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SPECIAL FEATURE: VEGETATION HISTORY

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The role of climate, forest fires and human population size in Holocene vegetation dynamics in Fennoscandia

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Abstract

Questions: We investigated the changing role of climate, forest fires and human population size in the broad-scale compositional changes in Holocene vegetation dynamics before and after the onset of farming in Sweden (at 6,000 cal yr BP) and in Finland (at 4,000 cal yr BP).

Location: Southern and central Sweden, SW and SE Finland.

Methods: Holocene regional plant abundances were reconstructed using the REVEALS model on selected fossil pollen records from lakes. The relative importance of climate, fires and human population size on changes in vegetation composition was assessed using variation partitioning. Past climate variable was derived from the LOVECLIM climate model. Fire variable was reconstructed from sedimentary charcoal records. Estimated trend in human population size was based on the temporal distribution of archaeological radiocarbon dates.

Results: Climate explains the highest proportion of variation in vegetation composition during the whole study period in Sweden (10,000–4,000 cal yr BP) and in Finland (10,000–1,000 cal yr BP), and during the pre-agricultural period. In general, fires explain a relatively low proportion of variation. Human population size has significant effect on vegetation dynamics after the onset of farming and explains the highest variation in vegetation in S Sweden and SW Finland.

Conclusions: Mesolithic hunter-gatherer populations did not significantly affect vegetation composition in Fennoscandia, and climate was the main driver of changes at that time. Agricultural communities, however, had greater effect on vegetation dynamics, and the role of human population size became a more important factor during the late Holocene. Our results demonstrate that climate can be considered the main driver of long-term vegetation dynamics in Fennoscandia. However, in some regions the influence of human population size on Holocene vegetation changes exceeded that of climate and has a longevity dating to the early Neolithic.

KEYWORDS
climate, fire, human population size, pollen, REVEALS plant abundance, variation partitioning

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Special Feature "Millennial to centennial vegetation change" (Eds. Thomas Giesecke, Petr Kuneš & Triin Reitalu).

1 | INTRODUCTION

Pollen-based reconstructions of Holocene vegetation dynamics have demonstrated the influence of anthropogenic activity on forest composition and landscape openness since the mid-Holocene in Central and Northern Europe (Fyfe, Woodbridge, & Roberts, 2015; Marquer et al., 2014, 2017). Fennoscandian pollen data demonstrate the regional differences in forest composition throughout the Holocene, and this variation has been generally connected to the changes in climate (Birks, 1986; Heikkilä & Seppä, 2003; Miller et al., 2008). In addition, fire is an important disturbance factor in boreal forests that profoundly affects forest age, structure, composition and succession dynamics (Bradshaw, Lindbladh, & Hannon, 2010). Although Mesolithic hunter-gatherers may have altered local-scale vegetation composition through fires and favouring food plants (Hörnberg et al., 2005; Regnell, Gaillard, Bartholin, & Karsten, 1995), the regional scale vegetation change in Fennoscandia presumably remained under natural drivers longer than in other European regions. The current intensive anthropogenic influence and predicted accelerated warming of the boreal biome (Christensen, Kumar, & Aldrian, 2013) may cause compositional and structural changes to the present vegetation. Therefore, understanding the complex interactions between natural- and human-induced changes in the past regional vegetation dynamics can shed light on the future effects of a changing climate on ecosystems that are heavily influenced by human activity.

The strongest effect of human impact on vegetation in Fennoscandia is connected to the onset of agriculture, which was often accompanied by increased human-induced fires (Granström & Niklasson 2008; Huttunen, 1980). The earliest signs of agriculture are found at ca. 6,000 calibrated years before present (cal yr BP) in S Sweden (Sørensen & Karg, 2012; Welinder, 2011). In SW Finland the first unambiguous evidence of cultivation is dated 4,000–3,500 cal yr BP (Lahtinen, Oinonen, Tallavaara, Walker, & Rowley-Conwy, 2017; Taavitsainen, Simola, & Grönlund, 1998). In E Finland, earliest signs of cereal cultivation in palynological records are reported already from the early Neolithic ca. 6,400–5,200 cal yr BP (Alenius, Mökkönen, Holmqvist, & Ojala, 2017; Alenius, Mönkkönen, & Lahelma, 2013), whereas first archaeological evidence of cultivation, alongside increasing palynological evidence, is detected after 3,200 cal yr BP (Lavento, 2001; Taavitsainen et al., 1998).

Studies concerning the role of human impact and climate on vegetation changes during the mid- and late Holocene in N Europe have been mainly qualitative, based on interpretation of pollen data or archaeological findings. Recently, Reitalu et al. (2013), Kuosmanen et al. (2016) and Marquer et al. (2017) have addressed this question by means of variation partitioning, using different proxies to assess the role played by the anthropogenic influence. Reitalu et al. (2013) derived the human impact variable from pollen records, Marquer et al. (2017) used the anthropogenic land-cover change scenario (ALCC; Kaplan et al., 2010), while Kuosmanen et al. (2016) utilized a human population size proxy, based on the temporal frequency distribution of radiocarbon-dated archaeological findings (Lechterbeck et al., 2014; Woodbridge et al., 2014). This approach assumes a correlation between the amount of archaeological material at any particular time point and the human population size at that time (Shennan & Edinborough, 2007; Tallavaara, Pesonen, & Oinonen, 2010). An advantage of this proxy is its independence from the reconstructed vegetation dynamics.

Here we employ this independent proxy of human population size together with climate and regional fires to statistically assess their relative importance on the variation in the Holocene vegetation composition in Fennoscandia during three time periods: (1) the whole study period in Sweden (10,000–4,000 cal yr BP) and Finland (10,000–1,000 cal yr BP); (2) before the onset of farming in Sweden (at 10,000–6,000 cal yr BP) and in Finland (at 10,000–4,000 cal yr BP); and (3) after the onset of farming in Sweden (at 6,000–4,000 cal yr BP) and in Finland (at 4,000–1,000 cal yr BP). The length of the study periods between Sweden and Finland differs due to the limitations of data on human population size.

2 | METHODS

2.1 | Study area

The study area is located in Fennoscandia and is divided into four regions; (1) southern (S) Sweden, (2) central (C) Sweden, (3) southwest (SW) Finland and (4) southeast (SE) Finland (Figure 1). The northern limit of the study region in Sweden is located at 61.5° N, while the border between S and C Sweden is at 58.3° N. In Finland, the northern limit of the study region is at 62.5° N, and the border between SW and SE Finland is at 25.5° E (along Lake Päijänne). These study regions were chosen because the availability of a high amount of data for pollen-based REVEALS estimates, human population size data and charcoal data.

2.2 | Regional plant abundances

We used pollen records from 33 lakes selected from the European Pollen Database (Fyfe et al., 2009; Giesecke et al., 2014), the LANDCLIM pollen data archive (Marquer et al., 2017; Trondman et al., 2015, 2016) or provided directly by data contributors (Appendix S1). An important criterion for the selected pollen records was robust chronological control and adequate Holocene time resolution. The REVEALS model (Sugita, 2007) was run separately for each study region using five pollen records for C Sweden, 17 for S Sweden, five for SE Finland and six for SW Finland (Figure 1).

Within each region, the REVEALS model was used to convert pollen percentages of the 23 most important pollen taxa into proportional vegetation cover (Appendix S4) for 200-year time windows following Mazier et al. (2012), Trondman et al. (2015) and Marquer et al. (2017). Descriptions of Holocene changes in vegetation cover are depicted in Figure 2 and Appendix S4. The study period covers 10,000–1,000 cal yr BP corresponding with the time of available human population size data. Additionally to taxa-specific REVEALS estimates, nine plant

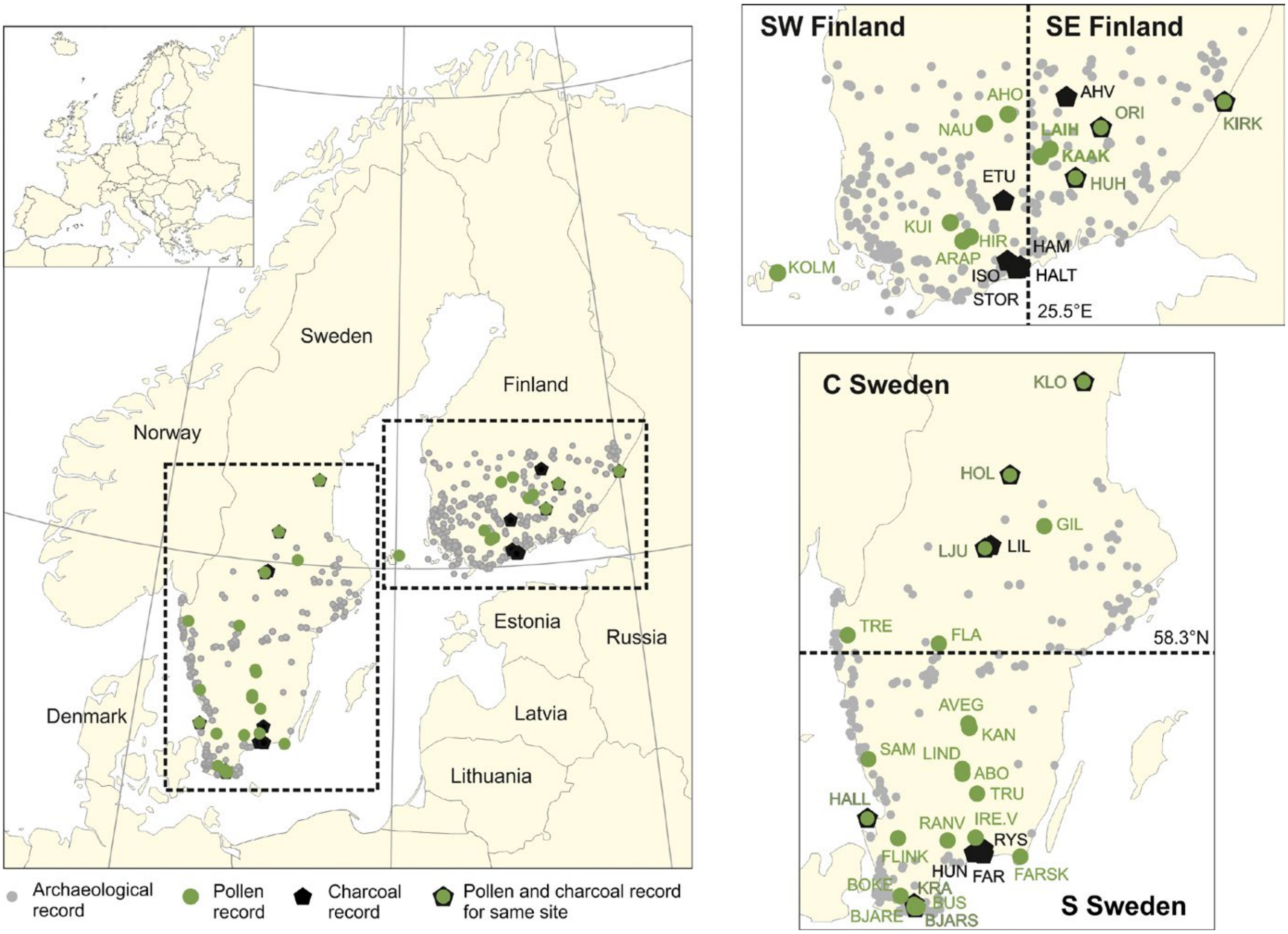


FIGURE 1 Location of the four study regions. The radiocarbon-dated archaeological sites for human population size proxy are shown as grey circles, sites with pollen record are marked as green circles and sites with charcoal record are marked with black polygons. The correspondence between the label of each site, the site name and the characteristics of each site are given in Appendices S1 and S2

functional types (PFTs; Appendix S5), grouped in terms of bioclimatic limits after Trondman et al. (2015), were defined in order to assess broad-scale trends in different plant ecosystems during the Holocene.

2.3 | Explanatory variables of Holocene vegetation changes

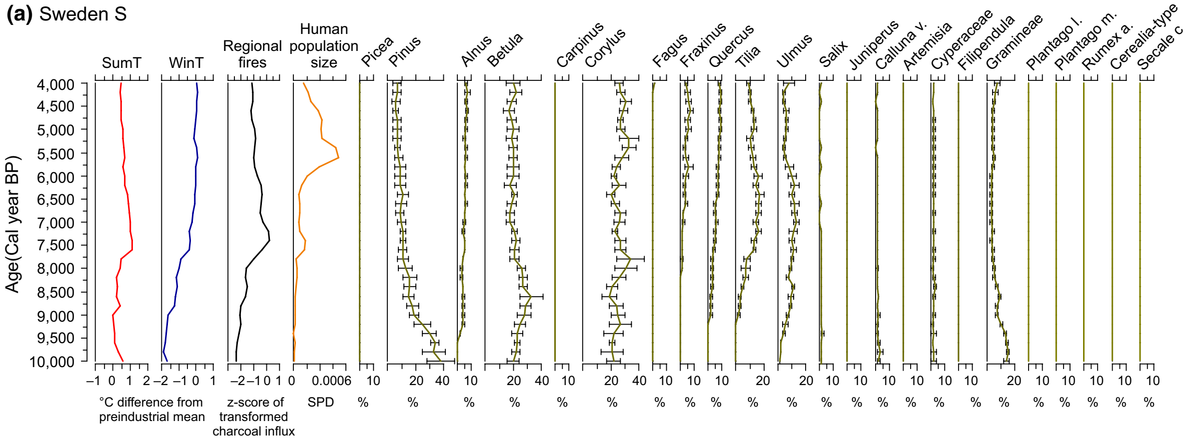
2.3.1 | Climate

The climate variables for the study regions were obtained from the LOVECLIM climate model as presented by Zhang, Renssen, and Seppä (2016). The version applied in this study explicitly represents components of the atmosphere, oceans (including sea ice) and vegetation in the climate system with intermediate complexity (Goosse et al., 2010). The spatial resolution of the model is 5.6° × 5.6° and three grid cells were used to provide regional temperature data for the study regions. S and C Sweden fell into the same latitudinal band, and thus the climate data are the same for these regions. The climate variables include winter December–January–February (DJF) and summer June–July–August (JJA) temperatures expressed as 30-year average and as anomalies from the preindustrial mean (550–250 cal yr BP). Climate parameters were averaged over 200-year bins for the statistical analyses (Figure 2; Appendix S4). Precipitation data were excluded due to the large uncertainty in the simulations. The applied climate simulation provides realistic trends on large sub-continental scale, especially for Fennoscandia, as demonstrated by inter-model and model data comparisons (Zhang, Renssen, Seppä, & Valdes, 2017a,b).

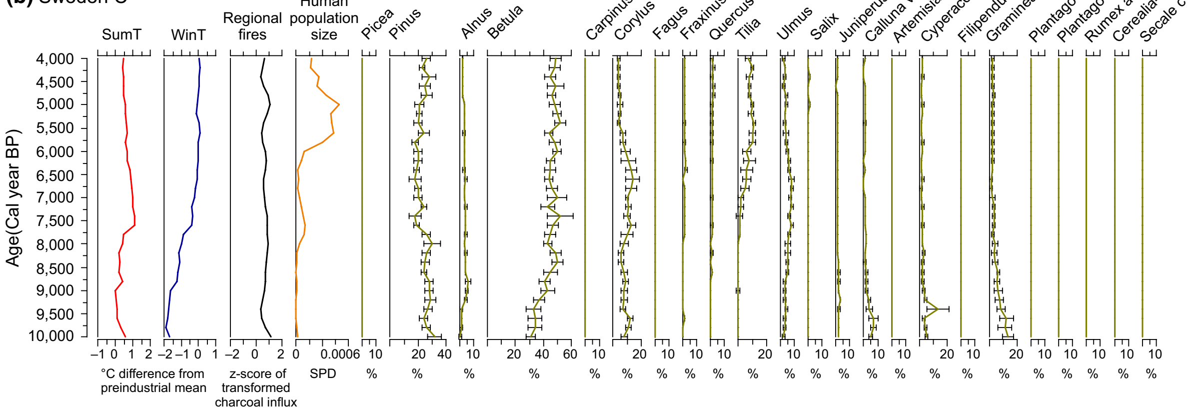
2.3.2 | Forest fires

The regional fire variable was reconstructed based on sedimentary charcoal records from 19 lakes. Charcoal data covering part or all of the last 10,000 years were acquired from the latest version of the Global Charcoal Database (GCD v3; Marlon et al., 2016), from previously published syntheses (Clear, Molinari, & Bradshaw, 2014) or provided directly by the authors (Appendix S2). To retrieve regional composites of changes in fire activity over the Holocene, charcoal accumulation in sediments was transformed and standardized according to a protocol

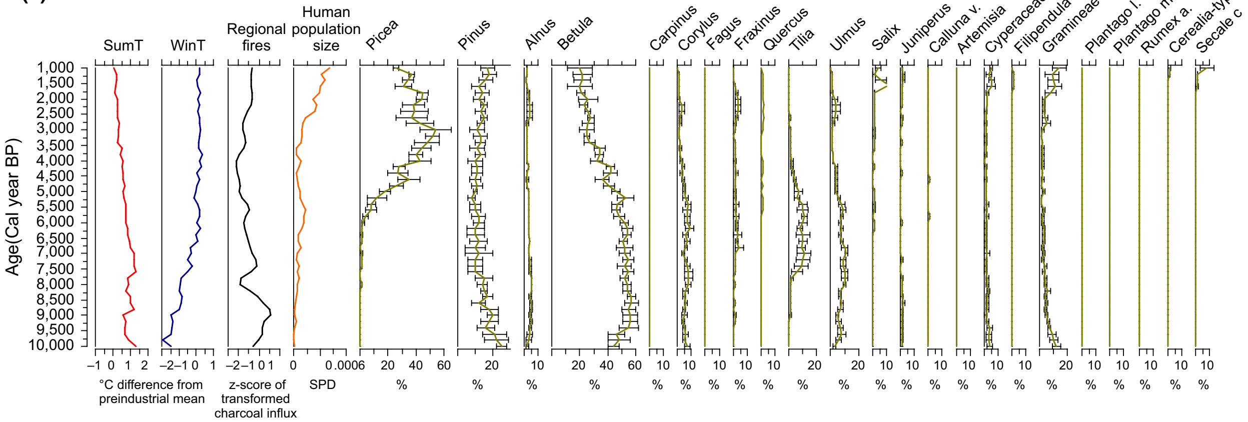
(a) Sweden S



(b) Sweden C



(c) Finland SW



(d) Finland SE

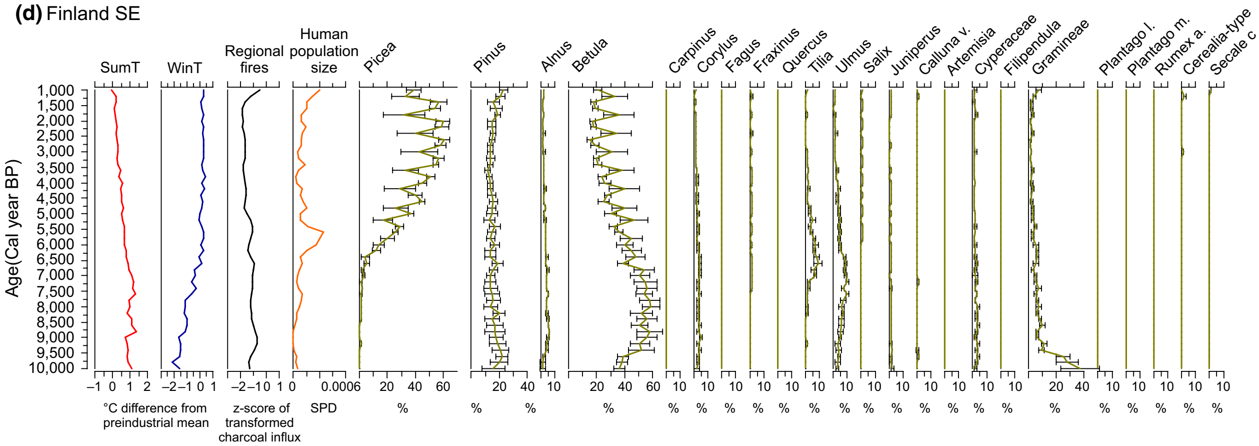


FIGURE 2 Holocene changes in the explanatory variables: simulated summer (SumT) and winter (WinT) temperatures (from the LOVECLIM model), fires (charcoal influx *z*-scores) and human population size data expressed as summed probability distributions (SPD) at each study region (a) S Sweden, (b) C Sweden, (c) SW Finland and (d) SE Finland (see Figure 1) and the mean of REVEALS estimates of 23 taxa

described by Power, Marlon, Bartlein, and Harrison (2010) and widely used within the paleofire community (Daniau et al., 2012; Molinari et al., 2013). The smooth curves were constructed by determining fitted values at 200-year intervals (Figure 2; Appendix S4). Composite curves were produced with the R package paleofire (Blarquez et al., 2014; R Foundation for Statistical Computing, Vienna, Austria).

2.3.3 | Human population size

Changes in human population size were reconstructed using the temporal frequency distribution of archaeological radiocarbon dates (Shennan & Edinborough, 2007; Shennan et al., 2013). The Swedish data were extracted from the EUROEVOL data set that contains over 14,000 archaeological radiocarbon dates from the Neolithic in NW Europe, spanning the Late Mesolithic and Early Bronze Age (Shennan et al., 2013; Timpson et al. 2014; Manning, Colledge, Crema, Shennan, & Timpson, 2016). The Swedish samples were supplemented by Mesolithic dates (Edinborough, 2005) and divided into southern (414 dates) and central (352 dates) subsets according to the study regions. Due to the Neolithic focus of the EUROEVOL data, the Swedish samples were restricted to cover the period of 10,000–4,000 cal yr BP. The Finnish data set (Oinonen, Pesonen, & Tallavaara, 2010; Tallavaara et al., 2010) covers the period of 10,000–1,000 cal yr BP both in SW (692 dates) and SE (315 dates) regions.

Summed probability distributions of calibrated radiocarbon dates (SPDs) were created for each region, and evaluated for random sampling bias and calibration effects using a Monte-Carlo simulation approach (Shennan et al., 2013; Timpson et al. 2014) and by implementing the methodology used in Crema, Habu, Kobayashi, and Madella (2016; Appendix S6). To reduce the potential bias of oversampling within sites, multiple dates from individual sites were grouped into non-overlapping bins, such that after ordering the dates at one site, the next date was only assigned to a new bin if there were more than 200 radiocarbon years between it and the previous date (Shennan et al., 2013; Tallavaara et al., 2010). Finally, SPDs were binned into conservative 200-year bins by averaging summed probability values within each bin (Figure 2, Appendix S4).

2.4 | Statistical analysis

Variation partitioning (Borcard, Legendre, & Drapeu, 1992) was performed to assess the relative importance of climate, regional fires and human population size on variation in Holocene vegetation composition. In the analysis, vegetation composition derived from the REVEALS estimates were used as response matrix, while climate, regional fires and human population size were used as explanatory variables. REVEALS estimates were Hellinger-transformed (Legendre & Gallagher, 2001) to assess the significance of each constraining variable and an ANOVA permutation test was run with 999 randomizations.

Variation partitioning was first performed for the whole study period in all regions, namely at 10,000–4,000 cal yr BP in S and C Sweden, and at 10,000–1,000 cal yr BP in SW and SE Finland. In order to evaluate the effect of the explanatory variables on vegetation before the onset of farming, variation partitioning was performed for the period of 10,000–6,000 cal yr BP for C and S Sweden, and for the period of 10,000–4,000 cal yr BP for SW and SE Finland. To assess the relative importance of the explanatory variables on vegetation changes after the beginning of agriculture, variation partitioning was performed for the period of 6,000–4,000 cal yr BP for S and C Sweden, and for the period of 4,000–1,000 cal yr BP for SW and SE Finland. To separately evaluate the relative importance of summer and winter temperatures on vegetation, variation partitioning with summer and winter temperature as individual explanatory variables was performed for all three study periods, the whole Holocene, the pre-agriculture and the agricultural periods, for all the study regions.

In order to assess the change in the role of climate, regional fires and human population size during the Holocene, a moving window approach (Reitalu et al., 2013) was employed. This approach enables performing variation partitioning for subsets of data in shorter time periods, hence providing information on how the relative roles of climate and human population size change over time. Moving window analysis was performed for all study regions in 2,000-year time windows, with ten 200-year bins in each time window.

3 | RESULTS

3.1 | Variation partitioning results

3.1.1 | The Holocene

Climate alone explained the highest fraction of variation in vegetation during the whole study period for all regions (Figure 3). The relative importance of winter temperature had high explanatory power for the variation in vegetation cover in S and C Sweden, while summer temperature explained a higher proportion of the variation in vegetation in SW and SE Finland (Appendix S7). The variation explained by human population size and forest fires was relatively low. Human population size had a significant impact on vegetation changes in C Sweden and SW Finland, while forest fires had a significant effect in S Sweden and SE Finland. Climate, forest fires and human population size together explained at least 70% of the variation in long-term vegetation in all regions. Variation partitioning performed with PFTs showed similar results as the taxa-based analysis, with overall higher explanatory power of the used explanatory variables in each study period (Appendix S8).

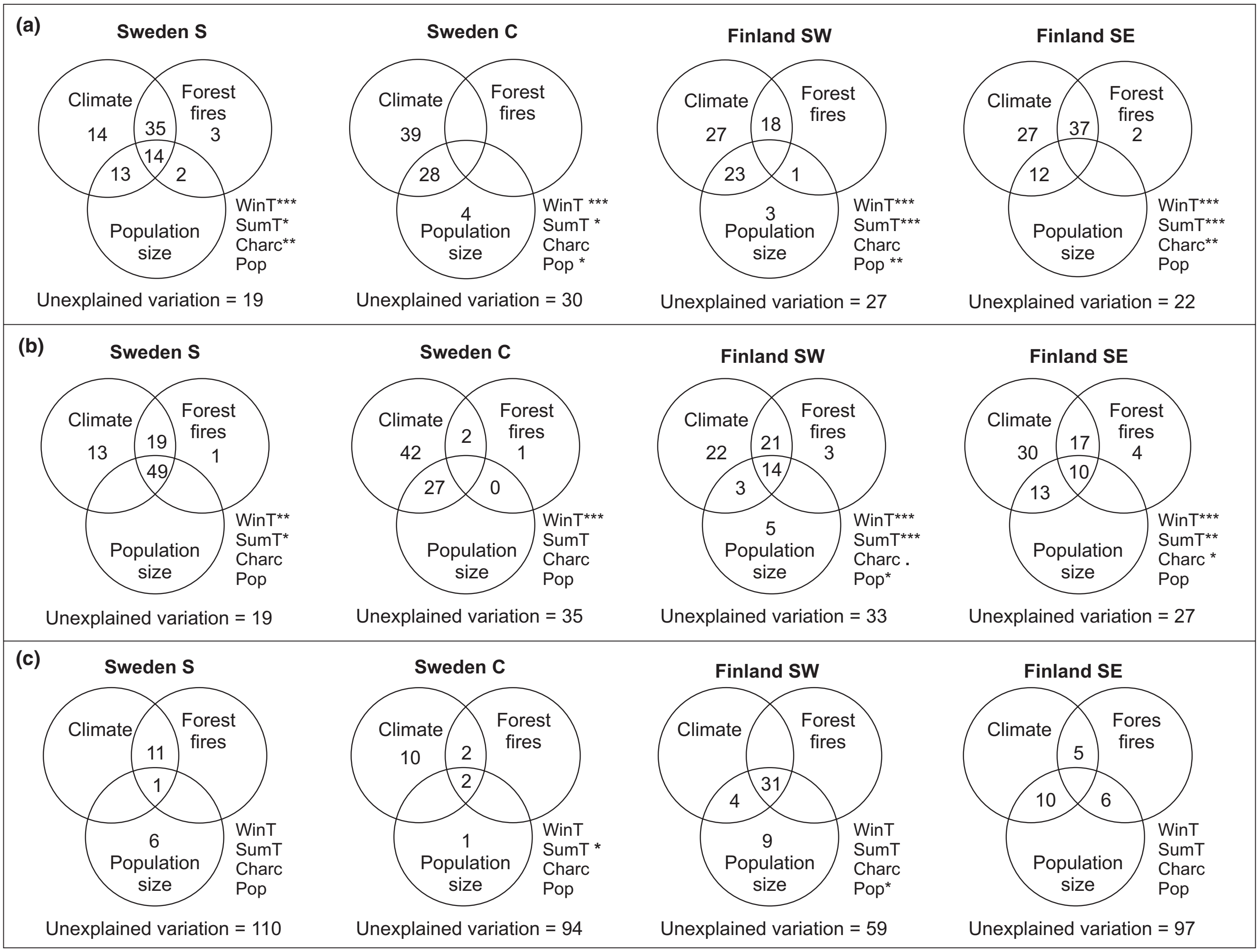


FIGURE 3 Percentage of variation in vegetation composition explained by climate (winter temperature: WinT, summer temperature: SumT), forest fires (Charc) and human population size (Pop) in S Sweden, C Sweden, SW Finland and SE Finland during a) the whole study period (10,000–4,000 cal yr BP in Sweden and 10,000–1,000 cal yr BP in Finland), b) before the onset of farming at 10,000–6,000 cal yr BP in Sweden and at 10,000–4,000 cal yr BP in Finland, and (c) after the onset of farming at 6,000–4,000 cal yr BP in Sweden and at 4,000–1,000 cal yr BP in Finland. Values <0 are not shown in the figure. Statistical significance (****p* < .001; ***p* < .01, **p* < .05 and *p* < .1) of each parameter on variation in vegetation is shown next to the corresponding Venn diagram

3.1.2 | Pre-agriculture

Before the onset of farming climate alone explained most of the variation in vegetation, with winter temperatures explaining a higher proportion of variation than summer temperatures (Figure 3; Appendix S7). Fires had a significant effect on vegetation composition in Finland, explaining 3% of the variation in vegetation in SW and 4% in SE Finland. Human population size explained 5% of the variation in vegetation in SW Finland, but was not significant in other regions. Climate, forest fires and human population size explained at least 65% of the variation in vegetation composition before the onset of agriculture in all regions.

3.1.3 | Agricultural time

Human population size explained the highest amount of the variation in vegetation composition in S Sweden and SW Finland (6% and 9%, respectively; Figure 3). Individually, climate explained a relatively low fraction of variation in vegetation in all regions, with summer temperature driving a higher proportion of variation than winter temperature (Appendix S7). Forest fires did not explain individually any variation in vegetation. However, together with human population size, they explained 6% of variation in vegetation dynamics in SE Finland. In general, a relatively high proportion of variation in vegetation was left unexplained in all regions.

3.1.4 | Moving window approach

Results of the moving window approach (Appendix S9: Figure S1) demonstrate the strong impact of climate on vegetation dynamics from the early to the mid-Holocene in S and C Sweden, especially between 8,600–6,500 cal yr BP, when climate explained 40%–60% of the variation in vegetation. In both regions the relative importance of climate was notably lower at 6,500–5,000 cal yr BP. The relative importance of fires was generally low, explaining ca 10% of the variation between 9,000–8,000 cal yr BP in both regions, and also between 6,000–5,500 cal yr BP in S Sweden. In S Sweden the importance of human population size increased at 7,000–6,500 cal yr BP, explaining up to 60% of the variation in vegetation (Figure 4). In C Sweden the explanatory value of human population size remained relatively low throughout the Holocene.

In Finland, the results of the moving window approach (Appendix S9: Figure S2) demonstrate notable fluctuations in the importance of climate in both regions. In SW and SE Finland climate explained 20%–60% of the variation during ca. 1,000-year periods around 8,000, 5,700 and 3,800 cal yr BP with lower importance in between. In SW Finland the explanatory value of fires was higher (20%) around 6,000 cal yr BP, with lower values during the late Holocene. In SE Finland fires explained the highest amount of variation in vegetation during the early Holocene. In general, the importance of human population size was low, except around 5,000 cal yr BP, when it explained over 20% of the variation in vegetation. In SW Finland the relative importance of human population size increased from 3,500 cal yr BP exceeding the explanatory value of climate by explaining 20% of the variation in vegetation (Figure 4). In SE Finland the relative importance of human population size remained low during the Holocene.

4 | DISCUSSION

4.1 | Role of climate in Holocene vegetation dynamics

The importance of climate as a driver of vegetation change was highest during the beginning of the Holocene Thermal Maximum (HTM) ca. 8,000–7,000 cal yr BP, and again around 6,000–5,000 cal yr BP, corresponding to the main temperature shifts during the Holocene. This can be seen especially in S Sweden and SW Finland (Figure 4). A similar trend of higher relative importance of climate in the early Holocene is also suggested by Marquer et al. (2017; Figure 4). The strong role of climate in vegetation dynamics at the beginning of the HTM is in agreement with the well-established northward range shift

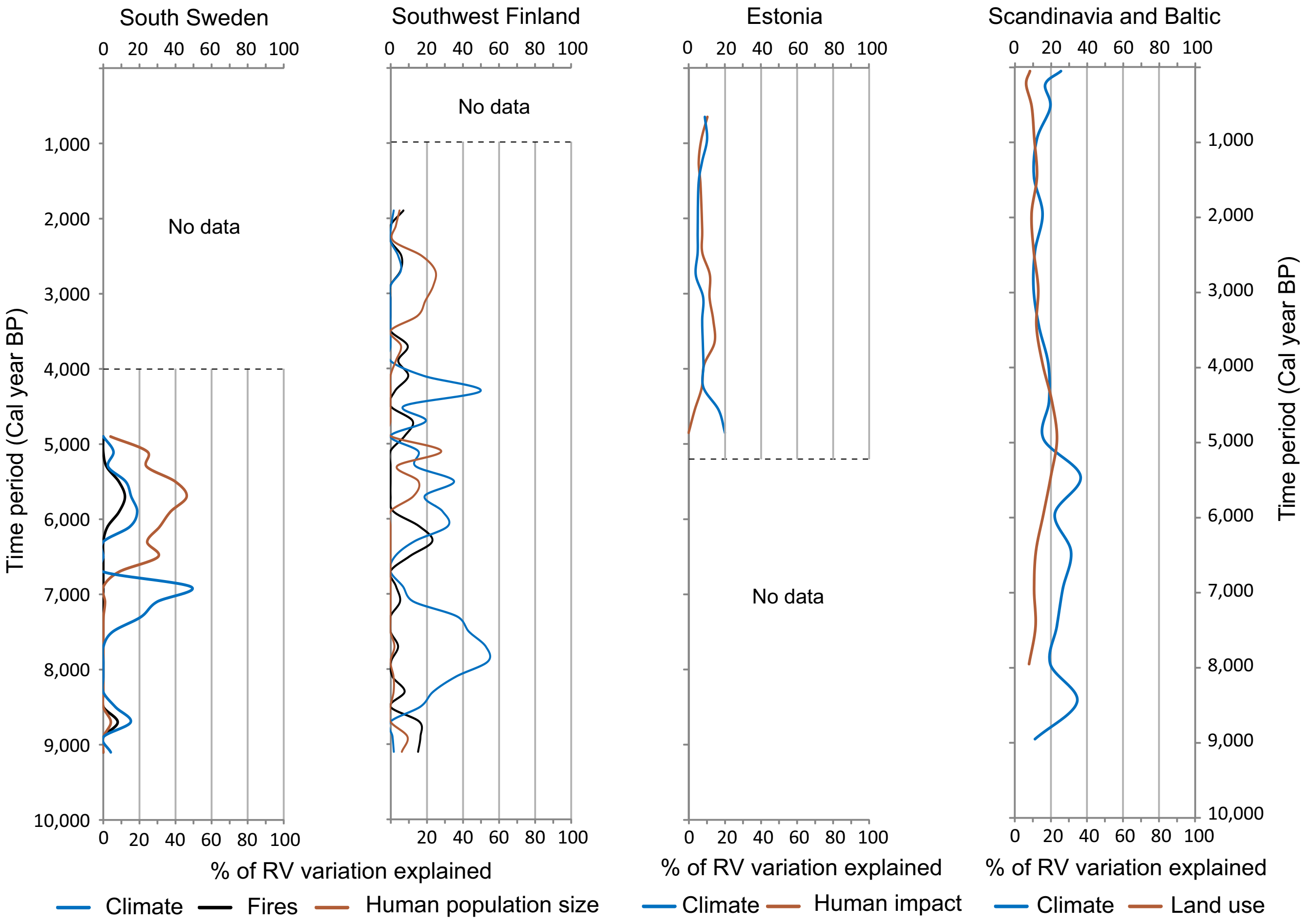


FIGURE 4 Relative importance of climate, fires and anthropogenic influence on variation in vegetation dynamics through the Holocene in N Europe. The fraction of variation in vegetation explained by human population size, regional fires and climate in (a) S Sweden and (b) SW Finland for ten 200-year subsets of data in 2,000-year moving time windows. (c) The fraction of variation explained by climate and human impact for 14 subsets of data in 1,200-year moving time window in Estonia (Reitalu et al., 2013). (d) The fraction of variation explained by climate and land use average across southern Scandinavia and Baltic countries (Marquer et al., 2017). For S Sweden, SW Finland and Estonia the results of each time window are shown from the midpoint of the time period. The used time windows are shown in Appendix S9: Tables S1, S2

of temperate tree taxa such as *Corylus*, *Tilia*, *Ulmus* and *Quercus* during this period (Miller et al., 2008; Seppä et al., 2015), and can be seen as an increase of temperate broad-leaf forest cover in Fennoscandia. This corresponds with the present ecological understanding that temperature is one of the main limiting factors for the northern limits of the temperate tree species (Jackson, Betancourt, Booth, & Grayd, 2009; Woodward, Lomas, & Kelly, 2004).

Although the importance of human population size on vegetation dynamics increases from the early Neolithic in Sweden and during the late-Holocene (ca 3,500 cal yr BP) in Finland, climate remains an important driver behind vegetation cover changes, especially in C Sweden and SE Finland (Appendix S9: Figures S1, S2). Similarly, the results of Reitalu et al. (2013) and Marquer et al. (2017) demonstrate the strong effect of climate on vegetation dynamics in Estonia and southern Scandinavia during the last 1,000 years. If this control of climate on boreal forest composition will prevail, the projected accelerating future warming in northern regions (Christensen et al., 2013) will act as the main driver of future changes in the boreal ecosystems, at least at regional scale.

4.2 | Role of fires in Holocene vegetation dynamics

The change from a natural to a more human-induced fire impact on vegetation dynamics is not clearly defined in our data. A higher influence of forest fires on vegetation composition during the pre-agriculture period was detected for both Sweden and Finland. In S Sweden, the slight increase in the role of fires during the beginning of the agricultural period coincides with the increasing effect of human population size (Figure 4.), while in C Sweden fires did not show any effect on vegetation composition. It is plausible that during this time human-induced fires were local fires, which did not have notable impact on regional vegetation composition. Since slash-and-burn practices were often used in connection with early farming (Alenius, Haggrén, Koivisto, Sugita, & Vanhanen, 2017; Huttunen, 1980), the notably low importance of forest fires on vegetation during the agricultural period in SW Finland was surprising. Although the charcoal data used in this study reconstruct the regional fire history, the uneven distribution of the sedimentary charcoal records in the study regions might bias the results. However, changes in vegetation dynamics are partly explained by the joint effect of fires and human population size, whereas pre-agriculture fires and climate have a notable joint effect on variation in vegetation. Therefore, it is plausible that the increased joint effect of human population size and fires indicate the change from natural- to more human-induced fires affecting vegetation dynamics during the late Holocene.

4.3 | Increasing anthropogenic influence from early Neolithic

The comparison between our results and those of Marquer et al. (2017) for S Scandinavia and the Baltic region demonstrate an increasing role of human population size on vegetation dynamics from the mid-Holocene in S Sweden suggesting increasing land use by the growing population (Figure 4). It is plausible that the rapid increase in human population size in S Sweden was due to suitable climate conditions during the HTM (Tallavaara & Seppä, 2012) and the spread of more intensive land-use practices from Central Europe. The shift to agrarian society gradually changed the landscape, when Neolithic communities started to migrate inland. Broad-leaf forests were first used as woodland pastures and then cleared for cultivation (Lagerås, 1996; Sköld, Lagerås, & Berglund, 2010).

The low human impact on vegetation dynamics in SW Finland until 3,500 cal yr BP is in line with the small human population size and with the later anthropogenic influence on vegetation in Finland compared to S Scandinavia and the Baltic region (Fyfe et al., 2015; Marquer et al., 2017). The increasing importance of human impact in SW Finland corresponds with the onset of agriculture ca 4,000–3,500 cal yr BP (Taavitsainen et al., 1998), suggesting that human population size was the major driver of vegetation dynamics during the late Holocene, especially during the period of 3,000–1,000 cal yr BP. Growing agrarian communities cleared the forest for pastures and arable land. Cultivated fields were commonly left as fallow for a few years in order to maintain soil productivity. This may have caused an increase in the proportion of *Betula* and *Alnus* together with shrubs in the vegetation cover (Reitalu et al., 2013).

The lower importance of human population size on regional vegetation change in C Sweden and SE Finland could be explained by the fact that these regions were more forested and less populated during the study period. Alenius et al. (2013) showed that, for example, in E Finland forest clearances and cultivation intensified only from AD 600 onwards, coinciding with increasing human population size. Due to the land uplift, substantially large areas of SE Finland were raised rapidly above the Baltic sea level after the deglaciation, in contrast to SW Finland (Tikkanen & Oksanen, 2002) and therefore SE Finland lacks thick, fine-grained mineral soil layers, such as clay and silts, which provide fertile soils for cultivation in SW Finland. It is plausible that, due to the lack of suitable areas for more intensive field cultivation, human population size remained relatively low in SE Finland and animal husbandry together with sporadic slash-and-burn cultivation were practiced longer than in SW Finland (Taavitsainen et al., 1998).

4.4 | Issue of causality in the variation partitioning analysis

It is also important to note that variation partitioning as a method does not consider the causality, but only the co-variation between variables through time. The causality between climate and vegetation is relatively clear, while the causality between changes in vegetation and in hunter-gatherer population size and forest fires is more difficult to deduce. Hunter-gatherer populations were small and scattered, affecting mainly the local-scale vegetation dynamics (Hörnberg et al., 2005; Regnell et al., 1995). In Finland, the decline in hunter-gatherers along with the decline of temperate forests coincides with the expansion of spruce and consequently the boreal ecosystem

(Seppä et al., 2009). Boreal forests provide lower food abundance compared to temperate mixed forests, and it has been argued that this ecosystem change caused the decline in hunter-gatherer population size (Tallavaara & Seppä, 2012). It is also probable that instead of a causal relationship between human population size and vegetation, these variables co-vary because of the changes in climate. Similarly, the causality may be difficult to distinguish between fires and vegetation. Ohlson et al. (2011) showed that fire frequency in Fennoscandia decreased after the spruce expansion. However, it is still speculative if spruce expanded because of fire reduction or the fires decreased due to the spruce expansion. Since disentangling these issues of causality with variation partitioning is challenging, future studies would benefit from the use of other methods that provide more insight into the direction of the interaction between response and explanatory variables.

5 | CONCLUSION

Hunter-gatherer populations did not significantly affect vegetation dynamics in Fennoscandia. Climate was the main driver of change during the Holocene and large-scale shifts in vegetation were likely driven by climate. However, with relatively stable climatic conditions, the role of climate may decrease and other factors, such as disturbances, site characteristics, competition and human impact may have a greater effect on vegetation composition. Agricultural populations, however, highly affected vegetation composition, and the role played by human population size became more important during the late Holocene. There is a clear regional dependence related to human population size, i.e. the effect of human impact on vegetation change was notably higher in S Sweden and SW Finland, where land use was more intensive, than in C Sweden and SE Finland.

The variation partitioning approach provides important insights into the drivers of past vegetation dynamics and provides a stepping stone for finding more precise methods to assess the processes behind past changes in long-term vegetation dynamics. The relatively high importance of climate throughout the Holocene suggests that – even after the onset of farming – climate, together with human impact, remained an important driver of changes in broad-scale vegetation dynamics. Although the anthropogenic impact may have periodically and regionally overruled the effect of climate already from the early Neolithic, climate can be considered the main driver of long-term regional vegetation dynamics in Fennoscandia during the Holocene.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1 Metadata for pollen records

Appendix S2 Metadata for charcoal records

Appendix S3 The REVEALS corrections for the 23 plant taxa

Appendix S4 Vegetation composition and explanatory variables

Appendix S5 Plant functional types (PFTs)

Appendix S6 Summed probability distributions (SPD) of archaeological radiocarbon dates

Appendix S7 Variation partitioning results for winter and summer temperature

Appendix S8 Variation partitioning results with plant functional types (PFTs)

Appendix S9 Results from moving window analysis

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