scale and local. Only from AD 550 onwards does the regional vegetation show a significant reduction of forests along with the presence of domesticated cereals, meadows and grasslands and, from AD 750 onwards, the spread of slash-and-burn practices. The expansion of slash-and-burn practices becomes visible in the regional charcoal composite curve and, locally, at Huhdasjärvi A. The expansion of slash-and-burn practices during the Iron Age is also known from other sources (e.g. Taavitsainen 1987; Taavitsainen et al. 1998). All of this indicates a shift towards agricultural communities, where farming is the predominant activity and determines the main diet, although hunting, fishing and gathering may have continued. Both slash-and-burn and permanent field cultivation were in use from the 17th century onwards in eastern parts of Scandinavia, and
slash-and-burn cultivation remained the major method of cereal crop cultivation in eastern Finland until the late 19th century (Soininen 1974; Taavitsainen 1987; Taavitsainen et al. 1998; Alenius and Laakso 2006; Alenius et al. 2017). The timing of the shift towards agricultural communities suggested by the REVEALS results from eastern Finland agrees with the date range AD 400–1000 that is obtained genetically with ancient DNA at the time of the actual burst of animal husbandry in north-east Baltic Sea region (Niemi 2018). The rise and expansion of human activities from ca. AD 400 have further affected the regional plant composition, and in particular the evenness index. The regional climate-induced evenness change, i.e. high (6850–3450 BC) and decreasing evenness (3450 BC–AD 550), starts to increase from AD 500 until AD 1875. This increase in REVEALS evenness followed by a decline after AD 1875 is similar to the pattern reported by Fredh et al. (2017) in southern Sweden. Fredh et al. state that the highest evenness refers to the period of traditional cultural landscape while later evenness decrease refers to modern land use over the last century.

Conclusions

This article contributes to the discussion about Neolithic land use at local and regional scales in eastern Fennoscandia. The LRA allows us to compare the regional- vs. local-scale land use from fossil pollen records, and to underline main differences in the local land use between the study sites; the traditional use of pollen percentage/concentration data alone cannot achieve these objectives. Detailed, local scale investigations are therefore crucial in demonstrating the varieties of land use practices among hunting, fishing and gathering societies, and in providing a long-term background of human modifications and sustainable use of local resources.

In particular, we show that during the Early Neolithic, vegetation composition and fire activity were similar between the regional and local scales, mainly driven by natural and climate-induced factors. From ca. 4000 BC onwards, the trends in vegetation and fire dynamics start to differ between the regional and local scales, probably due to local land use being overshadowed at the regional scale by climate-induced factors. The LOVE model is therefore useful in pollen-based reconstruction of past vegetation to highlight the local land uses that are not visible through the REVEALS applications.

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